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REVIEW OF THE EARLY LIFE HISTORY OF PUGET SOUND FISHES

by

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1. INTRODUCTION

A large amount of information on the early life history and reproductive biology of fish species found in Puget Sound, Washington is currently available. This information, however, is contained within a variety of sources, including published and unpublished literature from both foreign and domestic origins. This project represents an attempt to consolidate this material into a single-source reference. The specific objectives of this project were two-fold:

1) Identify the available sources of information on reproductive ecology and early life history of Puget Sound marine fishes, and,

2) Summarize the information for each species.

The ichthyfauna of Puget Sound is composed of 60 fish families and 218 species which can be divided into 49 teleost or bony fish families (200 species) and 11 non-teleost families (18 species)(Miller and Borton 1980). This report includes summaries and references for 175 of the teleost species. For the remaining 25 teleost species, only references are provided. With the exception of the Salmonidae, most of these include species which are only incidentally found in Puget Sound. It is the hope of the authors that summaries for these remaining species will be added in the future. Also at this time no attempt has been made to consolidate information on the non-teleost fishes (sharks, rays, skates, lampreys).

Literature references used in this project were collected from a variety of sources which included primarily personal index card files but also published and unpublished bibliographies on early life history and reproduction of fishes. Current references were obtained since 1978 by reviews of weekly material received at the University of Washington Fisheries-Oceanography Library. Bibliographies which were searched for references were Day et al. (1971), Kernehan (1976), and Donaldson (1977). Additional sources of references included 1976 class notes compiled by E.H. Ahlstrom and a bibiliography presented by English (1976).

The bulk of the material was summarized from published journal articles (primarily U.S., but also including Canadian, Japanese, and Soviet literature), but appropriate theses and agency reports were also included. Only a small amount of material was available on studies conducted within Puget Sound, so information for most species was based on studies from other locations. It should be kept in mind that aspects of reproduction of a particular species may vary geographically, and information obtained from other areas may not be directly applicable to fish species in Puget Sound.

Spawning biology and early life history summaries are presented on a species by species basis arranged within families. In most cases, references cited are presented by family at the end of each section.

Because of time constraints it was not always possible to locate or review all the available references on a particular species. In these cases, the references are included under a separate heading "Additional References".

This work is intended to provide students and researchers with access to the early life history and spawning biology literature for one group of fishes. In addition, these summaries provide insight into the present state of knowledge for each species and help focus on gaps or absences of information which may be topics for future research.

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2. ACIPENSERIDAE

Acipenser medirostris - Green sturgeon

Acipenser transmontanus - White sturgeon

(available literature not reviewed)

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3. NEMICHTHYIDAE

Nemichthys scolopaceus - Slender snipe eel

(available literature not reviewed)

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4. CLUPEIDAE

Alosa sapidissima - American shad

Range: Baja California to Kodiak, Alaska; Kamchatka; in Atlantic from Florida to Newfoundland

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic, marine

Spawning habitat: anadromous

Spawning season: spring

Mode of reproduction: oviparous

Eggs: demersal

Larvae: pelagic

Shad are not native to the Pacific Ocean but were transplanted from the Atlantic into the Sacramento River, California, in 1871. By 1876-1880 they ranged as far north as the Columbia River and in 1882 were reported in Puget Sound. They were first observed in the Fraser River and parts of southeast Alaska in 1891, Cook Inlet in 1904, and Kodiak Island in 1926 (Welander 1940). At present, shad are known to occur from Todos Bay, Baja California to Kodiak, Alaska and off Kamchatka. In the Atlantic, shad range from Florida to southeast Newfoundland (Hart 1973).

In Puget Sound, shad have been taken in salt water from Bellingham Bay to near Olympia and have been reported in the Skagit, Stillaguamish, Snohomish, and Nooksack rivers (Miller and Borton 1980).

On both the Atlantic and Pacific coasts, shad enter rivers to spawn, but spend the majority of their life in waters along the continental shelf. They are believed to associate with waters of 13-18^{o}C, in both oceans, which governs their seasonal distribution. Although there is no definite information on shad migration routes in the Pacific, Leggett and Whitney (1972) postulate that during December-April, shad are restricted to waters off southern California and the tip of Baja. A general oceanic warming trend in May-June would allow shad to move northward and by July-August, they could range as far north as Alaska. Cooling temperatures in September could move shad southward again.

Spawning shad are known to enter rivers on both the Atlantic and Pacific coasts when water temperatures approach 18^{o}C. In the Columbia River, 90% of the run generally takes place when river temperatures are between 16.0-19.5^{o}C (June-July) (Leggett and Whitney 1972). Shad which

enter the Columbia River at this time are reported to spawn in tributaries as far upstream as the Snake River (Browning 1974).

In California, no spawning runs are thought to occur south of San Francisco Bay (Leggett and Whitney 1972). In the Sacramento-San Joaquin River delta, shad become abundant in spring during the spawning migration which takes place between April and June. Shad are present in the delta area when water temperatures range from 11.1-21.2°C and most spawning occurs far upstream although some spawning takes place in the brackish water of the delta. Many of the shad die shortly after spawning, but some spent shad migrate back to sea. The young-of-the-year shad migrate downstream and out of the delta in September-November. Preliminary observations indicate that these shad begin to migrate immediately upon hatching and their migration is not triggered by flow or stream temperature (Stevens 1966). From California, there is also evidence that shad can successfully reproduce in a landlocked lake (Von Geldren 1965).

In Canada, shad ascend rivers in spring, depending on the water temperature, but mostly in May-June and into July (Scott and Crossman 1973). The Fraser River is thought to be the most northern river in which shad spawn along the Pacific Coast (Carl et al. 1967, cited by Leggett and Whitney 1972).

In Puget Sound, shad are reported from a number of rivers (Miller and Borton 1980), but details on spawning activity do not exist.

The majority of information on the spawning biology and early life history of shad comes from Atlantic coast populations. Jones et al. (1978) provide a compilation of the available literature from which most of the following summary was taken.

Along the Atlantic coast, the first runs begin in the south in November, but most spawning runs occur during spring and continue into summer in more northern locations. Peak movement into rivers corresponds to temperature of 18.5°C, and spawning has been reported at a range of temperatures 8-26°C, but usually occurs within a range of 12-21°C.

Fecundity estimates range from 58,534 to 659,000 eggs per female. Both males and females reach sexual maturity at 2-7 years, although the average spawning age for males is 4, and 4-5 for females. Spawning males range from 305-447 mm FL and females are 383-485 mm FL.

Unfertilized eggs are 1.8 mm and pale amber with a wrinkled capsule. After exposure to water and fertilization take place, they increase to 2.5-3.8 mm and are transparent, pale amber or pink, and spherical. The yolk is distinctly granular and the perivitelline space is about half the egg radius. Eggs are largely demersal, but may also be found in the water column as they are only slightly more dense than water. At least on the Atlantic coast, most spawning occurs in tidal

freshwater, and less frequently in nontidal water. Eggs are deposited at random and are dropped loosely and singly to the bottom usually in river areas dominated by extensive flats, but also over sandy or pebbly shallows. Spawning occurs frequently near mouths of creeks and in clear to very turbid water. Spawning activity has been noted at current velocities of 0.3 to > 0.9 m/sec and at depths of 0.9 to 12.2 m.

Shad probably spawn at all hours of the day or night with greatest activity between noon and midnight or from sunset to midnight. Spawning probably occurs at night in clear water and begins later in the day or all day in turbid water.

Eggs develop on the stream bottom and hatch in 2 days at 27°C and 17 days at 12°C. The optimum conditions for development were calculated at ∿ 17°C, 7.5°/oo, and darkness. At 24°C, the blastodisc is formed within 30 minutes of fertilization and the first cleavage furrow is complete at 1.3 hours. At 4-5 hours after fertilization, the morula is completed. The blastula stage is brief and the blastocoel is kidney-shaped when viewed from above, but soon becomes crescent-shaped. There are 3 or 4 somites evident on the embryo at blastopore closure, and Kupffer's vesicle, optic vesicles, auditory vesicles, and choroid tissue are evident shortly thereafter. During the tail bud stage, 32 somites are evident and hatching occurs soon after this stage (Fig. 4.1).

Larvae are elongate and slender, at hatching, with a body depth of 5% of total length. Larvae are 5.7-10.0 mm TL and have a large ovoid yolk sac and a mouth which is open, but not functional. In three days, the jaws, gill arches, and two pairs of recurved teeth on the lower jaw are forming. The young shad larvae are transparent and the yolk sac is covered with a diffuse network of stellate chromatophores. A midventral line of pigment is sometimes present on the isthmus. A line of chromatophores is present along the dorsal surfaces of the yolk sac where it meets the body and continues posteriorly along the dorsal gut surface to the anus. On the ventral surface of the gut a closely approximated double line of pigment spots extends from about the 18th myomere to the anus. A fine network of pigmentation is usually present on the lateral surface of the gut and is most dense near the anus. On the lateral body surface, between the level of the notochord and the gut are several stellate chromatophores which extend from the yolk sac to beyond the anus. There are also a few spots below the notochord in the area of the future caudal fin.

The yolk sac is absorbed in 4-5 days at 17°C and in 7 days at 12°C when larvae are 9-12.2 mm. At yolk absorption, pigment consists of a continuous midventral line on the isthmus and a dorsally oriented row of 2-3 spots at the base of the pectoral fins. From this point, the midventral pigment forms two lines which diverge somewhat shifting to the dorsal surface of the gut at the junction of the intestine and the body (Fig. 4.2). On the midventral gut surface a complete series of closely paired or slightly alternating pigment lines originate at the 18th myomere and extend to the anus. There are 2-3 midventral postanal spots

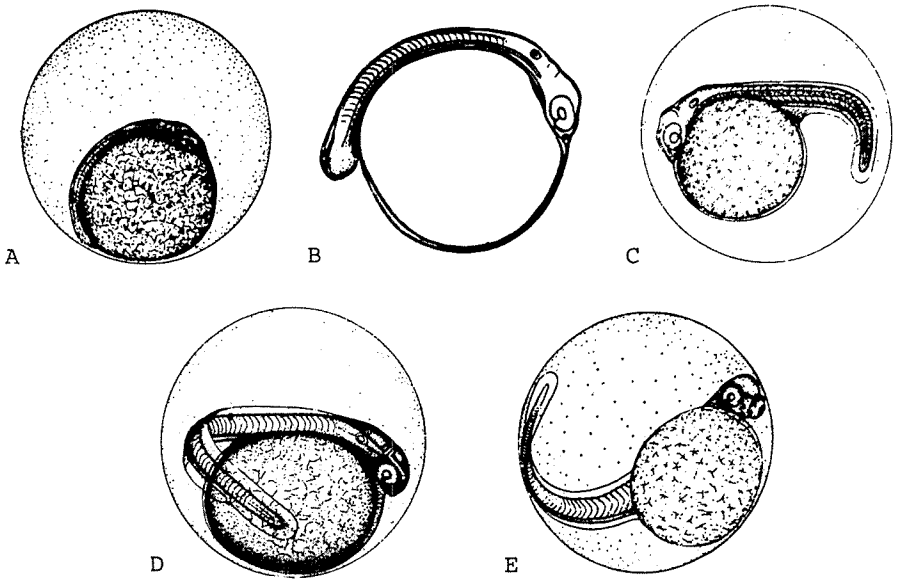

Fig. 4.1. Development of eggs of American shad, Alosa sapidissima: A) just after blastopore closure, 20 myomeres visible; B) tail-free embryo, egg capsule removed, 32 myomeres, heart thickening just posterior to eye; C) egg, 44 hr; D) egg, 48 hr; E) egg, 72 hr, yolk covered with stellate chromatophores, mouth open, rudimentary gill arches, pectoral fin buds formed. (Source: Jones et al. 1978.)

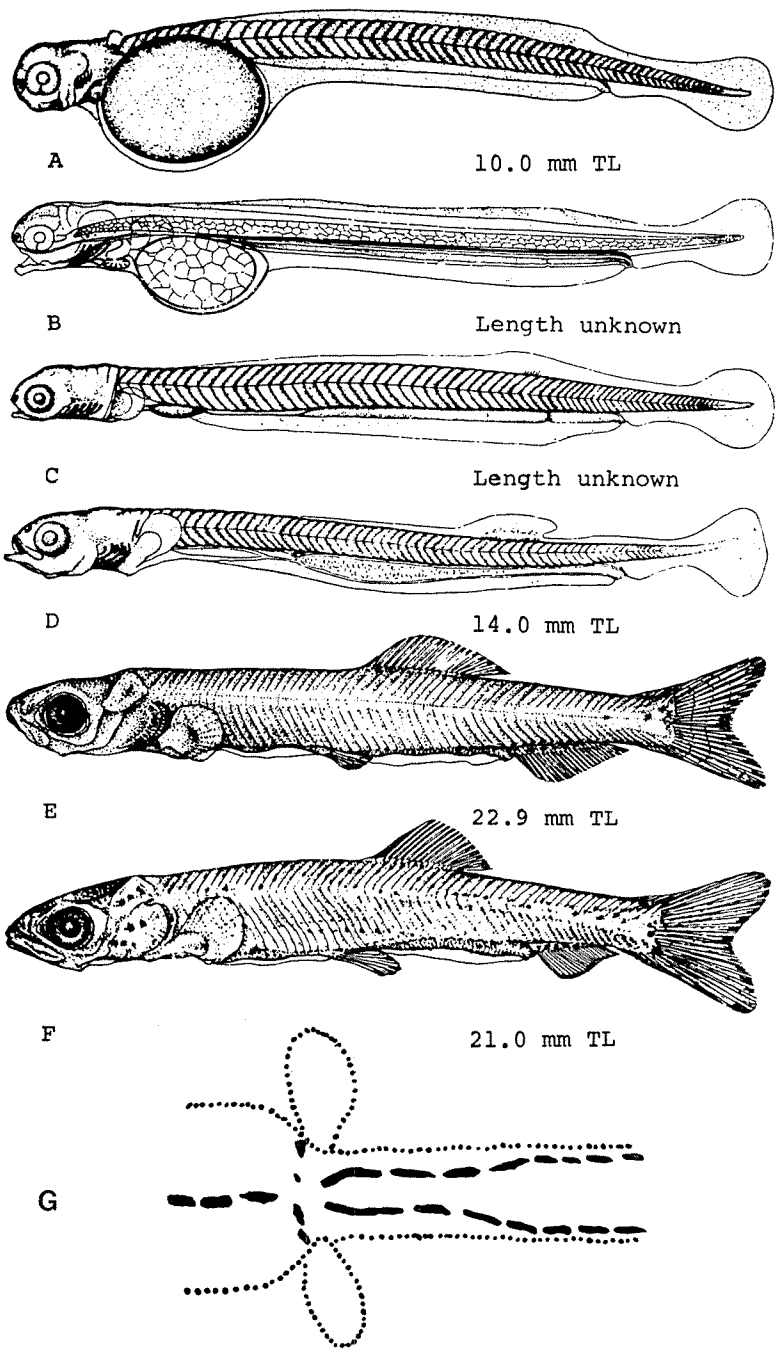

Fig. 4.2. Larval stages of American shad, Alosa sapidissima: A) yolk sac larva, 10.0 mm TL, newly hatched, preanal myomeres 43, pigment on yolk and along intestine not shown; B) yolk sac larva, length unknown, 3 days old, urogenital system shown as dark line over intestine; C) yolk sac larva, 5 days old; D) 14.0 mm TL, 17 days old, 9 incipient rays in dorsal fin; E) 22.9 mm TL, 20.0 mm SL, 12 days old; F) 21.0 mm TL, 17.8 mm SL, 18 days old; G) ventral pigment pattern found on larvae from yolk absorption to ∿ 13.0 mm TL. (Source: Jones et al. 1978.)

and 5-10 spots on the caudal fin. The lateral body pigments spots are reduced. Up to 16 mm, there is a continuing reduction in pigment spots with the diverging pigment line terminating at about the 14-15 myomere. By 21 mm, melanophores begin to be added to the head, operculum, and at the base of the anal fin. Significant additions of pigmentation occur during transformation at about 28 mm.

Larval pectorals are present at hatching and by 14 mm, the anlage of the dorsal fin is developed, incipient caudal rays are formed and flexion is underway. At 18 mm, the pelvics which are the last fins to develop, appear, but rays are still forming in the pectorals and pelvics at 21.0 mm TL. Scales are first evident above the midlateral area at 34.5 mm and are nearly complete at 51.8 mm (Fig. 4.3). (Larval descriptions from Jones et al. [1978] and Leim [1924]). Photos of 9, 10.5, 12.0, 20.5, 21, 28, and 38 mm TL larvae are presented by Leim (1924).

On the Atlantic coast, juvenile shad begin to form schools at 20-30 mm TL and spend their first summer in the river where they hatched. They begin to move downstream to the sea in the fall, and their migrations are probably triggered by temperature as they appear to move downstream when temperatures of the water drop below 15.5°C (Leggett and Whitney 1972). Some juveniles along the Atlantic coast migrate to sea, but others may remain in estuaries for the first year.

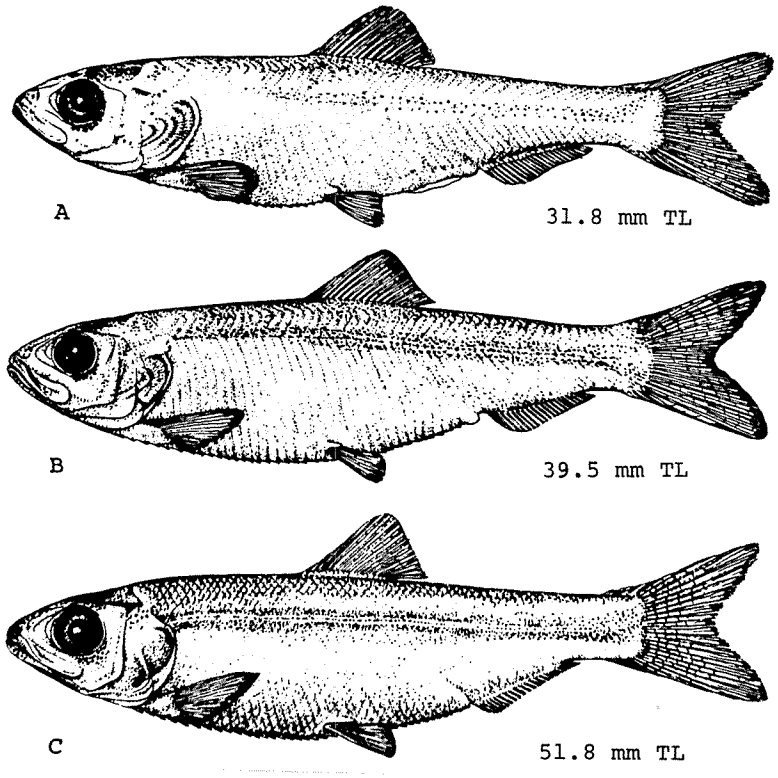

Fig. 4.3. Juvenile stages of American shad, Alosa sapidissima: A) 31.8 mm TL, 26.7 mm SL, 38 preanal and 15 postanal myomeres; B) 39.5 mm TL, 33.5 mm SL, 38 preanal and 16 postanal myomeres, scales forming above mid-lateral region, dark stripe along side; C) 51.8 mm TL, 41.5 mm SL, almost fully scaled, lateral stripe still evident. (Source: Jones et al. 1978.)

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Clupea harengus pallasi - Pacific herring

Range: Baja California to Beaufort Sea; Tena River (Arctic Ocean) to Korea.

Occurrence in Puget Sound: common

Adult habitat: pelagic, schooling

Spawning habitat: demersal, nearshore

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached

Larvae: pelagic

Because of their commercial importance in many areas of the North Pacific, the biology of Pacific herring has been under study for many years (e.g., Thompson 1917). Since all available references on Pacific herring spawning biology could not be reviewed, an emphasis was placed on those references dealing with Pacific herring stocks from Puget Sound. Additional references on spawning biology of Pacific herring from other parts of the Pacific were included as needed, and unreviewed references are presented in the appended bibliography.

Pacific herring are an important food and forage fish species which range in the eastern Pacific from Baja California to the Beaufort Sea and in the western Pacific from Tena River in the Arctic Ocean to coastal waters of Korea (Hart 1973). In Puget Sound, adults are common and widespread in bays and inlets throughout (Miller and Borton 1980), and are commercially exploited by three fisheries. These include a sac-roe fishery in the U.S. Strait of Georgia during April and May which utilizes the mature gonads (Trumble 1979b), a general purpose fishery in northern Puget Sound during fall and winter, and a year-round salmon bait fishery which operates throughout Puget Sound (Trumble 1979a).

Because of this commercial importance, the Washington Department of Fisheries (and other agencies) have been documenting areas of spawning activity of Pacific herring within Puget Sound. Spawning has been found to occur in specific areas throughout the Sound from the eastern Strait of Georgia in the north, to the area around Hunter Point in southern Puget Sound (Fig. 4.4). The adults appear to return each year to the same general area where they hatched, thus forming discrete spawning populations which do not appear to interbreed to any great extent (Trumble 1979a). Although the general spawning locations are specific and predictable, migratory or behavioral changes in the adults may cause some variation between years within a particular spawning ground. For example, within a documented spawning site, not all areas may be used

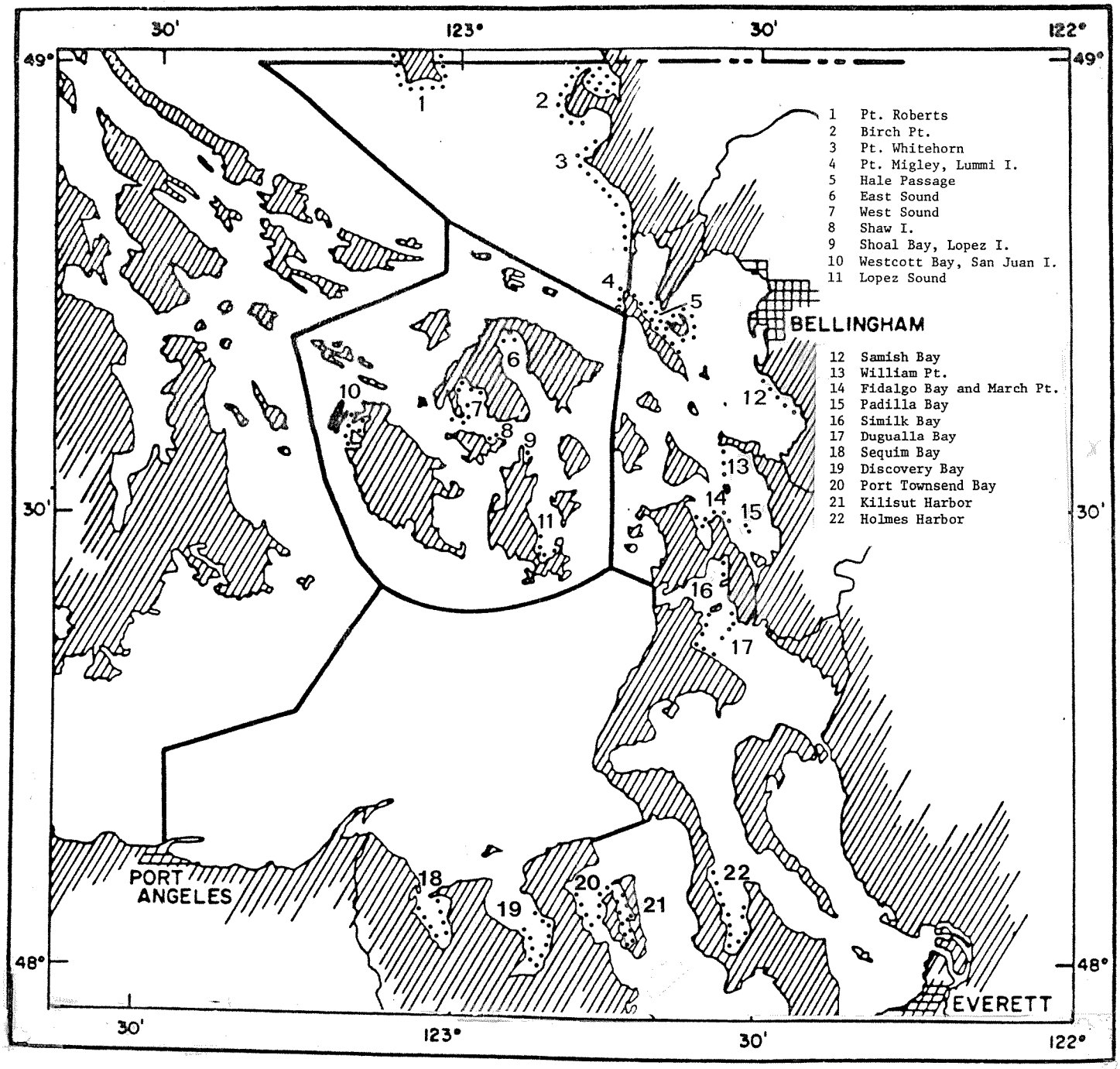


Fig. 4.4. General location of spawning grounds of Pacific herring, Clupea harengus pallasi, in northern Puget Sound. (Source: Koons and Cardwell 1981.)

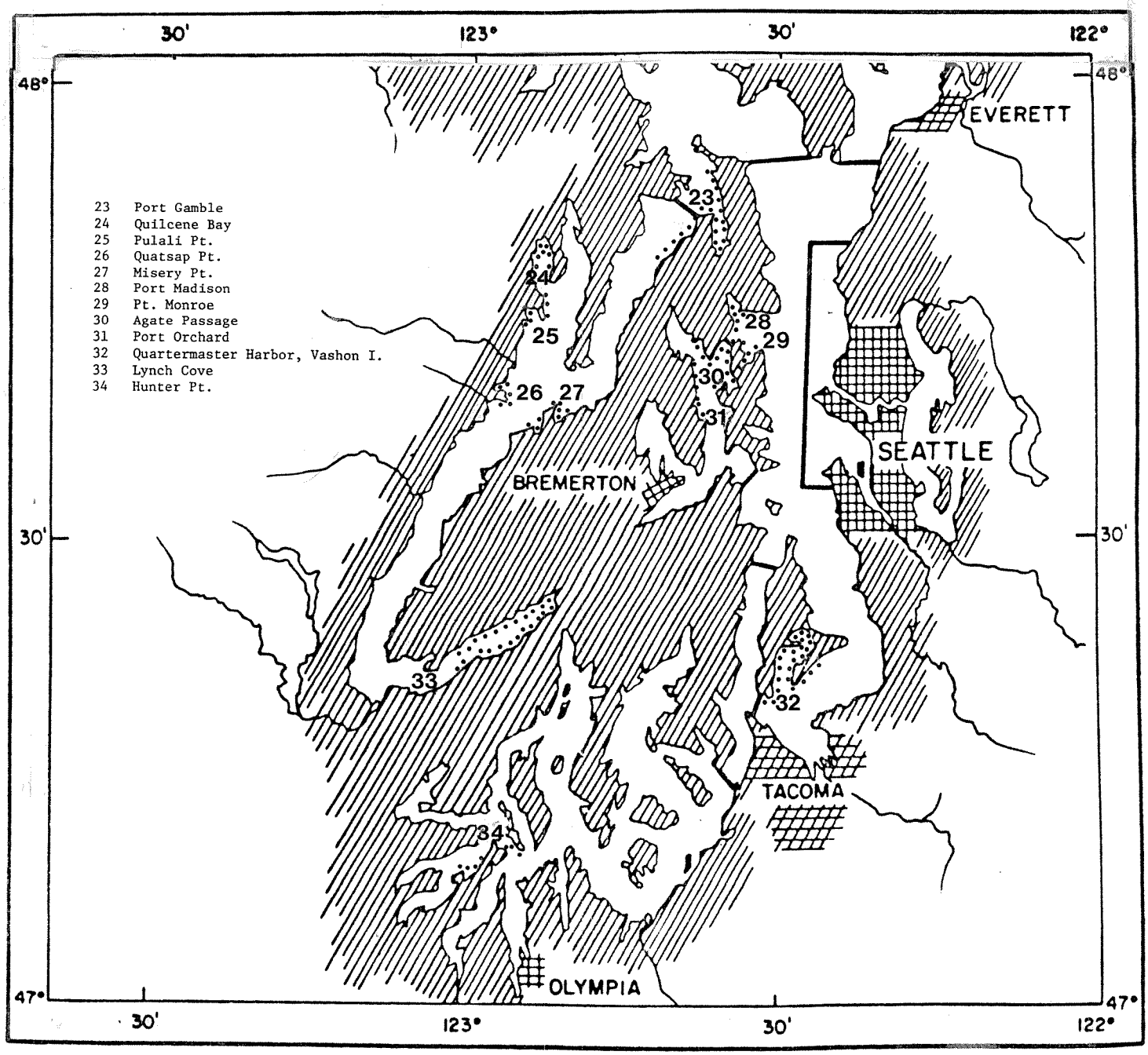


Fig. 4.4. (Cont.) General location of spawning grounds of Pacific herring, Clupea harengus pallasi, in southern Puget Sound. (Source: Koons and Cardwell 1981.)

each year or some areas may receive several separate bouts of spawning activity each year (R. Trumble, Wash. Dept. Fish., pers. comm.).

In Puget Sound, most spawning takes place in February-March, although spawning herring may be found somewhere in Puget Sound from January to June (Fig. 4.5). Adults arrive in the spawning area where they may spend a month or more undergoing final maturation. Spawning in any one area may extend over a long period (up to several months), but the spawning peak usually occurs at a similar time each year (Meyers and Adair 1978, cited by Trumble 1979a).

The largest spawning stock of Pacific herring in the Puget Sound region occurs in the U.S. Strait of Georgia and spawning occupies most of the shoreline between Pt. Roberts and Pt. Francis with the exception of some areas of Birch and Lummi bays. The herring which spawn in this area are migratory and begin to congregate along the eastern part of the Strait in March where they mature and spawn on adjacent beaches primarily from April to May. This spawning stock supports the herring sac-roe fishery mentioned earlier and represents about 10,000 tons of spawning fish.

Minor spawning grounds are found in several bays in and around the San Juan Islands, including East and West sounds in Orcas Island, and on northern San Juan Island, Shaw Island, and northern and southern Lopez Island. Spawning activity in these areas occurs between January and April.

East of the San Juans, herring are known to spawn in Samish, Fidalgo, Padilla, Similk, and Dugualla bays during February and March. These areas also include juvenile stocks in protected nursery areas and migratory populations of immature and adult fish.

Herring spawning grounds in the Pt. Townsend area include Sequim Bay, Discovery Bay, western Pt. Townsend Bay, and Kilisut Harbor. The area south of Protection Island has been found to be an important "holding area" for migratory herring. During the winter, sexually-maturing adults congregate in this area and after reaching maturity move to adjacent beaches to spawn. This area also contains large numbers of immature herring.

On the southeast side of Whidbey Island, herring spawn in Holmes Harbor in February-April. Northern Hood Canal spawning grounds have been documented in Port Gamble Bay, Quilcene Bay, and near Pulali, Quatsap, and Misery Points. In southern Hood Canal, herring are composed of 0+, 1+, 2+ immature, and maturing adults, which may be migratory or resident fish. Hood Canal is also an important nursery area in spring and summer for juvenile and immature herring.

Relatively small populations of spawning herring occur in the Port Madison - Port Orchard area, primarily in February-March. Spawning activity also occurs in Quartermaster Harbor from January to March by a

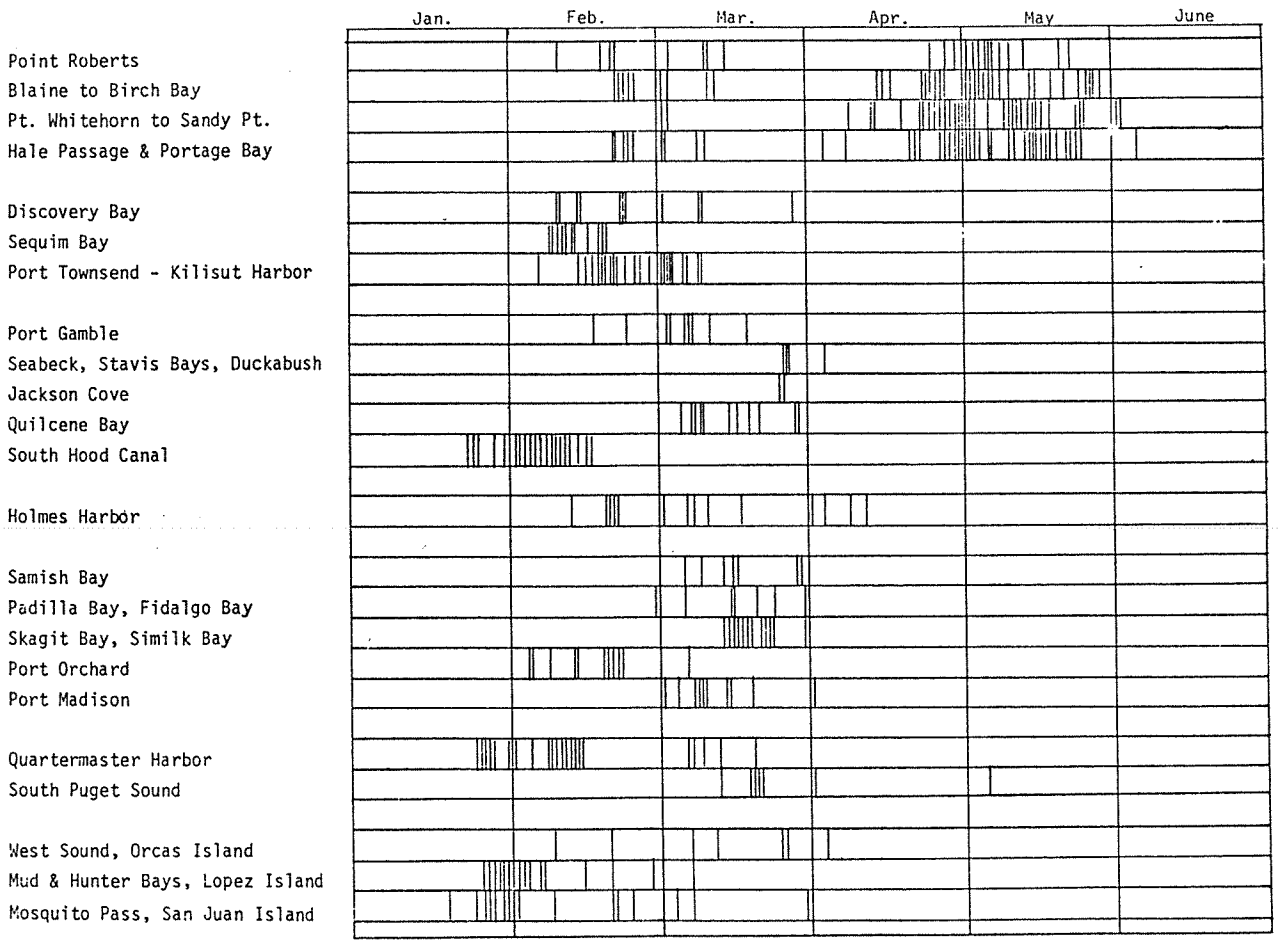


Fig. 4.5. Timing and location of documented herring spawning in Puget Sound. (Source: Trumble 1979a.)

herring stock of moderate size. Limited spawning is known to occur in the area south of the Tacoma Narrows, but this area also serves as a holding area for migratory adults, a nursery area for juvenile herring, and a habitat for resident herring (Trumble et al. 1977; Lemberg 1978; Trumble 1979a; Koons and Cardwell 1981).

Pacific herring also spawn along the British Columbia coast from January to June, although the average median date of spawn deposition occurs between mid-March and mid-April in most areas. The duration of spawning in any one area may range from as short as one day to as long as 90 days, and in most areas extends for more than one week (Hourston 1980). In some areas of B.C., herring arrive inshore just prior to spawning, but others may arrive early and remain in dense schools for several months before spawning (Outram and Humphreys 1974).

The spawning season of Pacific herring from other areas of the Pacific were summarized by Macy et al. (1978) (Table 4.1). Geographically, there is generally a shift to a later starting date of herring spawning as you move from south to north. In California to British Columbia, spawning may begin in January-February with a shift to March-April in southeast Alaska and Gulf of Alaska, and to May in the Bering Sea.

In Puget Sound, Pacific herring may reach sexual maturity at age 2 and lengths of 14-16 cm (Katz 1942), but some may not reach maturity until age 4, as in the Strait of Georgia population (Trumble 1979a). The bulk of the spawning population in Puget Sound, however, is 3-6 years old and it is presumed that adults can spawn several times during their lifetime. In Alaskan water, age of first maturity is 3-4 years and 2-6 years in the Bering Sea (Table 4.2).

Katz (1942) examined the fecundity of 55 female Pacific herring from Seal Rock in Puget Sound. The number of eggs produced per female ranged from 6307 to 40,918 (Table 4.3) and fecundity increased with length according to the relationship:

$$F = .000000436 \times L^{4.71}$$

(F = number of eggs; L = standard length, mm).

Fecundity was also dependent on age, although to a lesser extent, such that for herring of the same length, more eggs were produced by the older spawners. Relationships of fecundity to age and length have also been reported for British Columbia herring (Nagasaki 1958) and Alaska herring (Paulson and Smith 1977).

On a large geographic scale, there appears to be a decline in fecundity for a given length when moving from south (Puget Sound) to north (Prince William Sound) and northwest (Peter the Great Bay) (Fig. 4.6). However, in moving northward, there is an increase in the mean length of the spawning females such that the mean fecundity also

Table 4.1. Spawning time, by area and water temperature, of Pacific herring, Clupea harengus pallasi. (Source: Macy et al. 1978.)

Reference	Area	Spawning time	Water temperature, °C
Scattergood et al. 1959	California	January-April	8.0-10.0
Scattergood et al. 1959	Oregon	January-April	3.8-12.3
Outram and Humphreys 1974	British Columbia	February-early June	4.5-10.0
Scattergood et al. 1959; Skud 1959	SE Alaska	March-early June	6.1-11.0
Rounsefell 1930	Prince William Sound	April-May	----
Kasahara 1961	Kodiak Island	late April-early June	(4.0-9.0)
Scattergood et al. 1959	W. Alaska	April-May	3.0-5.5
Rumyantsev and Darda 1970	SE Bering Sea	May	---
Rumyantsev and Darda 1970	NE Bering Sea	May-early June	---

Table 4.2. Approximate age and length of first maturity, by area, of Pacific herring, Clupea harengus pallasi.

Reference	Area	Age, yr	Length, cm
Reeves 1972[1]	Alaska	3-4	15-20
Shaboneev 1965[1]; Rudomilov 1972[1]	E. Bering Sea	2-6 50% mature at 4 95% mature at 5	19-26
Rounsefell 1930(a)[1]	Cook Inlet and SE Alaska	0% mature at 2 32-84% mature at 3 60-100% mature at 4 100% mature at 5	---
Katz 1942; Trumble 1979a	Puget Sound	2-4	14-16

[1]Summarized from Macy et al. 1978.

Table 4.3. Fecundity of Seal Rock, (Puget Sound) herring, by length and age. (Source: Katz 1942.)

Standard length, mm	Age	No. of eggs	Standard length, mm	Age	No. of eggs
139	2	8,005	168	4	16,380
142	2	7,614	169	?	11,491
143	2	6,479	171	4	16,135
144	2	6,307	171	3	18,966
146	2	6,624	172	3	16,035
147	2	7,917	172	4	13,526
149	2	9,661	176	4	15,025
149	2	8,792	177	3	15,130
150	2	7,477	178	?	14,393
150	3	9,168	178	3	14,509
151	2	7,057	178	3	18,099
152	2	7,321	179	3	17,080
154	3	8,985	179	3	15,629
154	2	8,675	180	?	14,393
155	3	9,402	182	5	20,645
156	2	9,384	183	3	21,369
156	3	9,773	187	3	23,959
157	2	7,863	187	3	28,088
159	2	10,272	193	4	25,294
160	?	8,854	194	4	24,309
161	3	13,007	194	?	29,184
161	2	16,119	203	7	29,641
161	3	12,834	207	6	38,736
163	4	14,083	208	8	39,914
163	2	10,781	214	5	32,158
165	3	16,823	220	7	40,918
168	4	10,985			

Table 4.4. Mean fecundity (F) versus age (A) for Pacific herring, Clupea harengus pallasi, by area. L = mean standard length, mm. (Source: Paulson and Smith 1977.)

	Seal Rock[a] Washington		Southern[b] British Columbia		Northern[b] British Columbia		Prince William Sound Alaska			Peter The Great Bay[c] Siberia	
A	*F*	No.	*F*	No.	*F*	No.	*F*	No.	*L*	*F*	No.
I	8,808	11	10,244	4	—	—	—	—	—	25,534	28
II	15,815	17	14,570	48	14,298	10	13,992	4	182	57,435	57
III	16,842	8	18,811	65	20,416	153	17,965	21	200	67,851	30
IV	26,414	2	22,404	29	24,695	45	22,528	26	214	96,096	8
V	38,376	1	25,695	7	31,098	19	23,391	98	214	102,610	10
VI	35,279	2	27,072	1	41,052	4	24,347	7	219	104,106	4
VII	39,914	1	26,287	1	34,639	1					
VIII										134,000	1
Mean length spawning females	169 mm		195 mm		197 mm		212 mm			288 mm	
Mean fecundity	15,819		18,361		22,274		22,317			60,661	

[a] Katz (1948).
[b] Nagasaki (1958).
[c] Ambroz (1931).

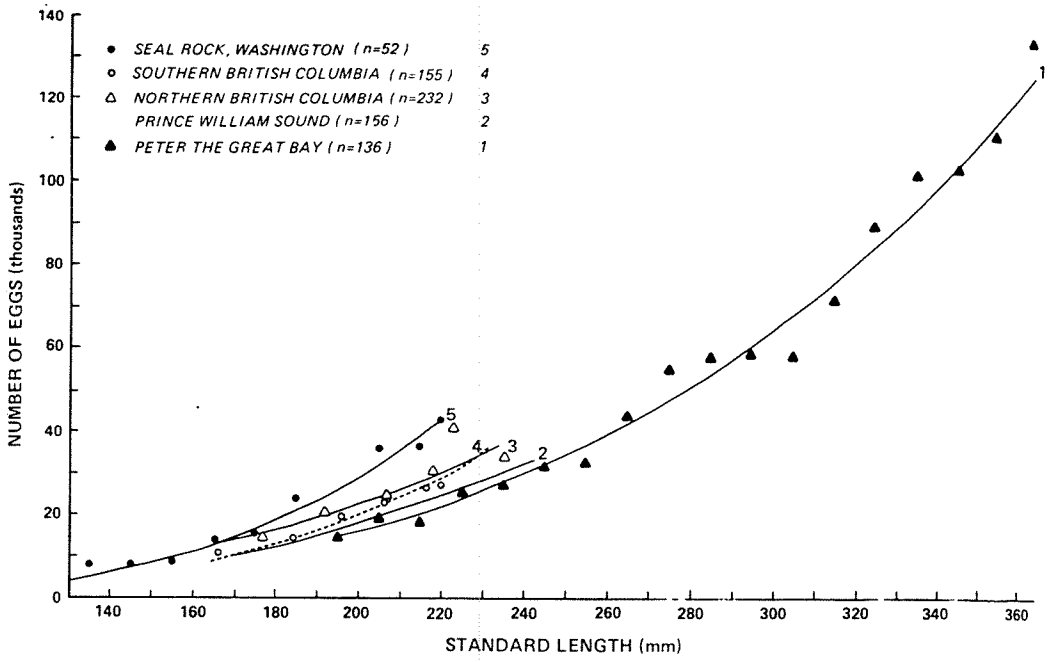


Fig. 4.6. Relationship of fecundity to length for Pacific herring from various regions. (Source: Paulson and Smith 1977.)

increases in a northernly direction (Fig. 4.6; Table 4.4). Hence, it appears that as latitude increases, the decline in fecundity vs. size is offset by an increase in mean length of the reproductively active females (Paulson and Smith 1977).

The factors which initiate spawning activity in Pacific herring at a certain time and location are not well-known, and there is no concrete evidence for a preferred time of day or tidal stage at which herring spawning occurs in Puget Sound (Trumble, pers. comm.). As the herring prepare for spawning, they form schools which move inshore, and the sexes do not appear to pair off (Schaefer 1938; Hourston et al. 1977; Outram and Humphreys 1974). Instead, males discharge their milt more or less randomly into the water, turning it opaque. Sperm densities at peak coloration of the water have been found to be on the order of 80-210 sperm/ml at the surface (Hourston and Rosenthal 1976).

Herring spawning on eelgrass in Holmes Harbor, Puget Sound was observed and described by Schaefer (1937) and was similar to observations made by Hourston et al. (1977) on herring spawning behavior in captivity:

> "Spawning females, usually one or two at a time, reduced their swimming speed as they neared the center of the tank. When about 5 cm from the central standpipe, each fish turned on its side, with the ventral surface toward the standpipe and the pectoral fins extended. While orienting to and contacting the standpipe, the fish took on a more rigid appearance. Amplitude of the tail movement was reduced while the frequency was increased. Usually contact with the standpipe was made with the lower jaw or anterior portion of the central surface. At this time, the back was arched and the extended papilla was readily visible. As a result, the papilla was generally the first (and sometimes the only) part of the posterior portion of the fish to make contact with the standpipe."
>
> "As the papilla was brushed over the substrate, a string of adhesive eggs was deposited. Each such 'egg deposition' lasted 3 to 8 seconds, involving 4 to 7 tail beats, before the fish broke contact with the standpipe. The fish then either swam a few body lengths, turned, and continued the spawning 'bout' by carrying out another egg deposition, or returned to the school. After staying in the school for as little as 20 seconds or as long as 20 minutes, it returned to the standpipe or seaweed and began another bout of egg deposition. One female observed over a 50-minute period performed 44 such spawning bouts, involving 304 egg depositions. Most (37) of the 44 spawning bouts involved more than one deposition."

Each act of egg deposition resulted in the release of less than 50 eggs.

Hourston et al. (1977) also observed two types of egg deposition patterns produced by herring spawning in the tank. In one case, eggs were deposited in rows of 1-4 eggs in width with the female in direct contact with the substrate. These egg "tracks" tended to run at a slight angle from the vertical. Eggs were also scattered randomly over the bottom indicating eggs were released into the water column and settled on any available substrate. Both patterns are also observed under natural spawning conditions, and Hourston et al. hypothesized that random scattering of the eggs may occur during high sperm density which would reduce visibility causing females to release their eggs without contacting the substrate.

In Puget Sound, most spawn densities are of the order of a single layer of eggs or less, although multi-layered deposition (2-6 egg layers) may be found in the Strait of Georgia population (Trumble 1979a; Trumble et al. 1977). In the Sea of Okhotsk, as many as 6-15 and even 16-20 layers of eggs have been observed (Galkina 1971).

Under conditions of natural spawnings, herring may deposit their eggs on a variety of substrates including marine plants and algae, brush, rocks, pilings, worm tubes, hydroids (Obelia sp.), burlap, or old lumber, and at both intertidal and subtidal depths. Most spawning, however, occurs on patches of vegetation, but spreads to nearby objects or lying loose on sandy patches between eelgrass beds as the vegetation becomes saturated with eggs (Millikan and Penttila 1973; Outram and Humphreys 1974). Before the 1970's it was thought that herring eggs were spawned primarily in the intertidal zone on eelgrass (Zostera), rockweed (Fucus), japweed (Sargassum), or laminarians (e.g., Taylor 1964). However, it is now generally concluded that the type of vegetation used and depth of spawning varies depending on location (Haegele et al. 1981; Millikan and Penttila 1973; Penttila and Day 1976). In Puget Sound, eelgrass is a commonly utilized spawning substrate, although in many mud-bottomed bays, such as in southern Puget Sound, red algae Gracilariopsis sp. and Agardhiella sp. may dominate in deeper water and are commonly used by spawning herring. In central Puget Sound, spawning substrates include Sargassum, Zostera, and occasionally Ulva (sea lettuce) in addition to red algae. Hood Canal spawning substrates are similar to central Puget Sound with the addition of Laminaria sp. In the Strait of Georgia and San Juan Islands, herring spawning occurs on low intertidal rocky-shore beaches which support a more diverse community of marine plants. In these areas, Laminaria saccharina, Alaria marginata, and Sargassum muticum overlie an understory of short red algae (Odonthalia, Microcladia, Gigartina, Iridea, and Cryptopleura) which may be used more extensively than nearby eelgrass beds (Penttila and Day 1976; Millikan and Penttila 1973).

Haegele et al. (1981) have suggested that beach slope may influence the distribution of herring spawn as eggs were deposited to deeper

depths on steeper sloping beaches and the highest deposits of eggs were found on the most gradually sloping beaches. In British Columbia, eggs have been found intertidally up to +3.7 m (+ 12′) above 0 tidal height, and may extend to depths of 16-20 m (Humphreys and Haegele 1976; Hourston et al. 1977; Taylor 1964). Regardless of the slope of the beach, Haegele et al. (1981) found the greatest spawning density from 1 m above Chart Datum (defined as the "plane of lowest normal tide") to 2 m below, after which density declined gradually with depth. In Puget Sound, herring spawn from the low intertidal to subtidal zones, between +1.2 m (+4′) to -6.1 m (-20′) in tidal elevation (Trumble, pers. comm.).

In North American waters, the largest schools of herring occur in those areas where spawning temperatures are 5.0-5.5°C to 8.8-9.0°C. The southern limit of spawning distribution coincides with water temperatures of 10°C, but Asian stocks of Pacific herring may be able to tolerate egg development at lower temperatures ($\leq$ 4°C) than British Columbia or Washington herring. Pacific herring eggs and larvae are tolerant, however, to a wide range of salinities (12-26°/$_{oo}$) (Alderdice and Velsen 1971).

A ripe, unfertilized herring egg averages about 1.0 mm (Outram 1955) and ranges from 1.2 to 1.5 mm after exposure to sea water (Hart 1973). Unfertilized eggs are opaque, spherical, and consist mainly of a large mass of colorless yolk globules. At extrusion they are sticky and adhere readily to the substrate. Herring sperm is a minute, mobile cell about 0.044 mm in length with a rounded head and a thin movable tail. In normal sea water, sperm will survive and remain active for 4-5 hours (Outram 1955).

In laboratory experiments, development of artificially reared eggs was significantly affected by temperature, but there was no clear relationship between the salinities tested and the rate of development (Table 4.5, Fig. 4.7). At 13.29°C, development time to 50% hatch was about 9 days and increased to 35 days at 4.0°C (Alderdice and Velsen 1971). Outram (1955) determined that eggs began to hatch after 14-15 days at 8.5°C, 11-12 days at 10.7°C, 18-19 days at 7.0°C, and 28-40 days at 4.4°C. The "optimum" conditions for egg and larval survival were calculated by Alderdice and Velsen (1971) to occur between 13-19°/$_{oo}$ and 5.5 to 8.7°C which are contained within the ranges in which most natural spawnings in B.C. occur. In Alderdice and Velsen's experiments, most of the hatching occurred during dark periods between 5 p.m. and 7 a.m.

The development of Pacific herring eggs incubated at 8.5°C was described by Outram (1955): The first cleavage is complete after 3 1/4 hr and the blastula forms after 15 hr. At the end of 24 hr, the bottom and central cells of the blastodermal cap become raised up to form the segmentation cavity. At 40 hr, the first rudiments of the early embryo are seen and at 54 hr, the head is well-formed with the optic lobes visible as expansions of the head. The embryo continues to lengthen and at 4 days the tail is raised off the yolk. On the 7th day, the eyes are becoming pigmented and the body encircles more than once around the

Table 4.5. Duration of hatching period, incubation time (from fertilization to 50% hatch) and rate of development of Pacific herring (Clupea harengus pallasi) eggs at various salinities and temperatures. (Source: Alderdice and Velsen 1971.)

Trial	Test conditions		Duration of hatching interval (*hr*)	Incubation time (*hr*)	Rate of development (%/*day*)
	Salinity (‰)	Temp (*C*)			
1	7.83	4.71	359.1	674.8	3.56
2	7.83	13.29	156.6	217.0	11.06
3	42.17	4.71	–	–	–
4	42.17	13.29	133.0	216.5	11.09
5	25.00	9.00	239.4	354.8	6.76
6	25.00	9.00	246.2	390.6	6.14
7	5.00	9.00	251.7	344.8	6.96
8	45.00	9.00	272.5	377.2	6.36
9	25.00	4.00	503.3	833.7	2.88
10	25.00	14.00	137.2	222.1	10.81
11	16.41	6.85	345.9	517.8	4.63
12	16.41	11.15	198.9	273.9	8.76
13	33.59	6.85	345.6	502.9	4.77
14	33.59	11.15	215.8	286.4	8.38

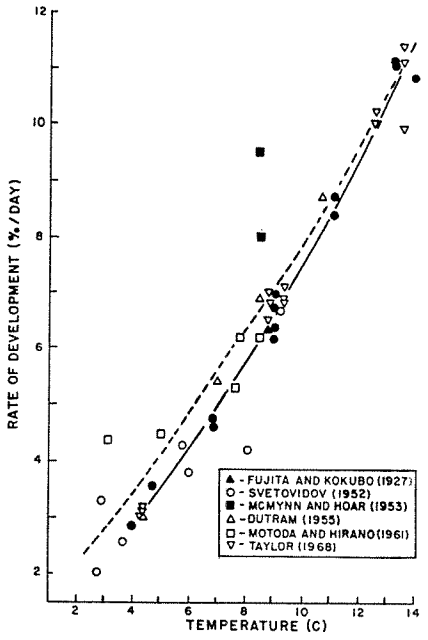


Fig. 4.7. Effects of temperature at various salinities on the rate of development of eggs of Pacific herring. Solid line from data of Alderdice and Velsen 1971 (solid circles); dotted line from Blaxter (1956) for Atlantic herring. (Source: Alderdice and Velsen 1971.)

yolk. In 11-12 days the embryo almost encircles the yolk twice and hatching occurs in 14-15 days (Table 4.6; Fig. 4.8).

Mortality during the egg stage can be quite high, and may be as much as 99% of the eggs (Taylor 1964). Possible causes of egg mortality include damage from wave action and storms, exposure to detrimental air temperatures, and predation by birds, including gulls and diving ducks which uproot spawning vegetation (Jones 1972; Taylor 1964; Hart and Tester 1934; Cleaver and Franett 1945; Outram 1958; Tester 1942). Haegele et al. (1981), however, recently pointed out that if only a small fraction of the total egg complement is intertidal, as when subtidal spawning occurs, only about 10% egg loss can be attributed to bird predation (gulls) and wave action.

The thickness of spawn deposition may also have a significant effect on the hatching process. Survival of eggs has been shown to decrease sharply with egg mass thickness, possibly due to decreased oxygen in the lower levels. Maximum larval production is estimated to occur at light to medium intensities (2-6 layers) of deposition (Galkina 1971; Taylor 1971).

Herring larvae hatch at 4-8 mm SL ($\bar{x}$ = 6 mm SL). In the yolk sac stage (up to 9 mm SL) they are semi-transparent and threadlike and have darkly pigmented eyes. The snout to anus length is long and larvae are virtually unpigmented. With development, a characteristic pigmentation occurs along the ventral surface of the body. It consists of two rows of chromatophores which are widely separated along the anterior half of the body (approximately lateral to the gut), but lie close together from the middle of the body back to the anus (i.e., on the ventral surface of the gut). In addition, a small number of larger melanophores is located posterior to the anus and on the isthmus (Stevenson 1962). Larvae of 8, 11, 29 and 46 mm have been illustrated by Taylor (1964) and Marliave (1975) (Fig. 4.9).

The pectoral fins (no rays) are present in yolk sac larvae and the dorsal and caudal fin are distinguishable by 12 mm and dorsal rays appear at 14 mm. The anal fin is evident at 20 mm and pelvic fins appear when larvae are 21-24 mm. At 35 mm, definite pectoral rays appear. Notochord flexion begins at 18 mm and is complete at 20 mm. Metamorphosis from the larval stage to the juvenile begins at about 26 mm and is complete by 35 mm. Scales begin to grow when larvae are 35-40 mm, marking the transition to the juvenile stage (Fraser 1922, Stevenson 1966).

Larval and juvenile stages (5.6 mm to 42.0 mm) have also been illustrated by Uchida et al. (1958) (Figs. 4.10, 4.11).

Larvae grow from about 6 mm at hatching to 38 mm in 6-10 weeks (Taylor 1964), to about 60 mm at 6 months and to 90-100 mm at about one year (Fraser 1922).

Table 4.6. Developmental stages of eggs of Pacific herring, Clupea harengus pallasi, reared at 8.5°C. (Source: Outram 1955.)

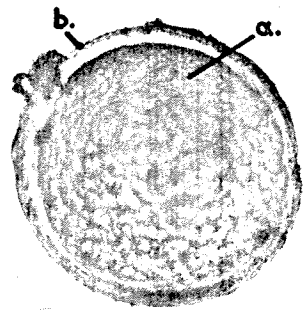
Age (in hours)	Embryonic Stage	Description of Embryonic Stage	Reference to figure illustrating embryonic stage
0	Unfertilized egg	Egg appears whitish and opaque. Note granular yolk cells enclosed in an outer membrane, the chorion.	1
		FIRST PHASE	
1½	Fertilized egg	After fertilization the yolk contracts forming a perivitelline space between yolk and chorion. The thin layer of protoplasm (blastodisc) enveloping the yolk is shown accumulating at one pole. It should be noted that the yolk occupies nearly all of the egg. The yolk is the food source of the developing embryo. As the embryo grows the volume of yolk decreases until by time of hatching it is reduced to about half its original volume.	2
3¼	first cleavage	The first of a series of cleavages or cell divisions has occurred dividing the blastodisc (one cell) into two cells.	3
5¾	third cleavage	The third cleavage or division results in formation of 8 cells, arranged in 2 rows of 4 cells each. Subsequent cell divisions results in 16, 32, 64, etc. cells.	4, 5
15	Early blastula	Continued rapid cell division results in the formation of a dome-shaped blastodermal cap above the yolk which consists of large-size cells.	6
24 (1 day)	Late blastula	Cell division continues resulting in blastodermal cap of cells greatly reduced in size as compared to cells of the 15 hour stage. The bottom and central cells of the blastodermal cap become raised up from the yolk to form an internal segmentation cavity between themselves and the yolk.	7

Table 4.6 (Cont.). Developmental stages of eggs of Pacific herring, Clupea harengus pallasi, reared at 8.5°C. (Source: Outram 1955.)

Age (in hours)	Embryonic Stage	Description of Embryonic Stage	Reference to figure illustrating embryonic stage
		SECOND PHASE	
40	Embryonic shield	At this stage the blastodermal cap becomes known as the embryonic shield. Here the first rudimentary indications of the early embryo are seen as a thickening of the median portion of the shield. The yolk sac now forms about 3/4 of the volume of the egg.	8
45	Early neurula	The cells at the edge or rim of the embryonic shield (the germ ring) divide rapidly and spread peripherally over the yolk surface while the cells towards the centre of the future embryo differentiate into a definite head region and a long thin body.	9, 10
54	Late neurula	Head of embryo is now well formed with the optic lobes showing as expansions of the head. The body of the embryo has lengthened and encircles about 3/4 of the yolk sac.	11
72 (3 days)	Early embryo	The brain region differentiates further and the lens of the optic vesicles can be seen. The body has divided into 15 conspicuous muscle segments or somites. Embryo has grown in length so that the tail is almost touching the head.	12
96 (4 days)	Early embryo	Embryo continues to grow in length so that the tail has become raised off yolk sac and is almost touching head. Body is almost completely divided into somites.	13
		THIRD PHASE	
120-144 (5-6 days)	Early embryo	The first convulsive body movements can be observed and the heart is formed and beats irregularly. Eye region is well developed but lacks pigmentation.	Not illustrated

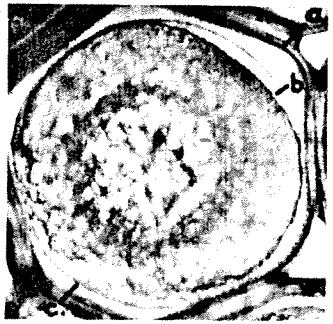
Table 4.6 (Cont.). Developmental stages of eggs of Pacific herring, Clupea harengus pallasi, reared at 8.5°C. (Source: Outram 1955.)

Age (in hours)	Embryonic Stage	Description of Embryonic Stage	Reference to figure illustrating embryonic stage
168 (7 days)	Early embryo	Body has grown until tail is well past head. Pigmentation of the eye is taking place. The black eyes are the most distinctive visible structures of the embryo. Otic vesicles or ears are well developed. Yolk sac is becoming reduced in size as embryo grows. Considerable twitchings of the body take place from now until hatching.	14
264-288 (11-12 days)	Late embryo	Growth of all organs continues gradually. Eyes are darkly pigmented and the embryo is twisted almost twice around yolk sac.	15
336 hours (14-15 days)	Hatching	Remains of ruptured egg cases present. The embryo ruptures the external membrane and hatches out head first. Newly hatched herring larvae are 5-6 mm (1/4") in length and are quite unlike adult herring in appearance. The attached yolk sac is absorbed in 4-5 days. The transparent and fragile larval herring live a hazardous existence for several months, at the mercy of ocean currents and predators, until such time as they can actively swim and school up.	16



1 - 0 HOURS

a. yolk
b. chorion

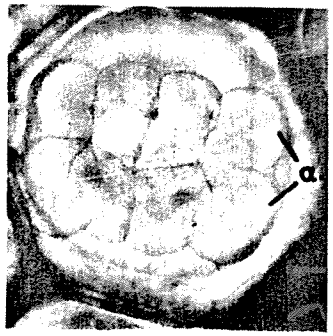


2 - 1½ HOURS

a. vitelline membrane
b. blastodisc
c. plasma membrane

3 - 3¾ HOURS

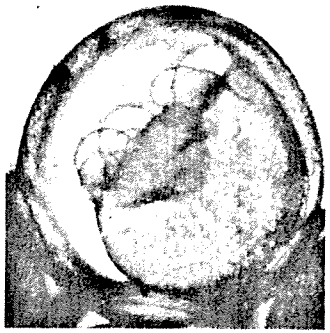
a. two cells
b. perivitelline space



4 - 5¾ HOURS

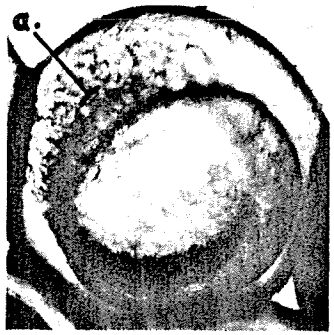
a. two rows of four cells

(top view)



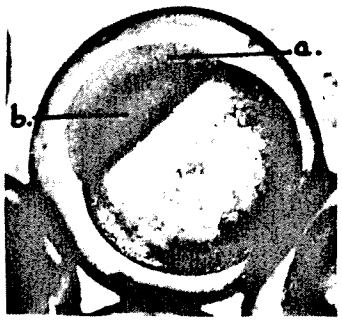
5 - 5¾ HOURS

(side view)



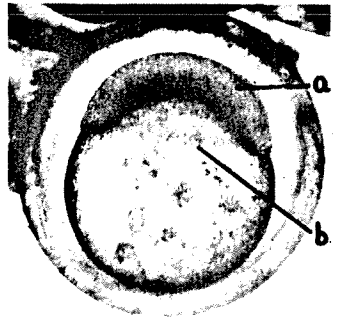
6 - 15 HOURS

a. dome-shaped cap of large size cells



7 - 24 HOURS

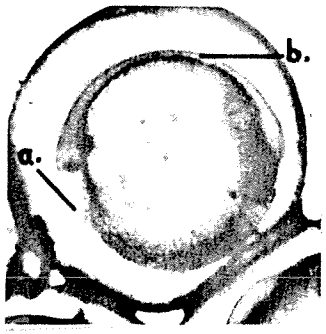
a. dome-shaped cap of small size cells
b. segmentation cavity



8 - 40 HOURS

a. thickening of cells in mid line
b. germ ring

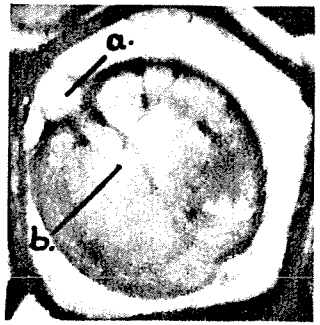
Fig. 4.8. Development of eggs of Pacific herring, Clupea harengus pallasi, at 8.5°C. (Source: Outram 1955.)



9 - 45 HOURS

a. head region
b. body of embryo

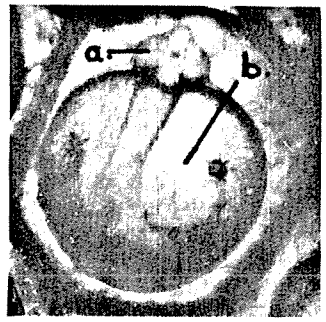
(side view)



10 - 45 HOURS

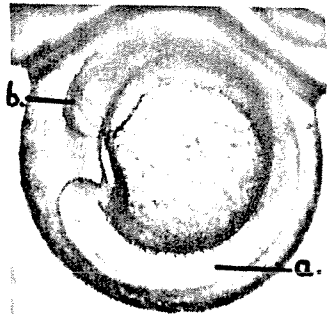
a. head region
b. form of body

(top view)



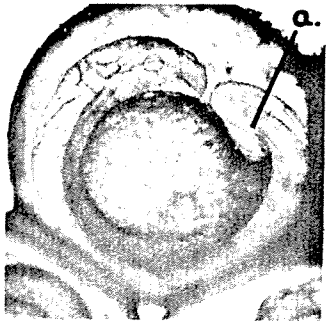
11 - 54 HOURS

a. optic lobes
b. yolk sac



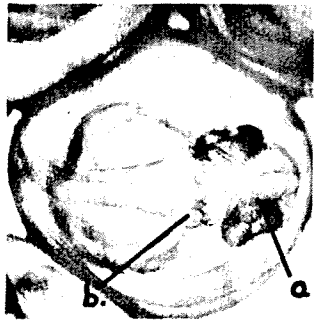
12 - 72 HOURS

a. somites
b. head region



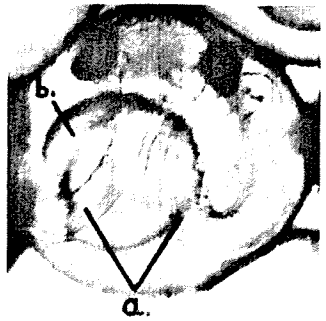
13 - 96 HOURS

a. tail raised off yolk and almost touching head



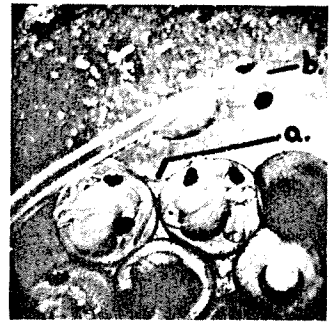
14 - 168 HOURS

a. black eyes
b. ear vesicles



15 - 264 to 288 HOURS

a. body encircles yolk twice
b. yolk sac much reduced in size



16 - 336 HOURS
(hatching)

a. remains of egg case
b. hatched larval herring

Fig. 4.8 (Cont.). Development of eggs of Pacific herring, Clupea harengus pallasi, at 8.5°C. (Source: Outram 1955.)

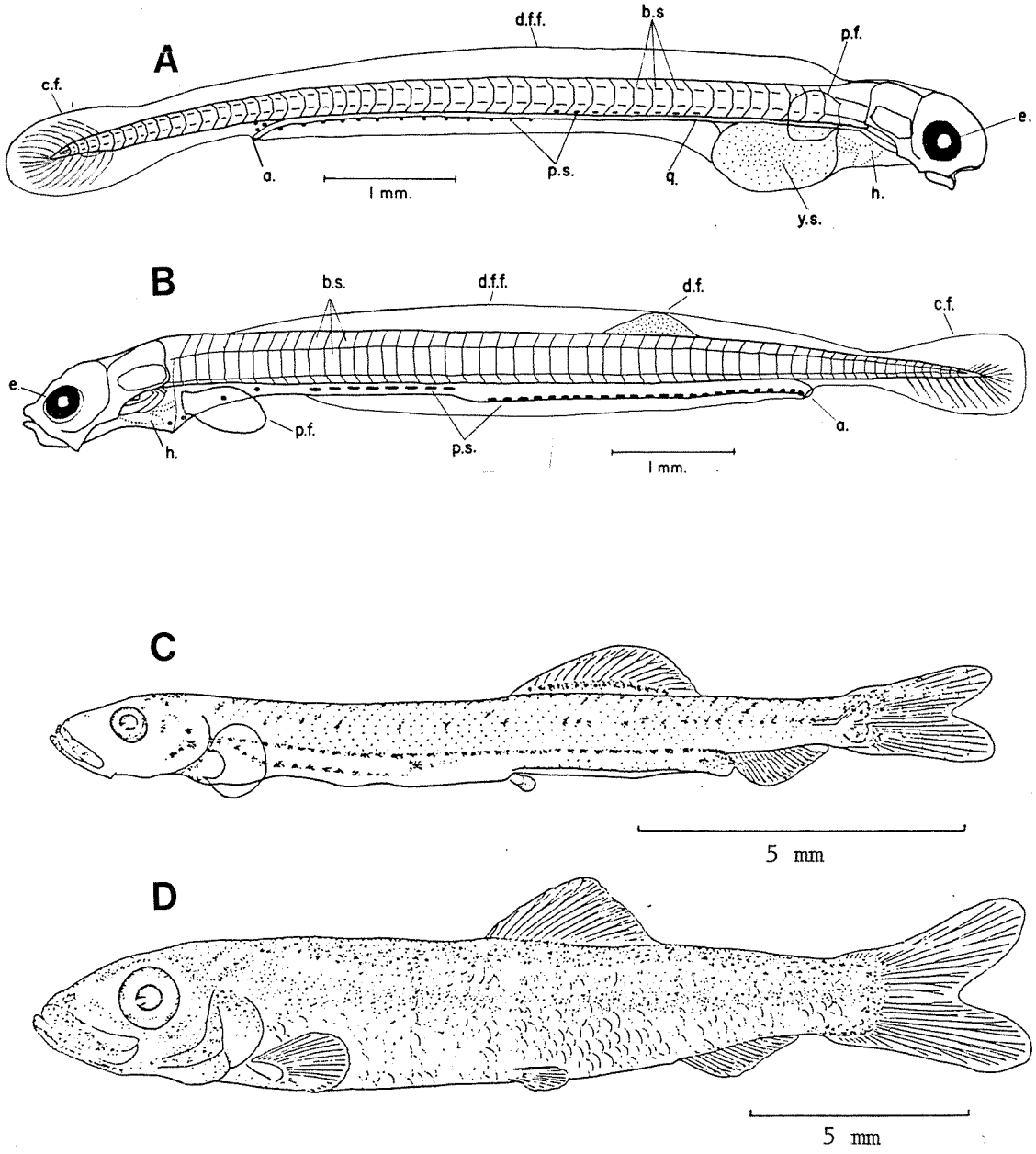


Fig. 4.9. Larvae of Pacific herring, Clupea harengus pallasi: A) ∿ 8 mm, 2-days old; B) ∿ 11 mm, 14-days old; a-anus, bs-body segments, cf-caudal fin, dff-dorsal finfold, df-dorsal fin, e-eye, g-gut, h-heart, pf-pectoral fin, ps-pigment spot, ys-yolk sac (Source: Taylor 1964); C) 29 mm TL, 43-days old; D) 46 mm TL, 83-days old. (Source: Marliave 1975.)

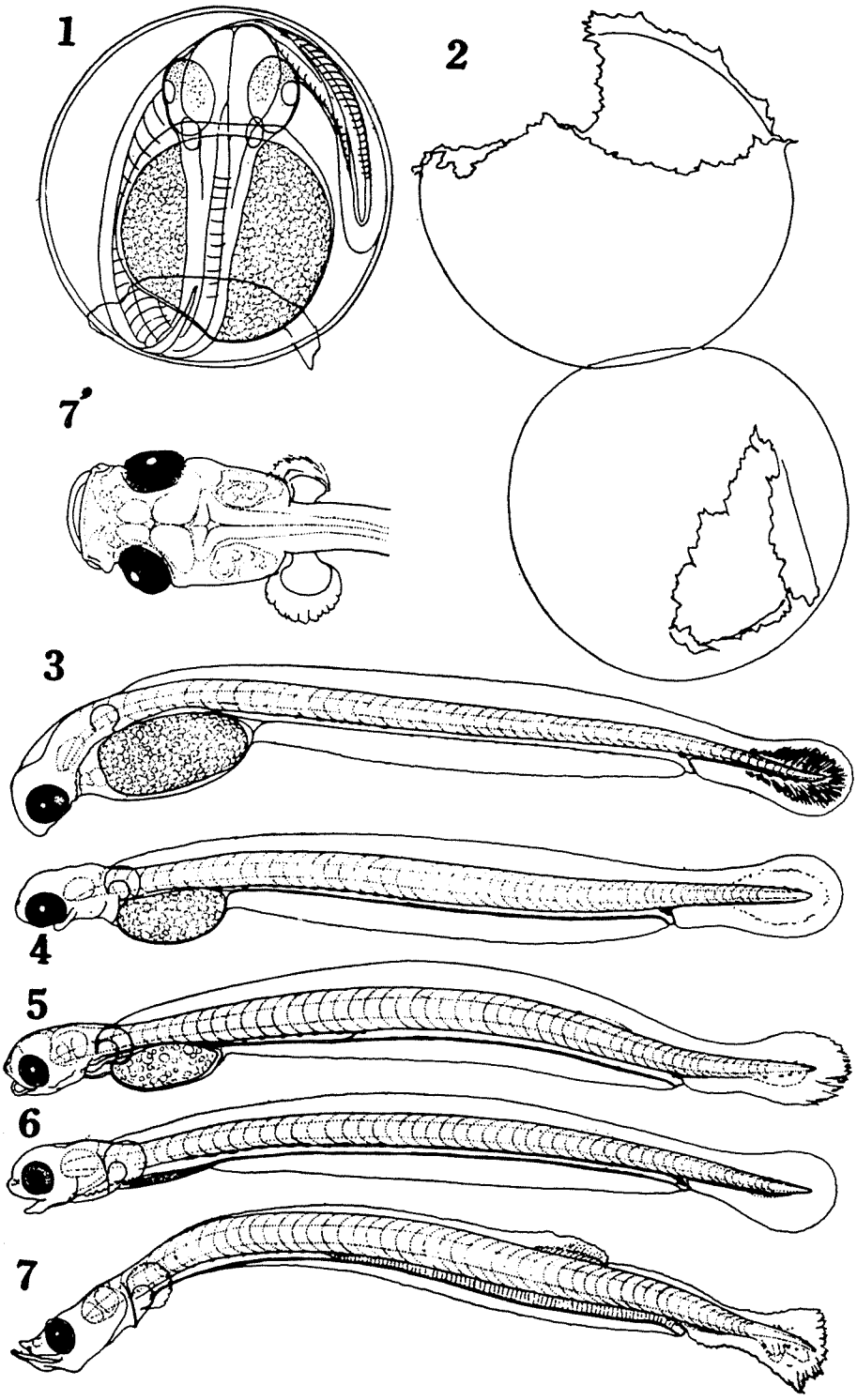


Fig. 4.10. Eggs and larvae of Pacific herring: 1)demersal, attached egg, 1.4 mm in diameter; 2) empty eggs; 3) newly hatched larva, 5.6 mm TL; 4) 6.5 mm, 12 hr after hatching; 5) 8.6 mm; 6) 8.6 mm, 7 days after hatching; 7) 10.4 mm TL; 7') 10.4 mm, dorsal view of head. (Source: Uchida et al. 1958.)

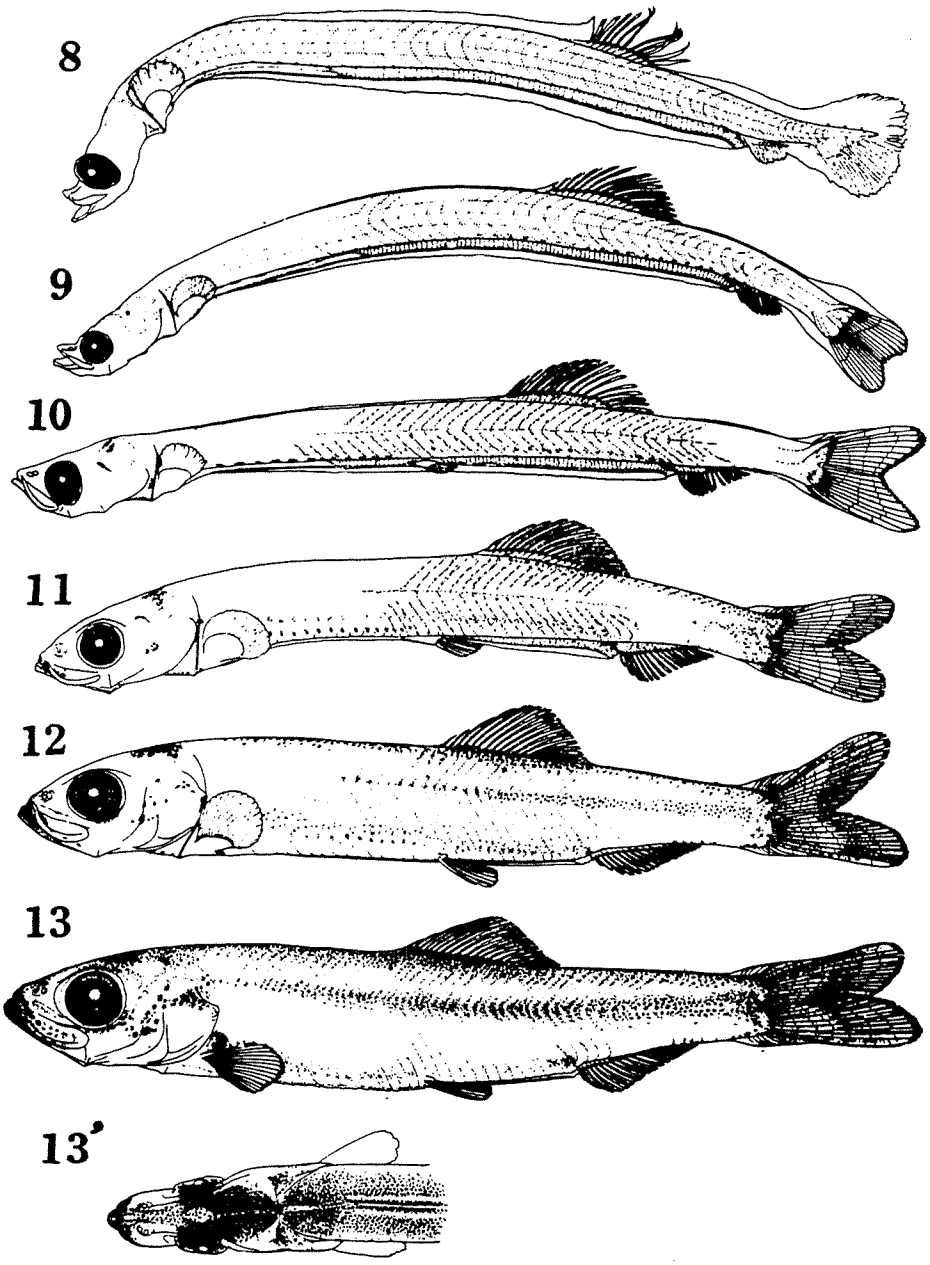


Fig. 4.11. Larvae and juveniles of Pacific herring: 8) 14.3 TL; 9) 16.8 mm; 10) 24.0 mm; 11) 30.0 mm; 12) juvenile, 36.0 mm; 13) 42.0 mm; 13') 42.0 mm, dorsal view of head. (Source: Uchida et al. 1958.)

Mortality during the larval stage may also be quite high and may be 99% of the herring larvae. Possible contributing factors include predation by ctenophores, jellyfish, chaetognaths, and other marine animals, starvation, and water conditions (salinity and temperature). However, Stevenson (1962) concluded that none of these factors alone or together could account for the high mortality. He believed that the major cause of larval mortality in B.C. herring was the transport of larvae by surface currents to the open sea, where the factors directly causing death are unknown, but may be connected to the higher salinities of the open sea. Stevenson concluded that the transport of larvae to unfavorable areas determines the relative strength of the year class.

Herring larvae are usually concentrated in inshore, near surface waters (Stevenson 1962). Marliave (1980) observed that schooling behavior in aquarium conditions began after 16 days from hatching and was fully developed by 25 days.

In Puget Sound, herring have completed metamorphosis by late-spring and early summer and move into shallow water rearing areas. During summer and autumn, juveniles reside in schools along the shoreline and in September-October move offshore into deeper open water. By November-December, they are about 4" in length and remain in Puget Sound through the next summer until they are about 5-6." At about a year and a half, they migrate out of traditional fishing areas during late summer to early winter. Although the migration routes are not well-known, some Puget Sound herring move to waters off Cape Flattery and Vancouver Island. As they approach maturity they migrate back into Puget Sound to spawn (Trumble 1979a).

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Sardinops sagax - Pacific sardine

Range: Baja California to southeast Alaska; also off Peru and Chile from 5 to 42°S

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic, schooling

Spawning habitat: near surface in waters of continental shelf

Spawning season: spring-summer (California)

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Pacific sardines or pilchards range along the continental shelf of North America from Baja California and Gulf of California to southeastern Alaska. While the primary commercial centers of abundance of sardines are off southern California, sardines are known to undertake seasonal migrations which increase in distance with age. The northward migrations in early summer result in the largest and oldest fish migrating as far as Vancouver Island, with a subsequent southward migration to Californian spawning grounds in autumn. These migrations have resulted in some commercial take of Pacific sardines off British Columbia, Washington, and Oregon in past years (1916-1950) (Hart 1973).

A marked decrease in the abundance of Pacific sardines during the 1940's led to an increase in studies to determine the factors responsible for their fluctuation in abundance, distribution, and availability. Among these studies were extensive investigations of the egg and larval populations off California. Conducted primarily by the California Cooperative Oceanic Fisheries Investigation (CalCOFI), quantitative plankton hauls have been made over an established pattern of stations occupied at regular intervals during the year (e.g., Ahlstrom 1948, 1952, 1953, 1958, 1959, 1966; Ahlstrom and Kramer 1955, 1956, 1957; Kramer 1970).

In Puget Sound, the recorded sitings of Pacific sardine are few (Miller and Borton 1980) and it has never been established that they spawn in Puget Sound. The bulk of the early life history and reproductive ecology summarized below is from studies conducted off California.

The CalCOFI studies showed that the main spawning area of Pacific sardine is between Point Conception and Southern Baja (Ahlstrom 1966), although the general spawning area may extend as far north as San Francisco in some years (Scofield 1934). Spawning of Pacific sardines has also been known to occur off central and northern California, and

possibly as far north as Oregon. The Gulf of California contains a separate, discrete spawning population of sardines (Ahlstrom 1966).

Pacific sardines spawn off California in spring through summer (February-August) with a peak in April-May (Clark 1934). Ahlstrom (1954), however, has found sardine eggs in every month off central Baja, although the majority of eggs do occur in February-May.

Clark (1934) estimated the age of maturity of female sardines (from commercial catches) to be at 160 mm or greater. Fifty percent of the females were mature at 180-190 mm, 90% were mature at 200 mm, and 100% were mature at 210-220 mm. MacGregor (1957) concluded that the age of maturity for females was reached at two years and at length of 175 mm and greater.

The spawning behavior of Pacific sardine has not been directly observed, although Wolf (1964) encountered a school of ripe and running sardines in South Bay, Cedros Island off Baja, and noted their behavior which may or may not have been related to spawning. The activity began immediately after dark throughout the bay with the sardine school spread in a loose aggregation at or near the water's surface. Individual fish were observed to dart about at random and often leaped clear of the water, causing the surface to appear as if pebbles were continuously dropped upon it. Subsequent plankton hauls determined that newly spawned eggs were most abundant below the surface, indicating spawning had occurred somewhat below the surface.

Females outnumbered males in sardines sampled near San Pedro, Monterey, and Vancouver Island, with the greatest difference in the sex ratio found off Vancouver Island. Females were also of a greater length than males in all three locations which may be due to age differences. These findings led Watanabe and Hart (1938) to suggest there was a differential mortality rate, with a higher mortality for males than females.

Clark (1934) was the first to report on the fecundity of Pacific sardine which ranged from about 30,000 to 60,000 eggs per female at lengths between 191 and 267 mm (Fig. 4.12c, open circles).

Later, MacGregor (1957) studied the fecundity of sardine in relation to fish weight, fish length, and age of the spawner (Fig. 4.12). In all cases, the left and right ovaries of each pair were at the same stage of maturity and neither ovary had a consistently higher or lower count than the other. Fecundity of individual fish of the same length varied considerably and the relationship of fecundity to weight of the female proved to be the better indicator of fecundity than either length or age. Over all fish examined, fecundity ranged from less than 10,000 to about 60,000, although one individual contained close to 100,000 ova.

The number of spawnings per female per season has been under debate for many years. Clark (1934) reported finding four distinct size

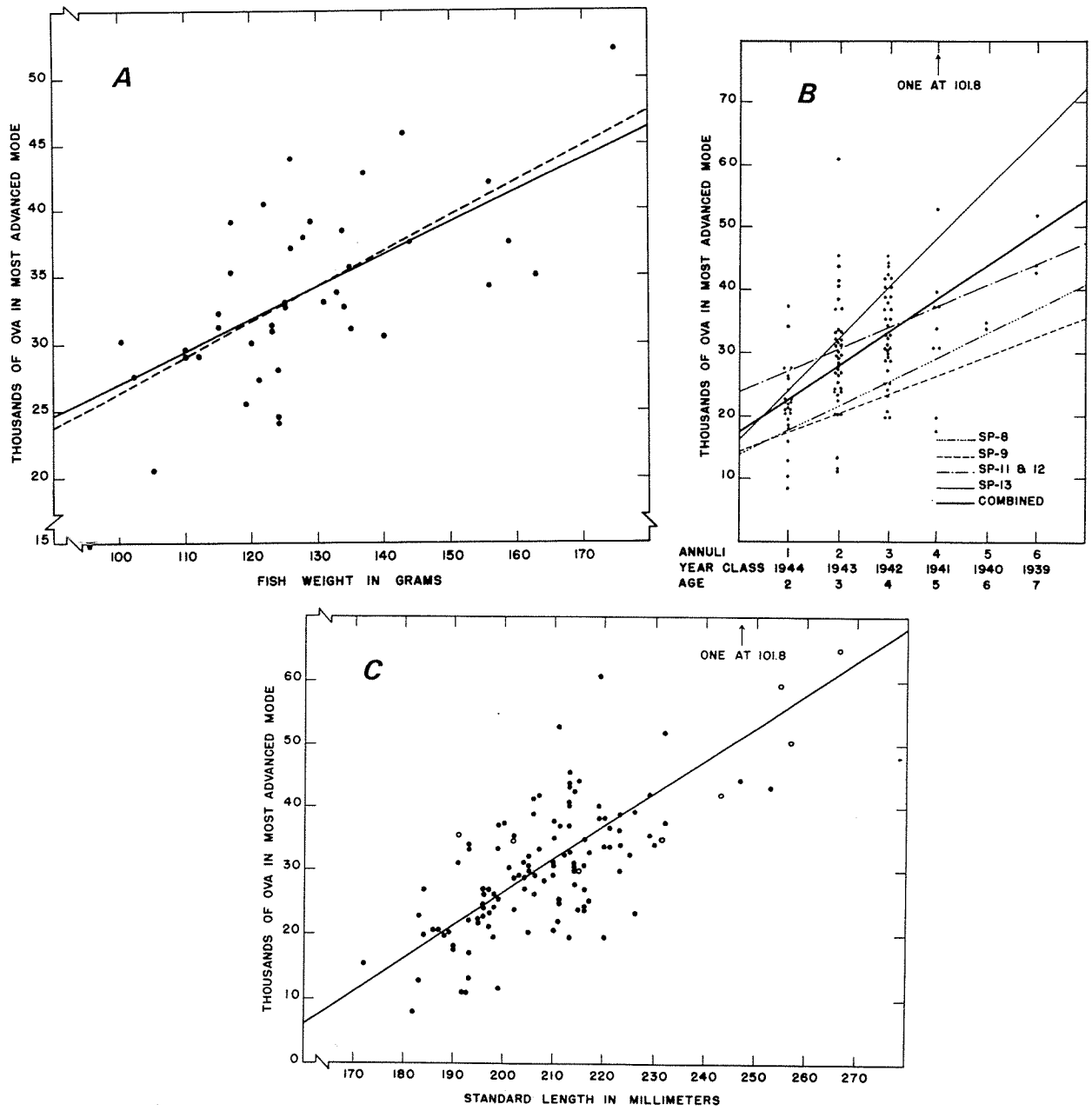


Fig. 4.12. Relationship of weight, age, and length to number of ova in the most advanced mode, for Pacific sardine, Sardinops sagax from San Pedro: A) fecundity-weight of 40 fish; dashed line, y = .2628 x and solid line, y = 2.94 + .2402 x; B) fecundity-age for 4 different samples of sardine and all samples combined; C) fecundity-length for 116 sardines, open circles are from Clark (1934). (Source: MacGregor 1957.)

classes of eggs and concluded there was sufficient evidence to justify the conclusion that individuals spawned more than once per breeding season. She suggested that up to three batches per year are possible. MacGregor (1957) also reported finding two or more size groups of yolked ova in ovaries, but after reviewing the evidence for and against multiple spawning, decided it was not possible to determine the number of batches spawned per season.

In the 1930's, Tibby (1937) observed a definite relationship between surface water temperature and the extent and abundance of sardine spawning. He estimated the minimum temperature at 13°C with an "optimum" at 15-18°C. It has since been determined that most sardine spawning occurs within a 4 degree temperature range of 12.5-16.5°C although eggs have been taken over a range of 11°C to 27.4°C. The lower temperature threshold appears to be near 13°C as only negligible amounts of spawning have been found at temperatures below this (Ahlstrom 1943, 1954, 1959).

Pacific sardine spawning occurs primarily at night from about 8 p.m. to midnight (Ahlstrom 1943) and the eggs are limited in their distribution to the upper mixed layer. The depth of the mixed layer varies from location to location and the eggs may be variously distributed within the mixed layer. In some cases, eggs occur in concentrations near the surface or within the upper 10-20 m, but may also be more widely distributed or found only in the lower portion. On the average, however, most eggs are concentrated between the surface and 20 m (Ahlstrom 1959, 1948). Larval Pacific sardines are also concentrated primarily between the surface and 42 m, and almost, if not all, are taken above 80 m (Ahlstrom 1948).

Sardine eggs were first identified and briefly described by Scofield and Lindner (1930) and additional descriptions were provided by Scofield (1934) and Ahlstrom (1943). Eggs are spherical, transparent, and with a thin unsculptured chorion which has a bluish or purplish cast. They contain a single oil globule which measures 0.16 mm in diameter and the yolk is irregularly segmented. Prior to fertilization, eggs range from 0.97-1.47 mm, and are about 1.2 mm on the average. After fertilization, the chorion begins to swell due to the development of a large perivitelline space and eggs reach their maximum diameter between 1.35 and 2.05 mm (Table 4.7). Miller (1952) successfully fertilized sardine eggs in the laboratory and observed that they achieved their maximum diameter after 10 hours (Table 4.8). At an incubation temperature of about 16.8°C, cleavage began at 1 1/2 hours after fertiliztion and sixten blastomeres were formed by 2 1/4 hours (Fig. 4.12). At the point of maximum egg diameter (10 hours), the blastodisc is well-formed and at 13 hours, the germ ring approaches the equatorial position. Blastopore closure is encountered at 19 hours and 6 somites are visible on the early embryo shortly after closure. The tail of the embryo lifts from the yolk sac during the 35 somite stage, or at 35 hours after fertilization. Heart beat is detectable at 43 hours of development and embryos begin to hatch during the 47th hour. At 16.8°C

Table 4.7. Average and range of diameter of eggs of Pacific sardine, Sardinops sagax. (Source: Wolf 1964.)

Reference	Average diameter, mm	Range, mm	No. eggs examined
Pre-cleavage (0-1 1/2 hr after fertilization)			
Ahlstrom 1943	1.20	1.02-1.38	591
Miller 1952	1.26	1.10-1.41	20
Wolf 1964	1.23	0.97-1.47	104
Developing eggs (10 hr after fertilization)			
Ahlstrom 1943	1.70	1.35-2.05	∿1000
Miller 1952	1.83	1.71-1.90	10
Wolf 1964	1.62	1.45-1.73	100

Table 4.8. Increase in size of eggs of Pacific sarding, Sardinops sagax, up to 10 hr after fertilization. After 10 hrs, all diameters of eggs are within the range of 1.71-1.90 mm. (Source: Miller 1952.)

Hours after fertilization	Stage of development	Average diameter in mm.	Range of diameter in mm.	Number of eggs measured
0	Just fertilized	1.15	1.10-1.20	10
1	Blastodermal cap	1.38	1.31-1.41	10
2	8-16 Blastomeres	1.64	1.62-1.67	3
3	64 Blastomeres	1.68	1.64-1.73	8
5½	Early Blastodisc	1.73	1.69-1.76	10
10	Early Germ Ring	1.83	1.71-1.90	10

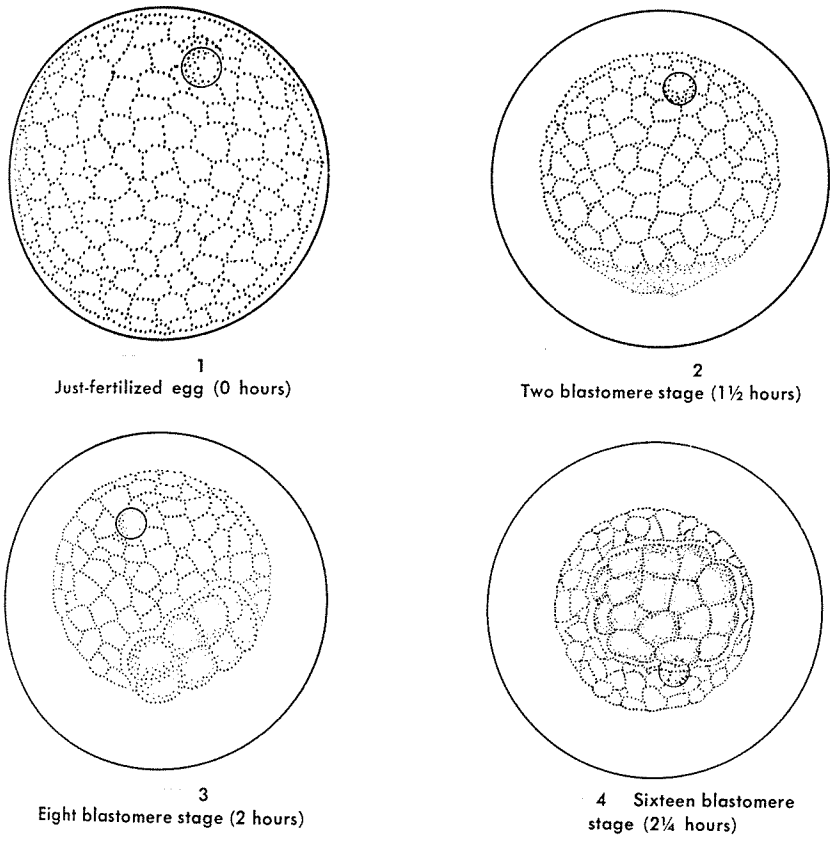


Fig. 4.13. Early developmental stages of eggs of Pacific sardine fertilized at about 16.8°C. (Source: Miller 1952.)

most eggs hatch between 54 and 56 hours after fertilization (Table 4.9) (Miller 1952). The later developmental stages of Pacific sardine eggs based on plankton collections have been illustrated and described (Fig. 4.14; Table 4.10).

Since sardine eggs in nature are present in water temperatures between 11 and 27°C, Lasker (1964) determined the amount of time required for eggs to develop at temperatures within this range:

Temperature, °C	Incubation time, hours
11	140
12	115
13	93
14	78.5
15	68.1
16	60.2
17	53.7
18	48.4
19	43.2
20	39.3
21	34.0

Although eggs developed at temperatures less than 14°C, mortality of the larvae was high and at temperatures less than 13°C, larvae failed to develop pigmented eyes and functional jaws. Since most natural spawning is between ~13-16°C, egg development is on the order of 2.5 to 4 days.

Illustrations and/or descriptions of various sized sardine larvae have appeared in reports by Scofield and Lindner (1930), 10.5 mm; Scofield (1934), 3.5, 10.5, and 34 mm; Ahlstrom (1948); Miller (1952), 4.11, 4.86, 5.30, and 6.03 mm; Ahlstrom (1966), 5.6, 12.5 and 31.3 mm (Fig. 4.15), and Kramer (1970), 3.0, 6.1, 9.1, 14.0, 19.7, 31.3 mm (Fig. 4.16). Larvae are slender and elongate with a thin straight intestine which extends along the ventral surface for about 5/6 of the larval length. At hatching, larvae are between 3.5 mm (Scofield 1934) and 3.75 mm (Lasker 1964). During the early larval period when the yolk sac is large, the sardine larvae float or swim about near the surface. After yolk and oil globule are absorbed, larvae sink if they remain motionless. In the laboratory they are observed to repeatedly swim upwards in short bursts followed by slow sinking (Miller 1952).

Larvae hatch in a relatively undeveloped stage with unpigmented eyes and unformed mouth and jaws. In laboratory hatched larvae, the eyes became pigmented after 3 days at about 16.8°C and 21°C, but not until about 9 days at 13°C (Miller 1952; Lasker 1964). Newly hatched larvae have two dorsal rows of pigment spots, parallel to each other on either side of the notochord. These spots migrate downward and become concentrated anteriorly over the gut and optic lobes and posteriorly in a position ventral to the gut and in the lower caudal finfold region

Table 4.9. Embryological development of eggs of Pacific sardine, Sardinops sagax, held at an average temperature of 16.8°C. (Source: Miller 1952.)

Hours after fertilization	Stage of development	Remarks
1	Blastodermal cap formed	Perivitelline space forming. Eggs near top of water. Yolk sac tends to remain in upper portion of the capsule, with the oil globule uppermost.
1½	2-4 blastomeres	
2	8 blastomeres	One 16 blastomere stage found at this time.
2¼	16 blastomeres	Blastomeres protruding well from the yolk material—easily seen.
2½	32 blastomeres	Eggs now suspended uniformly in jars, not all near the surface as previously.
3	64 blastomeres	The rate of cleavage is fairly uniform. There is very little overlapping of stages.
3½	128 blastomeres	
10	Blastodisc well formed. (Early germ ring)	"Water hardening" completed. (1.83 mm. average diameter).
13	Embryonic shield	Germ ring nearing equator.
19	Early embryo stage.	Blastopore closing. Yolk sac in upper portion of capsule.
20	6 somite stage	Only the somites clearly seen in the living material are counted. A few eggs are starting to die and turn white when they sink to the bottom of the jars.
24	12 somite stage	
30	28 somite stage	
35	35 somite stage	Tail coming free from yolk sac.
38	42 somite stage	Cerebral hemispheres now defined.
43	48 somite stage	Heart beats observed (120 per minute).
47	Starting to hatch	Probably eggs with damaged capsules.
55	Peak of hatching	Over three-fourths of the eggs hatched between 54 and 56 hours after fertilization. The prolarvae are suspended in water with the yolk sac upward. Capsules sink to the bottom of the jars upon hatching of the larvae.
60	Hatching completed	

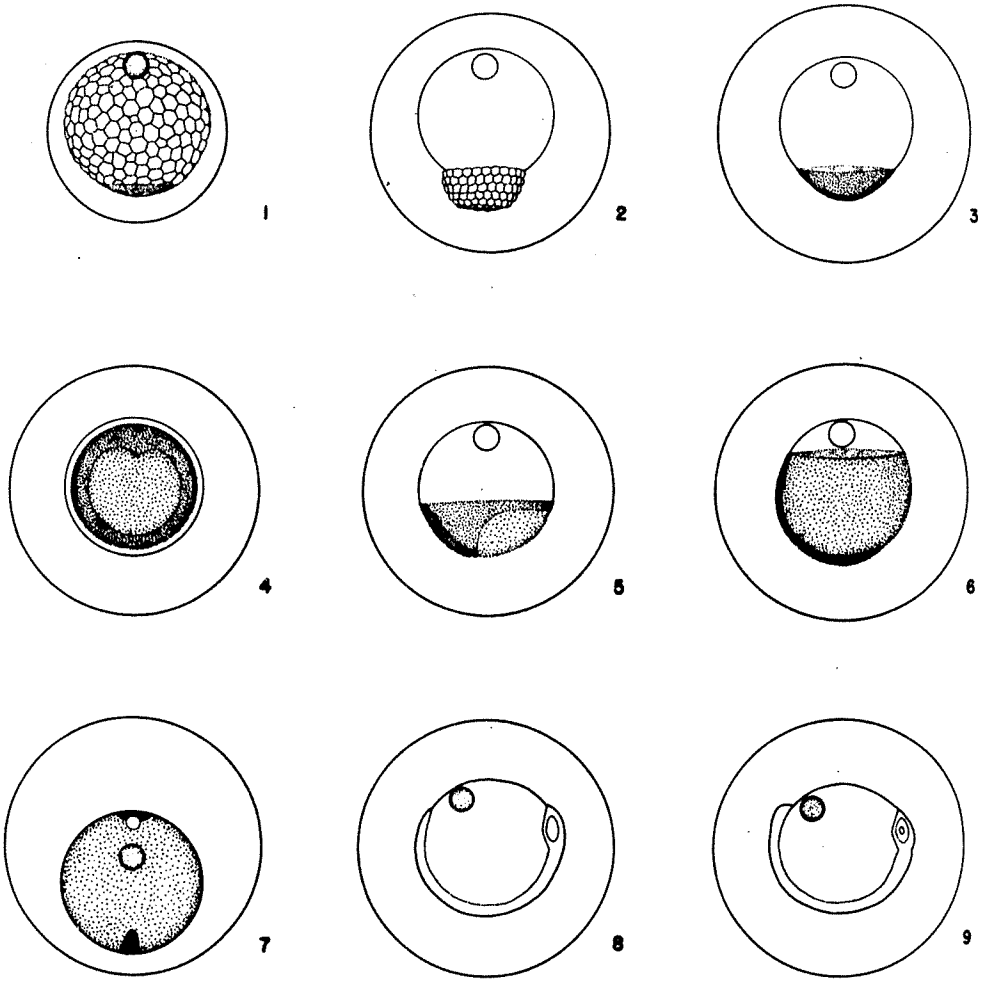


Fig. 4.14. Developmental stages of eggs of Pacific sardine, Sardinops sagax. Complete description of stages are given in Table 4.10: 1) stage I pre-cleavage egg; 2) early stage II, blastodermal cap; 3) late stage II, individual cells of cap not readily visible; 4) dorsal view of intermediate stage III, segmentation cavity; 5) beginning of stage IV, germ ring encloses a third of the yolk mass; 6) beginning of stage V, continuing growth of germ ring; 7) stage V, immediately before closing of blastopore, ventral view; 8) early stage VI, optic vesicles arise; 9) late stage VI, pupils appear in eyes. (Source: Ahlstrom 1943.)

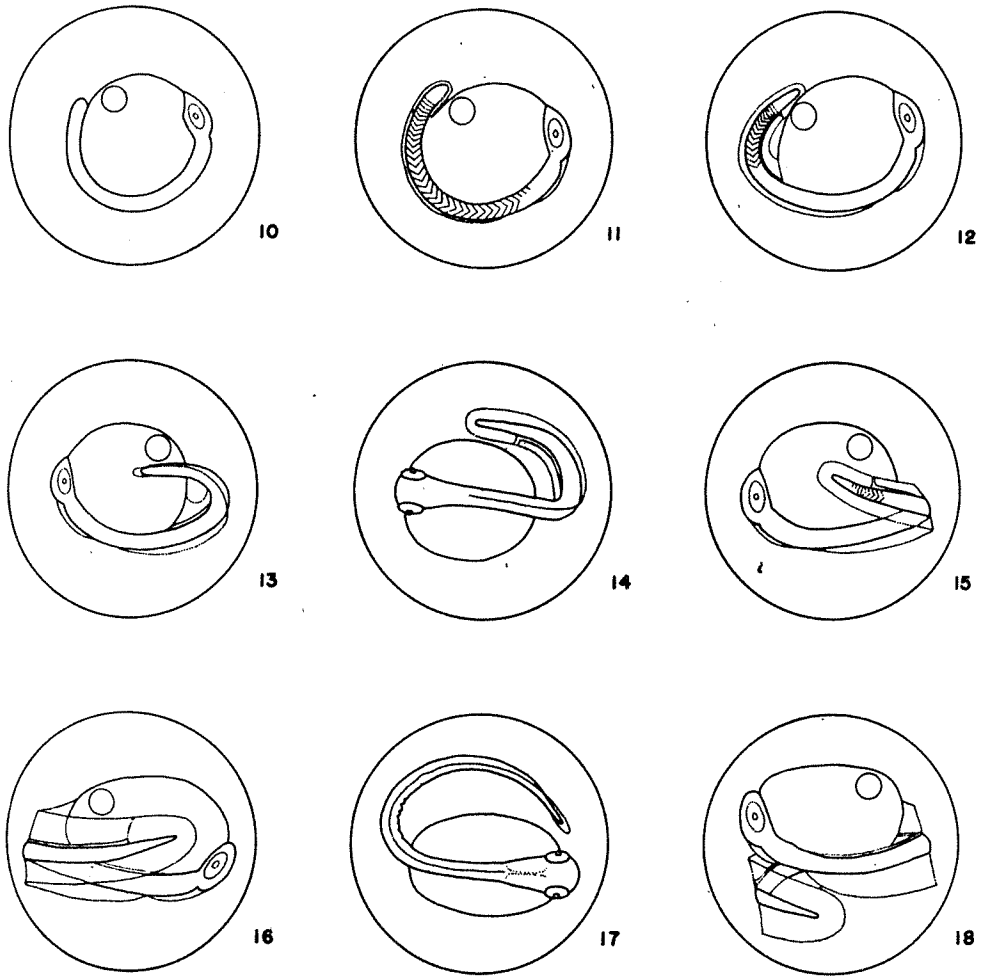


Fig. 4.14. (Cont.) Developmental stages of eggs of Pacific sardine, Sardinops sagax. Complete description of stages are given in Table 4.10: 10) early stage VII, tail bud begins to separate from yolk; 11) late stage VII, free portion of tail about equal to length of head, somites become distinquishable, finfold barely discernable; 12) late stage VIII, one-third of the body at the tail end is separated from yolk; 13) late stage IX, tail curves to one side of the yolk, pigment spots may appear in 2 parallel rows on the dorsum; 14) early stage X, dorsal view, free tail continues to lengthen and is oriented along the side of the yolk; 15) early stage X; 16) early stage XI, dorsal view, free tail length greater than portion attached to yolk sac, tail divided into somites to its tip; 18) late stage XI, just prior to hatching. (Source: Ahlstrom 1943.)

Table 4.10. Description of developmental stages of Pacific sardine, Sardinops sagax, eggs. (Source: Ahlstrom 1943.)

Stage I

In stage I were included all pilchard eggs that were not undergoing development, either because they were so recently fertilized that cleavage had not yet begun or because they were unfertilized. Pre-cleavage eggs are usually smaller in size than are pilchard eggs undergoing development; the difference is not in the yolk mass, which is fully as large in the pre-cleavage eggs, but in the width of the perivitelline space, which may be nearly wanting. Many eggs in this stage have an accumulation of protoplasm at the animal pole to form a blastodisc.

Stage II

The period of development of the blastodermal cap is covered in stage II. Although this stage includes the early cleavage divisions, no pilchard eggs have been observed in our samples with fewer than about 128 cells. The lack of material showing early cleavage divisions is hard to explain, especially since stage I eggs were taken previous to initiating cleavage. Such divisions must take place very rapidly, indeed. While the individual cells are fairly large and quite evident, the blastodermal cap has a rugged, berry-like appearance. As the cells become minute and indistinct through repeated divisions, the cap assumes the shape of a smooth, rounded, lenticular dome. The pilchard egg floats with the blastodermal cap downwards. At the opposite end of the yolk mass is the single, large oil globule. This stage persists until segmentation cavity is formed.

Stage III

Stage III covers the period of development from the first appearance of the segmentation cavity to the definite establishment of the embryonic shield. The segmentation cavity is formed when the blastodermal cap separates from the underlying periblast in the middle portion of the cap; the cavity forms somewhat eccentrically, leaving the blastoderm on one side of the cavity somewhat thicker than elsewhere. The thickened area is the region of the developing embryonic sheild. However, the outline of the embryo is not definitely defined in this area until after this stage. The germ ring begins the envelopment of the yolk with a cellular sheath; by the end of the stage the ring has enclosed a third of the yolk mass.

Stage IV

This stage begins when the general outline of the embryo can be discerned along the median line of the embryonic shield. The germ ring at the beginning of the stage encloses a third of the yolk mass; the end-point of the stage is arbitrarily fixed at the period of development when the germ ring encloses four-fifths of the yolk. By the end of the stage the embryo extends about two-fifths of the way around the yolk, with the cephalic region both thicker and wider than the remainder of the embryo.

Table 4.10 (Cont.). Description of developmental stages of Pacific sardine, Sardinops sagax, eggs. (Source: Ahlstrom 1943.)

Stage V

The period of development covered by this stage occupies the final enveloping of the yolk by the germ ring and the closure of the blastopore. The germ ring continues its centripetal growth until the yolk is completely encompassed by a cellular sheath; the final closure occurs just back of the posterior pole of the embryo. While the germ ring is completing this closure, there is a thickening all along the embryo, although the resulting dorsal ridge is still most pronounced in the cephalic region and tapers off posteriorward, so that even by the end of this stage the tail is hardly differentiated from the surrounding tissues, and the embryo itself is a simple, undifferentiated ridge in which somites are not yet defined. Eggs are considered as belonging to this stage until the optic vesicles are distinguishable in the head of the developing embryo.

Stage VI

This stage begins after the closure of the blastopore when the outline of the optic vesicles can be seen in the cephalic region of the embryo; it ends when the tail starts to separate from the yolk. The optic vesicles occupy fully half of the head during this stage; the somites take shape, being evident all along the embryo except in the immediate vicinity of the head and tail; the embryo extends about two thirds of the way around the yolk; the single oil globule in the yolk is a little beyond the posterior end of the embryo and retains this position in the yolk mass subsequently. This stage is of longer duration than any of the preceding three. By the end of the stage, the pupils can be discerned in the eyes, the embryo is about of equal thickness along its entire length, while the tail is somewhat swollen at its tip.

Stage VII

This stage commences when the tail begins to separate from the yolk mass; it covers the early growth of the tail until the free portion is about of equal length to the head of the embryo. Although the demarcation of the beginning of this stage is rather definite, its termination is somewhat arbitrary. All the remaining stages are separated primarily on the degree of development of the tail, as it offers the best landmarks on which to base separation into stages. During Stage VII the tail remains of uniform thickness along its length; the posterior end is rounded and even appears somewhat swollen in some individuals; the fin fold is barely discernible, extending around the free portion of the tail and along the dorsal side of the body to near the region of the head; there is either no differentiation of somites in the free portion of the tail or at best a few somites are formed at the base of the tail by the end of the stage; along the rest of the body the somites stand out sharply when viewed from above. By the end of this stage in most specimens the free tail extends up to, but not beyond, the position of the oil globule.

Table 4.10 (Cont.). Description developmental stages of Pacific sardine, Sardinops sagax, eggs. (Source: Ahlstrom 1943.)

Stage VIII

At the beginning of this stage the developing tail is free from the yolk mass for a length greater than the length of the head; by the end of the stage about one-third of the body at the tail end is separated from the yolk. The fin-fold is becoming conspicuous, although it is barely half as wide as the embryo by the end of the stage. The intestine can be seen as a line along the ventral side of the developing tail, and the position of the vent is indicated in the fin-fold. Somites are formed along the tail, at least as far as the end of the intestine. The tail tapers posteriorly, but the tip is still rounded.

Stage IX

Approximately one-third of the body is free from the yolk at the beginning of the stage and the tail is often bent to one side; by the end of the stage the tail is always curved, either to the right or left of the yolk, and comprises about two-fifths of the total length of the embryo. The fin-fold is about half as wide as the body at the beginning of this stage, it is somewhat broader along the free ventral portion of the body than along the dorsal side; by the end of the stage the ventral fin-fold is nearly as wide as the body proper, During stage IX pigment spots (melanophores) may appear on the dorsum in two parallel rows, one on either side of the notochord, with the spots more numerous immediately behind the head; on some specimens pigmentation does not appear until after this stage. The embryo conforms less to the shape of the yolk than previously and is beginning to straighten in its middle portion; at the end of this stage the tail is curved to one side of the yolk at about a 45° angle to the plane of the embryo.

Stage X

The free tail comprises at least two fifths of the length of the body at the beginning of the stage and is as long as the remainder of the body by the end of the stage. During stage X a fundamental change in the orientation of the embryo is completed, a change begun in the previous stage. This is accomplished by the straightening of the body of the embryo and the upward flexing of the tail. The embryo as a whole is no longer curved around the yolk; rather the plane of orientation has been rotated a complete 90°. Only the head end remains curved around the yolk, the remainder of the body being straightened out into one plane, although it is U-shaped due to the flexing of the end of the tail. During this stage the tail increases in length, until its tip is nearly as far forward as the base of the head; the fin-fold is about as wide as the body along the dorsal side and somewhat wider along the ventral margin.

Stage XI

This is the last stage before hatching. At the beginning of the stage the tail stretches as far forward as the base of the head, and the posterior portion of the body free from the yolk sac is longer than the portion carrying the yolk sac, and this disparity increases during the stage. The yolk mass is now oval-shaped; the fin-fold is wide, being 1 1/2 to 2 times as wide as the body; the tail is divided into somites to its very tip, which is now somewhat pointed. The eyes are still colorless, pigmentation taking place after hatching. This stage ends with the hatching of the egg.

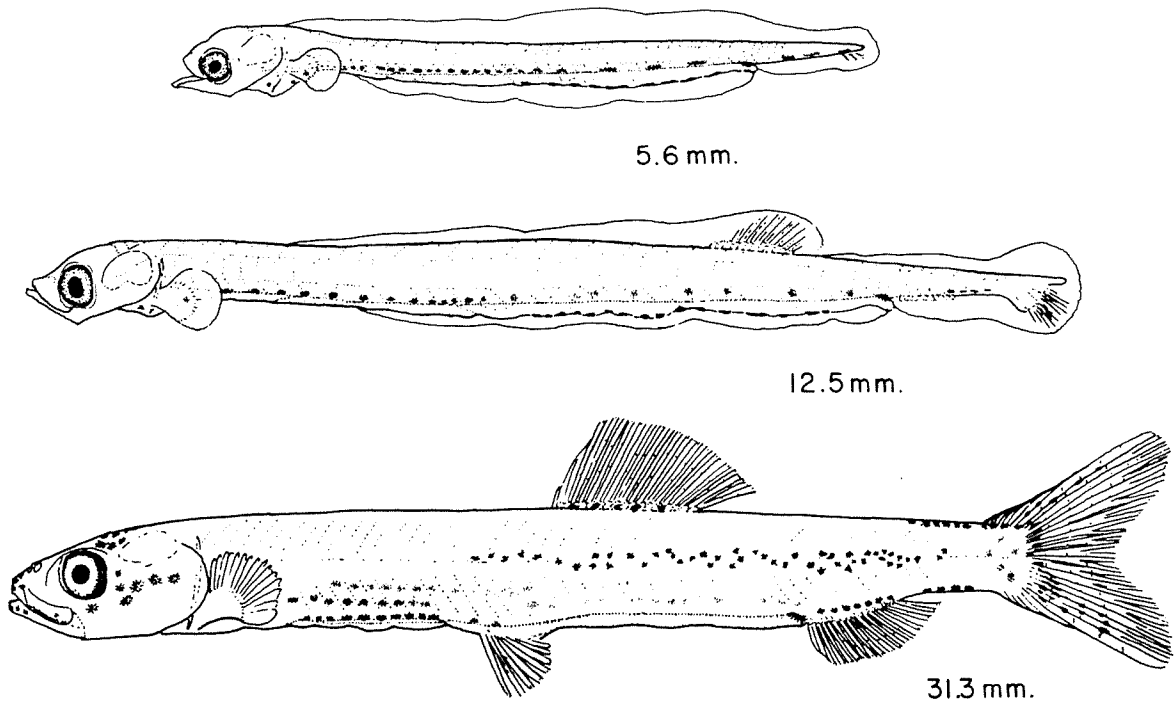


Fig. 4.15. Larvae, 5.6 and 12.5 mm, and metamorphosing specimen, 31.3 mm SL, of Pacific sardine, Sardinops sagax. (Source: Ahlstrom 1966.)

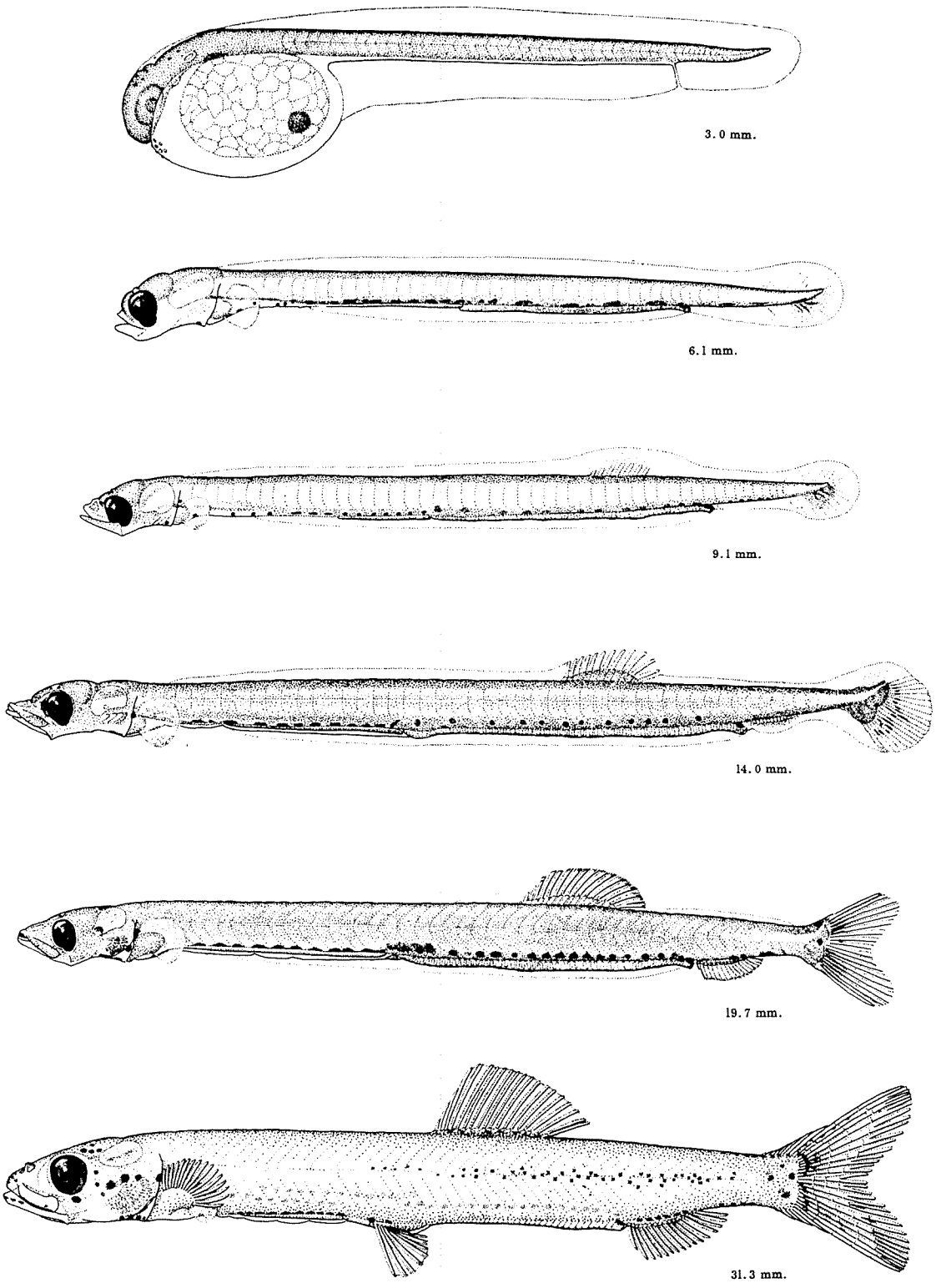


Fig. 4.16. Larval series of Pacific sardine, Sardinops sagax. (Source: Kramer 1970.)

(Fig. 4.17). This rearrangement of pigmentation is complete by about 60 hours after hatching (Miller 1952).

According to Ahlstrom (1948), fin development in the sardine proceeds in the following order: pectorals appear at about 5 mm; dorsal fin begins forming at 8 mm; caudal fin at 8-15 mm; anal fin at 12 mm; and pelvics at 20-25 mm. The position of the vent relative to the dorsal fin can aid in identifying Pacific sardine larvae from herring and anchovy larvae. In the Pacific sardine, the anus is located 5-7 myomeres beyond the posterior margin of the dorsal fin (Ahlstrom 1948; Scofield 1934). Pacific sardine larvae always possess 48 myomeres from the edge of the gill cover to the end of the tail (Scofield 1934).

In laboratory experiments, many larvae die soon after yolk absorption, but the survivors continue to show a steady increase in total length up to about the fifth day, after which there is a progressive decrease in length until death (Fig. 4.18). Early larval growth is temperature dependent with maximum lengths reached at 16°C (Fig. 4.18).

When provided with food, larval sardines in the laboratory exhibit swimming and feeding periods alternated with periods of rest. On the average, larvae spend about 40% of their time swimming and 60% resting. As the sardine larva grows, however, its swimming time increases and becomes continuous by the time it is about 9 mm. Feeding larvae in the laboratory exhibit a "search" pattern which may enhance its probability of catching additional food particles if prey are aggregated. After the larva has captured food or attempts to capture food, it moves a short distance in one direction, then turns 90° to the right or left and moves an equal distance before turning 90° again in the same direction. Some larvae were observed to turn six times, although the usual number of turns was three or four (Schumann 1965).

The feeding reflex of sardine larvae was observed by Schumann (1965) and demonstrated the visual nature of larval fish feeding:

> "The first active interest in food is seen when a larva apparently tries to focus on a particle in the water. The body is slightly drawn into an S-shaped position and the head is jockeyed back and forth in what seems to be an attempt to keep a moving particle within a critical point of focus ... In following periods the sinuous position of the body becomes more pronounced, the head moves rapidly back and forth, and the first attempt to capture a particle is made ... After the larva has reached 7 mm in length, the broad swimming undulations are followed by short, rapid undulations as food is sighted. The head of the larva moves from side to side and the eyes are in constant motion as the body is drawn into a pronounced S-shape and a rapid strike is made."

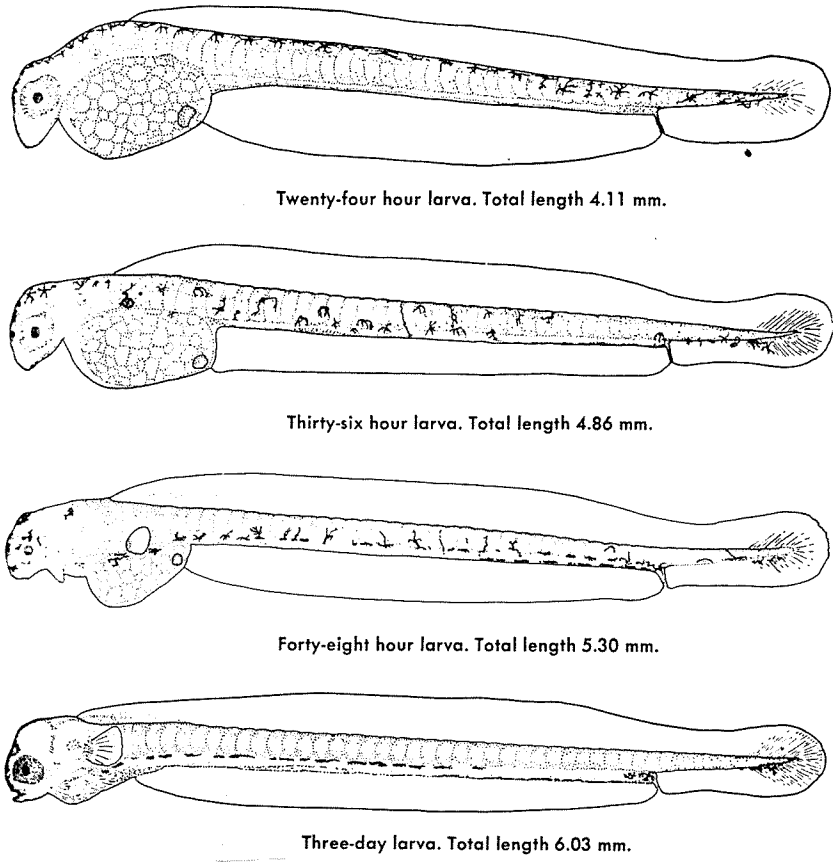
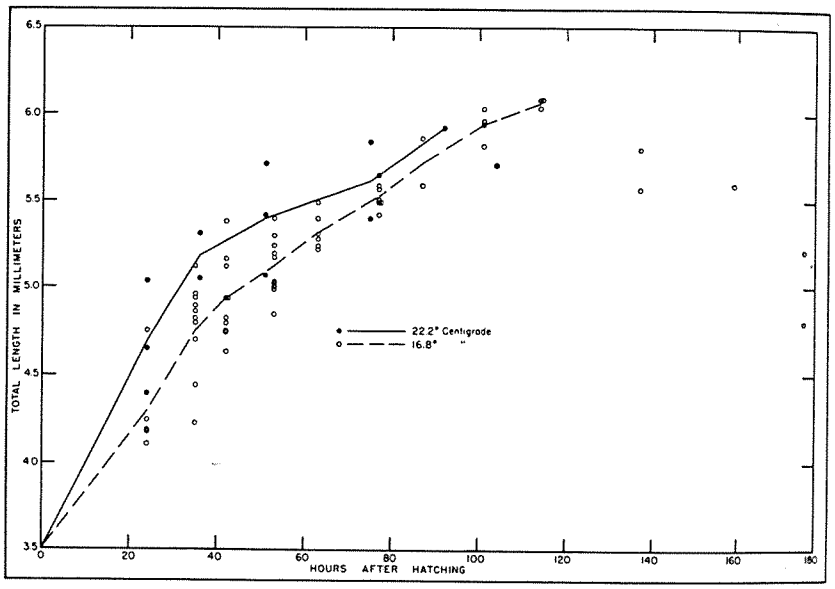


Fig. 4.17. Early larval stages of Pacific sardine reared in the laboratory. Note the downward migration of pigment cells, development of eye pigmentation, and reduction of yolk sac after 3 days. (Source: Miller 1952.)



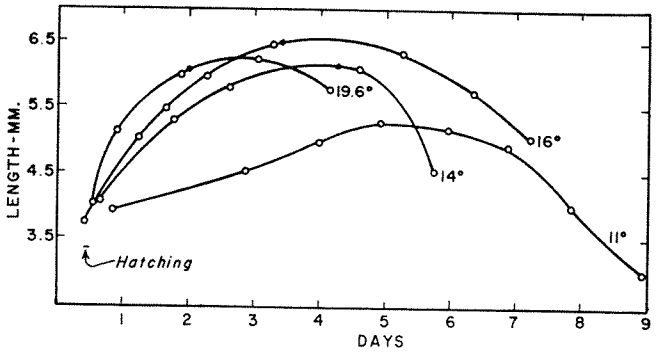


Fig. 4.18. Growth of unfed larval sardine, Sardinops sagax at various temperatures. Top: data from Miller (1952); bottom: data from Lasker (1964).

During the first attempts to capture food, the larva may abruptly break off its inspection of the food item and lapse into a motionless drift, or move away. If a strike is attempted, only one lunge at a particle is made. However, as sardine larvae become successful in their first feeding efforts, they begin to develop an obvious proficiency at capturing food and after a food particle is sighted, it is struck in rapid succession without the hesitancy seen during the first attempts at capturing food (Schumann 1965).

Under natural conditions, larvae have not been observed to contain food when yolk material is present. Eggs, nauplii, and juvenile stages of copepods compose almost all of the identifiable food consumed by sardine larvae up to 25 mm in length (Table 4.11). With growth, larvae consume more copepodid stages which is probably a function of larger larvae being able to capture and ingest larger sized prey (Fig. 4.19). Larvae appear to feed primarily during the day, when light conditions are better for visual feeding. Larger larvae demonstrate a faster return to low feeding incidence at night which may be attributed to faster digestion rates (Fig. 4.19)(Arthur 1976).

Scofield (1934) found that sardines between 40-100 mm fed primarily on copepods, young between 100-200 mm fed primarily on diatoms or copepods and adults $\leq$ 200 mm fed largely on diatoms and dinoflagellates. Scofield described the development of the gill rakers, which do not become fully developed until sardines are over 100 mm when diatoms become a major food item.

Larval mortality of Pacific sardines has been investigated from field and laboratory studies. Ahlstrom's (1954) field data of catches of larvae indicated a significant increase in larval mortality (i.e., "critical period") between the egg stage and 5.75 mm or about the time of yolk absorption, followed by a fairly constant mortality until 12 mm. However, he believed this was a sampling artifact due to undersampling of the smallest sizes which might be lost through the plankton meshes. Schumann's (1965) laboratory data seemed to also indicate a critical period at about 5.0-5.5 mm, but Lenarz (1972), when using a more efficient net for larvae could find no indication of an increase in mortality at this size in plankton-caught sardine larvae.

Eggs and larvae of sardines have also been the subjects of studies to determine their energetics, including O_2 consumption, osmoregulatory ability, caloric uptake and requirements, and growth (Lasker 1962; Lasker and Theilacker 1962; Lasker 1964). These articles are reviewed by Lasker (1965).

Transformation from the larval to the juvenile stage occurs at about 35 mm (Scofield 1934). Sardines begin to form schools when they are about 38 mm and two months of age and are transported or migrate inshore to nursery grounds. Off California, young are found off southern California and Baja California (Clark 1935; Scofield 1934).

Table 4.11. Food of larval Pacific sardine, Sardinops sagax, from the California Current region. (Source: Arthur 1976.)

	Size group					
	End of yolk-sac stage to 5.5 mm		6.0 to 9.5 mm		10.0 to 25 mm	
Food items	No.	%	No.	%	No.	%
Copepod eggs	141	22.0	35	10.8	10	28.6
Copepod nauplii:						
Calanoid	40		18		3	
Cyclopoid	68		39		3	
Harpacticoid	62		42		2	
Unidentified	179		149		5	
Total nauplii	349	54.5	248	76.3	13	37.1
Copepodid stages:						
Calanoid			1		7	
Cyclopoid	2		7		3	
Harpacticoid			2		1	
Unidentified			1			
Total copepodids	2	0.3	11	3.4	11	31.4
Dinoflagellates	5	0.8				
Tintinnids	20	3.1				
Foraminifera	3	0.5				
Unidentified crustacean eggs					1	2.9
Unidentifiable material	120	18.8	31	9.5		
Total number of food particles	640		325		35	

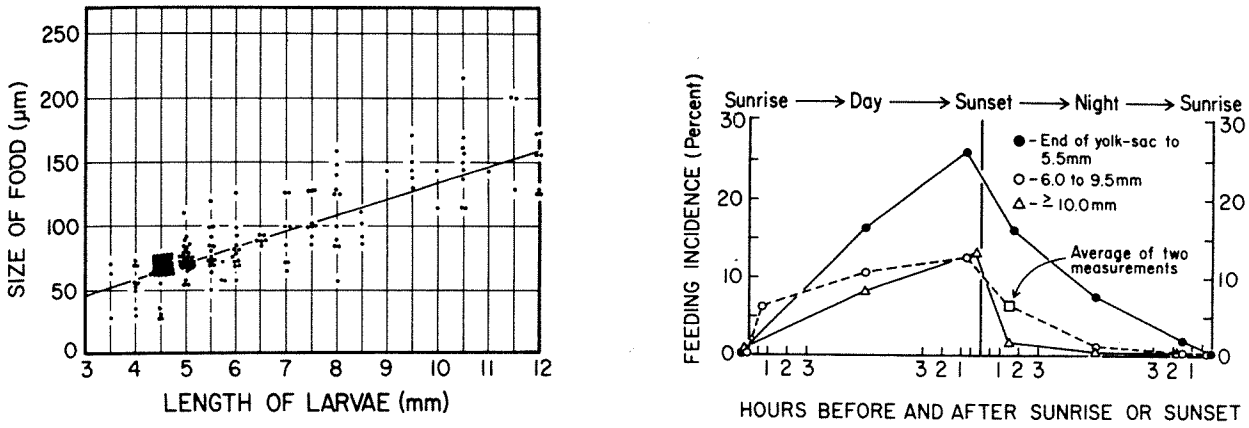


Fig. 4.19. Size of food organisms of Pacific sardine (on the left) where the line is a least squares fit to all data points and is expressed by the equation: $S = 13.04L + 5.70$ where S = width of food in microns, L = SL of larvae in mm; $r = 0.813$ and r^2 implies that 66% of the variation in food size can be explained by larval size alone. Feeding incidence of Pacific sardine (on the right). (Source: Arthur 1976.)

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5. ENGRAULIDAE

Engraulis mordax - Northern anchovy

Range: Cape San Lucas, Baja, to Queen Charlotte Islands, British Columbia

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic schooling, along coast

Spawning habitat: pelagic

Spawning season: mid-June to mid-August (Oregon)

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Northern anchovy are pelagic schooling fish which are generally found in coastal waters. They range from Cape San Lucas, Baja California, to the Queen Charlotte Islands (Hart 1973) and are distributed in three subpopulations (Tillman 1975; McHugh 1951; Vrooman and Paloma 1975, cited in Laroche and Richardson 1980). The northern subpopulation extends from British Columbia to north of San Francisco and the central and southern subpopulations occur off southern California and Baja California (Fig. 5.1). The major center of abundance of northern anchovy occurs in the central and southern subpopulations and most of the work on the reproductive biology and early life hstory is confined to anchovy within these areas. The spawning biology of the anchovy in the northern subpopulation, off Oregon, has only recently been investigated.

Spawning of northern anchovy has been recorded from British Columbia to Magdalena Bay, Baja with the heaviest spawning occurring off California and Baja between Point Conception and Point San Juanico (Baxter 1967). The southern extent of anchovy spawning and its offshore distribution between San Francisco and Magdalena Bay have been adequately described by the CalCOFI (California Cooperative Oceanic Fisheries Investigation) surveys (e.g., Ahlstrom 1952, 1953, 1958, 1959a, 1967; Ahlstrom and Kramer 1955, 1956, 1957; Kramer and Ahlstrom 1968). Most anchovy spawning in this region occurs within 60 miles of the coast, although eggs have been reported out to 300 miles offshore (Baxter 1967). Off California, northern anchovy spawn in all months of the year, although with a definite peak in February to April (Lasker and Smith 1977, cited in Hunter and Leong 1981).

Spawning season and location of anchovy in the northern population are less well-known. During July, Robinson (1969) found larval anchovies as small as 11 mm in the southern Strait of Georgia which were

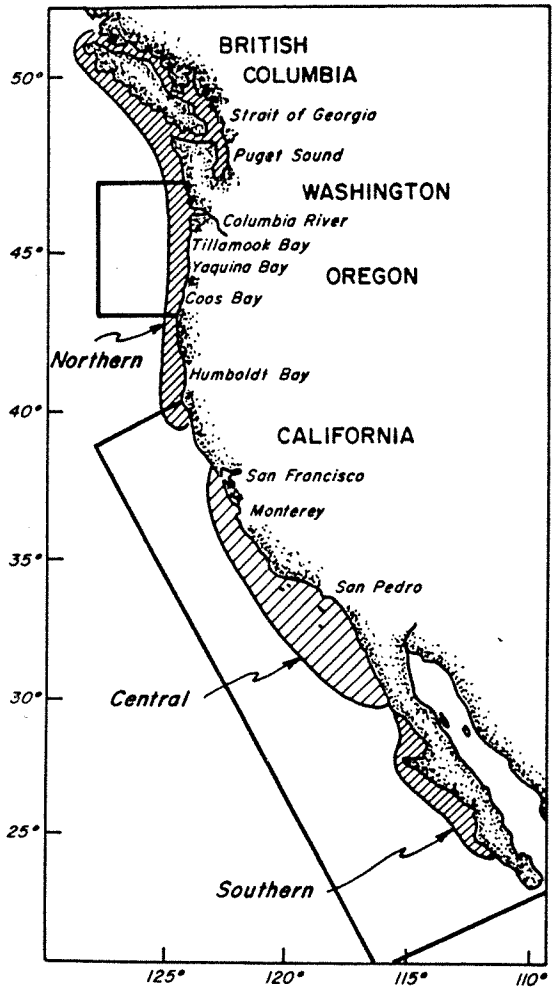

Fig. 5.1. Geographic ranges (shaded) of the three subpopulations of northern anchovy, Engraulis mordax. Upper rectangular area represents area surveyed for ichthyoplankton off Oregon and Washington by Richardson (1981). Lower rectangle shows approximate boundaries of the principal area surveyed by CalCOFI. (Source: Richardson 1981.)

probably locally produced. Ripening female anchovies have been collected in the Strait of Georgia, also indicating a possible spawning stock in this area (Pike 1951). In Puget Sound, adults have occurred at numerous locations throughout the Sound, but are not commonly found. Two occurrences of spawning fish have been reported, one in mid-Saratoga Passage and one in mid-Dabob Bay, but details are lacking (Percy Washington, personal communication, cited by Miller and Borton 1980). Northern anchovy eggs have been collected in Skagit Bay from late May through mid-August, although no larvae were found, but indicating northern anchovy may spawn in this area as well (Blackburn 1973).

Recently, Richardson (1973, 1981) described a spawning stock of northern anchovy off the coast of Oregon which is separate from the California population. Her data indicate that spawning is closely associated with the warm (>14^{o}C) near surface waters of the Columbia River plume and takes place over a relatively short time period, mid-June to mid-July. Spawning of the Oregon anchovies takes place further offshore than in California, which may be due to an avoidance of low water temperatures which occur in the coastal upwelling area off Oregon during the spawning season (Richardson 1981). Richardson (1981) also pointed out some other differences in spawning conditions between the Oregon and California anchovy populations. In the California subpopulation, spawning occurs when southward flow of the California current is minimal, the water temperature at 10 m is reaching minimum annual values, upwelling is minimal, but increasing, and day length is beginning to increase. Off Oregon, spawning occurs when current flow to the south is at a maximum, surface temperatures are reaching maximum values, upwelling is at a maximum, and day length is beginning to decrease.

Based on available catch information, Laroche and Richardson (1980) constructed the pattern of seasonal migration of northern anchovy in the northern subpopulation. In winter (January-March) both immature and mature anchovies (50-180 mm) occur in nearshore coastal areas off British Columbia, Washington, and Oregon. Off Washington, concentrations of fish are found between Cape Flattery and Destruction Island over depths of 31-313 m and between Grays Harbor and the Columbia River over 42-101 m depths. Off Oregon and Washington, anchovies are observed or captured near bottom or in midwater in coastal areas but are rarely taken in bays or estuaries. Infrequent catches occur in the Strait of Juan de Fuca, Puget Sound, Yaquina Bay, Humbolt Bay, or Tillamook Bay. During the spring (April to mid-June), anchovies remain in the nearshore coastal areas. In summer, mid-June to September, mature and immature anchovies reside in nearshore coastal areas of B.C., where spawning is reported to occur in bays and inlets around southern B.C. Off Washington and Oregon at this time, however, mature and immature anchovies are geographically separated. Adult fish in spawning condition are found offshore between 43^{o} and 47^{o} N at distances of 65 to 157 km from the coast, and immature anchovies remain in the nearshore coastal areas or bays. In the fall (October to December), adults are no longer abundant off the B.C. coast, and off Washington-Oregon adults return to coastal areas from the offshore spawning areas. Immature anchovies appear to leave the bays or

estuaries and return to mingle with adults in the nearshore coastal areas.

Size at sexual maturity varies between the subpopulations and may have varied within the central subpopulation over the last decade (Hunter and Leong 1981)(Table 5.1). In the northern subpopulation off B.C., a few anchovies may mature at less than age II, but the majority are mature at age II and lengths of 105-109 mm SL (Pike 1951). Off Oregon, northern anchovies do not mature until $\geq$ 85 mm SL and most anchovies > 101 mm SL (and age II) are mature (Laroche and Richardson 1980).

Sex ratios in northern anchovy populations are generally 1:1; however, samples have been taken which include greater numbers of either females or males. Possible reasons for changes in the sex ratio may be due to segregation of the population by sex or due to reproductive behavior of the anchovy schools (Klingbeil 1978; Hunter and Goldberg 1980; Pike 1951). Laroche and Richardson (1980), for example, found equal proportions of males and females except during active spawning periods when males outnumbered females on the average 2.6:1.

Estimates and methods for estimating the spawning biomass of northern anchovy are available (Stauffer 1980; Smith 1972; Parker 1980; Richardson 1981).

Despite differences in methods of estimating fecundity among various researcher, Laroche and Richardson (1980) concluded that the northern anchovies off Oregon and Washington have a higher fecundity (based on ovary-free body weight) than fish in the central population (Table 5.2). Their estimates of fecundity were: a total mean fecundity of 16,826 $\pm$ 1,563 oocytes per female, or 826 $\pm$ 49 oocytes per g of ovary-free body weight, compared to estimates by MacGregor (1968) and Hunter and Goldberg (1980) of 606 and 389 oocytes per g of ovary-free body weight, respectively. Laroche and Richardson (1980) also determined a similar fit to the linear and exponential expressions of the relationship between total fecundity and total body weight and between total fecundity and standard length. The relationship between total fecundity and ovary weight was also highly correlated (Table 5.3).

There is some evidence that northern anchovy in the central subpopulation are multiple spawners. Based on histological and laboratory observations, a female anchovy may be able to spawn at 7 to 10 day intervals (Hunter and Goldberg 1980; Hunter and Macewicz 1980), and may be capable of spawning up to 20 times per year (Hunter and Leong 1981). In the northern subpopulation, Laroche and Richardson (1980) observed several size modes of eggs in the ovary prior to hydration, but could neither confirm nor discount multiple spawning by northern anchovy in this area.

Off California, most northern anchovy eggs are encountered between the surface and 50 m, and mostly in the upper 20 m. Temperatures associated with these catches of eggs range from 9.9-23.3°C with the majority

Table 5.1. Summary of information on the length and age of sexual maturity of northern anchovy, Engraulis mordax, in the central and northern subpopulations.

Reference	Area, Subpopulation	Length, age	% mature
Clark and Phillips 1952	California, central	100-120 mm SL and age I-II.	30%
		120-139 mm SL and age II-III.	50%
Huppert et al. 1977 (cited in Laroche and Richardson 1980)	California, central	≥ 120 mm and age 24 mo.	100%
Hunter and Macewicz 1980	California, central	96 mm SL	50%
Pike 1951	British Columbia, northern	105-109 mm SL and age II	96%
		100-104 mm SL and < age II	14%
Laroche and Richardson 1980	Oregon, northern	< 85 mm SL	0
		85-100 m SL	31%
		101-120 mm SL	95%
		121-128 mm SL	98%
		> 128 mm SL	100%

Table 5.2. Summary of available estimates of fecundity of northern anchovy, Engraulis mordax from the northern and central subpopulations.

Reference	Area, subpopulation	Fecundity estimate	Comment
Pike 1951	British Columbia, northern	1,369 oocytes per g total body wt.	Estimate based on counts of all oocytes > 0.20 mm.
Laroche and Richardson 1980	Oregon, northern	16,826 ± 1,563 oocytes, total mean fecundity of 21 fish; 720 ± 40 oocytes per g total body wt; 826 ± 49 oocytes per g ovary-free body wt.	Estimate based on the most advanced oocytes in ripe or nearly ripe fish.
MacGregor 1968	California, central	574 oocytes per g total body wt; 606 oocytes per g ovary-free body wt.	Estimates based on counts of advanced, nonhydrated, yolked oocytes ≥ 0.50 mm.
Hunter and Goldberg 1980	California, central	389 oocytes per g ovary-free body wt.	Estimate based on ripe, hydrated oocytes.

Table 5.3. Functional (geometric mean) regression equations, sample size (N), standard error of the regression coefficient (SE), and correlation coefficient (r) for the relationship between total fecundity (TF) and total body weight (W), standard length (SL), and ovary weight (OVW) in northern anchovy, Engraulis mordax, collected off the Oregon-Washington coast. (Source: Laroche and Richardson 1980.)

Equations	N	SE	r
Ovarian stages 6-10:			
$TF = -13{,}889.91 + 1{,}339.57W$	21	176.54	0.82
$Log_{10}\ TF = 1.91 + 1.69\ log_{10}W$	21	0.24	0.77
$TF = -76{,}286.31 + 738.99SL$	21	108.56	0.77
$Log_{10}\ TF = -6.80 + 5.23\ log_{10}SL$	21	0.82	0.73
Ovarian stages 6-8:			
$TF = -1{,}181.63 + 11{,}506.73\ OVW$	11	1,534.23	0.92
Ovarian stage 10:			
$TF = -2{,}654.20 + 4{,}637.89\ OVW$	10	433.83	0.96

occurring at temperatures between 13 and 17.3°C (Ahlstrom 1959b, 1956). Ahlstrom (1961) set the lower threshold temperature for northern anchovy spawning at 11°C, with peak spawning corresponding to temperatures of about 14°C. Development time from egg stage IV (germ ring encloses 1/3 to 4/5 of yolk) to hatching at 14°C is about 50 hours (Fig. 5.2). In laboratory experiments, Lasker (1964) noted that development from egg stage IV to hatching was faster for northern anchovy than for Pacific sardine (Sardinops sagax) at temperaturess between 11-12°C. He also noted that at 11-12°C, northern anchovy developed a functional jaw before hatching, whereas Pacific sardines did not, which may give northern anchovy larvae, at these temperatures, a competitive feeding advantage over the sardine larvae.

Development of oocytes in the ovary of northern anchovy was described by Laroche and Richardson (1980). Small oocytes are spherical, but become elliptical at 0.2 mm. Most oocytes less than 0.38 mm lack yolk and are transparent. Vitellogenesis becomes evident in oocytes larger than 0.38 mm, and most oocytes greater than 0.50 mm are completely opaque. At 0.7-0.9 mm, the developing ova appear grainy because yolk globules have replaced the single amorphous yolk mass of smaller oocytes. The yolk of hydrated eggs, 0.9 to 1.42 mm, is segmented. Eggs are released from the follicles and lie loose in the ovary at 1.10 to 1.42 mm. In addition to normally developed oocytes, Laroche and Richardson (1980) found degenerating or atretic oocytes in ovaries collected before, during, and after the spawning season. Photos of normal and degenerating ovarian oocytes are provided by Laroche and Richardson (1980).

Mature northern anchovy eggs are ellipsoidal with a major axis of 1.23-1.55 mm, and a minor axis of 0.65-0.82 mm. Prior to development, eggs are colorless, transparent, lack oil globules, and contain a segmented yolk and a thin, delicate unsculptured egg membrane. During early development, eggs are slightly more dense than sea water and float with the blastoderm at the lower end of the major axis. As the embryo advances, the egg rolls over on it side so that the major axis is horizontal and the embryo hangs underneath (Bolin 1936).

Beyond the 8-16 cell stage (Fig. 5.3A, B), cleavage occurs regularly at about 1/2 hour intervals to produce a dome-shaped blastoderm (Fig. 5.3C) and the protoplasm around the periphery becomes concentrated in the form of a flattened ridge or periblast (Fig. 5.3D). The segmentation cavity appears beneath the blastoderm and invagination begins shortly thereafter, and the germ ring is distinctly visible when the egg is viewed from the end (Fig. 5.3E). After the germ ring differentiates, the blastoderm begins a rapid growth over the yolk (Fig. 5.3F, G). The embryo remains relatively undifferentiated, until blastopore closure; however, as soon as the blastopore closes, rapid changes occur. The eyes become visible, body segmentation appears, and Kupffer's vesicle is apparent (Fig. 5.3H). As soon as Kupffer's vesicle disappears (several hours), the tail becomes free and lifts from the yolk. Also, the pupils become visible, auditory capsules and otoliths appear, the heart develops and the median finfold forms (Fig. 5.3I). During development, the

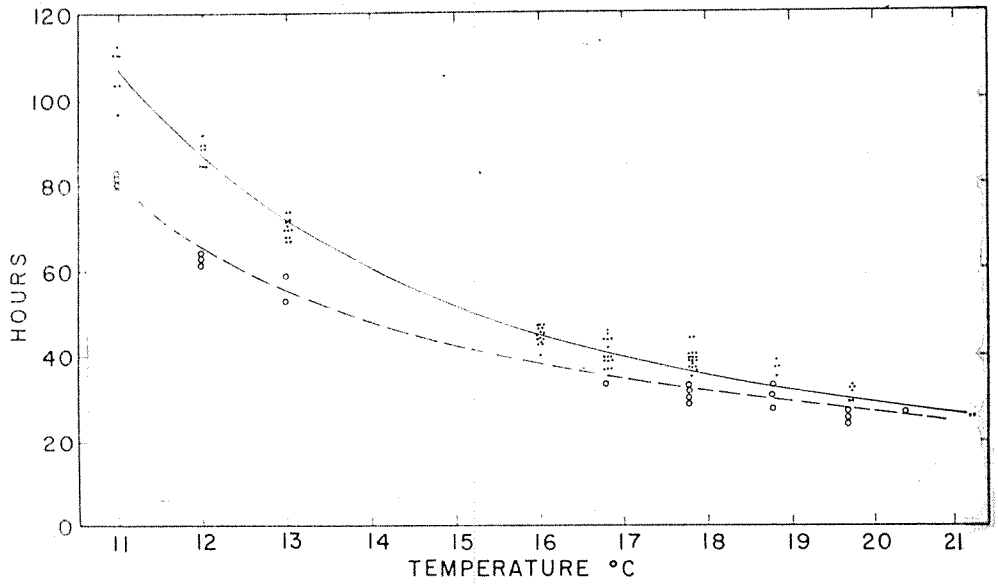

Fig. 5.2. Development time from egg stage IV to hatching at various temperatures; solid line - Pacific sardine, Sardinops sagax, and dashed line - northern anchovy, Engraulis mordax. Each dot represents a single embryo. (Source: Lasker 1964.)

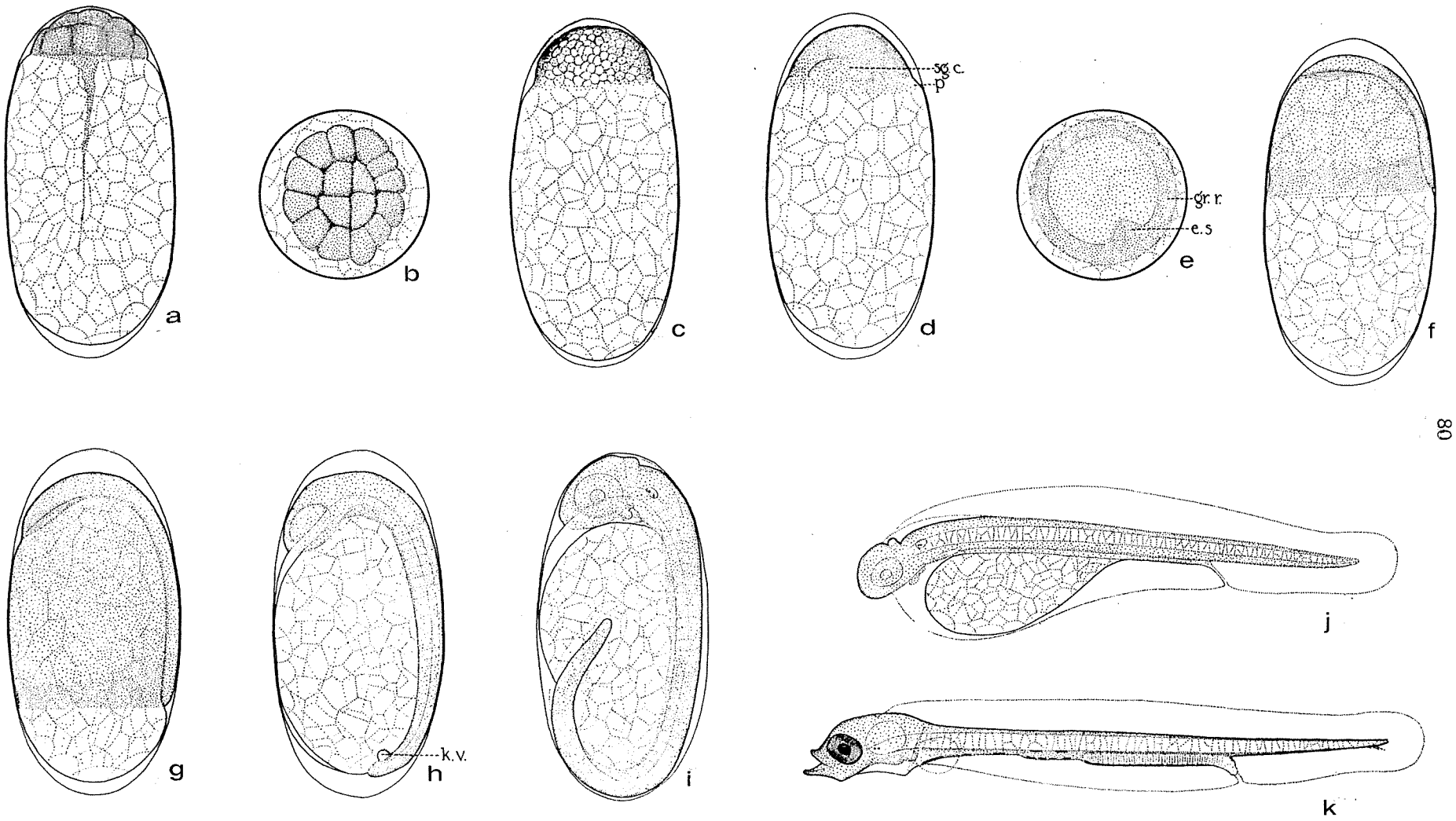

Fig. 5.3. Development of eggs and early larvae of northern anchovy, Engraulis mordax: a) 16-cell stage, side view; b) 16-cell stage, end view; c) well developed blastoderm; d) segmentation cavity (sg.c.) and periblast (p.) well developed; e) germ ring (gr.r.) and embryonic shield (e.s.) forming; f) embryonic axis well established; g) just before blastopore closure; h) just after blastopore closure, Kupffer's vesicle (k.v.); i) just prior to hatching; j) newly hatched larva, ∿ 3 mm; k) 5-day old larva. (Source: Bolin 1936.)

tail is flexed to the right or left, but never extends as far as the head. A few hours before hatching, the embryo is active, moving its tail from side to side, but cannot turn in the egg capsule (Bolin 1936).

Northern anchovy larvae have been well-illustrated (Bolin 1936: 3 mm, 6 mm; Kramer and Ahlstrom 1968: (Fig. 5.4); Ahlstrom 1965, 1966: 6.0, 11.5, 31.0 mm). Hatching occurs when larvae are ~2.7-3.0 mm (Lasker 1964; Bolin 1936). They possess a large elongated yolk sac, the mouth and jaws are often unformed, and the vent is located midway between the posterior end of the yolk sac and the tip of the tail. The larvae are transparent and lack pigment, even in the eyes (Fig. 5.3J) (Bolin 1936). According to Bolin (1936), the yolk sac is absorbed in 36 hours and the eyes become pigmented soon after hatching. The pectoral fins become large and the posterior portion of the gut begins to show signs of convolutions. On the fourth day after hatching, the mouth is functional and the lower jaw is long and protruding. Larval pigment on the fifth day consists of a few elongated melanophores on the ventral border of the body which extend in an irregular series from the base of the pectoral fins halfway to the vent. Another series is located on the postanal midventral margin of the tail, and a small patch of melanophores near the tip of the tail extends posteroventrally into the finfold (Fig. 5.3K).

Off California, larvae of northern anchovy are taken between a temperature range of 10 and 19.7°C, with most larvae associated with temperatures between 14 and 17.4°C. Larvae are distributed throughout the water column, primarily between the surface and about 75 m, with most found above 50 m (Ahlstrom 1959b).

In the northern subpopulation off Oregon, larvae are transported southward off Washington-Oregon during summer. In the fall, a shift of surface currents toward the north and inshore results in juveniles located in bays and rivers where spawning is rare or unsuccessful. To date, there is no evidence of an additional offshore spawning center north of the Oregon study area to explain the recruitment of juveniles to Oregon bays and rivers (Richardson 1981).

Other important aspects of larval anchovy biology have been studied, primarily for anchovy in the central subpopulation. These studies were needed to assess the mortality and survival of larval anchovies and included dynamics of larval growth, physiology, and food habits (see Additional References).

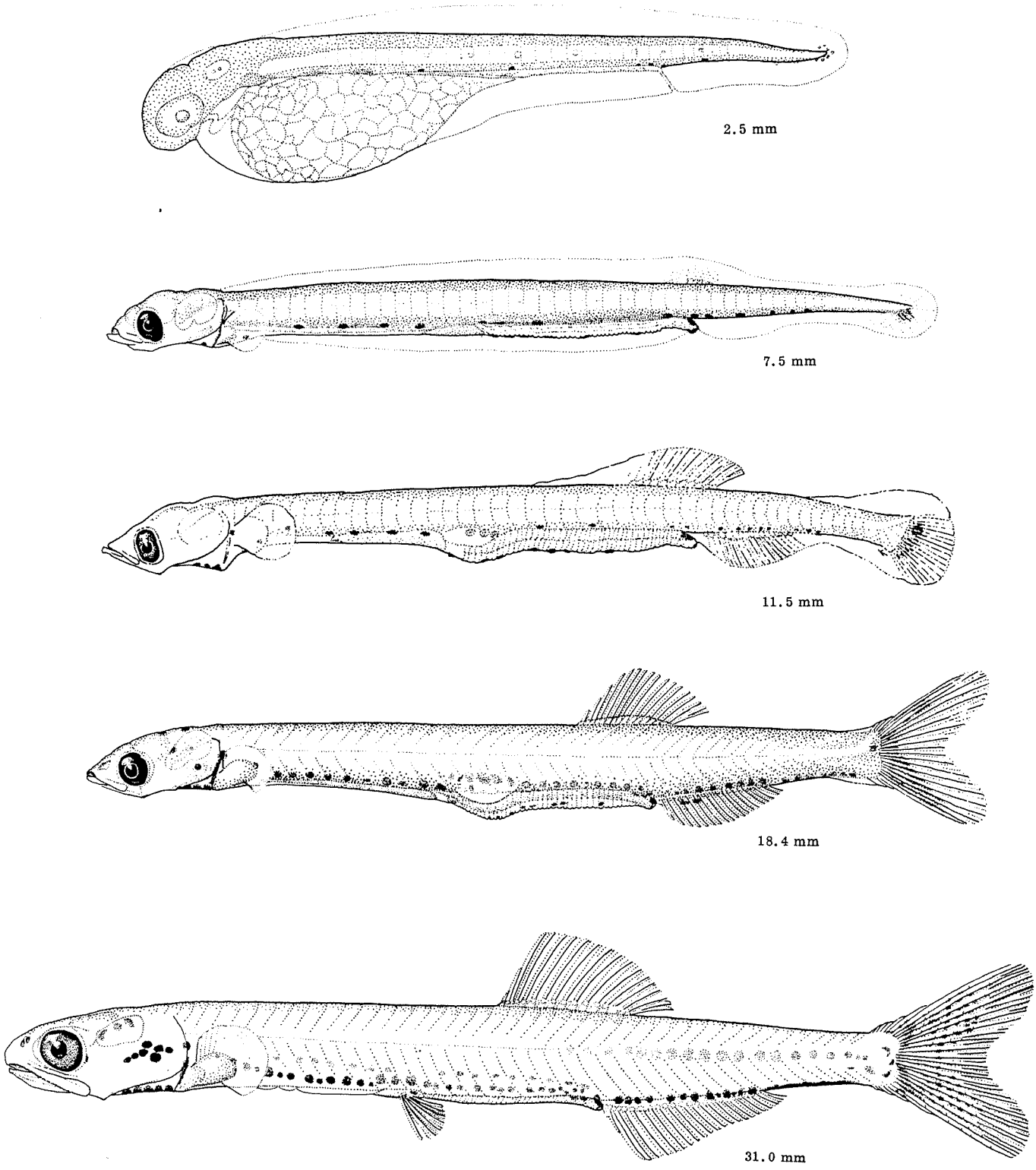

Fig. 5.4. Larvae of northern anchovy, Engraulis mordax. (Source: Kramer and Ahlstrom 1968.)

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6. SALMONIDAE

Onchorhynchus gorbuscha - Pink salmon

O. keta - Chum salmon

O. kisutch - Coho salmon

O. nerka - Sockeye salmon

O. tshawytscha - Chinook salmon

Salmo clarki - Cutthroat trout

S. gairdneri - Rainbow trout

Salvelinus malma - Dolly Varden

The available literature for the 8 species of salmonidae found in Puget Sound is quite extensive. While a comprehensive review of this material would not be practical, it is hoped that a synopsis of the early life histories of these important anadromous or freshwater fishes will be added to this report in the future. Meanwhile, the reader is directed to the references listed below.

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7. OSMERIDAE

Allosmerus elongatus - Whitebait smelt

Range: central California to Vancouver Island

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: undescribed

Whitebait smelt range from central California to southern Vancouver Island in the Strait of Juan de Fuca (Hart 1973; Barraclough and Wilson 1971). Adults have been reported only rarely from the Puget Sound area and include Sequim Bay and the San Juan Islands (Miller and Borton 1980).

No early life history information is available on this relatively uncommon species; however, it has been reported that whitebait smelt probably spawn in the ocean and that development of larvae may be protracted as translucent young up to 76 mm have been found (Hubbs 1925, cited in Hart 1973).

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Hypomesus pretiosus - Surf smelt

Range: Southern California to Gulf of Alaska

Occurrence in Puget Sound: common

Adult habitat: pelagic

Spawning habitat: demersal, on gravel beaches

Spawning season: continuous in Puget Sound

Mode of reproduction: oviparous

Eggs: demersal, attached

Larvae: pelagic

Surf smelt range from southern California to Prince William Sound and Chignik Lagoon in Alaska. In the eastern Pacific, they belong to a distinct subspecies, Hypomesus pretiosus pretiosus, to be distinguished from H. pretiosus japonicus, which occurs along the northeast Asian coat (Hart 1973).

Studies of the racial separation of Puget Sound surf smelt from coastal surf smelt, based on morphological and meristic characters, seriological techniques (antigen-antibody reactions), and parasite incidence indicate that surf smelt from Hood Canal are genetically most similar to Camano Island smelt and that these two stocks are statistically different on a number of points from coastal surf smelt (Kilambi 1965; Kilambi and DeLacy 1967; Kilambi et al. 1965).

Behavior and sexual characteristics of spawning surf smelt from Puget Sound have been studied in detail and information includes in situ observations of spawning activity, substrate preference, relationship of spawning to tide cycle and height, size and age composition of spawners, and fecundity. Development of fertilized eggs has been well-documented and larvae and postlarvae have been illustrated and described to some extent.

Surf smelt are widespread and common in Puget Sound and spawning beaches represent over 100,000 yards of shoreline. Major spawning areas are found in southern Puget Sound, southern Hood Canal, northern Saratoga Passage, and the Liberty Bay area. Other areas exist as well (Fig. 7.1) (Penttila 1978).

In Puget Sound, surf smelt spawn during most months of the year with the exception of late March through April (Penttila 1978). Throughout the Puget Sound spawning sites, spawning does not take place simultaneously on all beaches, but occurs at different times depending on location. At each beach, spawning may last from 2 to 4 months and

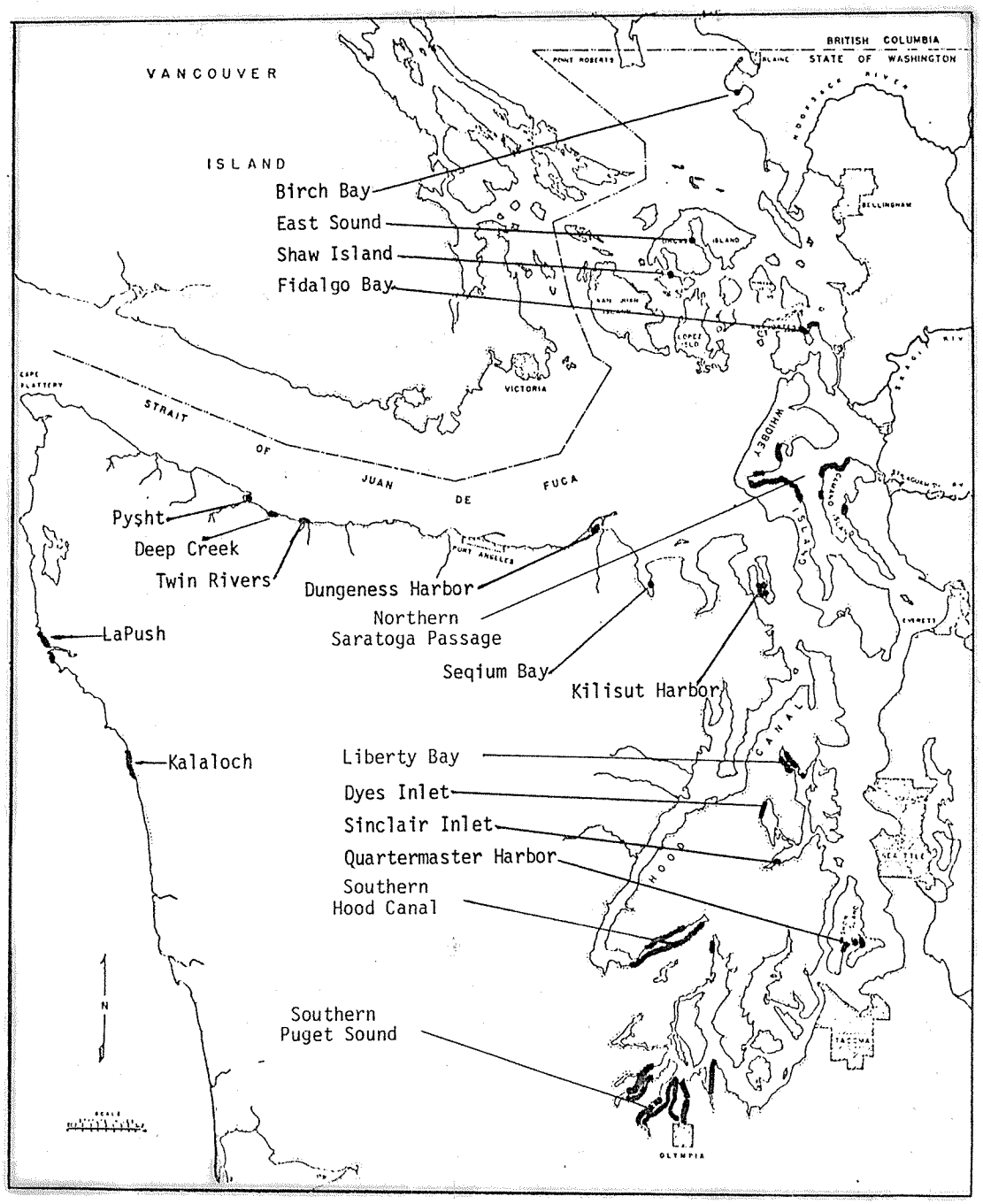

Fig. 7.1. Location of spawning beaches of surf smelt (Hypomesus pretiosus) in Puget Sound. (Source: Penttila 1978.)

typically occurs at the same sites at the same time each year (Schaefer 1936).

It has been established that surf smelt spawning beaches are similar in several ways. They are frequently at the heads of bays or inlets and usually somewhat shaded along the upper part by overhanging trees or by bluffs. Typical substrates are fine gravel and coarse sand, and in some cases, with broken shells mixed in. On some beaches, freshwater seepage through the gravel is present (Schaefer 1936). Temperature and salinity of the water over the spawning beach seems to have no relationship to spawning activity. Surf and wind factors may affect spawning activity as more spawning occurs on calm days, than on windy days when surf is heavier (Schaefer 1936).

The primary factors affecting spawning activity are tide stage and time of day, with heaviest activity during high tides which occur in the late afternoon or evening (Yap-Chiongco 1941; Schaefer 1936). While in some cases spawning may occur before high water (Loosanoff 1937) spawning generally takes place on the ebbing tide (Schaefer 1936; Thompson et al. 1936). In either case, eggs are rarely deposited on the highest point reached by the tide and are usually concentrated between the 7-foot and 11-foot tide levels (Penttila 1978).

Adult males in spawning condition can be distinguished from ripe females by color and morphology. Males are a dull olive green with a yellowish-silver abdomen, while females are bright bottle green with a metallic sheen and have a white underside. In addition, males develop small, wart-like excrescences, called pearl organs, on the body, head, and fins. They are also characterized by a lesser body depth and thickness, larger pectoral fins, swellings on either side of the anal fin, and wing-like flaps of skin on the anus (Yap-Chiongco 1941).

The majority of surf smelt spawn at the age of two years, although some three- to five-year-old females and some one-year-old males are found. Mature fish range from 81 to 178 mm (Yap-Chiongco 1941) with females usually averaging greater in length than males (Penttila 1978). It has been noted that larger individuals (primarily the two-year-old fish) arrive on the spawning grounds sooner and spawn earlier than smaller fish. These smaller fish may arrive toward the end of the spawning season and are primarily the one-year-old males (Schaefer 1936; Yap-Chiongco 1941; Penttila 1978). In one case, it was reported that sexes arrived on the spawning ground in separate groups (Loosanoff 1937), but this is not always the case (Yap-Chiongco 1941). If segregation by sex does occur, this can lead to erratic estimates of sex ratios. Many investigators reported that males outnumber females on the spawning ground; however, it is not known if this is because females remain in deeper water until they are ready to spawn.

Females do not spawn all their eggs in one batch, but may extend spawning over several days. During this time, a female may produce between 1,300 and 30,000 eggs (Leong 1967) and most commonly 15,000 to

20,000. Studies have shown that ovaries contain both ripe and unripe eggs; however, it is not known how many spawnings an individual fish may make.

The spawning activity of surf smelt has been observed and described (Loosanoff 1936; Schaefer 1936; Thompson et al. 1936; Yap-Chiongco 1941). The observations of Schaefer (1936) are reported below:

> "As the smelt prepare to spawn, large numbers of males are seen milling about and swimming rapidly back and forth, apparently in search of females. When a female is perceived, all the males nearby immediately pursue her and attempt to attain the spawning position. If she heads toward deeper offshore water, the males abandon pursuit. In the spawning act, one to five males approach the female from the side or behind. They take position on either side of the female so that all the vents are nearly in a line, the group of fish pressing tightly together. The snouts of the males, due to the smaller average size of this sex, are usually slightly behind that of the female. The sides, head, and fins, particularly the pectorals, of the males are covered with minute tubercules which help them in maintaining position. In these positions, the group of fish moves, just off the bottom, either toward shore or nearly parallel thereto. The bodies of the fish are held nearly rigid, and a rapid vibration of the bodies occurs as they move forward. At this time the ova and milt are emitted, the latter giving the water a cloudy appearance. The spawning act takes place in water not over two feet in depth, and usually just at the water's edge, where the water is only a few inches deep.
>
> "The entire spawning act requires less than one minute. Subsequently, the group separates and returns to deeper water a foot or two offshore. Only a few of the ova are, presumably, emitted at each attempt since both male and female individuals have been observed spawning several times in immediate succession."

After spawning, the spent individuals disappear from the immediate spawning area and there is no indication of the mass mortality of spawned-out fish, as in the case of eulachon (Penttila 1978).

Fertilized surf smelt eggs are spherical and average 1.02 mm in diameter (Schaefer 1936). The yolk contains numerous oil globules and the shell is transparent, although covered with numerous minute pores. The micropyle is surrounded with a cap-like structure called the zona radiata externa. When the egg is extruded into the water, this

structure everts itself and assumes a funnel shape, providing a guide for sperm to reach the micropyle (Fig. 7.2A). When the egg is fertilized, it settles to the bottom and attaches to the substrate by the zona radiata externa (Yap-Chiongco 1941). Surf smelt make no attempt to bury their eggs, but rely on wave action to cover them with a fine layer of sand. Since the eggs are deposited on the upper portion of the beach, they may be covered with water only a short time during the incubation period which lasts 2-4 weeks (Penttila 1978). Detailed studies of mortality among developing spawn have not been done. Thermal stress and desiccation may be the most important factors of mortality and initial estimates of mortality during the incubation period may be 20-30% under favorable conditions, and may be as high as 90%. The degree to which surf smelt spawn are eaten by predators is also unknown (Penttila 1978).

Development of surf smelt eggs has been described and illustrated (Yap-Chiongco 1941) (Figs. 7.2A-N). The germ ring appears by 20 hours, followed by the appearance of Kupffer's vesicle and optic vesicles at 40 hours. The heart can be seen faintly pulsating in 91-116 hour embryos and the eyes are developed by 144 hours. Hatching occurs after 216-240 hours. Other developmental events are summarized in Table 7.1.

Hatching may be stimulated by both mechanical and chemical means and newly hatched larvae are 4-6 mm. Larvae (5 and 6.5 mm), postlarvae (17 mm), and small juveniles (35, 45, 51, 68, and 75 mm) have been illustrated and described (Yap-Chiongco 1941). At hatching, the larvae are slender and transparent, with a prominent yolk mass located approximately one-fourth of the body length from the head. The body is surrounded by the finfold which runs from the nape around the tail and ends at the posterior edge of the yolk sac. Melanophores are localized on the ventral surface of the body forming a long chain of moderately spaced spots. Anterior to the anus, these melanophores originate at the median posterior wall of the yolk sac and continue posteriorly to the anus. These pigment spots range from 15 to 25 in number, but most frequently are 20-21. Posterior to the anus, the ventral melanophores number 7 to 12, and most commonly 8 or 9. A few melanophores also appear dorsal and lateral to the anus. One pair also occurs beneath the ventral base of the pectoral fin and a second pair occurs slightly above the esophagus and posterior to the pectorals (Fig. 7.3A). The yolk material is absorbed 4 to 6 days after hatching, and after two days, additional melanophores appear on either side of and slightly dorsolateral to the intestine. These extend from the pectoral fins to the anus and are further apart than the ventral line of melanophores. At five days or about 6 mm, fin rays of the caudal fin become faintly discernible (Fig. 7.3B).

Descriptions of larvae between 6 and 17 mm are lacking. At 17 mm, the body is well pigmented and melanophores are distributed about the bases of the pectoral fins, on either side of the abdomen, along the lateral line, on the ventral side posterior to the anus, and along the dorsal side from the tip of the snout to the tail (Fig. 7.3C). All the

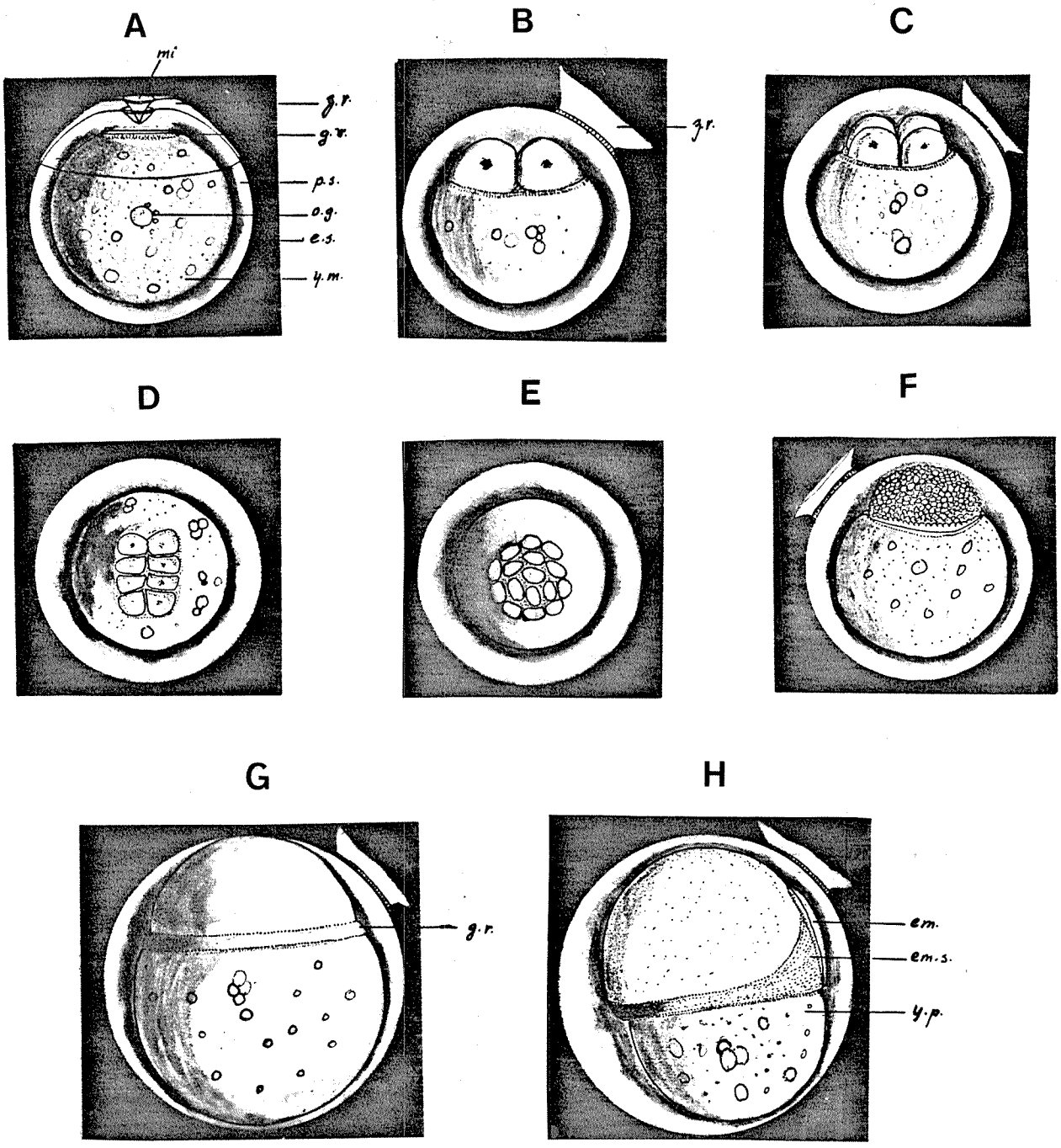

Fig. 7.2. Development of eggs of surf smelt, Hypomesus pretiosus: A) Unfertilized egg showing the micropyle and its relation to the germinal vesicle; zona radiata externa is in place prior to eversion, e.s. = egg shell, g.v. = germinal vesicle, mi = micropyle, o.g. = oil globule, p.s. = perivitelline space, y.m. = yolkmass, z.r. = zona radiata; B) two-cell stage; C) four-cell stage; D) eight-cell stage; E) sixteen-cell stage; F) late segmentation-16 hourembryo; G) commencement of the germ ring-18 hour embryo, g.r. = germ ring; H) 23-hour embryo showing the germ ring at the equatorial plate and the embryonic shield (em.s.) with the embryo (em.) on it. (Source: Yap-Chiongco 1941.)

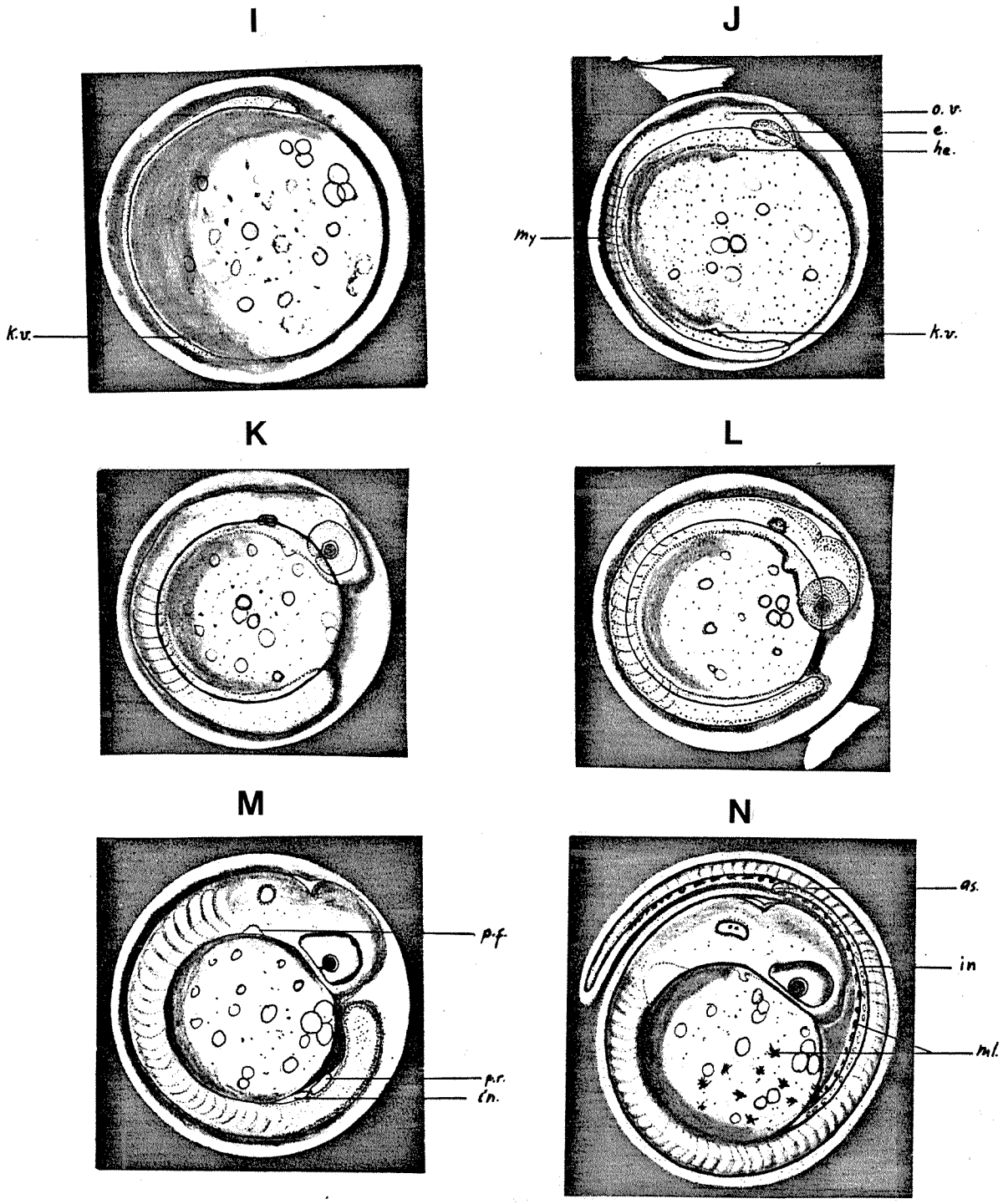

Fig. 7.2. (Cont.) Development of eggs of surf smelt, Hypomesus pretiosus: I) 39-hour embryo projected along the long axis of the embryonic shield, k.v. = Kupffer's vesicle; J) 50-hour embryo, my.= myotome, o.v. = optic vesicle, e. = eye, he. = heart; K) 67-hour embryo; L) 72-hour embryo, tail is freed from yolk; M) 97-hour embryo, intestine approaching the proctodaeum, p.f. = pectoral fin, p.r. = proctodaeum, in. = intestine; N) 147-hour embryo, characteristic pigment has formed on the ventral side from the yolk sac to the tail, also melanophores on yolk appear, as.= anus, ml. = melanophores.

(Source: Yap-Chiongco 1941.)

Table 7.1. Summary of major developmental events during incubation of surf smelt eggs (modified from Yap-Chiongco 1941.)

Incubation time (hours since fertilization)	Developmental event
2	Two-cell stage
4-5	Blastocoel beginning
17	Blastula
18	Germ ring and appearance of dorsal lip
23-28	Embryonic shield
31	Closure of blastopore
37	Appearance of Kupffer's vesicle and optic vesicle
57	Appearance of optic lens
66	Cephalic flexure of brain; appearance of auditory vesicle
72	Ventricle of brain distinct, first sign of wriggling
91-116	Heart faintly pulsating
96-144	Completion of pupil of eye; first anlage of pectorals; digestive tract advanced
111-120	Appearance of melanophores
113-137	Heart normally beating; embryos 1 to 1 1/2 loops
142	Anus fully established
151	Embryos constantly wriggling
216-240	Hatching

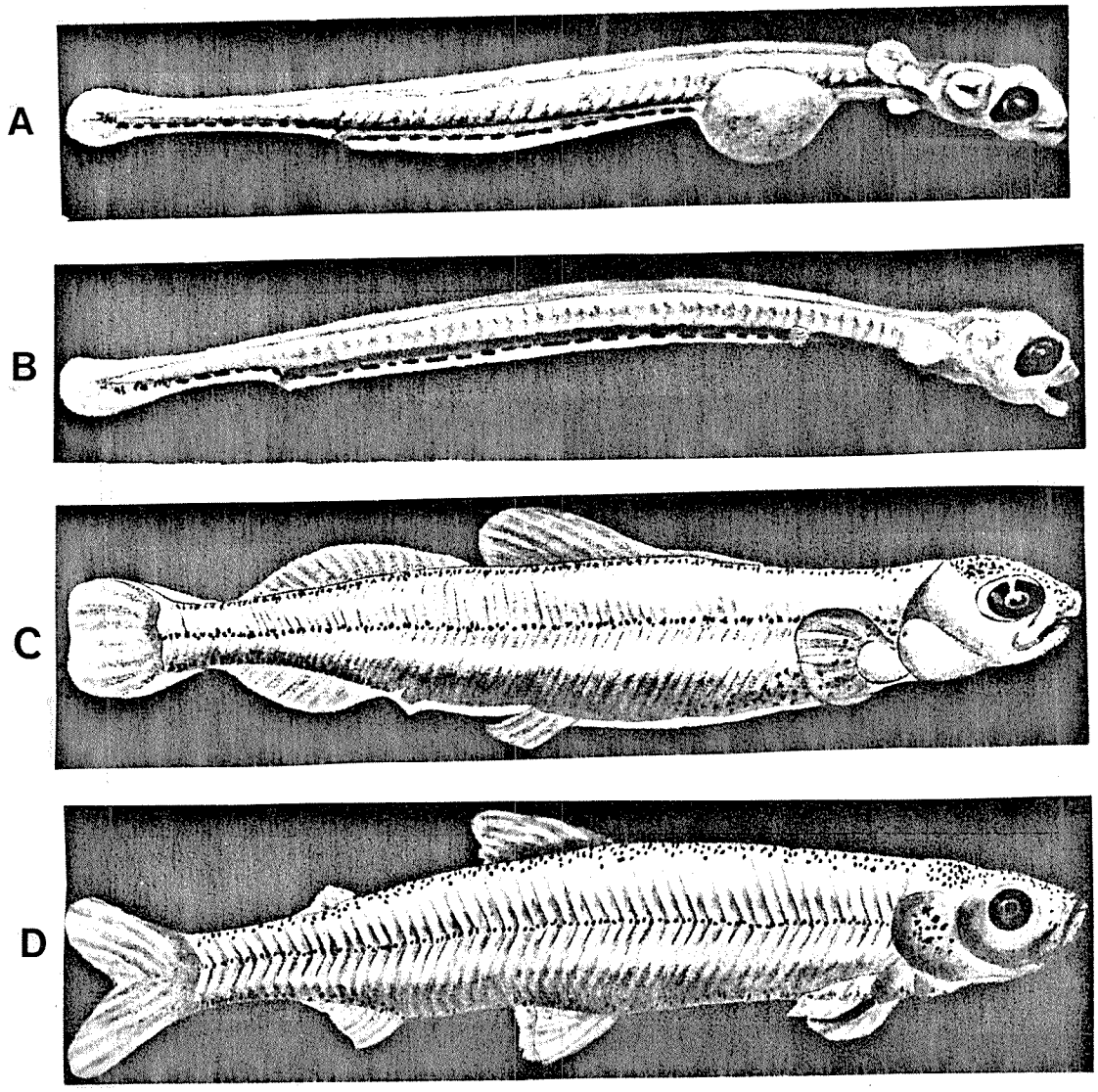

Fig. 7.3. Development of larval surf smelt, Hypomesus pretiosus: A) Newly hatched larvae, 5 mm; B) five-day old larva - 6.5 mm, yolk is fully absorbed; C) 17 mm larva showing the formation of the dorsal and adipose fins. Anal fin is advanced in development, but ventral fin fold is still intact; D) juvenile smelt - 35 mm, melanophores on dorsal surface are spreading laterally (Source: Yap-Chiongco 1941.)

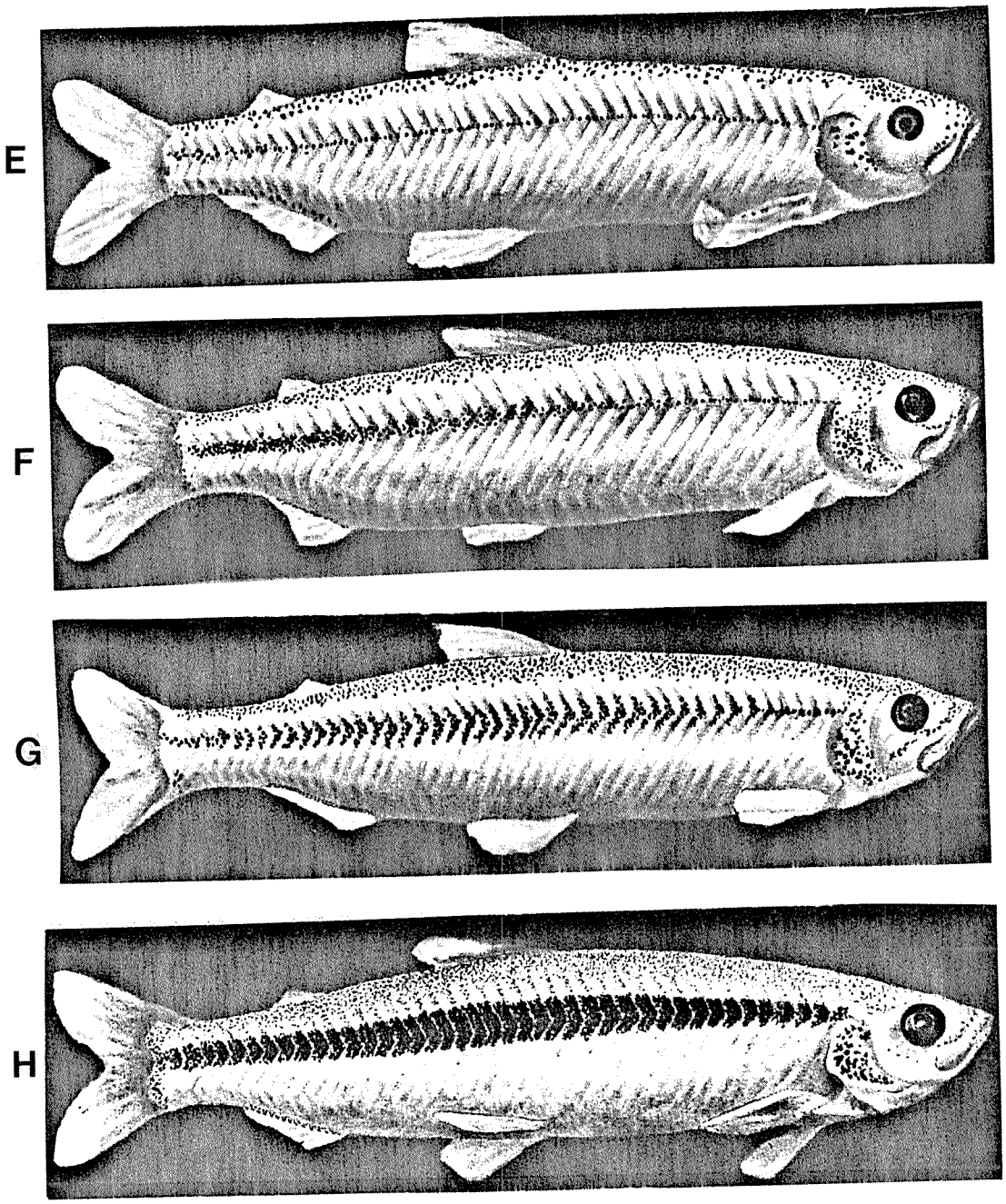

Fig. 7.3. (Cont.) Development of larval surf smelt, Hypomesus pretiosus: E) 45 mm; F) 51 mm; G) 68 mm; H) 75 mm (Source: Yap-Chiongco 1941.)

fins are advanced in development, but still somewhat larval in appearance. At 35 mm, the surf smelt is practically adult in form although pigmentation is still larval in character (Fig. 7.3D). Development of adult coloration can be seen in specimens larger than this size (Fig. 7.3E-H).

Not much is known about the aspects of the marine life of surf smelt from the time they leave the spawning beds until they return to spawn. It is not even known if they return to spawn on the beach they hatched from.

Several researchers have examined food habits of the young fish and found that food consisted of small planktonic organisms, especially copepods, Oikopleura, and Cladocera (Barraclough 1967a, b; Barraclough and Fulton 1968; Robinson et al. 1968a, b).

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Mallotus villosus - Capelin

Range: Juan de Fuca Strait to Arctic; Kamchatka to Korea; Labrador, Greenland, Iceland, Norway

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic, in schools

Spawning habitat: demersal, on gravel beaches

Spawning season: fall (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, attached

Larvae: pelagic

Capelin inhabit Pacific waters of North America from Juan de Fuca Strait through British Columbia and Alaska to the Arctic. It is primarily a northern species with centers of abundance in the Bering Sea and Arctic Ocean. Capelin also occur in the western Pacific along the Asian coast from Kamchatka to Korea and in the Atlantic from Labrador to Greenland, Iceland, and Norway (Hart 1973).

Capelin spawn along beaches in British Columbia in late September or October. Several isolated spawning populations are known from the central part of the Strait of Georgia, and capelin have also been recorded at Bentinck Island near Victoria and from Ladysmith on Vancouver Island (Hart and McHugh 1944). In Puget Sound, capelin are rare, but have been reported to spawn along the west side of Sequim Bay on the southern shore of the Strait of Juan de Fuca (Miller and Borton 1980). Spawning times for Pacific Ocean capelin in areas outside of B.C. and Washington was compiled by Macy et al. (1978) (Table 7.2). Locations of spawning grounds of capelin in Bristol Bay, Alaska are reported by Baxter (1975, cited by Macy et al. 1978) and distributions of capelin larvae in the Bering Sea have been mapped (Kashkina 1970; Musienko 1963; Faculty of Fisheries, Hokkaido University 1960, 1961).

At spawning, capelin exhibit sexual dimorphism and breeding males are characterized by a distinct ridge which develops along the lateral line. This ridge is formed by the elongation of the posterior edges of scale in this region such that males appear diamond-shaped in cross-section. Fins of the males are also longer and broader than in females and their pectoral fins bear membranous ridges on the anterior surface and tubercules on the posterior surface of the rays. Tubercules may also form on the heads of the males at spawning time. In addition, the first 10-12 rays of the male's anal fin become enlarged, particularly in their distal portion (Hart and McHugh 1944).

Table 7.2. Known spawning areas and times for Pacific Ocean capelin, *Mallotus villosus*. (Source: Macy et al. 1978.)

Area	Time	Reference
Asian side		
Peter the Great Bay	April-May	Nikol'skii 1954
Sea of Okhotsk	May-July	Nikol'skii 1954
Kamchatka	June	Nikol'skii 1954
Gulf of Anadyr	June-July	Musienko 1970
North American side		
Point Barrow	end of July-August	Andriyashev 1954
Bristol Bay	May 30-June 15	Baxter 1975
Sitka (S.E. Alaska)	October	Marsh and Cobb 1908
Strait of Georgia	September-October	Hart and McHugh 1944

There has been some confusion over the age of sexual maturity of Pacific coast capelin. Fraser (1915, cited in Macy et al. 1978) and Hart and McHugh (1944) believed that spawning fish were one year olds based on observing fish with scales showing zero or one growth ring. However, it was later determined that capelin do not form scales until 10-12 months after hatching. Thus no growth check would exist for the first winter, making the fish they observed at least 2 years old (Trumble 1973).

Pacific coast capelin reach sexual maturity at a smaller size than Atlantic capelin, 89-109 mm versus 129-166 mm (Schultz 1937, cited in Macy et al. 1978). Size range for mature British Columbia capelin is 94-115 mm for males and 90-112 mm for females (Hart and McHugh 1944).

Although the sex ratio of males to females on the spawning beaches indicates a predominance of males (Hart and McHugh 1944), this difference may be due to offshore schooling of non-spawning females (Trumble 1973); however, sex composition of non-spawning fish has not been studied.

During the spawning season, large schools of capelin appear along the shores of gravel beaches, and the actual spawning event takes place during high tide at night or on overcast days. Pairing of males and females during spawning has been observed to some extent. Two males may accompany a female toward the beach, pressing the body of the female between them in the area formed by the protruding lateral line ridges of the males. In this manner, eggs are spawned and fertilized. This process is repeated until all the ripe eggs are spawned, after which the female returns to deeper water. Males may remain inshore to fertilize other females (Trumble 1973; Hart and McHugh 1944).

Eggs are buried in the sand by wave action at about the +10 to +12 foot tide level and capelin appear to be substrate selective in their spawning grounds (Hart and McHugh 1944):

> "During spawning on certain beaches, considerable variation may be observed in the concentration of fish along the shore. This appears to be correlated with the nature of the beach surface, the fish tending to avoid both rocky and sandy patches. Later examination confirms this impression, the intensity of deposition being greatest where the particles are from 0.04 to 0.2 inches in diameter. A marked tendency is evident for the eggs to be attached to sharp corners and edges rather than to flat surfaces. This undoubtedly provides for free aeration during devleopment."

Fecundity of British Columbia capelin ranges from 3,020 to 6,670 eggs per female. Examinations of the size frequencies of eggs in the ovaries indicate capelin may spawn more than one batch of eggs; however, this is not known for sure (Hart and McHugh 1944).

Eggs range from 1.0 to 1.1 mm in diameter, are adhesive and may become buried to depths of ~15 cm (6 inches) in the substrate. Development of eggs in relation to temperature has been studied for capelin in the western Atlantic; eggs hatch in 30 days at 5°C, in 15 days at 10°C, and in 8.5 days at 15°C (Trumble 1973). British Columbia capelin eggs hatch in 2-3 weeks (Hart 1973).

The newly hatched larvae are slender, transparent, and between 5 and 8 mm in length. At hatching, the larva has a small yolk sac which contains a large oil globule, and has large well-pigmented eyes. Body pigment consists of three pairs of ventrolateral melanophores located between the pectoral fin base and the yolk sac, an almost continuous median line of melanophores on the ventral surface of the body from the anterior part of yolk sac to near the end of the notochord with a break in the line of pigment behind the anus, and a single large stellate melanophore on the dorsal surface of the anal pipe (Fig. 7.4A). At 7 mm, three pairs of ventrolateral melanophores begin to extend as a paired line of pigment spots which is dorsolateral to the intestine and extends posteriorly to the anus (Fig. 7.4B). At 16 mm, pigment has been added in the form of paired chromatophores anterior to the pectoral fin bases and along the throat. Pigmentation from this size on remains relatively unchanged until metamorphosis (Templeman 1948).

Only the pectoral fins (without rays) are present at hatching and the dorsal, anal, and caudal fin areas are covered by a continuous finfold. The yolk sac is absorbed by about 7 mm, and flexion begins at about 11 mm. At 16 mm, flexion is well underway, and rays are developing in the dorsal and anal fins (Fig. 7.4E). At 21 mm (Fig. 7.4F), rudiments of the pelvic fins are forming and at 29 mm (Fig. 7.4G), rays are beginning to form in the pelvic fins. At 40 mm, larvae are still extremely long and slender and have not metamorphosed in depth of body to the adult shape (Fig. 7.4H) (Templeman 1948).

Larvae are washed out to sea immediately upon hatching (Turner 1886, cited in Macy et al. 1978) and little is known about their development at sea. Some growth information has been reported for Bering Sea larvae (Nikol'skii 1954; Musienko 1970; both cited in Macy et al. 1978) and indicates a faster growth rate compared to Atlantic capelin and that most growth in length and weight occurs within the first two years.

Information is lacking on food habits of larval capelin. One 58 mm individual caught off the Strait of Georgia was reported to have eaten 12 Pseudocalanus minutus (Robinson et al. 1968). Food habits of larval Atlantic capelin have been studied to some extent (Bjørke 1976).

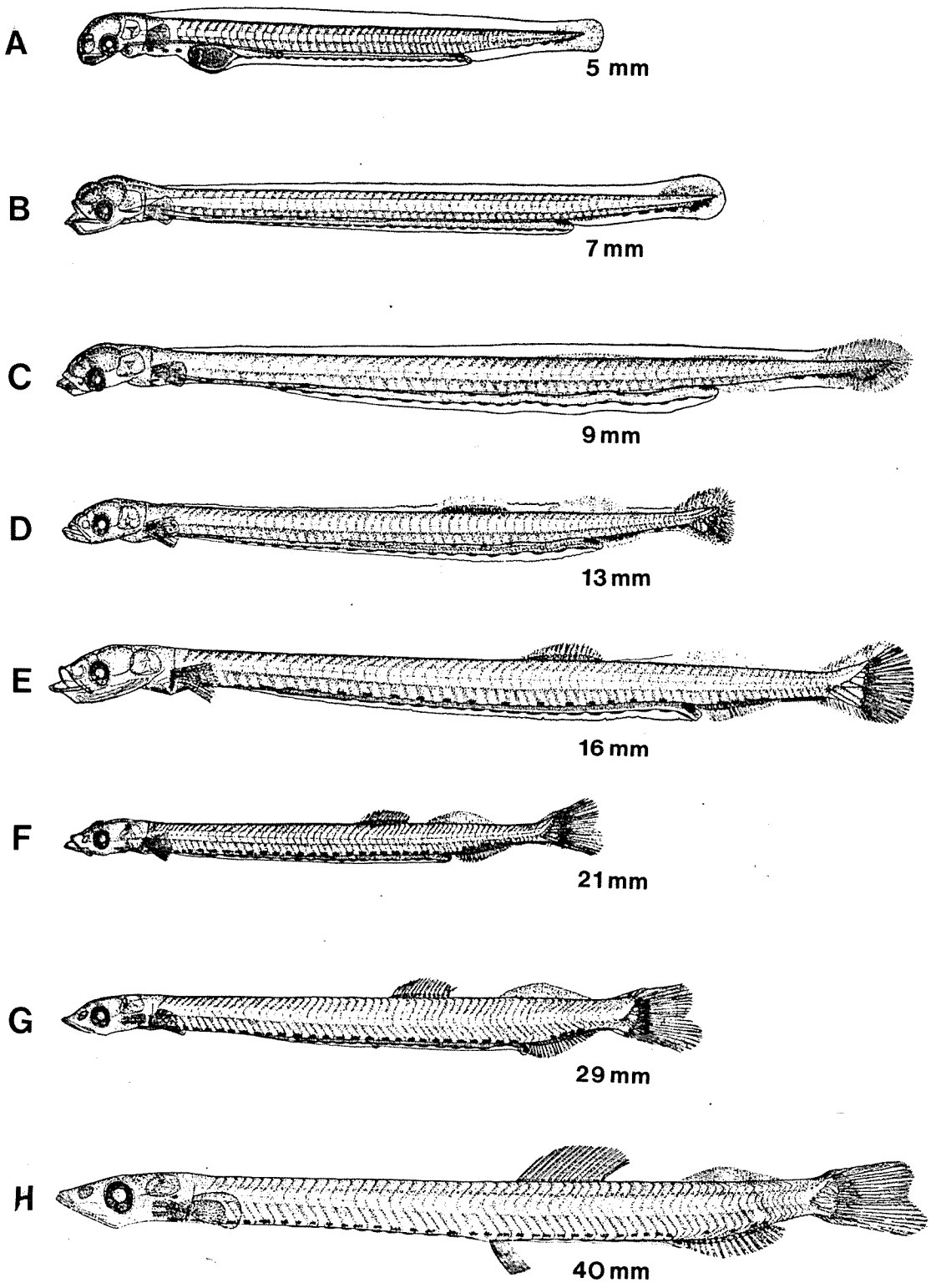

Fig. 7.4. Illustrations of larval capelin, Mallotus villosus, from 5 to 40 mm in length. (Source: Templeman 1948.)

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Spirinchus thaleichthys - Longfin smelt

Range: Central California to Gulf of Alaska

Occurrence in Puget Sound: common

Adult habitat: pelagic

Spawning habitat: anadromous or landlocked, with demersal spawning on gravel beaches

Spawning season: fall

Mode of reproduction: oviparous

Eggs: demersal, attached

Larvae: pelagic

Very little is known about the biology, distribution, and abundance of longfin smelt in the marine environment. They are reported to range from San Francisco, California to Prince William Sound (Hart 1973), but may extend as far north as Bristol Bay (Carl et al. 1967, cited in Macy et al. 1978).

Longfin smelt are anadromous and adults have been caught in Puget Sound from Olympia to Bellingham Bay (Miller and Borton 1980). Landlocked population also exist and are found in Harrison Lake, B.C., and Lakes Union and Washington in Washington State.

The majority of early life history data available are from studies of the Lake Washington stock of longfin smelt (Dryfoos 1965; Moulton 1970, 1974). The saltwater life history is virtually unstudied.

Longfin smelt are reported to spawn at the end of their second year between October and December. Actual spawning of anadromous fish has not been observed although it is thought to occur in rivers near the sea (Hart and McHugh 1944). Spawning males are darker in color on their sides than females and have profuse black stippling around the margins of the scales and along the back (Hart and McHugh 1944). In addition, some of the fin rays are enlarged and stiffened in the males and fine tubercules appear on their sides and paired fins. There is also a swelling of the body along the lateral line in males.

In anadromous stocks, the amount of time the young spend in freshwater is not well-known. Hart and McHugh (1944) found postlarval longfin smelt, 61-72 mm, in the Fraser River, and decided that the young spend a relatively long time in freshwater before migrating to sea. However, larvae as small as 22-23 mm have been reported from the Strait of Georgia, suggesting a shorter stay in freshwater (Barraclough 1967).

The only available description and illustration of longfin smelt egg development is provided by Moulton (1970). Eggs are characterized by a large number of oil globules in the yolk and by an anchor membrane used for attachment to the substrate. This membrane becomes adherent approximately five seconds after the egg enters the water.

After fertilization, development of the eggs proceeds as follows: At 9.6°C, the initial cleavage occurs after 7 hours and by 9 hours, all eggs are in the 4-cell stage. Cleavages to the 64-cell stage occur at 2-hour intervals. At 48 hours, the blastoderm begins moving down over the yolk and by 96 hours the blastopore is completely closed. The embryo is first discernible at 108 hours and by 5 days is readily recognizable. At this time, the optic lobes are apparent and the otoliths just visible. By 10 days, the embryo begins moving, and in 11 days the eyes are becoming pigmented. The heart is detected beating on the 13th day. The embryo increases in length from a full circle around the yolk mass on the 11th day to 1.5 circles on the 15th day and 3 circles on the 18th day. Prior to hatching, the embryos show about 4.5 circles. At temperatures ranging from 9.6°C to 10.6°C, development to the hatching stage is 25 days. Dryfoos (1965) found development took 40 days at 7.0°C.

Newly hatched larvae are about 7.5-9.8 mm total length (Moulton 1970). Pigmentation of the larvae is similar to descriptions given by Dryfoos (1965) and consists of a single row of melanophores on the ventral surface of the gut between the gut constriction and the anus. These melanophores range in number from 7 to 12 (Moulton 1970) and 8 to 10 (Dryfoos 1965), with differences due to merging of melanophores in some individuals.

Food of the young fish has been found to include Neomysis meredis (which occurs in fresh or brackish water). As the fish grow, they eat copepods and cumaceans, and later, euphausiids (Hart and McHugh 1944).

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Thaleichthys pacificus - Eulachon

Range: northern California to Bering Sea

Occurrence in Puget Sound: common

Adult habitat: pelagic

Spawning habitat: demersal, anadromous

Spawning season: spring

Mode of reproduction: oviparous

Eggs: demersal, attached

Larvae: pelagic

Eulachon range from northern California to the eastern Bering Sea and appear to be found only along the Pacific coast of America and not along the Asian continent (Hart 1973). They spend most of their lives in salt water, and unfortunately very little is known about them during this time (Barraclough 1964; Hart and McHugh 1944). In Puget Sound, adults have been collected from south Sound, near Seattle, off Everett, in the eastern Juan de Fuca Strait, and from the San Juan Islands (Miller and Borton 1980).

Like longfin smelt, eulachon are anadromous, returning to freshwater to spawn. The Columbia River has been the site of the largest commercial fishery (Browning 1974, cited by Macy et al. 1978) and other locations of spawning runs are reported to be the Fraser and Nass Rivers and other large B.C. rivers (Hart and McHugh 1944; Cobb 1907, cited by Macy et al. 1978). Eulachon have also been reported to spawn in Grays Harbor and Puget Sound (Swan 1881, cited by Macy et al. 1978). One spawning site has been located in Wapato Creek, which is about one mile upstream from the mouth of the Puyallup River in central Puget Sound (Miller and Borton 1980). Eulachon are not as abundant in Alaska as they are in B.C. and only occasional and brief spawning runs have been reported in the major rivers of southeast Alaska and Cook Inlet (Cobb 1907, cited by Macy et al. 1978). Marsh and Cobb (1908, cited by Macy et al. 1978) mention schools of eulachon in the Unuk, Stikine, and Chilkat Rivers, Dyea and Berners Bays, and Excursion Inlet in southeast Alaska and the important rivers of Cook Inlet. Runs are also reported from the Alaska Peninsula (Bean 1887; Marsh and Cobb 1908; both cited by Macy et al. 1978) and Bristol Bay rivers (Marsh and Cobb 1908; Gilbert 1895; both cited by Macy et al. 1978).

Spawning runs enter the larger mainland rivers and some smaller streams of B.C. in March through April (Barraclough 1964) or May (Hart and McHugh 1944), and fish may travel as far as 44 miles upstream to spawn (McHugh 1939). Timing of the runs from year to year appears to be

fairly constant in each locality (Hart and McHugh 1944). Spawning of the Columbia River eulachon occurs slightly earlier, February to March (Parente and Snyder 1970) and at temperatures of 4-10°C.

Spawning is thought to occur at night (Smith and Saalfeld 1955) although spawning activity has never been documented.

Like other species of smelt, eulachon exhibit a certain amount of sexual dimorphism which includes the presences of tubercules along the lateral line and on the head of the male. Also, muscles of the body wall are more developed in males, resulting in a more rigid fish, and the paired fins of males are longer (Hart and McHugh 1944).

By examining scales and otoliths of spawning B.C. eulachon, Hart (1939) and Hart and McHugh (1944) concluded that fish were in their second year of life and a few were 3 years of age. Later, however, it was shown that eulachon do not spawn until the end of their third year (Barraclough 1964). Columbia River fish are also reported to mature at 3 or 4 years (Smith and Saalfeld 1955). Most fish die after spawning as large numbers of dead fish have been observed near spawning grounds (McHugh 1939; Hart and McHugh 1944; Barraclough 1964). However, spent eulachon in good condition have been caught off the mouth of the Fraser River, suggesting that some fish recover and may spawn again (Barraclough 1964).

Gillnet samples taken of spawning fish have shown that males predominate early in the season, but decrease in abundance as the season progresses. This may be due to the higher incidence of dead males cast up on the beaches, and may not reflect the true sex ratio of the population as a whole (McHugh 1939).

Preferred areas for egg deposition are substrates of pea-sized gravel where currents are at a moderate velocity. In the Columbia River, eggs are found to a lesser extent on semi-sandy areas and on small sticks and debris. Laboratory experiments have demonstrated a spawning preference for gravel and coarse sand over rocks or sticks (Smith and Saalfeld 1955).

Fecundity of B.C. eulachon ranges from 17,000 to 40,000 eggs per female and is relative to the size of the fish, although the data show considerable variation (Hart and McHugh 1944). The average size of Fraser River eulachon is 52-178 mm standard length, with no size differences between the sexes (McHugh 1939). In the Columbia River, fecundities have been reported at 7,000 - 31,000 eggs per female (Parente and Snyder 1970) and 20,000 - 60,000 eggs for 40-195 mm females (Smith and Saalfeld 1955).

Eulachon probaly spawn en masse, no nests are built, and eggs are shed, fertilized, and abandoned (Scott and Crossman 1973, cited in Macy et al. 1978). The eggs show considerable irregularity in shape and have numerous oil globules in the yolk. The average size of the egg is ~1 mm

(.03-.04 inches). The mature egg has an outer membrane which separates from the inner covering after fertilization and turns itself inside out. It remains attached to the inner membrane over a small area and forms a short stalk or peduncle (Fig. 7.5A). The free edges of the outer membrane are extremely adhesive and become attached to particles of sand forming an anchor (Hart and McHugh 1944).

During development, eggs follow typical teleostean development. At three hours after fertilization, the blastodisc can be seen as a transparent yellow cap on the yolk, at 30 hours cleavage is underway and at 60 hours invagination is in progress. After 120 hours, head, eyes, and auditory capsules are formed. A weak heart beat is detected at 300 hours and the eyes have darkened and formed lenses. After 400 hours, the yolk has been reduced to half its original size and the heart is beating strongly. After 500 hours, the embryo becomes active and hatches (Parente and Snyder 1970).

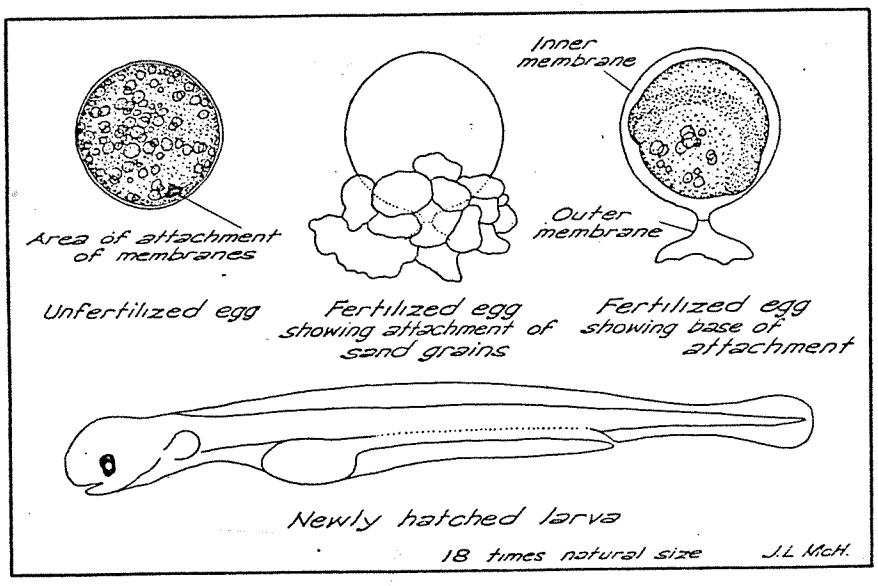
The artificially reared eggs described above hatched in about 22 days at 6.5-9.0°C. At slightly warmer temperatures (8.5-11.5°C) eggs hatch in 19 days (Smith and Saalfeld 1955), and at colder temperatures 4.4-7.2°C development is longer, 30 to 40 days (Hart 1973).

Newly hatched larvae are slender, transparent, about 4-7 mm in length, have rather small eyes and a yolk sac that is placed fairly far back on the body (Fig. 7. 5A,B). Larvae are almost completely outlined by dorsal and ventral finfolds that are continuous with the caudal fin (Hart and McHugh 1944). Pigment of a 6 mm larvae consists of several melanophores on the ventral surface of the gut and yolk sac, and a few postanal pigment spots (Fig. 7.5B). In larvae measuring 18-32 mm fork length, there is a distinct row of small black melanophores along the ventral surface of each side of the abdomen and above the anal fin (Fig. 7.5C). Fry measuring 46-51 mm have melanophores confined to the region above the anal fin. The caudal fin and dorsal body surface are sparsely covered with a strippling of very small melanophores, and the peritoneum is densely lined with small black pigment cells. Adult pigmentation seems to be complete in juvenile fish at the end of one year (Barraclough 1964).

Upon hatching, larvae are feeble swimmers and are carried out to sea. There are no records of larvae remaining in the rivers or feeding before reaching salt water. Barraclough (1964) collected larvae (17 mm was the smallest) and juveniles from the echo-scattering layers of coastal waters at various seasons of the year. He suggested that eulachon may spend a considerable portion of their first two years of life in these food-rich layers. Smallest feeding eulachon eat copepod nauplii and phytoplankton. Copepod eggs, copepods, mysids, ostracods, barnacle larvae, cladocera, worm larvae, and even eulachon larvae have been found to be the food of larvae and postlarvae 25-51 mm (Barraclough 1967 a, b; Barraclough and Fulton 1967; Robinson et al. 1968 a, b).

Eulachon are an important intermediate step in the food web between zooplankton and larger organisms. Small salmon, lingcod, and other fish

A



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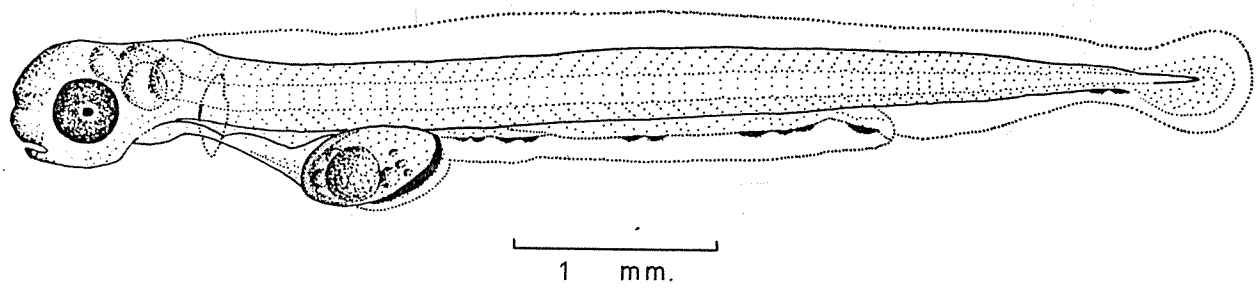

C

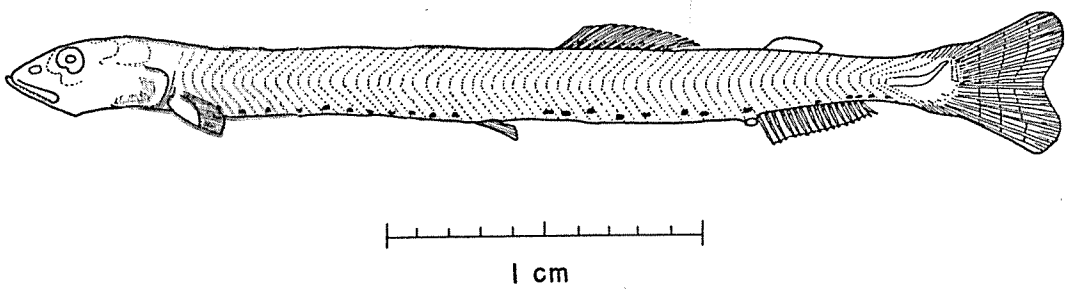

Fig. 7.5. Eggs and larval stages of eulachon, Thaleichthys pacificus: A) Method of attachment in eulachon eggs (Source: Hart and McHugh 1944); B) 6 mm larva (Source: DeLacy and Batts 1963); C) 30 mm larva (Source: Barraclough 1964).

feed on the larvae and postlarvae near river mouths (Hart 1973). Adult eulachon may contribute only seasonally to the diets of predators and during the spawning migration probably contribute a major part of the food of accompanying predators. Known predators include halibut, cod, dogfish, other sharks, seals, sea lions, porpoise, finback whales, killer whales, gulls, ducks, and other seabirds.

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8. PARALEPIDAE

Notolepis rissoi rissoi - Ribbon barracudina

(Available literature not reviewed.)

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9. SYNODONTIDAE

Synodus lucioceps - California lizardfish

(Available literature not reviewed.)

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10. ALEPISAURIDAE

Alepisaurus ferox - Longnose lancetfish

Range: from the equator to Alaska, Aleutian Islands, Bering Sea; Kurile Islands, Japan, Okhotsk Sea; also found in the Atlantic

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic or bathypelagic, surface to 1280 m

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: oviparous, possibly hermaphroditic

Eggs: undescribed

Larvae: pelagic

This widely ranging species is reported from tropical, temperate, and Arctic waters in both the Pacific and Atlantic oceans (Hart 1973) and has been reported on a few occasions from waters of Puget Sound (Miller and Borton 1980). It is pelagic or bathypelagic in nature and may be taken at depths ranging from the surface to 1280 m. Adult longnose lancetfish are characterized by an elongate scaleless body, very high and long dorsal fin, and large fang-like teeth (Hart 1973).

Lancetfish have been known to exhibit hermaphrodism. Individuals have been found which contain both testicular and ovarian material in which eggs are developing and cells of testes show meiotic activity. However, it is unknown if both sets of reproductive organs are functional (Gibbs and Wilimovsky 1966).

The spawning season in the Pacific is unknown except for one specimen taken off California in May which showed indications that spawning was imminent (Fitch and Lavenberg 1968).

Egg stages of longnose lancetfish are undescribed, but larvae from the Atlantic have been identified to species and may be either Alepisaurus ferox or A. brevirostris (Rofen 1966). At 7-8 mm, these larvae are characterized by large, stalked pectoral fins and dentition on the lower jaw which consists of long lateral canines (Fig. 10.1A, B). Pigmentation pattern of the 7-8 mm larva includes light pigment along the edge of the upper jaw, scattered melanophores on the top and postorbital regions of the head, scattered melanophores on the nape and along the dorsum posteriorly as far as the greatest height of the dorsal

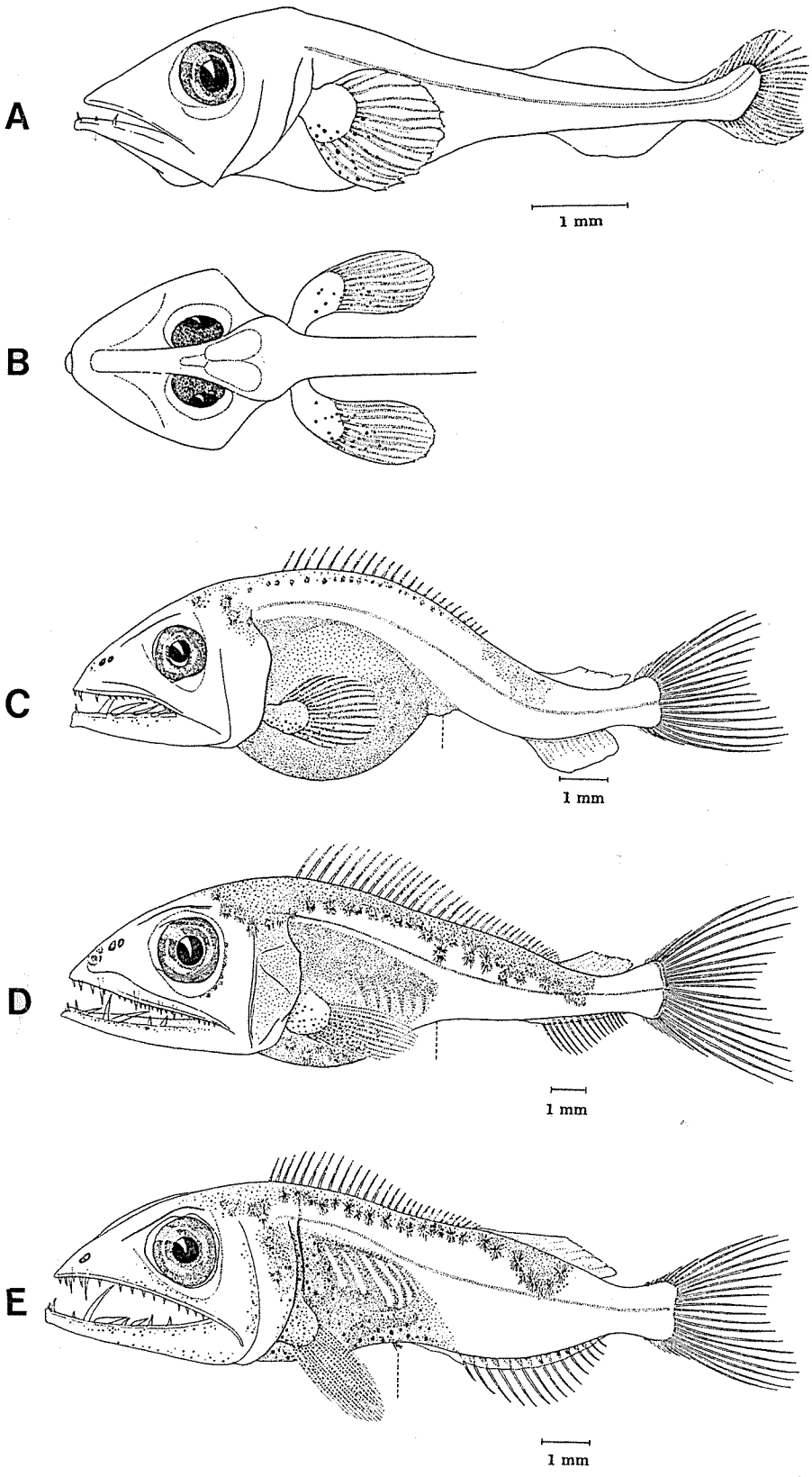

Fig. 10.1. Larval Alepisaurus spp. collected from the plankton off Bermuda in the Atlantic Ocean: A) 6.9 mm; B) 6.9 mm dorsal view: C) 12.1 mm; D) 17.2 mm; E) 11.8 mm. (Source: Rofen 1966.)

finfold where it expands on the uppper sides of the body as a broader pigmented area, and scattered melanophores on the gut region, throat, and stalks and rays of the pectoral fins. Pigment is lacking on the posterior lower regions of the body, and on the finfolds and caudal fin. With development (11-17 mm), the gut becomes well-pigmented and the melanophores form a pattern of numerous vertical bars. In addition, lateral and median dorsal body pigmentation becomes more extensive (Fig. 10.1 C, D, E).

Large fan-like pectorals are present in 6.9 mm larvae and rays of the caudal fin are developing (Fig. 10.1 A, B). By 12.1 mm, the dorsal finfold exists in the adipose fin region only, and rays are developing in the dorsal and anal fins. With development, the stalks of the pectoral fins become reduced and the pectoral fin rays become markedly elongated. Also with development, dentition becomes well-formed with prominent lateral canines (Rofen 1966).

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11. MYCTOPHIDAE

General

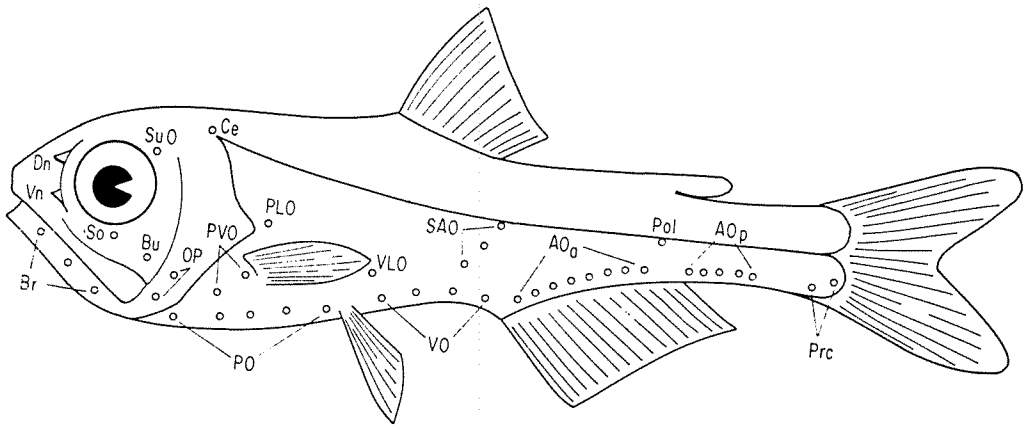
The lanternfish family, Myctophidae, represents the most speciose and widespread family of mid-water fishes in the world ocean. Presently, about 30 genera and 300 species are recognized. Adults are bathypelagic, usually at intermediate depths, although some are taken at depths of several thousand meters. Many species undertaken vertical migrations to the surface during the night.

In Puget Sound, three species of myctophids have been reported - Diaphus theta (California headlightfish), Stenobrachius leucopsarus (northern lampfish), and Tarletonbeania crenularis (blue lanternfish). In each case, only a few recorded sitings are known (Miller and Borton 1980).

While larval myctophids are known to make up almost 50% of all larvae taken in open-ocean plankton tows, the eggs of lanternfish are virtually unknown. Over twenty years of extensive plankton collection off California by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has failed to produce any positively identifiable myctophid eggs. While this situation would seem to imply that myctophids are viviparous, most investigators believe them to be oviparous (see Moser and Ahlstrom 1970, p. 10). CalCOFI researchers speculate that myctophid eggs are fragile and rupture or collapse during collection and are lost through the plankton net mesh (Moser and Ahlstrom 1970).

Extensive work (relative to other families) has been done on describing larval myctophids and using their larval characters to discuss taxonomic relationships within the family (e.g., Moser and Ahlstrom 1972; Moser and Ahlstrom 1974; Okiyama 1974). Currently, on the basis of eye shape, myctophid larvae fall into two "phylogenetically natural groups," those with narrow or elliptical eyes (Subfamily Myctophinae) and those with round or nearly round eyes (Subfamily Lampanyctinae) (Moser and Ahlstrom 1970). Species of either group may develop a mass of choroid tissue below the eye, but this is most marked in elliptical-eyed larvae. Narrow-eyed larvae in some genera may be stalked.

Another prominent feature of myctophids is the presence of photophores or light organs. In most species at least one pair of photophores, the Br_2 (Fig. 11.1), forms during the larval period. Some species, for example California headlightfish, develop additional photophores during the larval period. At transformation, the remaining photophores develop but do not form simultaneously. Usually the ventral series forms first in a posteriad sequence followed by formation of the lateral body photophores which form in a dorsad sequence. The sequence of appearance and position of photophores can be used in some cases to differentiate between species of lanternfish.



Paired photophores of a generalized myctophid

AOa	(1–7(9)) *Anterior anals*	OP	(1–2) *Opercular*s	SAO	(3) *Supraanals*
AOp	(1–7(9)) *Pedunculars*	PLO	*Suprapectoral*	So	*Suborbital*
Br	(3) *Mandibulars*	PO	(1–5(6, 7)) *Thoracics*	SuO	*Supraorbital*
Bu	*Buccal*	PVO	(1–2) *Subpectorals*	Vn	*Ventronasal*
Ce	*Cervical*	Prc	(1–4) *Precaudals*	VLO	*Supraventral*
Dn	*Dorsonasal*	Pol	(1(2)) *Posterolaterals*	VO	(1–4(5)) *Ventrals*

Fig. 11.1. Arrangement of photophores of a generalized myctophid. (Source: Hart 1973.)

Myctophid larvae differ markedly in the sequence of fin formation as compared to most clupeiform fishes. In myctophids, rudimentary pectoral fin are present at hatching and ossification is initiated at an early stage often before ray formation in the other fins or immediately following ossification of principal caudal rays. In addition, some species, for example blue lanternfish, develop more pectoral rays during the larval period than are present in the adult form. "Excess" rays are lost during transformation, probably by resorption. In most species the caudal fin is usually the first to develop ossified rays, which form just before and during notochord flexion. The anal fin forms next followed by the dorsal fin which in some species may initiate ossification as early as the anal fin. The pelvic fins are usually the last to form. Moser and Ahlstrom (1970) present a detailed discussion of the sequence of ossification of bony elements of the skull and skeleton of myctophid larvae.

Some myctophid larvae develop specialized structures which are present only during the larval period. Blue lanternfish larvae, for example, develop a pair of elongate lower pectoral rays which terminate in a series of pigmented spatulate processes, although these are usually broken off during collection. In addition, these larvae develop a voluminous sac-like median finfold. The functions of these structures are unknown, although it has been hypothesized that the enlarged finfold may be a hydrostatic organ that allows larvae to remain at a certain depth or that it functions as a nutrient storage organ (Moser and Ahlstrom 1970).

Another special larval structure is the lunate or conical tissue mass found on the ventral surface of the eye. Found in several myctophid genera including Tarletonbeania, it is present until metamorphosis when it disappears fairly rapidly. Moser and Ahlstrom (1974) speculated that this preformed choroid tissue provides the necessary vascular system for the rapidly expanding eye.

Differences in pigmentation among myctophid larvae can aid in identification and are worth mentioning. In the Puget Sound species, the earliest larvae of northern lampfish and California headlightfish possess a series of pigment spots along the ventral midline of the tail, blue lanternfish larvae do not. In northern lampfish, 19-21 pigment spots are present in early larvae, but decrease to 1-3 in late-stage larvae. In California headlightfish, the ventral postanal midline melanophores persist in number during larval development.

Diaphus theta - California headlightfish

Range: Baja California to Gulf of Alaska; Kurile Islands

Occurrence in Puget Sound: uncommon

Adult habitat: bathypelagic

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Hart (1973) reported that California headlightfish are bathypelagic in the northeast Pacific where they range from Baja California to Alaska. A few specimens of this lanternfish have been recorded in Puget Sound (Miller and Borton 1980).

Very little is known about the reproductive biology of California headlightfish. Eggs have not been found, although most evidence indicates that lanternfish are oviparous (Moser and Ahlstrom 1970).

The California headlightfish belongs to the subfamily Lampanyctinae which is characterized by larvae with round or nearly round eyes (Moser and Ahlstrom 1970). A 7.0 mm larval Diaphus theta was illustrated by Moser and Ahlstrom (1974) and has a slender body, small head, and a series of persistent melanophores on the ventral midline of the tail. Embedded melanophores also form at the base of the caudal fin rays (Fig. 11.2). Although only the Br_2 photophore is developed in the illustrated larvae, the PO_5 may appear by 6.2 mm and consecutive photophores development is shown in Table 11.1.

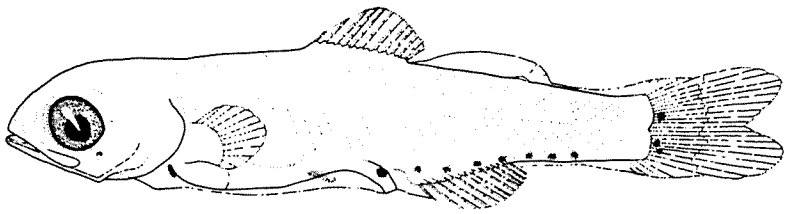


Fig. 11.2. Larva of California headlightfish, Diaphus theta, 6.9 mm. (Source: Moser and Ahlstrom 1974.)

Table 11.1. Sequence of photophore development in larval California headlightfish, Diaphus theta. (Source: Moser and Ahlstrom 1974.)

Species	Size larva (mm)	Photophores	No. of photophore pairs	Smallest juvenile (mm)
D. theta	6.2	Br_2 PO_5	2	ca. 12.0
	7.6	Br_2 PO_5 PO_1	3	
	8.2	Br_2 PO_5 PO_1 VO_1	4	
	8.6	Br_2 PO_5 PO_1 VO_1 PO_2 Op_2	6	
	9.0	Br_2 PO_5 PO_1 VO_1 VO_1 PO_2 Op_2 PO_3 PO_4 VO_5	9	
	9.2	Br_2 PO_5 PO_1 VO_1 PO_2 Op_2 PO_3 PO_4 VO_5 VLO	10	

Stenobrachius leucopsarus - Northern lampfish

Range: California-Mexico border to Bering Sea; Kurile Islands to Japan

Occurrence in Puget Sound: uncommon

Adult habitat: bathypelagic

Spawning habitat: unknown

Spawning season: winter-spring (Oregon)

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Inhabiting depths down to 3000 m, northern lampfish range from southern California to the Bering Sea (Hart 1973).

Off Oregon, northern lampfish are reported to reach sexual maturity at 65 mm or at about 4 years in age. Maturation of gonads begins in October and spawning takes place from December to March, with only one spawning per fish per season taking place (Smoker and Pearcy 1970).

In California, spawning lasts from November to August and occurs when fish are 3 years old. Ova diameters of mature fish range from 0.01-0.61 mm and when the majority of the eggs in an ovary are 0.45-0.61 mm, they begin to loosen from the ovary wall. Northern lampfish spawn only once per life time as only about 1% of the population survive beyond 3 years (Fast 1960).

Ahlstrom (1965) illustrated several sizes (5.3, 7.8, and 12.5 mm) of northern lampfish larvae and Fast (1960) described their larval development from plankton samples collected off California. The smallest identifiable larvae are 3.0 mm, and slender with elongate bodies. The head is small with a relatively high crown due to the size of the brain. The anus is located at about 33% of the total body length and the anal pipe is at an angle of 90° to the body axis. At this size, larvae are devoid of pigment except for a small amount of melanin on the eye (Fig. 11.3A). With development, the round eyes become heavily pigmented, the mouth shifts from an inferior to a terminal position, and rudiments of the caudal fin rays appear. At about 6.5 mm in length, three distinguishable gut melanophores appear. One is on the anterior ventral surface of the gut, another is on the posterior gut, and the third, which is the presumptive PO_4 photophore, is on the lateral body wall at about the seventh or eighth anterior myomere. Postanal midventral melanophores are also present (Fig. 11.3B). At about 10 mm, flexion is

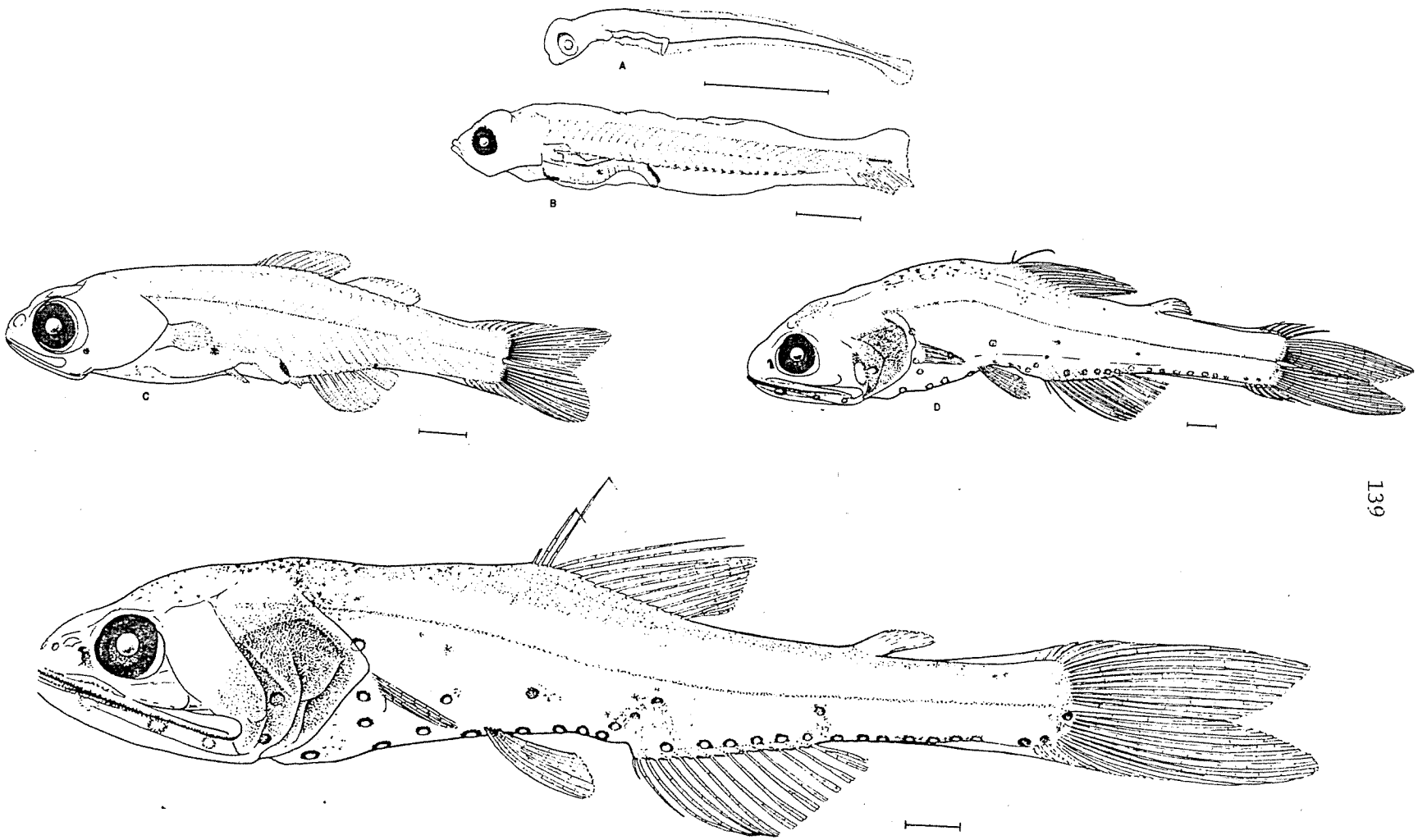


Fig. 11.3. Larvae and early juvenile of northern lampfish, Stenobrachius leucopsarus: A) ∿3.0 mm; B) ∿6.5 mm; C) 9.7 mm SL; D) 16.8 mm; Bottom) 19.2 mm SL. (Source: Fast 1960.)

complete and the specimen resembles a juvenile in morphology. The finfold is reduced to a narrow band near the caudal peduncle and the fins become well-differentiated with rays at various stages of development. As well as the PO_4 photophore, two other areas of melanation, indicating photophores, are present, the Op_2 and the AO_2. In addition, the postanal ventral melanophores have coalesced into one or two spots (Fig. 11.3C). By 16.8 mm, northern lampfish can be recognized by their photophore counts and patterns, although the heavily pigmented areas surrounding the photophores in larger juveniles are still lacking (Fig. 11.3D). Metamorphosis from larva to juvenile includes the following changes: Marked elongation of the jaws, posterior migration of the Op_2, increase in space between the dorsal and adipose fins and reduction in the base of the adipose fin (Fig. 11.3, bottom.

The pelagic, young northern lampfish larvae inhabit surface waters until they are about 10 mm TL. At this size, they descend to deeper water (400-500 m) where they undergo metamorphosis. Soon after, they rise to the 200-300 m level, and as they grow older there is a gradual tendency to seek deeper water until at sizes of 40 to 70 mm they are once more concentrated toward the lower limit of their bathymetric range (Fast 1960).

At the end of one year, northern lampfish range from 20-38 mm SL ($\bar{X}$ = 29 mm SL), are 40-60 mm SL ($\bar{X}$ = 50 mm SL) after 2 years, range from 60-72 mm SL ($\bar{X}$ = 66 mm SL) at the end of three years and are greater than 70 mm after four years (Fast 1960).

Tarletonbeania crenularis - Blue lanternfish

Range: Mexico to Alaska; Japan

Occurrence in Puget Sound: uncommon

Adult habitat: bathypelagic

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Although they range from Mexico to Alaska (Hart 1973), adult blue lanternfish have only been reported on two occasions from Puget Sound (Miller and Borton 1980).

Little information on spawning bilogy of this myctophid is available, although their larval development was studied in detail by Moser and Ahlstrom (1970). During early stages, larvae are slender, but become deep-bodied during late larval stages. In newly hatched larvae, the anus is located at midbody but increases to 70% of body length in 13-14 mm larvae and then to 54-56% at transformation. In contrast to the round-eyed larvae of northern lampfish and California headlightfish, larval blue lanternfish eyes are elliptical with a prominent mass of choroid tissue which develops on the ventral surface of the eye. The choroid is covered with pale melanistic pigment and the mass becomes broadly conical and enlarges throughout the larval period before disappearing during transformation.

The most striking features in the devleopment of blue lanternfish larvae are the presence of heavily pigmented voluminous dorsal and ventral median finfolds and the development of a pair of greatly enlarged and elongated lower pectoral fin rays. During the larval stage, the pectoral fin count contains 4 more rays than are retained in the adult. Extra rays, including the elongate rays, are lost during transformation.

Pigmentation of newly hatched larvae consists of a median dorsal and ventral melanophore opposite each other near the end of the tail, which may coalesce into a band (Fig. 11.4A). The ventral melanophore is lost by 5 mm, but the dorsal one persists in newly transformed juveniles. A large shield-like melanophore is present at the junction of the anal pipe and the ventral body surface and two embedded melanophores are present anteriorly - one dorsal to the foregut and one between the pericardial and perivisceral cavities. The posterior gut melanophore disappears in 8-9 mm larvae, and the melanophore on the dorsal foregut is lost by

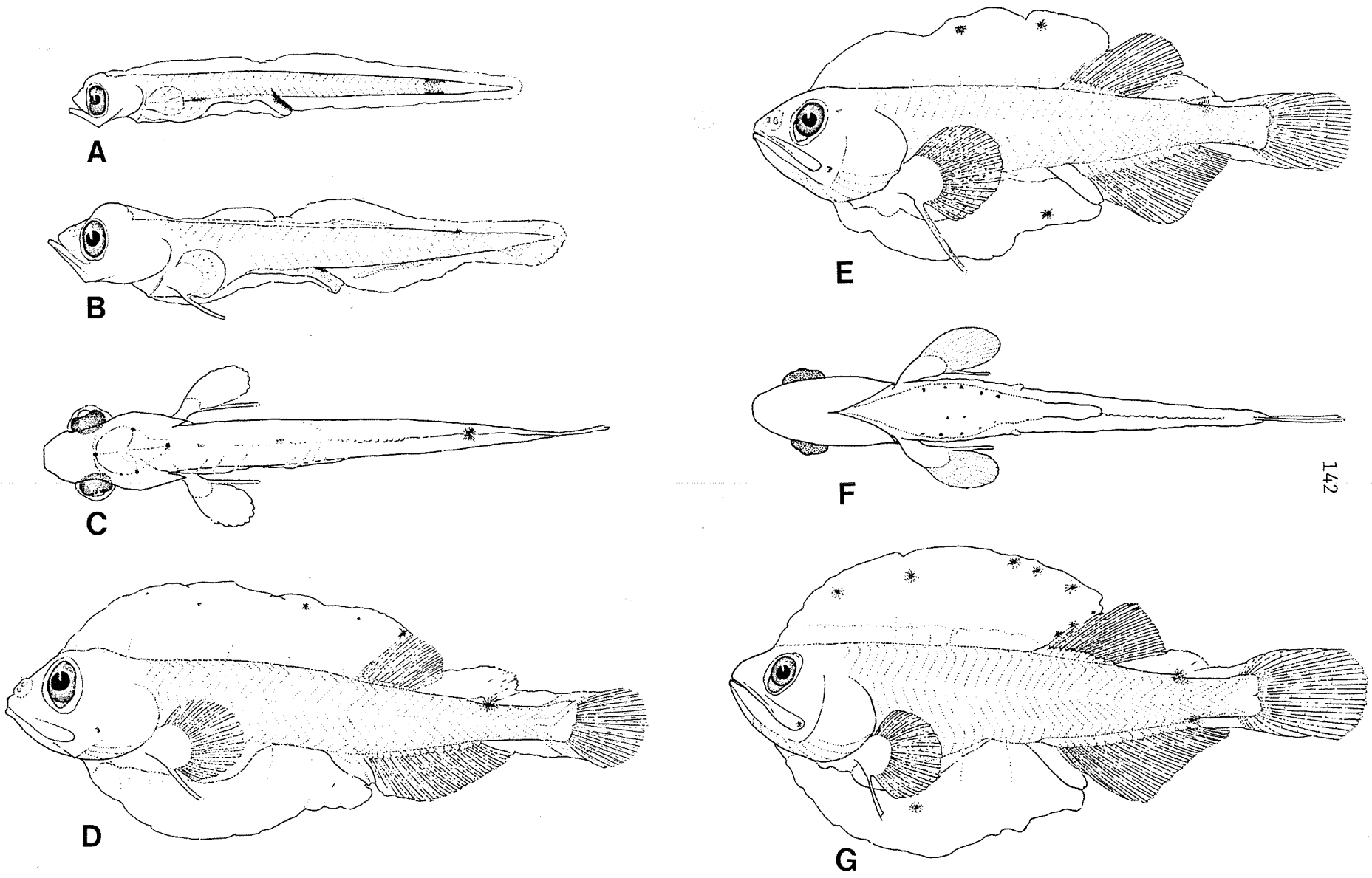


Fig. 11.4. Larval development of blue lanternfish, Tarletonbeania crenularis: A) 3.7 mm; B)7.5 mm; C) 9.6 mm - dorsal view; D) 10.5 mm; E) 13.8 mm; F) 13.8 mm-ventral view; G) 18.9 mm. (Source: Moser and Ahlstrom 1970.)

5 mm, but the spot at the transverse septum remains throughout the larval period and additional melanophores may develop in this reion. At 6 mm, melanophores first appear on the margin of the enlarged dorsal finfold, and spread along the margins of both fins and into the interior. Numerous small melanophores appear on the pectoral fin rays at 7 mm, and at 9 mm, melanophores appear on the ventral surface of the bulbous foregut becoming arranged in four longitudinal rows. During transformation, these rows coalesce into a median longitudinal line. Also at 9 mm, melanophores develop on the dorsal head region (Fig. 11.4C) and along the upper jaw.

The Br_2 photophores are the only light organs to develop during the larval period, and first appear in 10 mm larvae and are well-developed in late-stage larvae. A 19.3 mm specimen has all the ventral photophores developed, but few of the lateral ones. At this time, besides the Br_2, the best developed are the Br_1, Br_3, and superior Op. The six pairs of Po are visible, two pairs of PVO are barely discernible, but the PLO, VLO, SAO, and POL are not evident. At 21.7 mm, the PLO and VLO are present, but the SAO and POL have yet to develop (Fig. 11.5).

Sequence of fin formation and ossification proceeds in the following order: pectorals, primary caudals, dorsal and anal, and pelvics (Table 11.2).

Table 11.2. Sequence of ossification of fins of blue lanternfish, Tarletonbeania crenularis. (Source: Moser and Ahlstrom 1970.)

Length, mm	Development of fin rays
5	Elongate pectoral ray appears on ventral margin of fin; caudal fin begins to develop.
6	Enlarged pectoral ray begins to ossify.
7	Other pectoral rays begin to ossify; primary caudal fin rays also begin to ossify; adipose fin first appears.
7.5	Notochord flexion begins.
8	Larval complement of 15-17 pectoral rays is ossifying; bases of anal and dorsal fins developing and rays begin to ossify.
9	Hypural elements are differentiating; adult complement of primary caudal fin rays is ossifying; secondary caudal fin rays begin to ossify; pelvic fin buds appear.
10	Hypural elements begin to ossify; adipose fin well formed.
10.5	Flexion complete.
11	Adult complements of rays of dorsal and anal fins are ossifying.
13	Caudal rays ossified; pelvic fin rays begin to ossify.
14	Four superior and three inferior hypural elements are ossifying.
15	Adult pelvic fin rays present.

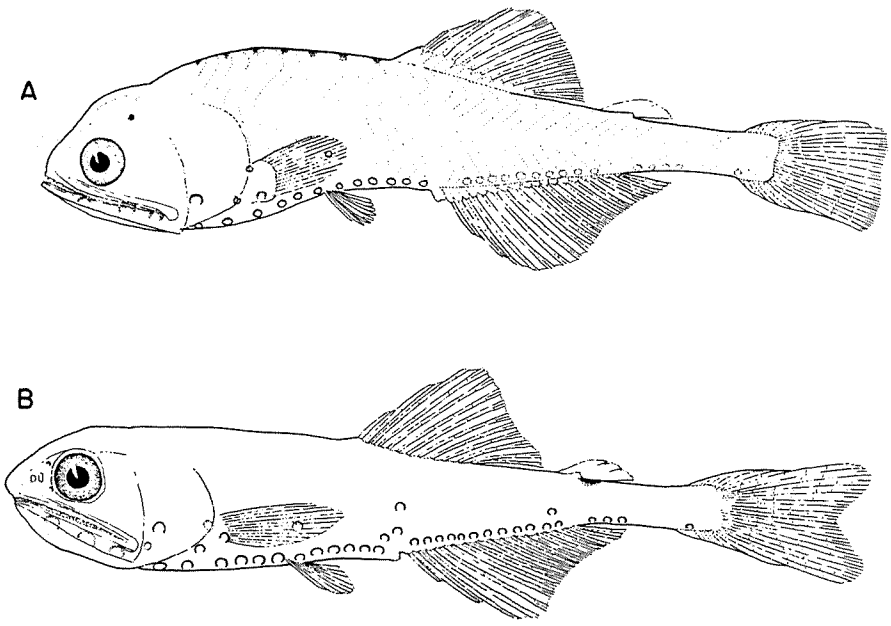


Fig. 11.5. Late transformation stage, 21.7 mm A), and juvenile, 21.6 mm B), of blue lanternfish, Tarletonbeania crenularis. (Source: Moser and Ahlstrom 1970.)

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12. BATRACHOIDIDAE

Porichthys notatus - Plainfin midshipman

Range: Gulf of California to southeast Alaska

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal and deeper

Spawning habitat: demersal, intertidal to subtidal

Spawning season: late spring - early summer

Mode of reproduction: oviparous

Eggs: demersal, attached, guarded

Larvae: demersal, attached, guarded

Plainfin midshipman are known from the Gulf of California to southeast Alaska (Hart 1973). They are also found throughout Puget Sound (Miller and Borton 1980) where they may be common in intertidal areas and deeper water to 265 m (Hart 1973).

Adults of this species are characterized by two unusual features. One feature is the presence of about 700 photophores or luminous organs which are arranged symmetrically in rows primarily along the ventral and ventrolateral surface, and to a lesser extent on the dorsal body surface. These organs have received a fair amount of attention as to their structure, mechanism of lighting, and possible function (Greene 1889; Greene and Greene 1924; Crane 1965; Strum 1969 a,b; Baguet and Case 1971). Crane (1965) observed male and female Porichthys from southern California waters illuminating together and hypothesized a likely function of these displays in courtship. It is interesting to note that the Porichthys found in Puget Sound do not luminesce (Strum, 1969b). This may be due to the absence of an ostracod prey, Cypridina, which occurs in California and provides luciferin, a chemical needed by Porichthys in order to bioluminesce (Tsuji, et al. 1972).

The second unusual feature of this species is the ability to emit grunts and croaks which are audible up to 40 feet. These sounds are achieved by contractions of muscles surrounding the swimbladder which force air through a small opening in its drumlike end (Greene 1924 a,b). There has been no clear correlation of the types of sounds produced and the behavior of the fish (Cohen and Winn 1967).

During the fall and winter months, plainfin midshipman are offshore and little is known about their life history. But during late spring and summer they undertake a shoreward migration into shallow bays or sandy intertidal pools. Spawning occurs under rocks or

boulders which are partially buried in sand or broken shell substrate, and the adults may use their pectoral fins to scoop out cavities under the rocks. The female deposits her eggs in a single layer on the roof of the cavity and leaves the nest, but the male remains to guard the eggs and larvae until they become free-swimming (Fig. 12.1). Males may be polygamous with several females contributing to the nest, which would be one explanation for the presence of eggs at various stages of development and possibly the wide range of egg sizes found within a nest (Arora 1948).

The male fasts while guarding the eggs and has been observed to fan the eggs with movement of the pectoral and caudal fins. In the aquarium, guarding males have been seen to brush and rub the eggs, possibly to remove debris, as unattended egg masses become overgrown with bacteria. Attendant males are also aggressive defenders of the nest and will attack other males or emit barks or croaks if approached. Males also protect the eggs from dessication during low tide by splashing them with water from the nest cavity (Arora 1948).

The number of eggs per nests can vary from 20 to 800, with the usual number about 200-300. The eggs are spherical, about 4-6 mm, and orange in color, resembling salmon eggs. The egg membrane is firm and attached to the rock by means of an adhesive disc. At the time of deposition, this disc is a transparent secretion at the vegetative pole of the egg. When the egg contacts with water, the adhesive disc becomes opaque and gluey, cementing the egg to the rock surface. Development of the eggs takes 16-20 days (Arora 1948).

At hatching, the egg membrane becomes weak and the embryo bursts the shell in the region near the tail. The tail then protrudes and may be seen lashing freely in the surrounding water. The split in the egg shell continues forward and downward uncovering the embryo and upper part of the yolk. At this stage, embryos are 7-8 mm and remain attached to the rock by means of the yolk sac which is connected to the adhesive disc (Fig. 12.1, top). The larvae remain in this position for about one month, deriving nutrition from the yolk sac (Arora 1948). While still attached to the rock, caudal and median fins develop, pelvic fins move forward to their permanent position, gill cover and pectoral fins become functional, the vascular system spreads over the yolk, head and mouth parts grow rapidly, and pigment and photophores begin to appear (Fig. 12.1, middle) (Arora 1948). Recent observations indicate that wild, attached larvae are capable of feeding on small copepods, such as harpacticoids and gnathostome cyclopoids (Crane 1981).

When the larvae are about 32-34 mm, they are ready to leave the rock. At this point, the yolk has been absorbed and the attachment organ has been reduced to a disc-like plate. By twisting back and forth, the larvae become detached from the rock and free-swimming. The remnant of the attachment disc drops off, and only a knob-like projection remains, which is ultimately absorbed (Fig. 12.1, bottom).

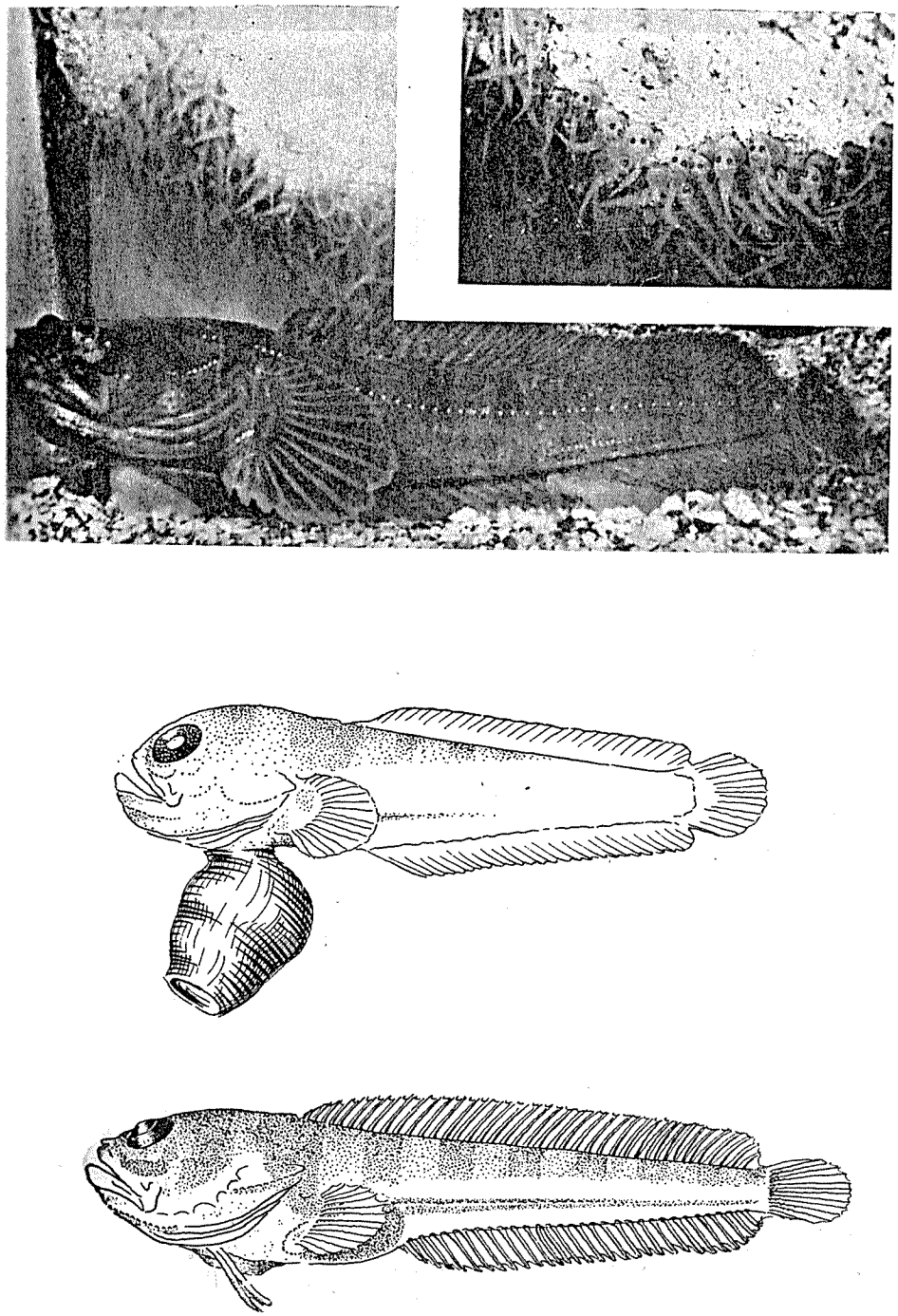

Fig. 12.1. Top) Male plainfin midshipman, Porichthys notatus, guarding a nest; Top-insert) close-up of larvae attached to undersurface of rock; Middle) larva 17 days after hatching; Bottom) young free-swimming juvenile just after leaving its anchorage. (Source: Arora 1948).

Free-swimming juveniles avoid light and remain buried in the sand during the day and come out at night to feed on small crustaceans and zooplankton (Arora 1948). The coloration of a 26 mm specimen consists of eight greenish black bars which extend from the mediodorsal region to the upper edge of a broad silvery stripe with metallic reflections, which occupies the middle third of the body. The fins are unpigmented, except for a basal caudal bar and the two dorsal spines. The top of the head is mottled with dark pigment, and is silvery on the sides and unpigmented ventrally except for a dark ring surrounding each photophore. A conspicuous narrow black streak is located below the eye and branches once or twice posteriorly (Hubbs 1920).

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13. GOBIESOCIDAE

Gobiesox maeandricus - Northern clingfish

Range: southern California to southeast Alaska

Occurrence in Puget Sound: uncommon, except common in northern Puget Sound

Adult habitat: demersal, on rocks or algae

Spawning habitat: demersal, on rocks

Spawning season: winter-spring (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, attached, guarded

Larvae: pelagic

Northern clingfish range from southern California to southeast Alaska (Hart 1973). They are equipped with a well-developed adhesive disc (Arita 1967) which enables them to cling to rocks or algae in the low intertidal zone (Hart 1973; Burge and Schultz 1973).

Spawning occurs during winter and spring in British Columbia and five or six fish may be present during spawning, but only one male remains to guard the eggs. The eggs average 2 mm in diameter and are bright yellow becoming golden near hatching. They are deposited on the underside of boulders and are laid as a monolayer in concentric rings with the most recently developing mode outermost (200-500 eggs per mode)(Marliave 1975).

Johnson (1970) found females of 64 mm in length or greater to be mature. From five ovaries examined, the mean number of ova was 296 (range 194-382) and egg diameters ranged from 1.25 to 1.90 mm($\bar{X}$=1.5 mm).

At hatching, larvae have a conspicuous bilobed yolk sac with a single oil globule (Fig. 13.1). They are short bodied, have a swim bladder (absent in cottid larvae), and large melanophores covering the dorsal surface of the gut. Pigment spots are also located on the snout, and as dashes extending into the anal finfold in the ventral postanal region. Development of the sucking disc takes place during the stage of caudal fin development, and is complete, but small with no papillae, when anal and dorsal fin ray development starts (Marliave 1975).

Late stage larvae accumulate in large schools around kelp beds in late May to late June in Barkley Sound, B.C. and begin to settle at

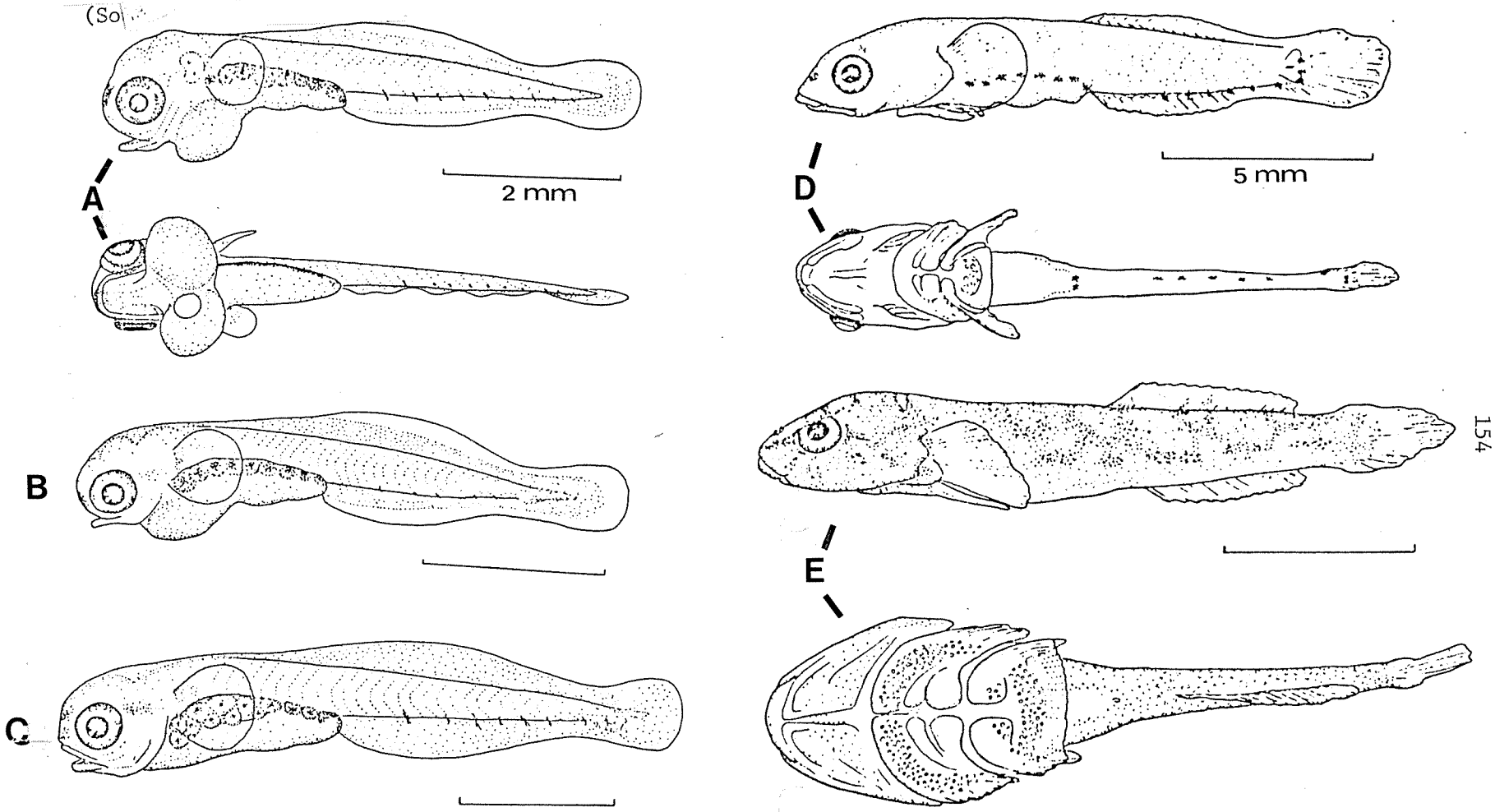

Fig. 13.1. Larvae of northern clingfish, Gobiesox maeandricus: A) 0-day, 6 mm TL (side and ventral views); B) 2-day, 6 mm TL; C) 6-day, 8 mm TL; D) settled stage, 54-day, 14 mm TL (side and ventral views); E) 65-day, 18 mm TL (side and ventral views). (Source: Marliave 1975).

lengths of 13-14 mm. In larval substrate preference experiments, northern clingfish young show an affinity for broad smooth surfaces such as Ulva or Nereocystis over sand, rock, or gravel. At this size (14 mm), the disc is small and lacks papillae. Juveniles remain on algae until ~ 19 mm TL when they transfer to rock surfaces or the tank bottom. Development of disc papillae may be one factor allowing them to switch to a rocky substrate (Marliave 1977).

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14. GADIDAE

Gadus macrocephalus - Pacific cod

Range: Santa Monica, California to Chukchi Sea; Kamchatka to Yellow Sea

Occurrence in Puget Sound: common

Adult habitat: semi-demersal

Spawning habitat: same

Spawning season: winter-early spring

Mode of reproduction: oviparous

Eggs: demersal

Larvae: pelagic

Pacific cod range from Santa Monica, California through Alaska and the Bering Sea to the Chukchi Sea. In the western Pacific, they occur off Kamchatka and in the Kuril Island, Okhotsk Sea, Sea of Japan, and near Port Arthur in the Yellow Sea. They are widely distributed over much of the shelf and occur as deep as 550 m (Hart 1973).

Areas of concentration of Pacific cod in British Columbia are found southwest of Vancouver Island, in Hecate Strait, and in Queen Charlotte Sound. They are also located off Washington State and are concentrated between Cape Flattery and Destruction Island. Lesser quantities occur off the Columbia River and coast of Oregon and small fishing grounds are reported in Puget Sound and the Strait of Georgia (Ketchen 1961).

Tagging studies carried out in Washington waters suggest that Pacific cod comprise a number of small subpopulations which remain relatively separate although some exchange may take place (Gosho 1976). In Puget Sound, Pacific cod are common and widely distributed, being found in practically all areas of the sound (Miller and Borton 1980).

Seasonal bathymetric migrations are documented for Canadian cod. These fish are located in deeper water (90-150 m) during the winter when spawning takes place (January to March). After spawning, migration to the shallower regions (30-70 m) of the coastal banks occurs. This lasts until late spring or early summer followed by a return to deeper water beginning in midsummer and lasting through November or December. Pacific cod distributions, at least off the Canadian coast, appear to be synchronous with the isotherms of 6-9^{o}C, although the evidence is incomplete. These isotherms are generally deeper during winter and shallower during late spring to early summer (Ketchen 1961).

In Port Townsend Bay, adults congregate for spawning during December to March and disperse over a wider area after spawning (Miller et al. 1978).

As a general rule, Pacific cod appear to spawn below the mixed layer at depths governed by its thickness. In most Asian waters, temperatures at these depths during the spawning period range from 0-5°C and in Canadian waters from 6-9°C. From observations on Asian cod populations and Canadian fish, it was concluded that cod neither enter nor spawn in areas where temperatures remain above 12-13°C, and spawning is probably inhibited at temperatures above 9°C or below 0°C (Alderdice and Forrester 1971).

Length and age of maturity differs between eastern and western Pacific cod. Ketchen (1961) reported that from the Strait of Georgia, 50% of male cod were mature at 48-49 cm and two years of age and at three years, all males were mature. Females were mature at a larger size (50% maturity level at 55 cm) and at a slightly older age (only 15-25% were mature at two years). Similarly, Port Townsend cod are small and relatively young at maturity - two years of age and about 44 cm (Miller et al. 1978). In contrast, Pacific cod off Kamchatka in the western Pacific reached the 50% maturity level at 73 cm for females, and 70 cm for males and age 6 for both sexes (Moiseev 1953).

Assuming a constant fecundity-length relationship for cod from the two areas, Ketchen (1961) suggested that the Canadian stock was approximately one-half as fecund as the northwest Pacific stock. Because Pacific cod from Canada mature at a smaller size and have a shorter life span, he assumed they would produce fewer eggs. Thomson (1962) studied the fecundity of cod from Hecate Strait and compared his data to data for cod in the western Pacific. He found that within the size range (40-88 cm) he studied, there was no difference in the production of eggs in proportion to body length between Canadian and Kamchatka cod. Hence, he concluded that Kamchatka cod do have a higher reproductive potential. Fecundity of Pacific cod is high and ranges from several hundred thousand eggs to 1-3 million eggs per female (Table 14.1). In Puget Sound, Karp (1982) determined the fecundity-length relationship for Pacific cod to be: $F = 12.024 \times \text{total length}^{2.959}$, where $r^2 = .653$. Calculated estimates of fecundity for 40, 50, and 60 cm females were 661,000, 1,280,000, and 2,195,000 eggs per female, respectively.

Studies of artificially fertilized Pacific cod eggs indicate they are demersal (Thomson 1963) and may be adhesive for a portion of their development (Forrester 1964). Eggs range in size from .98 - 1.08 mm (mean 1.02 mm). Several laboratory studies have been done on the development of Pacific cod eggs in relation to environmental parameters (Forrester 1964; Forrester and Alderdice 1966; Alderdice and Forrester 1971). At constant salinity ($26.5^{o}/_{oo}$) and different temperatures (5, 7, 9, 11°C), development times range from 8.5 days at 11°C to 17 days at 5°C. Egg development demonstrates a broad tolerance to various

Table 14.1. Length and fecundity (number of eggs) of Pacific cod, Gadus macrocephalus, from Hecate Strait (Source: Thomson 1962).

Length cm	Fecundity thousands	Length cm	Fecundity thousands	Length cm	Fecundity thousands
40	228	57	1,164	63	1,214
50	655	58	1,073	63	1,417
51	587	60	1,212	65	1,468
52	837	60	1,139	66	2,147
53	531	60	1,210	67	2,396
53	686	60	889	68	2,069
53	740	60	1,250	68	1,901
54	749	60	996	69	2,220
54	826	61	1,155	69	1,922
55	889	61	1,492	70	2,256
55	1,170	61	1,434	74	1,757
55	917	61	1,626	75	2,969
56	944	62	1,832	78	3,329
57	748	62	1,306	88	3,215
57	799	62	1,624		
57	974	63	1,020		

salinity and dissolved oxygen levels, but is restricted to a narrow range of temperatures. Maximum and near maximum viable hatches of eggs are associated with temperatures of 3-4.5°C over a range of 12.71-23°/$_{oo}$ and dissolved oxygen levels of saturation to 2-3 ppm. Stages of development of cod eggs are illustrated and described (Figs. 14.1, 14.2).

Eggs incubated at 5°C produce larvae of an average length of 4.45 mm (range 4.07-4.84 mm)(Forrester 1964), which is larger than lengths recorded for western Pacific cod, mean 3.6 mm (range 3.3-3.8 mm), and may be due to genetic or incubation differences. In the newly hatched larva, the head is inclined ventrally and the mouth is initially closed. Pigmentation is faint, but in two to three days, it becomes pronounced and characteristically concentrated along the upper part of the body cavity and in two conspicuous bands along the tail (Fig. 14.3). Illustrations and descriptions (in Russian) for western Pacific cod larvae appear in Gorbunova (1954) and Mukhacheva and Zviagina (1960).

Recently, Matarese et al. (1981) have provided descriptive characters for separating eastern Pacific gadid larvae (Pacific cod, walleye pollock, and Pacific tomcod) which prior to this time were difficult to identify from plankton samples when they co-occurred. For larvae less than 13 mm SL, separation is possible based on configuration and location of melanophores (Table 14.2; Fig. 14.4). These characters, plus counts of caudal fin rays on the superior hypural plate, may help identify larvae between 13 and 20 mm SL. After fin ray formation (> 20 mm SL) meristics can be used to separate these species.

Habits of the early larvae and juveniles of Pacific cod are virtually unstudied in Puget Sound. In Port Townsend Bay, a large catch of one-year-old prerecruit Pacific cod provided some evidence that these cod spend much of their early life in the bay, although more tagging information is needed (Miller et al. 1978). Due to to the previous problem in identifying gadid species from each other, little is known about the distribution and abundance of gadid larvae by species. Food items of young Pacific cod (21-22 mm) have been reported to be copepodites and Calanus pacificus and Pseudocalanus minutus (Barraclough et al. 1968).

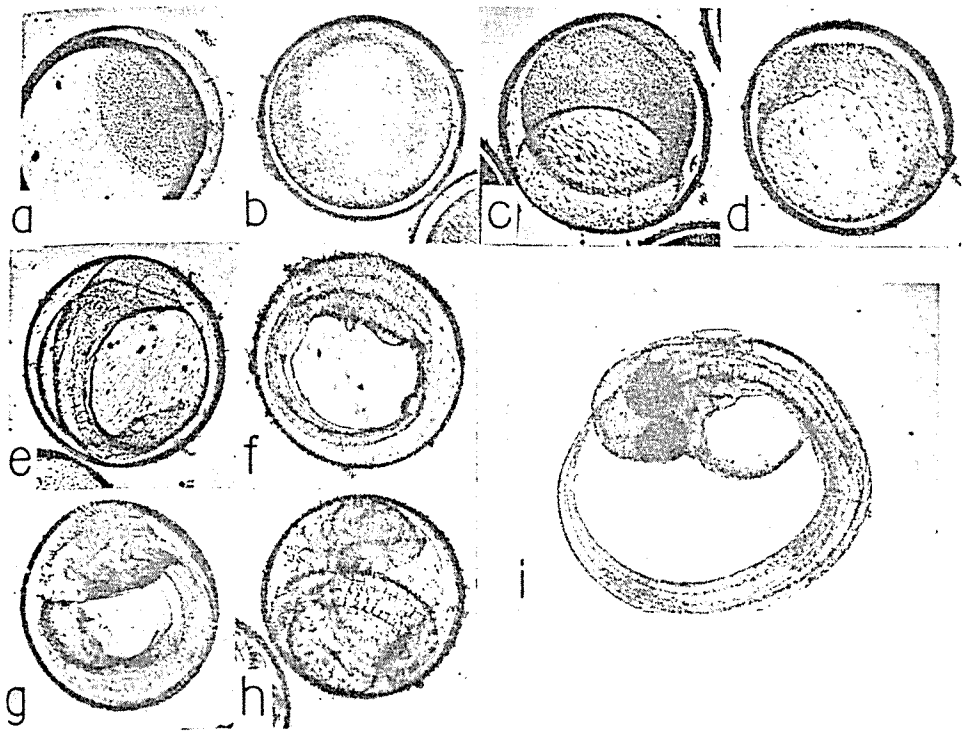

Fig. 14.1. Stages in development of Pacific cod eggs: a) Late blastodermal cap (7°C - 45 hr); b) early germ ring (5°C - 70 hr); c) migration of germ ring past equator (5°C - 70 hr); d) embryo approximately 1/2 circle (7°C - 70 hr); e) embryo 3/4 circle; somites and optic lobes readily distingishable, tail growing free of yolk sac (11°C - 70 hr); f) embryo full circle (5°C - 189 hr); g) tail of embryo starting past head (7°C - 167 hr, egg pigmented); h) embryo with tail well past head (7°C - 189 hr, heartbeat evident: i) newly-hatched larva (7°C - 333 hr). (Source: Forrester 1964).

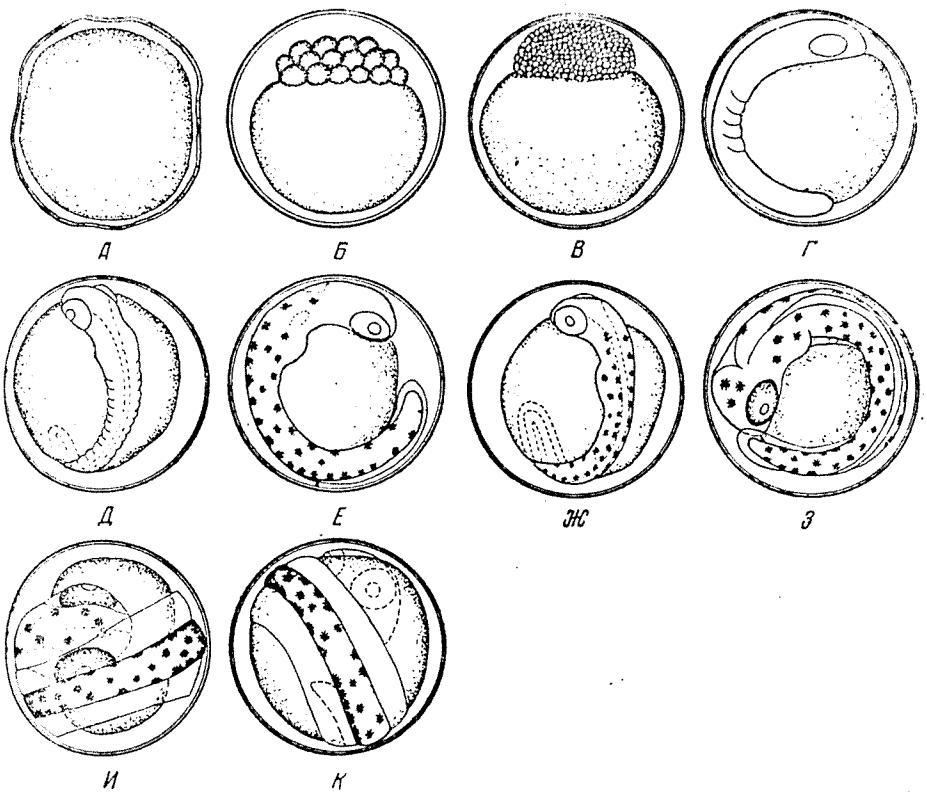

Fig. 14.2. Development of eggs of Pacific cod. (Source: Mukhacheva and Zviagina 1960.)

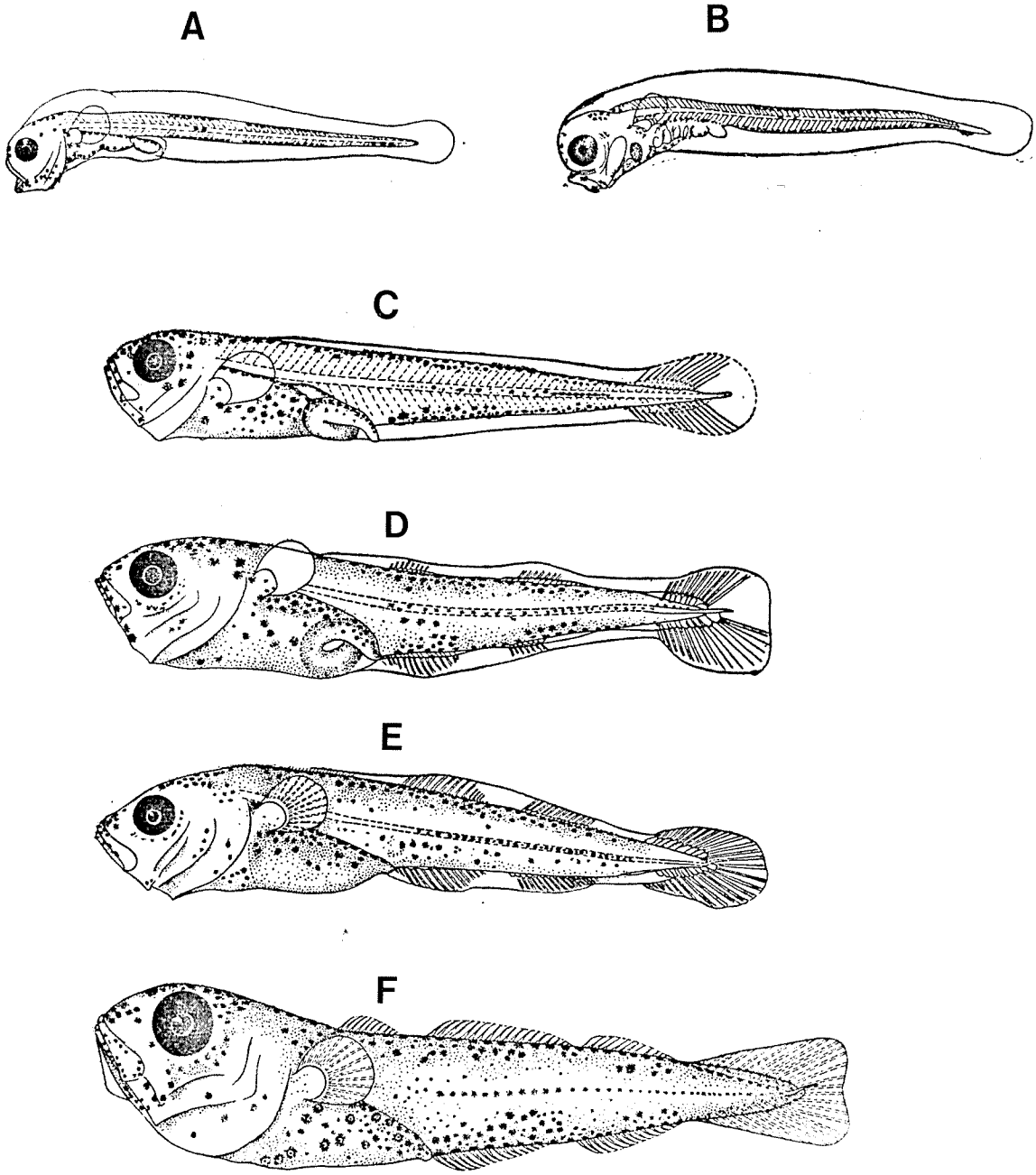

Fig. 14.3. Development of Pacific cod larvae: A) 5.25 mm; B) 6.8 mm; C) 10.0 mm; D) 13.0 mm; E) 15.0 mm; F) 20.0 mm. (Source: Mukhacheva and Zviagina 1960.)

Table 14.2. Characters useful in separating larvae of Microgadus proximus, Theragra chalcogramma, and Gadus macrocephalus at specific size ranges. (Source: Matarese et al. 1981).

Character	Size range (mm)	Microgadus proximus	Theragra chalcogramma	Gadus macrocephalus
Anterior pigment bar:	5-6			
Percentage of SL		41-53	47-55	40-57
Located at myomeres		14-23	21-26	16-26
Posterior pigment bar:	5-6			
Percentage of SL		61-74	69-79	59-81
Located at myomeres		28-39	36-43	26-42
Number of melanophores in each stripe of anterior bar:	3-4			
dorsal		2	5	7
ventral		4	5	8
Number of melanophores in each stripe of posterior bar:	3-4			
dorsal		7	5	11
ventral		7	7	10
Degree of stripe continuity:				
dorsal	5-13	separate	separate	continuous
ventral		continuous	separate	continuous
dorsal	13-16	separate	continuous	continuous
ventral		continuous	separate	continuous
Head melanophores:	4-8	-	-	More on dorsal surface and snout
Melanophores on ventral surface of gut:	>13	1-2 rows of spots	No spots or a few reduced spots	1-2 rows of spots
Lateral pigment on gut surface:	<13	-	much less	-
Mediolateral pigment in postanal region:	5-8	-	-	more
Ventral caudal pigment:	<10	Row of spots	Isolated spots	Isolated spots
Number of rays on superior hypural element:	>13	5	4	4

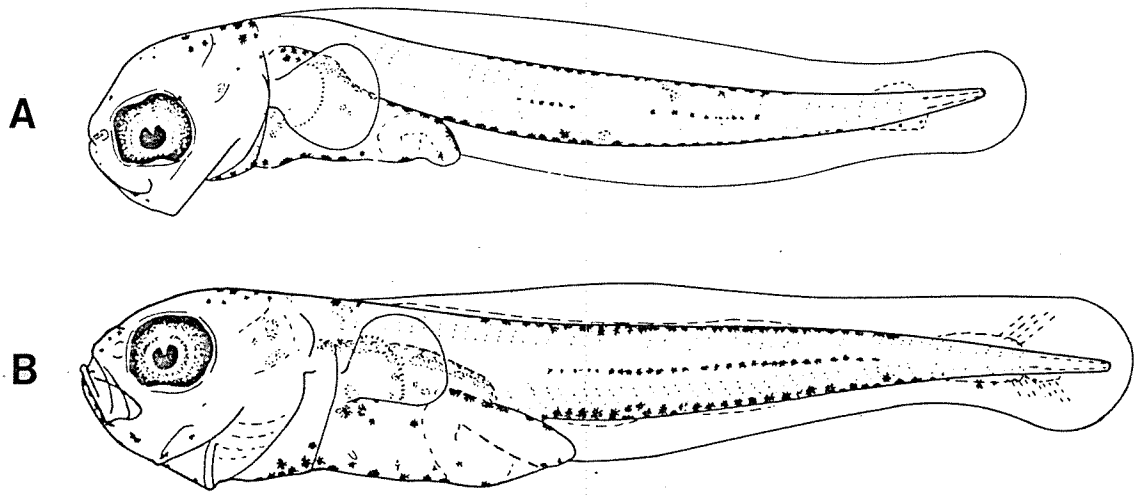

Fig. 14.4. Larvae of Pacific cod: A) 5.6 mm; B) 8.5 mm. Characteristic tail bands of pigment are less distinct in the Pacific cod as melanophores run together on the dorsal and ventral surfaces of the tail. (Source: Matarese et al. 1981).

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Merluccius productus - Pacific hake

Range: California to Alaska

Occurrence in Puget Sound: common

Adult habitat: semi-demersal

Spawning habitat: pelagic

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

In the eastern Pacific Ocean, hake are found from the Gulf of Alaska to the Gulf of California. They are especially abundant in the California Current area and their abundance decreases toward the north where they become largely replaced by Pacific cod and walleye pollock (Alverson et al. 1964, cited in Nelson and Larkins 1970). Most information indicates that hake inhabit the relatively deep waters of the continential shelf out as far as 550 m, but are primarily concentrated out to 180 m (Best 1963). During spawning they may become more pelagic, rising off the bottom to spawn at intermediate depths (Nelson 1967, cited in Dark 1975).

For oceanic hake, it has been hypothesized that adult hake undertake extensive annual migrations along the west coast of North America. This migration involves a northward movement of adult fish in the spring and summer to inshore feeding grounds primarily on the continental shelf, and a southward return movement beginning in the fall to the offshore spawning areas. One result of this migration is the seasonal abundance of adult hake off Washington and Oregon from spring to fall. Local concentrations of hake are also found off northern and central California at this time. In the winter, adults are essentially confined to offshore waters along the California-Mexico coast. There is some indication that only a small proportion of four-year-old (and younger) fish migrate into the fishing grounds off Vancouver Island, Washington, and Oregon (Nelson and Larkins 1970). Among fish five-years and older, the proportion of the larger, generally older fish increases in the northerly fishing areas.

Puget Sound contains a population of hake, which has been shown to be genetically isolated from the coastal population (Utter 1969; Utter and Hodgins 1971). No significant migration of coastal hake into Puget Sound is thought to occur, but data are lacking on emigration of hake from Puget Sound (Etchevers 1971). Within the Sound, hake are scattered over most areas (Miller and Borton 1980) and occur between 10 and

30 m above the bottom. Large concentrations are found in Saratoga Passage and in Port Susan (Etchevers 1971) and evidence from commercial fisheries suggests that hake in these concentrations originate from all over the Sound (Thorne et al. 1971). The hake which enter Saratoga Passage in October-December are about 70% mature. This concentration begins to disappear in late December and January and at the same time a large population begins to form in Port Susan. These fish are about 95% mature. It has been suggested that Saratoga Passage may be a "holding" area for maturing hake, which move into Port Susan to spawn from January to June (Kimura and Millikan 1977).

Hake are mature by age four with some larger three-year-olds also spawning (Best 1963), and some mature two-year-old fish have been found in Puget Sound, although they are rare (Kimura and Millikan 1977). Lengths at maturity are 300-600 mm (Best 1963; Kimura and Millikan 1977). Coastal hake are usually larger and live longer than Puget Sound fish (Etchevers 1971). In Saratoga Passage, the ratio of males to females is approximately equal. In Port Susan, however, males enter before females and usually dominate the population from January to March, but the ratio balances out in March (Etchevers 1971).

MacGregor (1966, 1971) looked at ovaries of hake ranging from 130 mm to 688 mm and found a large amount of variation in fecundity between fish. The number of advanced eggs per fish ranged from 3419 to 496,000 with a tendency for larger fish to have more eggs (Table 14.3). Because of the relatively short spawning season and the small percentage of immature eggs in the ovary, it is speculated that only one batch of eggs is matured per season (MacGregor 1971; Ahlstrom and Counts 1955).

Hake eggs are pelagic, spherical, and range in diameter from 1.07-1.18 mm. They are covered with a tough, transparent, unsculptured shell membrane and contain a single rather large oil globule (0.27-0.34 mm in diameter). The yolk material is clear, homogenous, and of a dark straw color, which may appear granular after being encased by the germ ring.

The embryonic development of hake eggs has not been studied in detail. Nelson and Larkins (1970) reported a development time from fertilization to hatching of 3.1 days at 16.6°C and 9.2 days at 8.4°C. Descriptions and illustrations of early, middle, and late stage eggs are provided by Ahlstrom and Counts (1955). Early stage eggs, (Fig. 14.5 A, B), have a clear unsegmented yolk and an oil globule situated at the vegetative pole. The developing egg floats with the oil globule upwards and situated immediately adjacent to the blastopore close to the tail of the embryo and maintains this position throughout development. When the embryonic shield has enveloped approximately three-quarters of the yolk, the embryo has discernible eggs. The early stage embryo is upigmented. Middle stage eggs, (Fig. 14.5 C, D), are characterized by pigmentation which develops immediately after blastopore closure. Pigment appears on the oil globule, on the head and

Table 14.3. Fecundity of Pacific hake, Merluccius productus, ranging in length from 130 mm to 688 mm. (Sources: top and middle table from MacGregor 1971; lower table from MacGregor 1966).

Standard length	Weight	Gonad weight	Gonad index	Advanced eggs		Eggs per gram of fish
				Size range	Number	
mm	*g*	*g*		*mm*		
130	22.1	0.928	4.2	0.50-0.67	3,419	155
131	23.3	1.345	5.8	.57- .73	7,049	303
135	25.2	1.320	5.2	.57- .77	3,564	141
137	22.4	1.518	6.8	.50- .67	6,469	289
137	29.3	1.795	6.1	.53- .70	7,139	244
138	24.8	0.987	4.0	.53- .70	4,048	163
140	28.8	1.350	4.7	.53- .70	4,956	172
140	34.5	2.241	6.6	.57- .77	7,926	230
141	30.5	1.222	4.0	.50- .70	4,534	149
150	21.2	1.198	5.7	.53- .73	4,257	201
150	37.1	2.481	6.7	.53- .73	10,864	293
160	31.5	1.875	6.0	.53- .73	6,447	205
162	30.3	1.957	6.5	.57- .73	7,633	252
170	32.3	2.000	6.2	.50- .70	8,741	271
172	37.7	1.863	4.9	.47- .70	10,731	285
174	37.7	2.000	5.3	.50- .70	7,559	201
202	57.0	4.002	7.0	.50- .67	19,564	343

Standard length	Weight	Gonad weight	Gonad index	Advanced eggs		Eggs per gram of fish
				Size range	Number	
mm	*g*	*g*		*mm*		
222	100	8.663	9.7	0.50-0.67	29,399	294
230	88	7.011	8.0	.50- .73	23,253	264
233	104	8.488	8.2	.60- .77	29,450	347
238	91	3.279	3.6	.57- .73	3,496	38
245	105	6.292	6.0	.50- .70	17,511	168
247	120	5.956	5.0	.60- .80	18,264	152
252	110	9.341	8.5	.53- .77	43,014	391
268	147	5.308	3.6	.60- .80	13,747	94
275	146	11.860	8.2	.57- .83	38,959	286
287	176	12.972	7.4	.67- .83	24,877	141
305	221	22.710	10.3	.57- .80	110,017	498

Standard length (mm)	Weight (grams)	Gonad weight (grams)	Advanced eggs		Eggs per gram of fish
			Number (thousands)	Diameter (mm)	
688	2,750	196.8	496	.60- .76	180
577	1,600	106.7	147	.56- .74	92
552	1,350	68.3	163	.58- .76	120
533	1,100	52.9	120	.60- .76	115
515	950	57.4	96	.80-1.00*	101
503	950	74.2	242	.64- .88	256
497	900	88.2	292	.68- .84	324
481	850	64.7	188	.70- .90	221
475	750	83.6	252	.70- .90	336
447	650	87.4	108	1.00-1.22*	166
442	600	43.8	137	.56- .74	228
433	600	42.9	64	.80-1.04*	107
431	600	49.9	93	.80-1.00*	155
422	550	41.2	122	.60- .80	221
395	500	82.0	278	.58- .76	556
391	400	24.8	72	.60- .80	179
384	350	18.5	43	.58- .78	122
373	400	13.1	38	.62- .80	96
367	400	13.7	33	.66- .82	83
358	450	51.4	113	.88-1.06*	251
351	300	30.0	46	.82-1.04*	153
346	500	45.4	80	.76- .92*	160

* Translucent eggs.

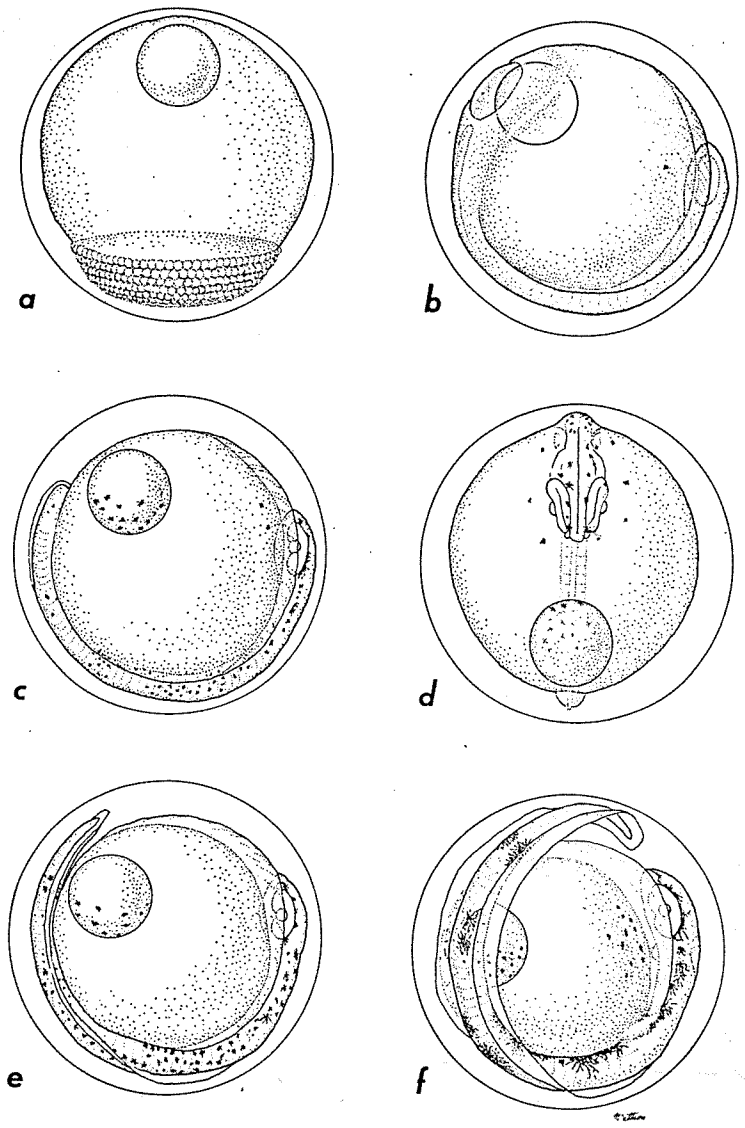

Fig. 14.5. Development of the eggs of Pacific hake, Merluccius productus: a) Early stage, at time of development of blastodermal cap; b) early stage, immediately preceding blastopore closure; c) middle stage, lateral view; d) middle stage, polar view; e) late stage, tail just beginning to twist out of plane of embryonic axis; f) late stage, just before hatching. (Source: Ahlstrom and Counts 1955).

dorsum of the embryo, and on the yolk mass. At the end of this stage, the tail has become partially lifted from the yolk and the embryo has its full complement of 50+ myomeres. In late stage eggs, (Fig. 14.5 E, F), the melanophores become restricted into several conspicuous patches of pigment. The pigment on the embryo occurs in four dorsal areas: on the head and four or five adjacent myomeres, on the body just anterior to the anus, on the body just behind the anus, and about midway between the anus and the end of the notochord. The only conspicuous ventral pigment on the embryo is a counterpart to the posterior-most dorsal patch. Some melanophores appear on the peritoneum, just prior to hatching. Buds of the pectoral fins may be seen.

Hake larvae hatch at about 2.4 mm and are in a relatively undeveloped condition, beginning postembryonic life before the mouth is formed or the eyes are pigmented. Although there is a considerable amount of variation in the amount of pigment found on individuals of the same size, hake larvae exhibit a species specific pigmentation pattern. Before the completion of yolk sac absorption, the young larvae are characterized by three conspicuous pigment areas: 1) a large spot on the back of the head (occipital spot); 2) a medio-postanal pigment area about midway between the anus and the end of the notochord; and 3) a heavy concentration of pigment along the dorsal peritoneal wall. In addition, there is a frontal patch of pigment between the eyes, spots on the ventral surface of the gut and a lateral spot immediately behind the anus. This pigmentation is found on larvae 3-10 mm (Fig. 14.6 A-G). Between 10 and 20 mm there is a rapid addition of pigment on both the body and head, but primarily on the dorsal surface (Fig. 14.6 A′ - D′). Fins do not become pigmented until the late larval period. When hake are about 36 mm, the characteristic larval pigmentation is obscured by the addition of more melanophores.

Hake larvae are moderately elongate with the greatest body depth at or near the pectoral fin, and with the body narrowing abruptly behind the anus. The digestive tract underlies only the forward part of the body, or approximately 40% of the total length and the intestine has a single loop, which can be easily seen in small larvae. Detailed morphometrics and sequence of ossificaion of hake larvae have been reported (Ahlstrom and Counts 1955). Fin formation begins on larvae as small as 3 mm and is completed in 30-35 mm larvae (Table 14.4).

Little information is available on hake from the larval period until they enter the commercial fishery at about 4 years. Ahlstrom and Counts (1955) attempted to look at vertical distribution of eggs and larvae in the California Current. They found that eggs were located between 27 and 102 mm while larvae occurred between the surface and 102 m. Most larvae were at depths where the temperature was 11.5-14.3^{o}C, but data are too limited for strong correlations. One-year-old hake have been reported in inshore waters of southern California and have been associated with schools of anchovy (Dark et al. 1970, cited in Dark 1975). It is not known when juveniles end their pelagic phase and become associated with the bottom (Dark 1975).

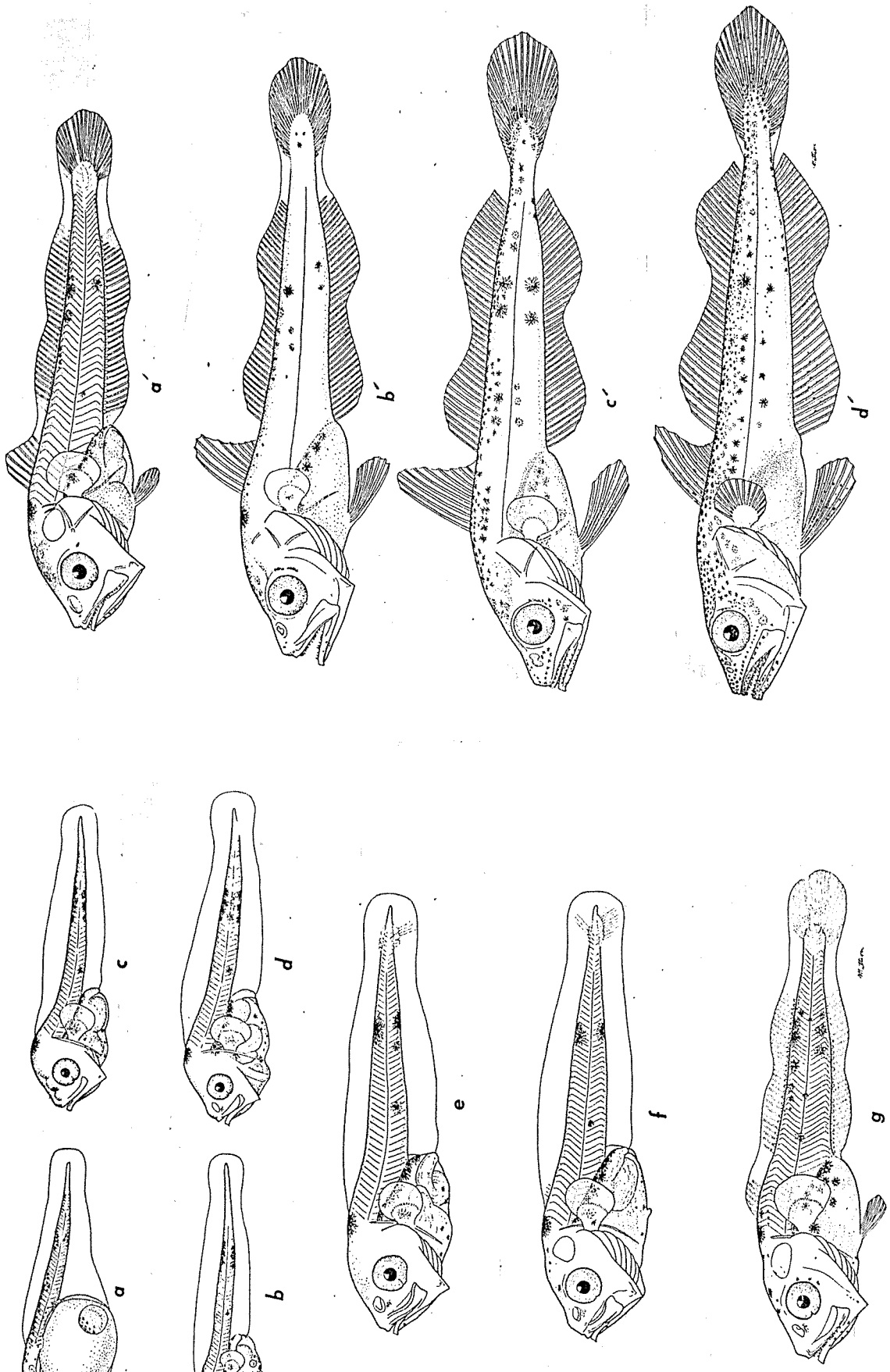

Fig. 14.6. Development of larvae of hake (Merluccius productus): a) Yolk-sac larva, 2.4 mm; b) 3.0 mm; c) 4.3 mm; d) 4.7 mm; e) 6.3 mm; f) 7.7 mm; g) 10.1 mm; a') 11.0 mm; b') 15.75 mm; c') 20.0 mm; d') early juvenile, 36.0 mm. (Source: Ahlstrom and Counts 1955).

Table 14.4. Sequence of formation of fins in larval hake, Merluccius productus. (Source: Ahlstrom and Counts 1955).

Fin	Size of larva when rays first appear (mm)	Size of larvae when fin rays are complete (mm)
Larval pectorals (without rays)	3	
Caudal	5.8	20
Pelvics	7.0	11
First dorsal	8.8.5	15.5
Second dorsal and anal	8.5-9.2	16
Pectorals (with rays)	17-25	30-35

Food habits of a few hake larvae from British Columbia showed that larvae as small as 4 mm had fed, consuming copepod nauplii. Food of larvae up to 40 mm consisted of various developmental stages of copepods, phytoplankton, and unidentified eggs (Barraclough 1968 a; Barraclough et al. 1968; Robinson et al. 1968 a, b).

Predators of young hake include rockfish, albacore, larger hake, arrowtooth flounder, and bigmouth sole. Adult hake have also been found in stomachs of Pacific lancetfish, bluefin tuna, sablefish, lingcod, sharks, and several types of marine mammals (Best 1963).

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Microgadus proximus - Pacific tomcod

Range: Central California to Alaska

Occurrence in Puget Sound: common

Adult habitat: demersal or pelagic

Spawning habitat: unknown

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: pelagic

Tomcod are common and are found throughout Puget Sound (Miller and Borton 1980); however, almost no information is available on their biology and early life history.

They range from off central California to the Gulf of Alaksa and Unalaska Island (Hart 1973), but their presence in the Bering Sea remains questionable (Matarese et al. 1981). Tomcod inhabit surface waters and down as deep as 220 m (Miller and Lea 1972). In British Columbia, they are not particularly abundant, but occur along the entire coast line and are found between 27-92 m (Hart 1973).

Recently, the larvae of Pacific tomcod were described and illustrated such that tomcod larvae can be distinguished from other gadid species (Matarese et al. 1981). Eggs and spawning behavior of Pacific tomcod remain unknown.

The larvae are slightly elongate with the greatest body depth occurring near the pectoral fin base. The gut is moderately long, approaching 50% SL in larvae and declining to 45% SL in juveniles. In larvae between 2.7 mm and 7.5-8.5 mm the vent opens laterally to the right, becoming vertical in larger larvae. This positioning of the vent has also been reported for other small gadid larvae (Marak 1967; Russell 1976; both cited by Matarese et al. 1981). All the yolk is absorbed in larvae > 3.0 mm. Transformation from larval to juvenile characters occurs at about 22 mm and is complete at about 27-28 mm. Detailed morphometrics of larval tomcod are provided by Matarese et al. (1981).

Pacific tomcod larvae show the typical gadid pigmentation in the postanal region consisting of dorsal and ventral pigment stripes confined to two bars (Fig. 14.7 A). The stripes within each bar are composed of double rows of melanophores with pigment spots on both sides of the body along the dorsal and ventral midlines. The number of

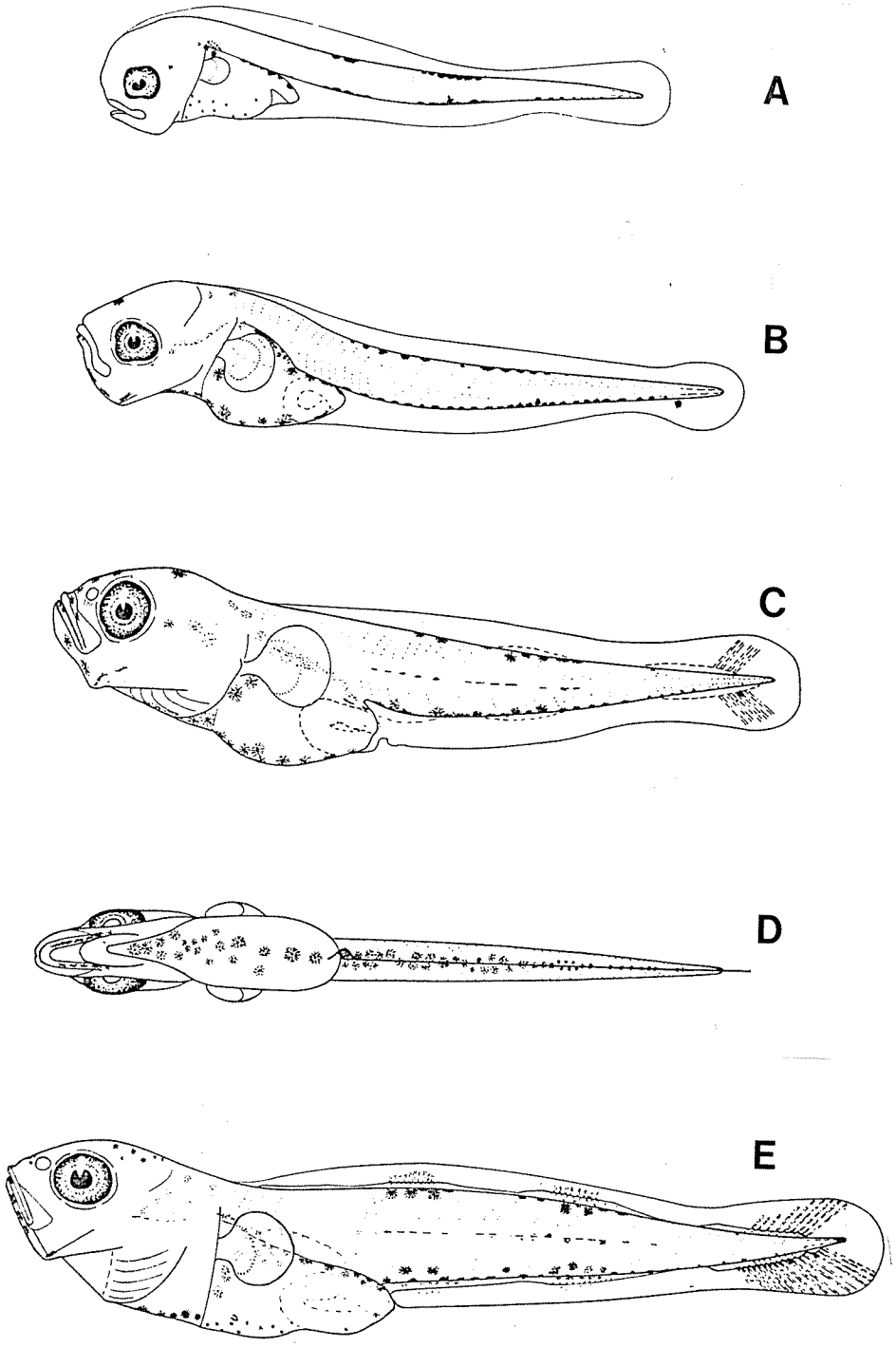

Fig. 14.7. Larval stages of Pacific tomcod, Microgadus proximus: A) 3.6 mm SL; B) 5.7 mm SL; C) 8.4 mm SL; D) 8.4 mm SL (ventral view); E) 10.7 mm SL. (Source: Matarese et al. 1981).

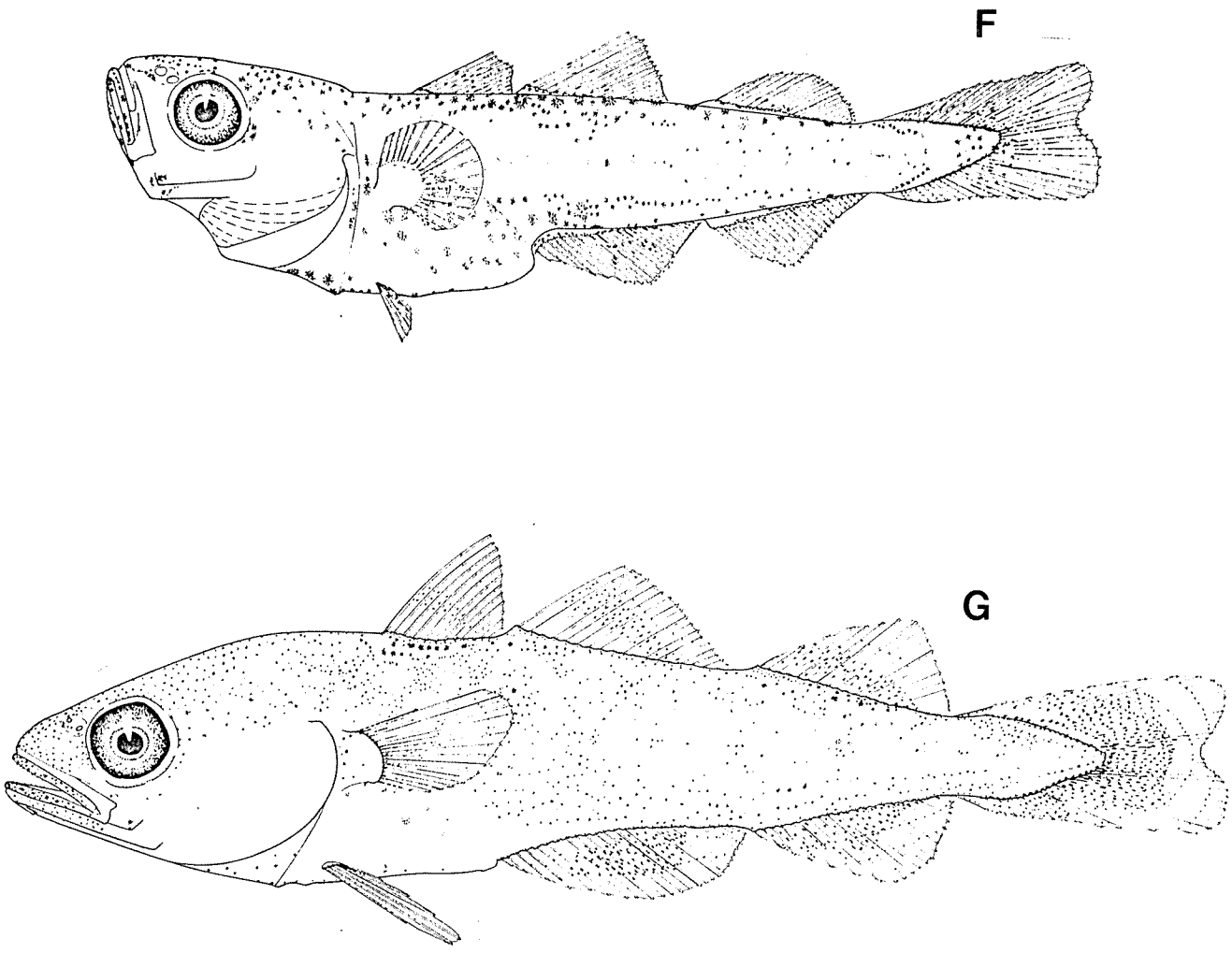

Fig. 14.7 (cont.). Larval stages of Pacific tomcod, Microgadus proximus: F) 16.0 mm SL; G) 27.0 mm SL (early juvenile). (Source: Matarese et al. 1981).

melanophores and lengths of these pigment bars are diagnostic for tomcod larvae (Table 14.2). In 3-4 mm larvae the dorsal stripes consist of 1-2 melanophores on each side of the dorsal midline, but increase to 2-3 in the anterior bar and 6-8 in the posterior bar with development. The ventral stripes have 4-5 spots on each side of the ventral midline in the anterior bar and 7-8 spots in the posterior bar. By 5.7 mm the ventral bars are continuous (Fig. 14.7 B), but the dorsal stripes remain separate until 15.0 mm SL. Postanal pigmentation changes little between 10.0-14.0 mm except for the addition of spots laterally and in the dorsal and anal finfolds. By 15.0-16.0 mm, additional melanophores occur along the dorsolateral and ventrolateral surfaces, but the spots in the bars remain distinctive (Fig. 14.7 F). After transformation, the larval pigment bars become obscured and the entire lateral area is pigmented (Fig. 14.7 G). Posterior to the second pigment bar, melanophores occur along the ventral body surface in the smallest larvae, connect with the ventral stripes by 5.7 mm, and extend to the notochord tip by 6.2 mm. These melanophores are smaller than the stripe melanophores and form a single ventral midline row (Fig. 14.7 D).

In larvae < 4 mm, pigmentation on the head is limited to a spot posterior to the eye and on the lower jaw. By 4.0 mm, 6-7 melanophoes appear on the nape and increase on the lower jaw and in the forebrain area. Pigment appears on the snout at 8.0 mm. Melanophores are also located on the dorsal surface of the gut cavity and on the ventral abdominal surface and isthmus and increase in number on the dorsal and ventral gut surfaces with development. Gut pigmentation changes little through transformation, except for additional melanophores on the lateral body surface.

Fin formation in larval Pacific tomcod proceeds as follows: larval pectoral fins; caudal fin; first anal fin; second anal fin; third, second, and first dorsal fin (nearly simultaneously); pelvic fins; and pectoral fins with rays. Detailed description of formation of the caudal fin structure is given by Matarese et al. (1981). Scales begin developing in the anterior portion of the body in specimens 28.6 mm and progress along the lateral line as the juveniles grow.

Because of the previous difficulties in identifying tomcod larvae, little information is available on distribution and seasonal abundance of tomcod larvae. However, off Oregon, it has been found that larval tomcod occur mainly within 18 km of the shore with peak abundances at 6 and 9 km. They are present in the plankton from February to August with a maximum abundance from March through July. Monthly length frequencies and median lengths indicate a winter-spring spawning period as small larvae, $\leq$ 5.0 mm were collected from February to June (Richardson 1977; Richardson and Pearcy 1977; summarized by Matarese et al. 1981).

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Theragra chalcogramma - Walleye pollock

Range: central California to Bering Sea; Kamchatka, Okhotsk Sea, Japan

Occurrence in Puget Sound: common

Adult habitat: demersal or pelagic

Spawning habitat: pelagic

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Walleye pollock range from central California to St. Lawrence Island in the northern Bering Sea. In the western Pacific, they are encountered off the Kamchatka coast, in the Okhotsk Sea, and the southern Sea of Japan. They are found from surface waters to below 365 m (Hart 1973).

The focus of attention on early life history of walleye pollock has been on stocks in the Bering Sea and western Pacific. No information is available on the reproductive characteristics of walleye pollock in Puget Sound, although they are a common and widespread species in this area (Miller and Borton 1980). The life history information presented in this section is based primarily on studies of walleye pollock in the Bering Sea. Eggs and larvae have been well-described and illutrated (Yusa 1954; Kobayashi 1963; Gorbunova 1954; Haryu 1980).

Walleye pollock are primarily winter-spring spawners throughout their range (Hart 1973; Hughes and Hirshhorn 1978; Serobaba 1968; Kanomaru et al. 1979), although eggs and small larvae have also been found during other months of the year (Kendall 1980; Rogers et al. 1979; Serobaba 1968). In the Bering Sea, the largest numbers of eggs are reported when temperatures in bottom and surface waters are 0.9 and 3.3^{o}C, respectively, and spawning grounds are located along the edge of the continental shelf between the 50 m and 300 m isobaths (Serobaba 1968).

One attempt was made to study the behavior of spawning pollock. These fish were observed to form schools of various shapes and sizes but the depths of the schools did not appear to be influenced by temperature or depth and topography of the bottom. There was some indication of independent schooling of the sexes with males inhabiting the upper layers, and females nearer the bottom. Immature pollock were

observed to accompany the migration of adults but remained separate from them by staying in shallower water than where spawning occurred (Takahura 1954).

Age and length of maturity of walleye pollock in the western Gulf of Alaska is age three for both sexes and 29-32 cm for males and 30-35 cm for females. A few (less than 5%) two-year-old males have also been found in a spawning condition. During spawning, the ratio of males to females fluctuates at 1:1 for fish up to 45 cm FL, but females become more dominant with larger size (Hughes and Hirshhorn 1978). In western Kamchatka, males reportedly dominate the catches during the spawning season, but this is not the case for other western Pacific areas (Zver'kova 1969).

Fecundity has been little studied and reports for western Pacific fish of 42-45 cm are 64,000-414,000 eggs per female (average 200,000) (Zver'kova 1969). It is unclear if more than one batch of eggs is spawned per season. Gorbunova (1954, cited by Zver'kova 1969) reported that spawning was a single time event, but protracted.

Eggs of walleye pollock are pelagic (Kanoh 1954) and may be abundant in the upper 50 m of the water column (Kanamaru et al. 1979). Serobaba (1968) claimed that the specific gravity of Alaska pollock eggs increases with development and they gradually sink out of the surface layers. Mature eggs are colorless, spherical, and transparent. They have no distinct oil drops, but contain many (5-6) small drops (5-10 μ in diameter) which are reported to be polysaccharide in nature and are not lipids (Kanoh 1954). In British Columbia, eggs are 1.35-1.45 mm in diameter, but larger diameters are reported for the Bering Sea - 1.48 to 1.66 mm (Serobaba 1968) and in the Sea of Japan, eggs are 1.41 - 1.55 mm, and sometimes are no larger than 1.20 mm (Gorbunova 1954, cited by Serobaba 1968).

When eggs were incubated at 6.7°C, hatching occurred after 12 days and larvae survived for another 25 days without feeding. Major developmental events of the eggs are outlined in Table 14.5 and illustrated in Fig. 14.8. The results of development of eggs at different temperatures showed the highest survival rate and longest incubation period at 2°C. Incubation time ranges from 10 days at 10°C with .3-32% successful hatch, to 13.8-14.4 days at 6°C and 72-83% survival, and 24.5-27.4 days at 2°C with 83-94% survival (Hamai et al. 1971).

Larvae hatch at about 3.5-4.5 mm (Hamai et al. 1971; Yusa 1954) and have about 43 myomeres. The eyes are from 250 to 330 μ in diameter and the mouth and vent are not opened. Just after hatching, pigmentation consists of scattered melanophores on the body of the larvae (Fig. 14.8,0). The young larvae float helplessly upside down at the surface due to the large buoyant yolk sac, but by energetic flicking of their tails and beating of the pectoral fins they can swim for short distances. After two days, pigment becomes concentrated in

Table 14.5. Development of fertilized eggs of walleye pollock, Theragra chalcogramma, reared at 6-7°C (Source: Yusa 1954).

Incubation time (time since fertilization)	Developmental event
1 hr	Blastodisc formation begins.
1 hr 50 mm	Protoplasm accumulates at the lower pole of the egg and surface of the yolk opposite to the blastodisc becomes flattened.
3 hr	2-cell stage.
5 hr	4-cell stage.
7 hr	8-cell stage.
9 hr	16-cell stage.
11 hr	32-cell stage.
13 hr	Morula stage.
1 day 3 hr	Blastula stage.
1 day 6 hr	First gastrula stage.
1 day 18 hr	Growth of the epiboly reaches about one-fifth of the egg surface, and the embryonic shield is differentiated.
2 days 22 hr	Germ ring near equatorial position; eyes formed, but are without pupils.
3 days 14 hr	Growth of the epiboly reaches about three-fourths of the egg surface; optic vesicles are well defined, medullary plate observed at the middle of the embryo.
3 days 19 hr	Growth of the epiboly reaches about four-fifths of the egg surface; first sign of brain; 5 or 6 somites at middle part of embryo.
4 days 1 hr	Blastopore nearly closed; embryo with 6 or 7 somites.
4 days 6 hr	Blastopore closed.
5 days	Embryo with 9-10 somites; heart appears as a slight bulge; auditory capsules appear.
5 days 3 hr	Embryo with 12-13 somites; pupils seen in both eyes: otoliths appear in auditory capsule; first appearance of Kupffer's vesicle.
5 days 22 hr	Embryo with 16-17 somites; Kupffer's vesicle well observed; olfactory pits appear; pigmentation appears.
6 days 8 hr	Liver and intestine observed; embryo with 18-20 somites; three parts of the brain are forming.
6 days 21 hr	Embryo with 25-30 somites; organs fully formed.
7 days 12 hr	Embryo with 35 somites; tail begins to lift.
8 days 12 hr	Tail encircles two-thirds of the egg membrane; embryo with 37 somites; heart pulsating; black pigment over the dorsolateral and ventral surface of the embryo.
9 days 12 hr	Embryo encompasses three-quarters of the circumference of the yolk mass; about 40 somites; Kupffer's vesicle has disappeared; embryo moves.
10 days 12 hr	Embryo almost one full circle.
11 days	Embryo encircles yolk mass.
12 days	Movement of embryo is vigorous; eyes are pigmented; hatching begins.

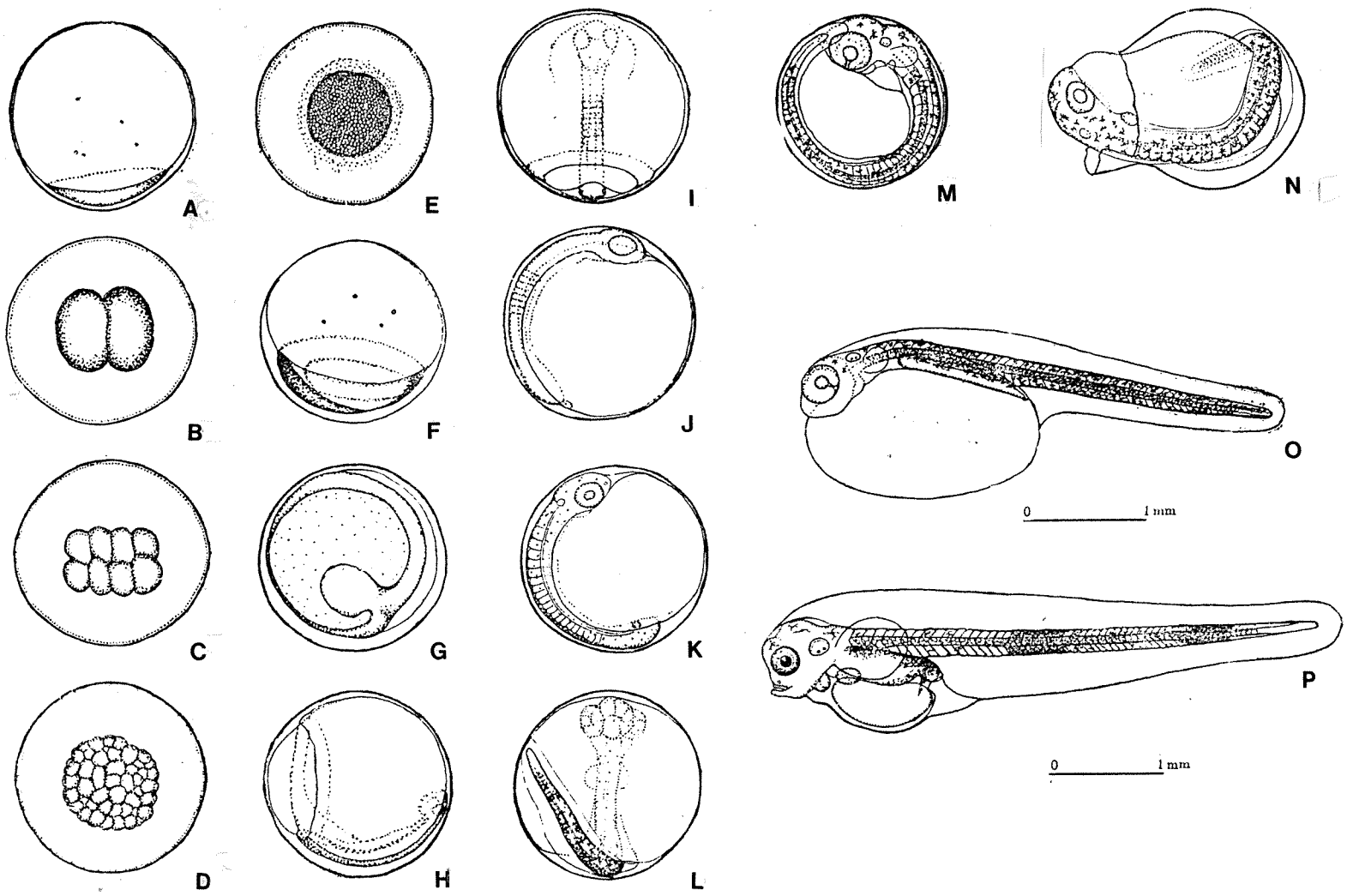

Fig. 14.8. Development of eggs of walleye pollock, Theragra chalcogramma, at 6-7°C: A) Blastodisc formation begins - 1 hr; B) two-cell stage - 3 hr; C) eight-cell stage - 7 hr; D) Morula stage - 13 hr; E) blastula stage - 1 day, 3 hr; F) gastrula stage - 2 days; G) germ ring near equatorial position - 2 days, 22 hr; H) epiboly reaches three-fourths of the egg surface - 3 days, 14 hr; I) blastopore nearly closed, embryo with 5 or 6 somites - 3 days, 19 hr; J) blastopore closed - 4 days, 6 hr; K) embryo with 16-17 somites - 5 days, 22 hr; L) embryo - 9 days, 12 hr; M) embryo - 11 days; N) hatching - 12 days; O) larva at hatching; P) larva at 5 days. (Source: Yusa 1954).

two distinct bars on the tail and is also located on the dorsal surface of the gut and on the head (Fig. 14.8P). (Refer to Table 14.2 for distinguishing pollock larvae from larvae of Pacific cod and Pacific tomcod at small sizes). By three days of age, larvae are swimming in an ordinary fashion for longer periods, but may resort to the upside-down floating position. The mouth is now well-formed and functional. Yolk sac absorption is observed after eleven days at 6-7°C in larvae which do not feed (Yusa 1954). When food (brine shrimp nauplii and rotifers) is offered, larvae begin to feed after the eighth day from hatching and yolk sac absorption is not complete until the twenty-first day after hatching (Hamai et al. 1974). Growth rate of larvae is rapid during the yolk sac stage and decreases thereafter (Hamai et al. 1971). Illustrations of pigmentation patterns and development of walleye pollock larvae are shown in Fig. 14.9.

In the ocean, larvae undergo vertical migrations which change with growth. Eggs and early larvae occur near or at the surface. Later, postlarvae and young occupy a wider range, rising up to the surface layers at night and sinking down to mid-depths or bottom waters by day. Juveniles and adults probably reside primarily in mid-depth or bottom waters (Kobayaski 1963). An interesting observation on young pollock (17-24 mm) behavior was noted by Van Hyning and Cooney (1974):

> "Our sightings of juvenile walleye pollock with Cyanea in Prince William Sound agree only in part with previous published accounts for other gadoid fishes. The young pollock were seen travelling with the jellyfish, apparently feeding as they drifted along together. However, when threatened from above, they always darted deeper into the water and away from the jellyfish rather than toward the safety of the umbrella. When undisturbed, the small fishes maintained their position near the periphery of the jelly-fish and none were observed at any time among the tentacles under the umbrella. Their behavior was more suggestive of the well-known orientation of some oceanic fishes toward a floating log or other object rather than for protection, although the presence of a large medusa may act as a deterrent to predatory fishes and sea birds."

The diet of small larvae (4-7 mm) has been found to include copepod eggs and nauplii and Pseudocalanus minutus (Barraclough 1967; Robinson et al. 1968 a, b). Small pollock up to 45 mm consume various stages of copepods including adults of Calanus pacificus, P. minutus, Microcalanus spp., Metridia spp., and Oithona spp. (Barraclough et al. 1968).

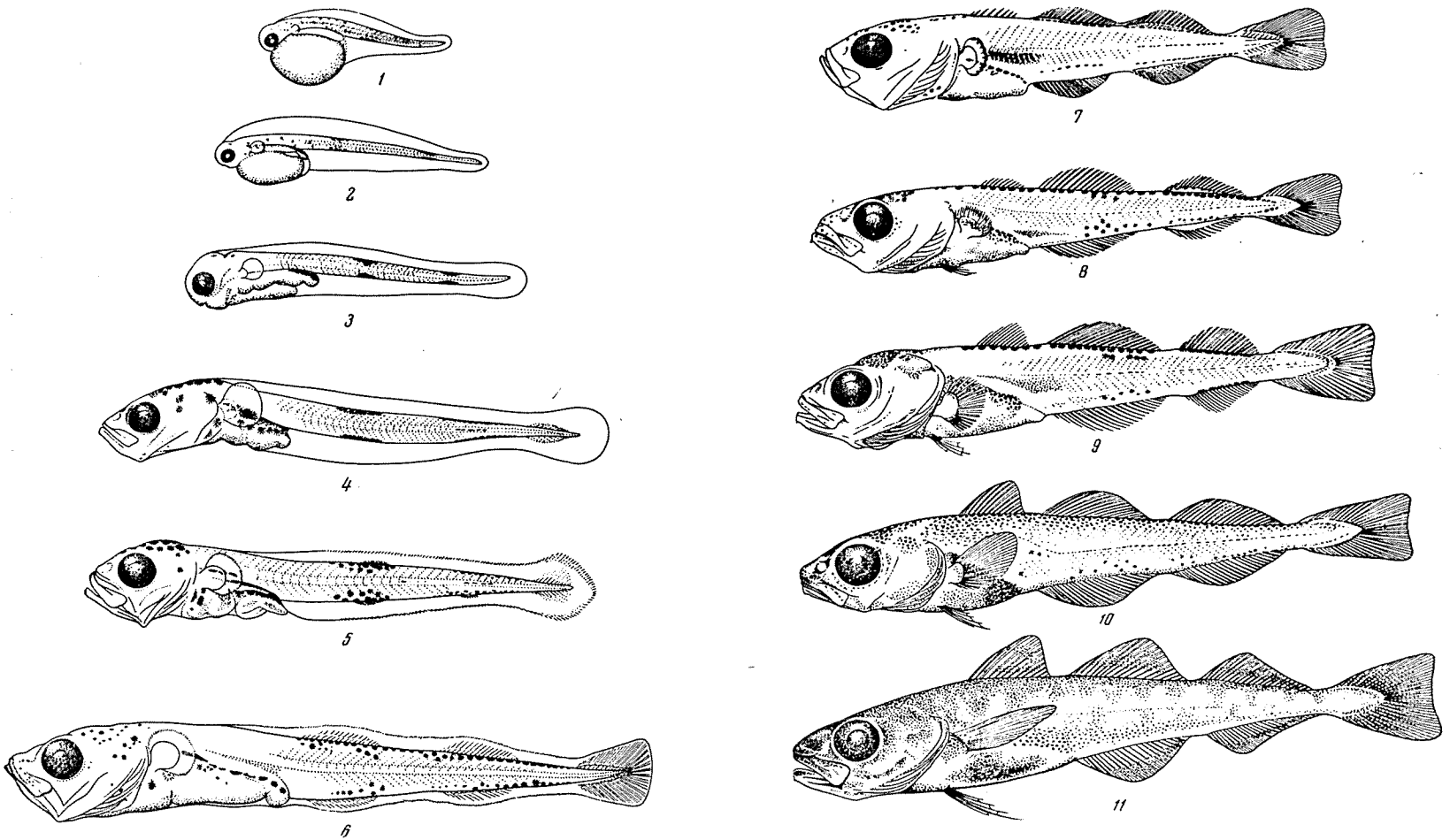

Fig. 14.9. Development of larval walleye pollock, Theragra calcogramma: (1) 3.5 mm; (2) 5.5 mm; (3) 6.5 mm; (4) 9.3 mm; (5) 9.8 mm; (6) 15 mm; (7) 16.7 mm; (8) 21.3 mm; (9) 30.0 mm; (10) 40 mm; (11) 100 mm. (Source: Gorbunova 1954).

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15. OPHIDIIDAE

Brosmophycis marginata - Red brotula

Range: Baja California to southeastern Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: spring

Mode of reproduction: ovoviviparous

Larvae: undescribed

Red brotula inhabit rocky areas (Miller and Lea 1972) from 55-180 m and range from Baja California to southeastern Alaska (Hart 1973) and Puget Sound (Miller and Borton 1980). Like other members of its family, it is ovoviviparous, but its reproductive behavior and embryonic development have not been studied to any large extent.

Fecundities of six fish between 260 and 305 mm ranged from 12,000 to 30,000 ova per female. During September and October the ova are about .7 mm and by February increase to 1.2 mm, although no embryos are evident until April or May. In May off Seattle, a 31 cm female extruded about 200 yolked larvae of an average size of 7 mm (Hart 1973).

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16. ZOARCIDAE

Lycodapus mandibularis -Pallid eelpout

Range: La Jolla, California to Prince William Sound, Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic

Spawning habitat: unknown

Spawning season: unknown (year-round in California)

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Apparently pelagic, adult pallid eelpout are found to various depths throughout their range (Hart 1973), and are frequently captured from the vicinity of submarine canyons and from deep inlets (Peden 1979; Peden and Anderson 1978). Pallid eelpout are relatively uncommon in Puget Sound, but have been reported from central Puget Sound, near Seattle, in Port Susan near Everett, and from Hood Canal (Miller and Borton 1980.)

Very little early life history or reproduction information is available for this zoarcid species.

Gonads of the male have been briefly described as elongate bilobed organs of equal size that are located in the posterodorsal portion of the body cavity. The sperm duct is located in a dorsal medial grove along each testis and there is no specialized genital pore or papilla. In the immature males, the testes are white and rod-like with rounded anterior tips and become expanded, dark grey, and "leaf-like" with maturity. In the females, a short oviduct connects the single dorso-medial ovary with the urogenital sinus. The immature ovary is thin, flaccid and contains ova of 0.05-0.2 mm in diameter. Females less than 120 mm SL carry up to 400 immature ova (< 0.2 mm diameter) while in the ripest females, about 100 $\pm$ 25 eggs are observed and range from 1.7 to 1.9 mm in diameter. The full compliment of mature eggs is spawned as eggs of this size are never found in spent ovaries (Anderson 1980).

In Monterey Bay, California, spawning of pallid eelpout is non-seasonal as ripe individuals are found year-round. Both males and females between the ages of three and five are mature (Anderson 1980). Anderson (1980) provides some evidence to support pelagic spawning in pallid eelpout.

Lycodes brevipes - Shortfin eelpout

Range: Oregon to Bering Sea; Okhotsk Sea

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: unknown

Larvae: unknown

Shortfin eelpout are taken at depths of 27 to 642 m from Oregon through Washington, British Columbia, Alaska and the Bering Sea, and are also found in the Okhotsk Sea (Hart 1973). They are apparently widespread throughout Puget Sound (Miller and Borton 1980) and common near the center of their range (Hart 1973).

No information is available on the early life history of shortfin eelpout.

Lycodes diapterus - Black eelpout

Range: San Diego, California to Bering Sea; Sea of Japan

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Black eelpout, ranging from southern California to the Bering Sea and Sea of Japan (Hart 1973), are fairly widespread in Puget Sound, although not particularly common (Miller and Borton 1980). No information is available on their spawning biology or early life development.

Lycodes palearis - Wattled eelpout

Range: Oregon to Chukchi Sea; Okhotsk Bay to northern Sea of Japan

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: possibly winter

Mode of reproduction: oviparous

Eggs: demersal

Larvae: undescribed

Wattled eelpout inhabit depths of 55-283 m and are reported from Oregon to the Chukchi Sea in the eastern North Pacific and from the Okhotsk Sea, Aniva Bay, and northern Sea of Japan in the western Pacific (Hart 1973). They are relatively rare in Puget Sound (Slipp and DeLacy 1952) and have been collected in five general areas of Puget Sound (Miller and Borton 1980).

Very little is known about the life history of this zoarcid. Two specimens maintained in a Tacoma, Washington aquarium generally remained immobile on a sandy bottom or side by side in a narrow space formed by a rock and the side of the tank. Eggs were taken from the female during January and were 6-7 mm, elliptical, and clear amber in color. After preservation, eggs showed a prominent disc of aggregated fat globules at the apex of the eggs. When spawned, the eggs were laid singly or in small clusters on the sand bottom (Slipp and DeLacy 1952).

Larval stages are undescribed.

Lycodopsis pacifica - Blackbelly eelpout

Range: Baja California to Gulf of Alaska

Occurrence in Puget Sound: common

Adult habitat: demersal, nearshore

Spawning habitat: probably same

Spawning season: late summer-fall (British Columbia)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: undescribed

Blackbelly eelpout range from Baja California to Afognak and Unalaska Islands in the Gulf of Alaska. They are the most common member of the Zoarcidae that occur in British Columbia, and are taken over muddy bottoms at 18-220 m (Hart 1973). They are also common in Puget Sound and widely distributed throughout the Sound (Miller and Borton 1980).

Males and females live up to five years (based on otoliths) and at age 3 to 5, males are usually larger. Males reach sexual maturity (50% level) at about 170 mm at which time males have larger heads and a shovel-like snout. Females reach sexual maturity at about 140 mm, with 50% mature at 150-159 mm (Levings 1969).

The male reproductive system consists of bilobed testes, each lobe roughly rectangular in shape, which lie in the posterodorsal part of the body cavity. Immature testes are light grey in color becoming white when mature. In British Columbia, mature males are found from September to January (Levings 1969).

The female reproductive system consists of a median unpaired ovary which lies in the posterodorsal part of the body cavity. The ovarian membranes are continuous with the oviduct and evidence of modifications for internal fertilization and incubation is absent, suggesting this species is oviparous (Levings 1969).

Ripe females have been found during August to December in British Columbia and mature a small number of large (~ 5 mm) yellow-orange eggs. Out of 51 specimens examined by Levings (1969), the mean number of mature eggs was 30 (range 7-52) and it is not known if parents guard the eggs or not.

Larvae of blackbelly eelpout are undescribed.

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17. SCOMBERESOCIDAE

Cololabis saira - Pacific saury

(Available literature not reviewed)

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18. CYPRINODONTIDAE

Cyprinodon variegatus - Sheepshead minnow

(Available literature not reviewed.)

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19. TRACHIPTERIDAE

Trachipterus altivelis - King-of-the-salmon

(Available literature not reviewed.)

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20. GASTEROSTEIDAE

Aulorhynchus flavidus - Tube-snout

Range: Baja California to southeast Alaska

Occurrence in Puget Sound: common

Adult habitat: nearshore, pelagic

Spawning habitat: demersal, on algae or marine plants

Spawning season: spring-summer (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: pelagic for brief time only

Tube-snout are small, slender nearshore fish which range from Baja California to southeast Alaska (Hart 1973) and are commonly found throughout Puget Sound (Miler and Borton 1980). Adults may reside in small to large (up to 2,000 individuals) schools in sheltered bays near shore where they have been observed in eelgrass beds, kelp beds, over rocky areas or over sand bottoms. Adults may inhabit depths from surface waters to 30 m and juveniles occur somewhat shallower, from the surface to 12 m (Limbaugh 1962).

In California, eggs and young are found throughout the year (Limbaugh 1962), but the spawning season in northern waters is probably restricted to late spring-summer. Marliave (1975) observed spawning tube-snout in Barkley Sound, British Columbia, during May and June, and Hart (1973) reported the occurrence of spawning tube-snout near Friday Harbor, San Juan Islands in late June, and in British Columbia in April.

Tube-snout may mature at less than one year (Limbaugh 1962). During spawning, they concentrate around algae and females may outnumber males 10 or 20 to 1 (Hart (1973). The males establish breeding territories as close as 2 feet apart and defend them by lunging at intruders (Hart 1973; Limbaugh 1962). Females have been observed schooling within 1 to 3 m of the male's territory. Each male breeds with several females and may accumulate up to 6 to 10 separate egg masses (Limbaugh 1962; Marliave 1975).

Eggs are round to slightly oval, are very adhesive, and are about 2 mm in diameter. They range in color from brown to pale honey-tan through various shades of brownish orange to dark reddish amber; however, within a particular cluster, eggs are uniform in color. Egg masses vary from 13-33 mm in diameter and contain 150 to 600 eggs (Limbaugh 1962; Marliave 1975).

The egg masses are deposited on young growths of algae or marine plants, including Alaria marginata, Nereocystis, Scytosiphon lomentaria (Marliave 1975), Macrocystis, Pelagophycus, eelgrass, coralline algae (Limbaugh 1962) or Desmarestia (Hart 1973). Eggs are laid just below the fast-growing tip of the young stipes that emerge from the holdfast. The eggs are adhesive to each other but not to the stipe and are attached at the junctions of the branches leading to the pneumatocyst-bearing fronds (Fig. 20.1). The male binds the seaweed together with very strong, silvery, weblike strands which are excreted from the urogenital region. This causes the stipe which bears the eggs to bend downward and creates a nest which is actually below the egg masses (Fig. 20.2) (Limbaugh 1962). In California, nests are found at depth of <11 m to 37 m, although the majority occur between 11 m and 18 m depths (Limbaugh 1962).

Because tube-snout spawn on the young, less sturdy growths of algae, the egg masses may be dislodged along with parts of the algae and carried away by surface currents. Marliave (1975, 1976) believed this dispersal mechanism may be important in establishing tube-snout in areas away from the spawning site. Parental behavior is adapted to periodic losses as new egg masses are spawned to replaced those removed by storms, which also ensures some hatching of larvae in the spawning area. Dispersal of the egg masses is also important as the period of larval pelagic drift is very short, less than one hour.

The egg masses begin to hatch after 2-3 weeks and hatching is protracted, lasting from 10 days to 6 weeks (Hart 1973; Limbaugh 1962; Marliave 1975). The newly hatched larvae, ~8.0 mm, rise to the surface and struggle to remain there, interrupted with periods of quiescence and sinking. Within 1/2 hour they begin to orient horizontally below the surface and sink slowly to the bottom where they begin schooling with other larvae on the bottom. For the first two weeks schools remain within 10 cm of the bottom and later stage schools also remain closely associated with the bottom, exhibiting no changes in behavior during metamorphosis (Marliave 1975, 1976).

In Barkley Sound, larvae hatch in June and July and form schools around kelp beds. Early larvae are recognized by unaligned lateral pigment bands. The anterior band is on the dorsal gut surface, and the posterior band is mediolateral on the musculature of the tail (Fig. 20.3). Later stage larvae are characterized by the development of the elongated snout which appears during fin ray formation, at ~16 mm (Marliave 1975). Metamorphosis to juvenile stage is complete within 2 months at which time tube-snout are about 40 mm TL (Marliave 1976). Schooling behavior continues throughout their life except during spawning (Limbaugh 1962).

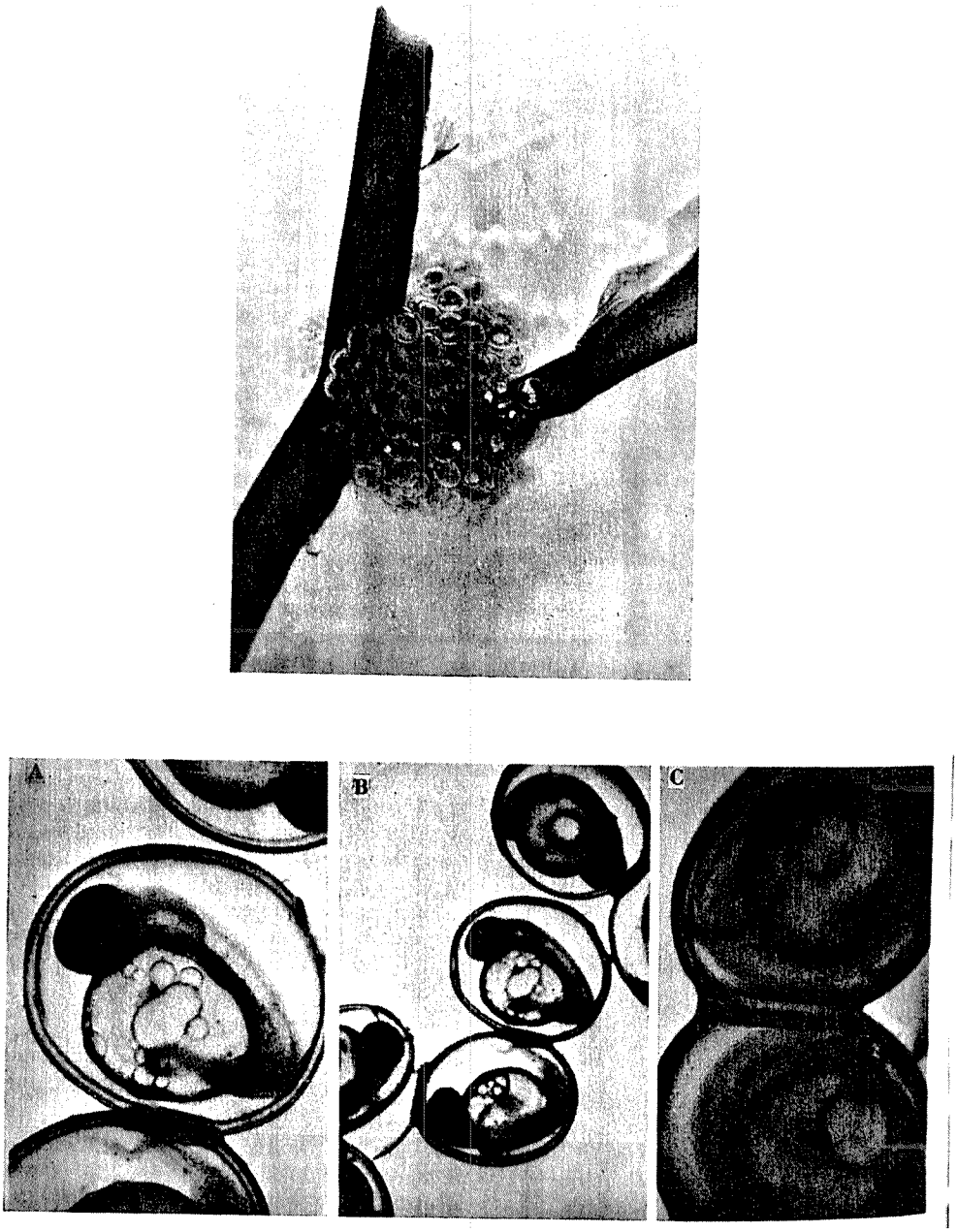

Fig. 20.1. Eggs of tube-snout, Aulorhynchus flavidus. Top) mass of eggs encircling the stipe of a Macrocystis plant; bottom) enlarged view of developing eggs, embryos well advanced. (Source: Limbaugh 1962).

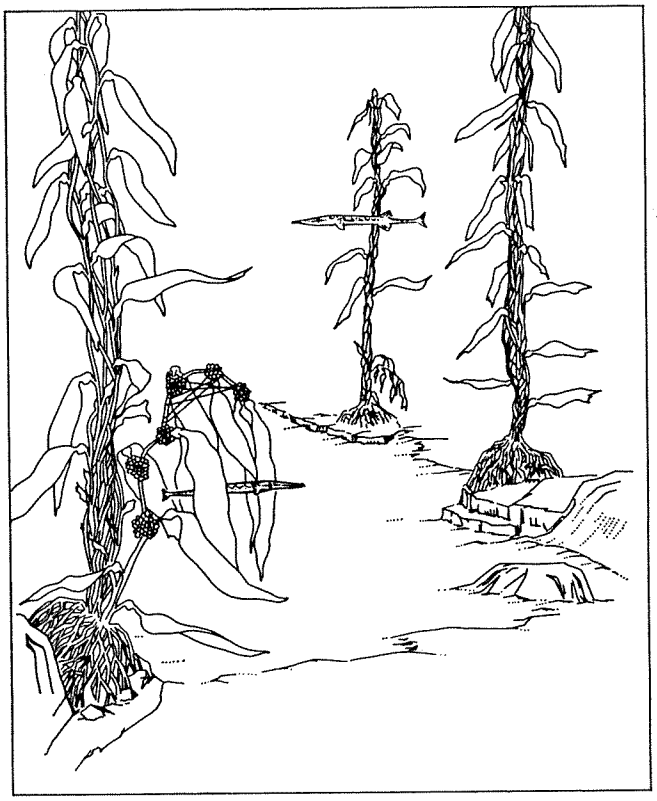

Fig. 20.2. Underwater view of nest of tube-snout, Aulorhynchus flavidus, showing how the stipe bearing the egg masses is bent downward. Male is shown residing in nest located beneath egg masses. (Source: Limbaugh 1962).

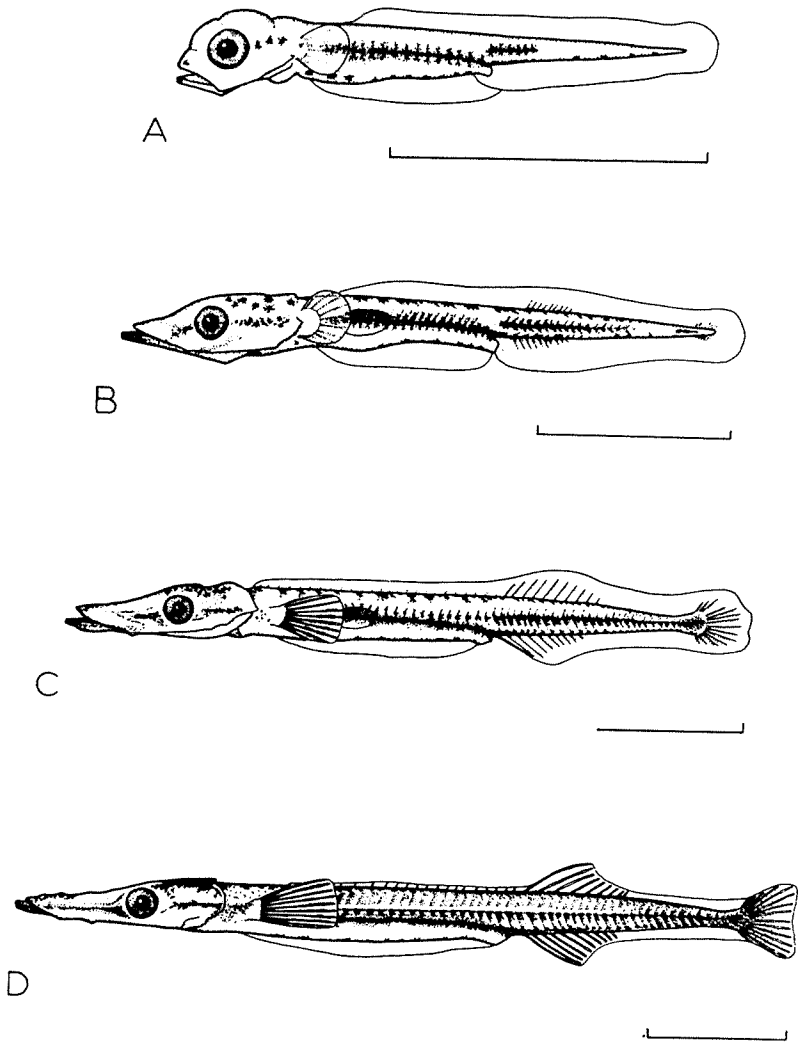

Fig. 20.3. Larval development of tube-snout, Aulorhynchus flavidus. Scale equals 5 mm: A) 0-day, 8 mm TL; B) 18-day, 16 mm TL; C) 32-day, 23 mm TL; D) 45-day, 30 mm TL. (Source: Marliave 1976).

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Gasterosteus aculeatus - Threespine stickleback

Range: Baja California to Bering Sea, Kamchatka to Korea; in Atlantic from Chesapeake Bay to Hudson Bay, from Spain to Norway and Greenland.

Occurrence in Puget Sound: common

Adult habitat: fresh or salt water

Spawning habitat: in lakes or streams, some are anadromous

Spawning season: spring

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: pelagic

Threespine stickleback occupy a wide range of habitats in both freshwater and saltwater, and are distributed over a large geographical range which includes most northern temperate areas (Hart 1973). They exhibit a wide variety of forms and have been separated into two major types (possibly subspecies or separate species) which are regarded as forms of Gasterosteus aculeatus (Hagen and McPhail 1970). The marine form, trachurus, can be separated from the freshwater form, leiurus, by possessing a complete series of lateral bony plates, a silvery color (opposed to olive-brown color of leiurus), and are of a larger size. Leiurus remains in freshwater all of its life and trachurus is believed to spend most of its life in salt water, migrating to freshwater to spawn (Scott and Crossman 1973). In freshwater, threespine sticklebacks form distinct populations and exhibit a wide variation in morphology between different areas (Hart 1973; Hagen and McPhail 1970). Along the coast, the marine form occurs in small schools in brackish water near wharves or in eelgrass beds and may also be encountered in large numbers far from shore (Clemens and Wilby 1961).

Most of the biological information available concerns the leiurus form of threespine stickleback found in freshwater where its breeding habits are well-known (see Additional References). The marine form, trachurus, is anadromous, entering streams in British Columbia during spring-summer to spawn. Hagen (1967) noted that very little cross-breeding between the two forms occurs, although crosses can result in viable hydrids which are intermediate in morphology between the two types. It is unknown if successful reproduction can occur in seawater. Vrat (1949) observed threespine stickleback spawning in a California slough of relatively high salinity, but observed a high mortality of eggs and larvae artificially reared in seawater, questioning the effectiveness of reproduction under marine conditions.

In freshwater, males of both forms assume bright spawning colors which include a reddish coloration of the throat, flank and ventral body surface, and bright blue eyes. During the spawning season, males become very aggressive and establish breeding territories. They build nests out of twigs, pieces of algae, or sand grains, cemented together with a sticky mucilaginous kidney-produced secretion. The male performs a courtship dance and entices a female to enter the nest and spawn. Several females may contribute to each nest and the male remains to fan and guard the eggs and young.

A nest may contain up to 600 yellowish semiopaque eggs which are 1.1-1.6 mm when freshly laid and increase to 1.5-1.9 mm ($\bar{x}$ = 1.7) after fertilization (Vrat 1949; Scott and Crossman 1973). The eggs are adhesive to one another but not to the substrate. The egg membrane is thick, smooth, and the yolk contains numerous oil globules of unequal size which are usually clumped toward one side, and smaller globules which are dispersed throughout the yolk.

According to Hagen (1967) females of the anadromous trachurus form produce more eggs, probably due to their larger size at sexual maturity, than the leiurus form or hybrid crosses (Fig. 20.4). The average numbers of eggs produced per female per spawning are 241, 105, and 190, respectively. Wooton (1973b) reviewed other studies on fecundity of the leiurus form and found the number, total wet weight, and total dry weight of eggs were highly correlated with both length and weight of the fish, and the larger fish produced eggs of the same size, caloric value, and water content as those produced by smaller individuals. A female stickleback may spawn several times in a breeding season and the number of spawnings is directly related to the size of the fish (Baggerman 1957; Wooton 1973a, cited in Wooton 1973b).

At 17°C, eggs develop in about 140 hours (Vrat 1949), and at 19°C, in about 168 hours (Scott and Crossman 1973). Embryology of threespine stickleback has been briefly described and illsutrated by Vrat (1949) (Table 20.1; Fig. 20.5) and Kutz and Radcliffe (1917).

Newly hatched larvae vary in size depending on location and are 4.71-4.91 mm in central California (Vrat 1949) and 4.2-4.5 mm near Woods Hole, Massachusetts (Kuntz and Radcliffe 1917). At hatching, the mouth is marked by a slight depression, but is closed, and the body is covered along the dorsal surface with dense, dark melanophores which are also located on the dorsal surface of the gut. Also, diffuse yellow pigment and small yellow chromatophores cover the entire body. With development, the number of melanophores increases along the dorsal and dorsolateral body surfaces and the xanthophores begin to disappear. The yolk sac is absorbed in 7 days and the mouth becomes functional. In 8 days, larvae grow to about 7 mm and after 30 days resembles a miniature adult except for the lateral plates which develop several days later (Vrat 1949; Kuntz and Radcliffe 1917)(Fig. 20.6).

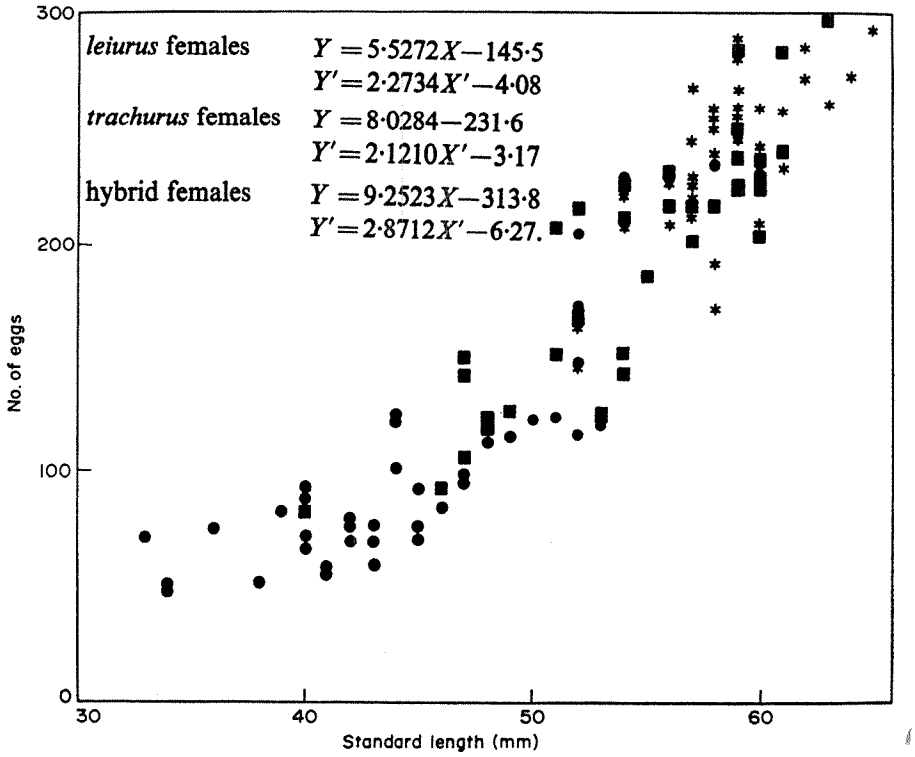

Fig. 20.4. Scatter diagram and regression equations of standard length vs. number of eggs produced at spawning by leiurus (•), trachurus (*), and hybrid females (■) of threespine stickleback, Gasterosteus aculeatus. Y = number of eggs, Y' = nat. log. of number of eggs, X = SL in mm, X' = nat. log. of SL in mm. (Data from Hagen 1967, figure and equations from Wooton 1973b).

Table 20.1. Development of eggs of threespine stickleback, Gasterosteus aculeatus (leiurus) at 17° C ± 0.6° C. (Source: Vrat 1949).

Time (hours from fertilization)	Developmental Event
1.5	Formation of blastodisc.
3	2-cell stage, plane of division is meridional creating 2 equal-sized blastomeres.
4	4-cell stage.
4.6	8-cell stage, arranged in two series of four cells each.
5.25	16-cell stage. All cleavages do not cut completely through the blastodisc, but leave a continuous layer of protoplasm investing the yolk at the base of the blastomeres.
9.6	Blastoderm cap.
11.6	Blastocoel is well formed, formation of early germ ring.
13	Germ ring migration begins
24	Blastopore closure, embryo clearly outlined.
25.3	Appearance of Kupffer's vesicle.
30	Eyes of embryo are outlined, Kupffer's vesicle at maximum size, 6 prs of somites are present, heart beat.
35	First melanophores appear on the dorsolateral surface of embryo.
38	12-body somites, embryo extends 3/4 of the way around yolk, pigment on dorsal surface consists of numerous black and brown melanophores and yellow xanthophores, pigment spreads toward cephalic region and eyes are becoming pigmented.
57	Otoliths appear.
59	Pigment on head and sides of yolk sac become heavy, embryo encircles more than once around yolk.
83–107	Embryo shows first movement.
140	Embryo completely formed and hatching begins.

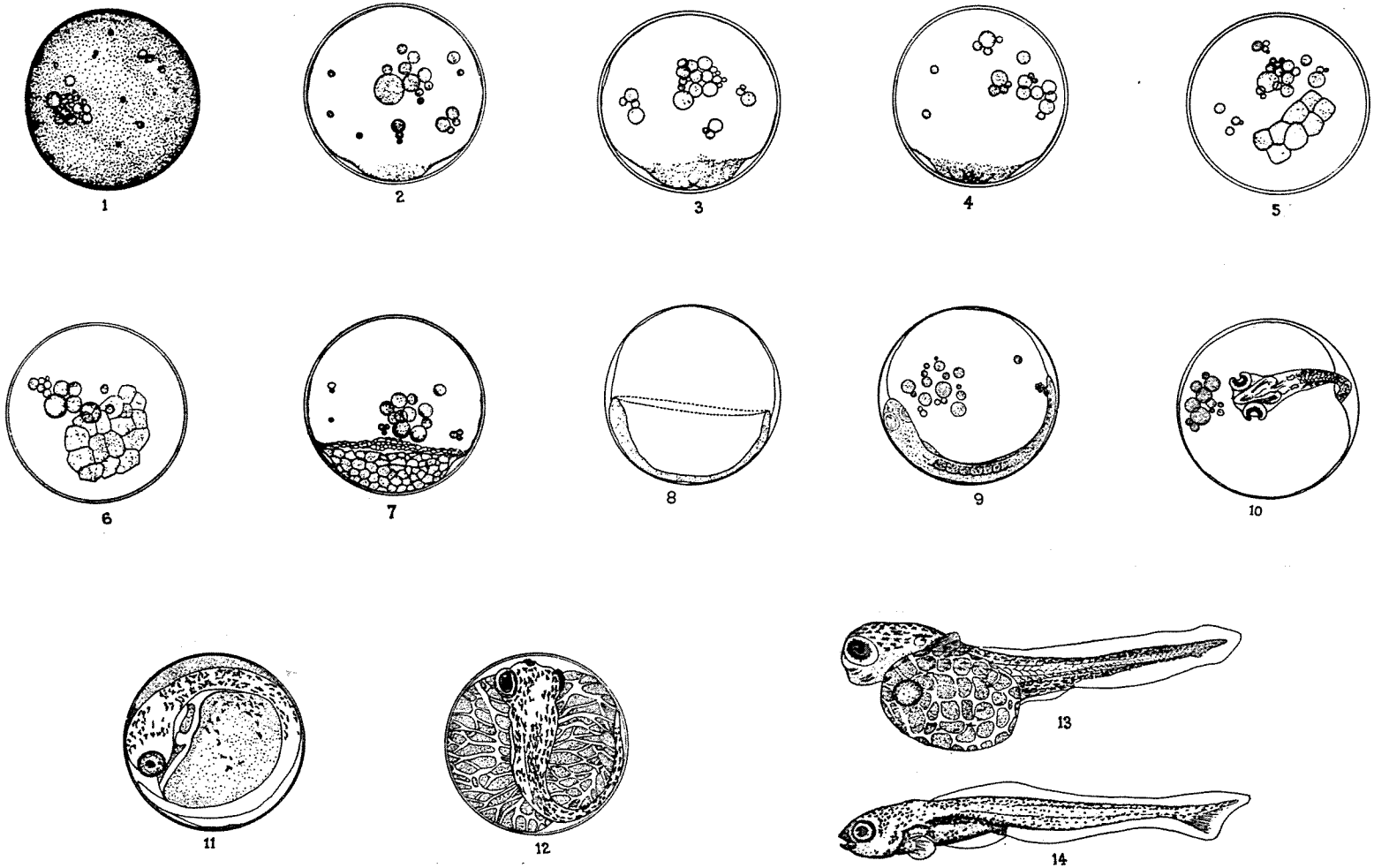

Fig. 20.5. Development of eggs and early larvae of threespine stickleback, Gasterosteus aculeatus: 1) Mature, unfertilized egg; 2) fully developed blastodisc; 3) 2-cell stage; 4) 4-cell stage; 5) 8-cell stage; 6) 16-cell stage; 7) advanced stage of cleavage, periblast differentiated; 8) embryonic axis and germ ring; 9) embryo with six somites, blastopore closed, Kupffer's vesicle well developed; 10) otoliths, pigment and brain divisions present; 11) embryo about 70 hrs-old; 12) advanced embryo, 4-days; 13) newly hatched, 4.71 mm; 14) 6-day, 7.2 mm larva. (Source: Vrat 1949).

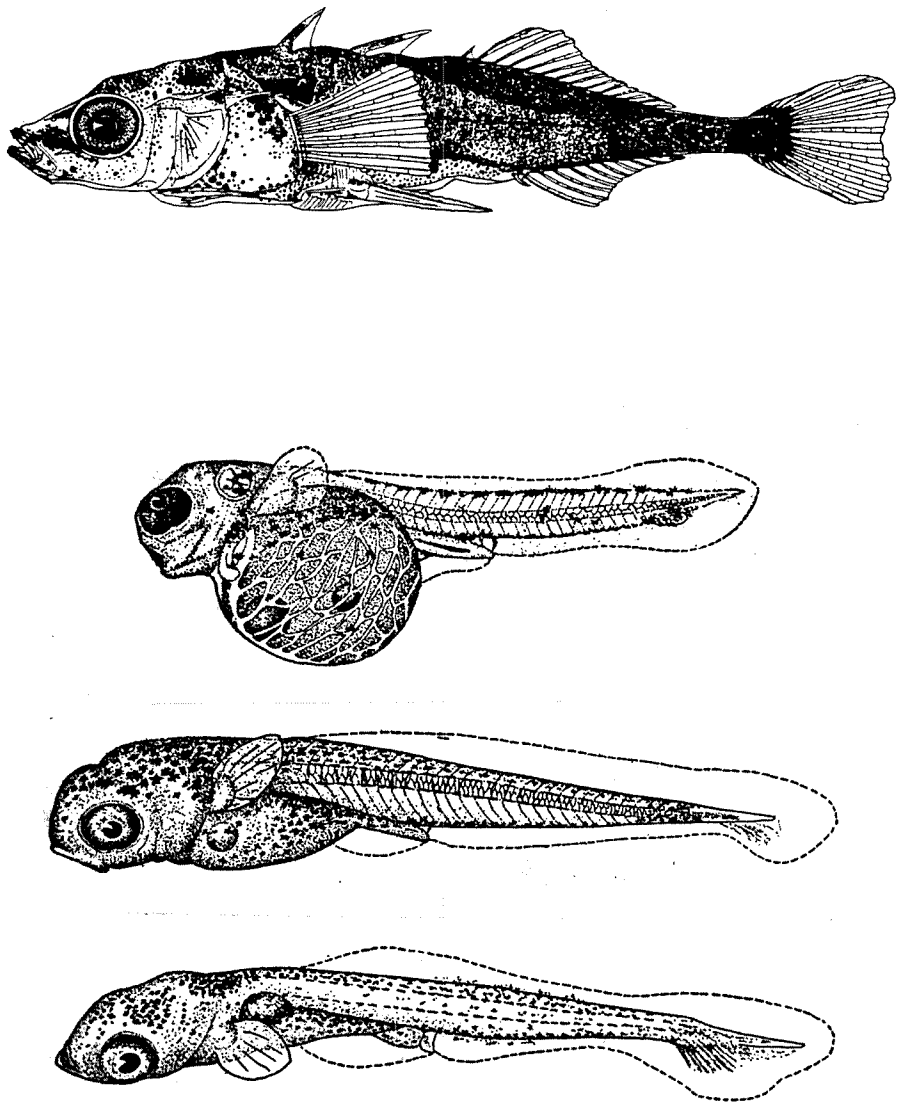

Fig. 20.6. Larval stages of threespine stickleback, Gasterosteus aculeatus: 19.8 mm TL juvenile (Uchida et al. 1958); newly hatched, 4.3 mm; 3-day, 6.3 mm; 8-day, 7 mm. (Source: Kuntz and Radcliffe 1917).

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21. SYNGNATHIDAE

Syngnathus griseolineatus - Bay pipefish

Range: central California to southeastern Alaska

Occurrence in Puget Sound: common

Adult habitat: inshore protected areas

Spawning habitat: same

Spawning season: summer

Mode of reproduction: oviparous

Eggs: undescribed, brooded by male

Larvae: undescribed

Belonging to the same order as seahorses (Syngnathoidei), this greatly elongated fish ranges from central California to southeastern Alaska. It is also characterized by an armor of bony plates which makes it quite rigid. Adults are common and widespread in Puget Sound (Miller and Borton 1980), most commonly encountered in protected inshore areas and sometimes observed drifting in shallow water or swimming along with jerky movements in eelgrass beds or near wharves. They may also be seen over deeper water (Hart 1973).

Sexual dimorphism is evident in that males have a postanal midventral slit which extends along about one-third of the fishes' length. The turned-in flaps of the body wall in this area form a brood pouch.

Spawning behavior has been observed in June in the San Juan Islands and involves an elaborate ritual in which the male shakes himself, nods his head, and periodically assumes a rigid vertical "S" position. The female then entwines around the male and presumably a transfer of fertilized eggs from the female to the brood pouch of the male occurs. The male broods the eggs and developing young until they are 19 mm. The spawning season is typically during summer and in British Columbia males have been found carrying eggs as early as May and may carry young as late as August (Hart 1973).

The size of the brood, length of development time, descriptions of eggs and larvae, and behavior of young fish when they leave the brood pouch are unknown.

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22. PERCICHTHYIDAE

Morone saxatilis - Striped bass

(Available literature not reviewed.)

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23. CARANGIDAE

Trachurus symmetricus - Jack mackeral

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24. BRAMIDAE

Brama japonica - Pacific pomfret; or related species

(Available literature not reviewed.)

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25. SCIAENIDAE

Cynoscion nobilis - White seabass

Genyonemus lineatus - White croaker

(Available literature not reviewed.)

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26. EMBIOTOCIDAE

General

In Puget Sound, embiotocids or surfperches are composed of six monotypic genera. Shiner perch, Cymatogaster aggregata, striped seaperch, Embiotoca lateralis, and pile perch, Rhacochilus vacca are the most commonly occurring species, and less commonly found are kelp perch, Brachyistius fienatus, silver surfperch, Hyperprosopon ellipticum, and white seaperch, Phanerodon furcatus (Miller and Borton 1980).

Surfperches have internal fertilization and embryonic development occurs in the ovarian cavity. Although the embryos develop in close contact with the female, they remain separated during most of their development by an egg membrane which surrounds each embryo. Hence surfperches are referred to as ovoviviparous (see Hempel 1979, p. 36).

Embryonic development of surfperches may require up to six months, during which time nutrition, oxygen and waste exchange, and respiration of the embryo are accomplished by contact with the richly vascularized tissue and fluids of the ovary. Young surfperches are released as active juveniles which soon form schools and begin feeding on their own.

Brachyistius frenatus - Kelp perch

Range: Baja California to southern British Columbia

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic, in kelp beds

Spawning habitat: pelagic

Spawning season: parturition in spring (California)

Mode of reproduction: ovoviviparous

Larvae: born as pelagic young

Adult kelp perch live closely associated with large kelp, particularly Macrocystis. They may occur near the rocky bottom at the base of the kelp, as well as at mid-depths next to the stipes, but are most abundant just under the kelp canopy near the water's surface (Hubbs and Hubbs 1954; Hobson 1971). Typically, kelp perch occur in aggregations of a dozen or more individuals, but larger individuals are often solitary, especially those near the sea bottom. Movement within the kelp bed or rearrangement of groups is limited (Hobson 1971).

In California, males and females reach sexual maturity late in their first year of life, and yearlings may be 85-105 mm in length. Kelp perch do not appear to live more than two years (Hubbs and Hubbs 1954).

The young perch are born in spring and are about 32-33 mm SL (Hubbs and Hubbs 1954). Additional information on kelp perch reproductive biology is unknown.

Cymatogaster aggregata - Shiner perch

Range: northern Baja California to southern Alaska

Occurrence in Puget Sound: common

Adult habitat: pelagic, nearshore

Spawning habitat: same

Spawning season: parturition and mating in summer (British Columbia)

Mode of reproduction: ovoviviparous

Larvae: born as pelagic young

Shiner perch inhabit bays and estuaries in large numbers during the summer months and are common in sandy or muddy shallows and around wharves, rocks, jetties and eelgrass beds. Generally, they leave the shallows for deeper depths during the winter (DeMartini 1969; Wilson and MIlleman 1969; Bane and Robinson 1970).

Young are released in April-May in California (Odenweller 1975), but not until June-July in British Columbia (Wiebe 1968b; Gordon 1965). Mating appears to ensue almost immediately after parturition of the young (Shaw and Allen 1977; Hubbs 1917; Wiebe 1968b). The ova do not begin to develop until October and the sperm are stored in the ovarian structure until eggs are matured and fertilized in December. Embryonic development requires ~5-6 months (Wiebe 1968b; Eigenmann 1892).

Males were originally thought to mature before birth (Hubbs 1921), but this was later shown to be incorrect (Hubbs and Hubbs 1954). Males actually mature during their first year and possibly mate within several months after their birth (Gordon 1965; Shaw et al. 1974; Shaw 1971). In British Columbia, no yearling females were observed to be carrying embryos, but 99% of two year old females were (Gordon 1965). However, from other areas (California, Oregon, and Puget Sound) females mate several months after birth and deliver their first brood at about one year of age (Shaw et al. 1974; Shaw 1971; Wilson and Millemann 1969; Turner 1938; Suomela 1931).

At the start of the breeding season in British Columbia (June-August), yearling fish are the first to arrive in shallow areas, followed by the appearance of the males, then females. Males and females form large schools in very shallow water, but move deeper as the season progresses. Young of the year form relatively compact schools that associate with kelp beds from July to mid-August. By the end of October, all groups of shiner perch move out of the shallow beach areas and into deeper water (Gordon 1965).

Photoperiod and water temperature are important cues of the reproductive cycle. An increasing or long photoperiod has been shown to initiate spermatogenesis, development of secondary sex characteristics, and reproductive behavior in male shiner perch. These processes are also enhanced by warmer temperatures. Oocyte formation is enhanced by warm temperatures found during summer and fall, but oocyte maturation (prior to fertilization) is fostered by colder temperatures of early winter. Although early gestation requires a cold temperature, warmer temperatures during late development enhances the growth of the embryos (Wiebe 1968a).

During the mating season, shiner perch exhibit sexual dimorphism. The males assume a jet black color over their entire body surface with the exception of a narrow band lining the ventral region of the operculum. In addition, during the breeding period, the anal fin of the male develops a modified anal fin appendage. The anterior rays of the anal fin become thickened and a bulbous gland with a tubular appendage appears on each side of the rays. The gland secretes a fluid of unknown function. Spermatophores are extruded from a genital papilla located between the anus and the anal fin (Fig. 26.1). The scales and epithelial tissue at the base of the anal fin rays are arranged so that a continuous canal is provided from the gonopore to the tubular appendage. Seminal fluid travels in this groove if external pressure is applied to mature testes and has been observed in males which attempted to copulate. This secondary sex characteristic is not evident in males at birth or during winter months, but becomes well-developed seasonally by the end of June (Wiebe 1968b; Shaw 1971).

Shiner perch exhibit a characteristic courtship behavior (Wiebe 1968b). A sexually active male pursues and attempts to isolate a female from the other males, and keeps other males at bay by aggressively charging them. The successful suitor, with his dorsal fin raised, performs a dance in front of the female in the form of an undulating "figure-eight" interspersed with wide circular sweeps (Fig. 26.2A). This may be repeated for several minutes, but may be interrupted by aggressive charges at intruders. The male attempts to mate by aligning parallel to the female, turning on his side and applying his modified anal fin appendage to the urogenital region of the female (Fig. 26.2B,C). The latter is accomplished while both fish swim slowly forward or hover briefly.

Females are not totally passive in the courting behavior as suggested by Wiebe (1968b), but are found to initiate many behaviors similar to those initiated by males, such as pursuing other males. However, females do not do the "figure-eight" dance. Gravid females seem more aggressive toward males than non-gravid females and males will court gravid as well as non-gravid females (Shaw and Allen 1977).

As mentioned earlier, males exhibit the courtship response and mate with females who are releasing their young or have just completed parturition and Shaw and Allen (1977) put forth the following hypothesis:

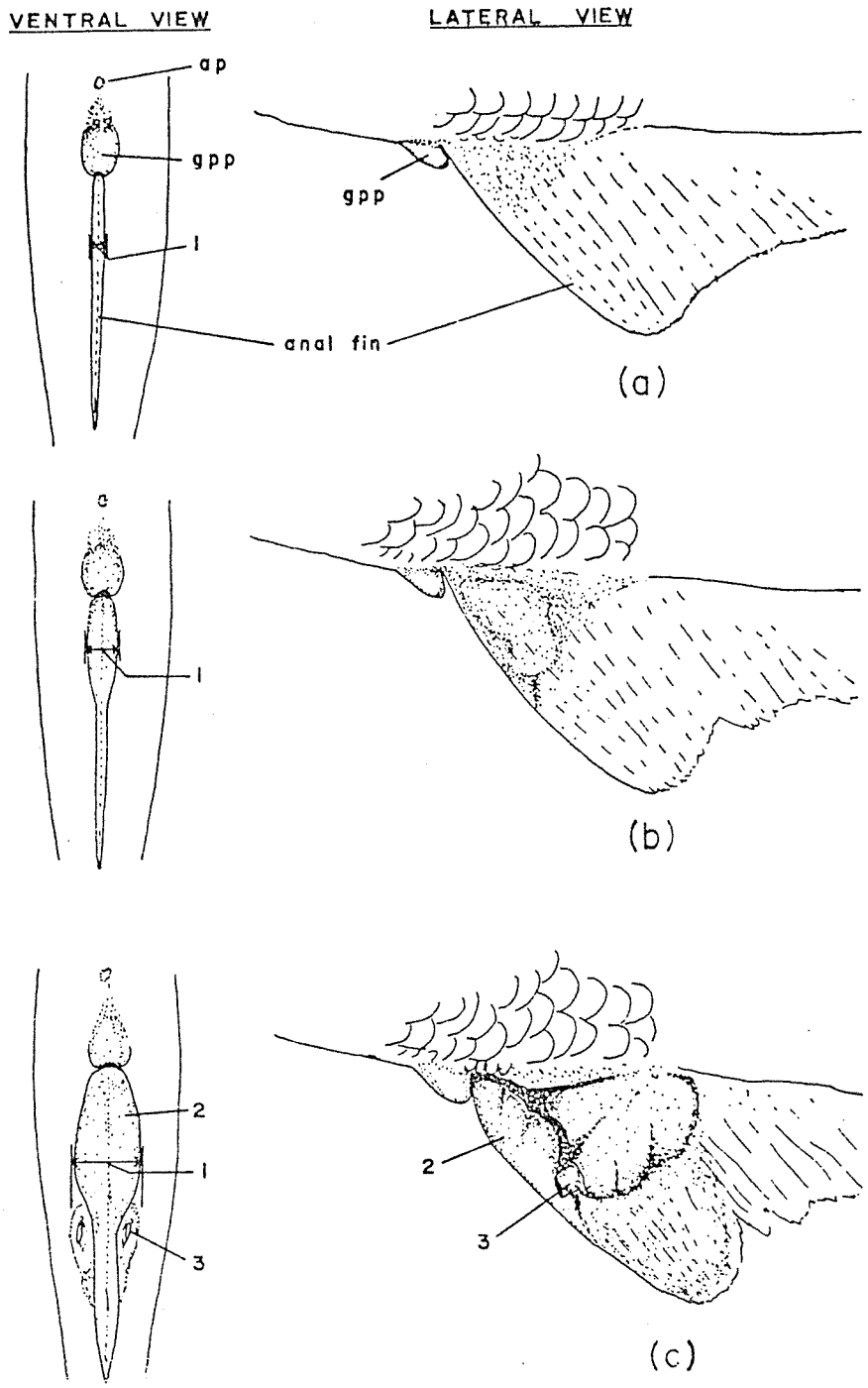


Fig. 26.1. Ventral and lateral view of modified anal fin structure of male shiner perch Cymatogaster aggregata: Appearance in a) December, b) May, and c) July. 1- region measured in determining index of anal fin structure, 2 and 3 - swelling and tubular structure of secondary sex character on anal fin; ap - anal pore, gpp - genital papilla. (Source: Weibe 1968b).

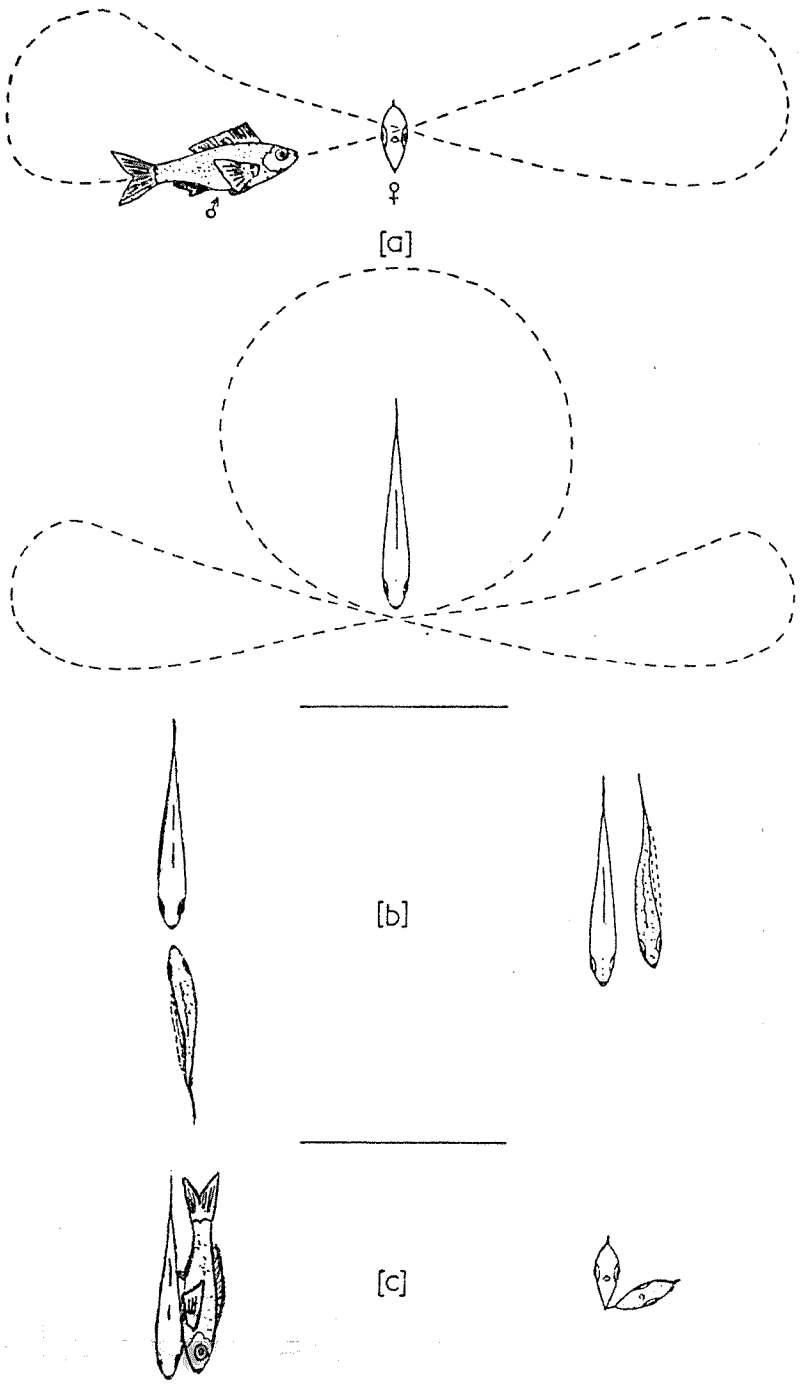


Fig. 26.2. Position of male and female shiner perch, Cymatogaster aggregata, during courtship and mating: a) Lateral and top view of path (dotted line) traced by male shiner perch during courtship "dance"; b) top view of position of male during "quiver", undulation of body and vertical fins and rapid jaw movements occur while the body appears limp; c) top and frontal view of position of shiner perch during mating. (Source: Weibe 1968b).

> "We believe the ideal time for insemination to occur is post-partum, since the ovary is highly distended and sperm can easily find their way through the large lumen, ultimately to embed in the ovarian wall. Subsequently, as the ovary shrinks, the sperm become closely packed and intimately connected with the ovarian tissue, from which they may derive nourishment during their period of waiting, until the eggs become mature in early winter."

Like other surfperches, shiner perch are adapted for ovovivipary. Turner (1938) described the ovarian structure of shiner perch females which consists of right and left tissue masses suspended from the mid-dorsal line of the ovarian sac. Each mass is partially divided internally by two dorsoventral longitudinal clefts, which form three longitudinal compartments that are open posteriorly but closed ventrally.

At maturity, eggs are only about 0.3 mm in diameter and are fertilized in the ovarian follicles (Eigenmann 1892). The fertilized eggs are not released into the ovarian cavity until or just before early segmentation stages. Embryos develop in the intra-ovarian cavity where they absorb nutritive material and oxygen from the female (Turner 1938; Eigenmann 1892). Detailed descriptions of ovarian development of shiner perch were provided by Eigenmann (1892).

The number of embryos carried by a female increases with increasing age and body length of the female (Tables 26.1A,B; Fig. 26.3) (Odenweller 1975; Gordon 1965; Wilson and Millemann 1969; Turner 1938; Eigenmann 1892). Broods range from about 6 embryos for a female < 100 mm and one year in age, to 15 or more embryos in older (4-6 yr) and larger (> 130 mm) females. The size and weight of the embryos also increases with size and weight of the female (Fig. 26.3). Hence, larger and older females produce larger young and more of them.

At birth, shiner perch are from 27-36 mm in length (Turner 1938) and emerge tail first. In some cases birth requires several hours per young. At the time of birth, the young are very dorsoventrally flattened and several tails may protrude from the distended oviduct at one time. The female remains swimming with no specific behavior accompanying the process. The young are active at birth and start feeding within a few minutes (Wiebe 1968b).

Table 26.1. A. Number of embryos developed, by size of female shiner perch, Cymatogaster aggregata, from California and British Columbia.

Length of female mm	Odenweller 1975 (Calif)		Gordon 1965 (B.C.)	
	No. fish examined	Mean No. embryos	No. fish examined	Mean No. embryos
90-94	1	6	-	-
95-99	-	-	12	7
100-104	6	7	21	9
105-109	3	9	56	9
110-114	5	9	19	10
115-119	6	9	23	10
120-124	3	11	11	13
125-129	-	-	8	12
130-134	1	15	-	-
135-139	1	16	-	-

Table 26.1. B. Mean lengths and weights of female shiner perch, Cymatogaster aggregata, and the mean number of embryos per female fish for each age class. (Source: Wilson and Millemann 1969 for Yaquina Bay, Oregon fish).

Age group	No. examined/ no. gravid	Mean fork length (cm)	Mean wt (g)	Mean no. embryos per female
I	51/46	9.32 ± 0.59[a]	13.65 ± 2.64	5.83 ± 0.86
II	32/28	11.11 ± 0.54	24.12 ± 3.55	9.30 ± 1.69
III	25/24	11.78 ± 0.61	28.00 ± 4.50	11.10 ± 1.89
IV	9/8	12.96 ± 0.84	37.09 ± 6.05	15.4 ± 4.33
V	2/1	13.35	44.95	15.0
VI	2/2	13.65	47.78	20.00
Total	121/109			

[a]Standard deviation of the mean.

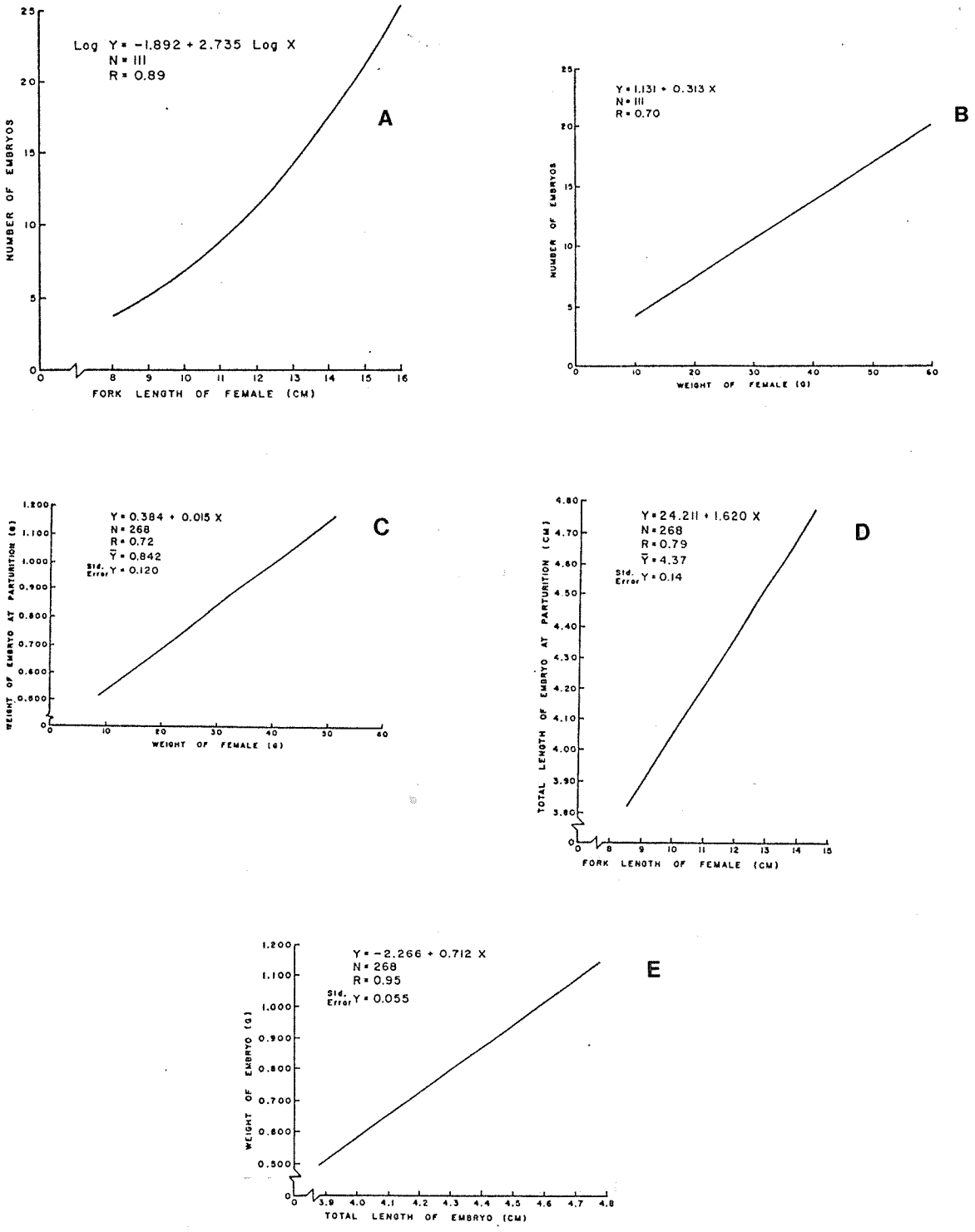


Fig. 26.3. Regression lines for various embryo and female-parent shiner perch, Cymatogaster aggregata, parameters: A) number of embryos compared to fork length of female; B) number of embryos compared to weight of female; C) weight of embryos compared to weight of female; D) total length of embryos of fork length of female; E) weight of embryo compared to total length of embryo. (Source: Wilson and Millemann 1969).

Embiotoca lateralis - Striped seaperch

Range: northern Baja California to southeast Alaska

Occurrence in Puget Sound: common

Adult habitat: pelagic

Spawning habitat: pelagic

Spawning season: parturition and mating in summer

Mode of reproduction: ovoviviparous

Larvae: born as pelagic young

Striped seaperch range along the Pacific Coast of North America from Baja California to southeast Alaska (Hart 1973). They are common around old underwater structures and pilings, in bays over mud flats where they occur in eelgrass beds, and are especially abundant along rocky shores where mussels and kelp are plentiful (DeMartini 1969; Gnose 1967). In kelp beds, they utilize the lower portions of the kelp columns for food and shelter (Alevizon 1975).

In Puget Sound, breeding occurs in June through August, and age of first maturity is reported to be 3 years for both sexes (Gnose 1967; Swedberg 1965). Males develop a modified anal fin structure, similar to male shiner perch (Gnose 1967; Blanco 1938) and striped seaperch also exhibit a mating position similar to shiner perch where the male assumes an oblique position to the female with anal fin areas touching (Edwards 1970).

After mating, sperm remain stored in the female's ovary until September when fertilization occurs. In October-November, eggs are in late cleavage, blastula, gastrula, or other embryonic stages and from December to July, larvae are present in the ovaries and reach 51 mm before their birth in July (Blanco 1938).

The female reproductive system consists of an ovary which is suspended from the dorsal wall of the abdomen (Fig. 26.4, 1). The anterior part of the ovary is divided into 2 horns and the left horn is generally smaller than the right. From the dorsal midline of the ovary, 2 ovarian sacs are suspended. These sacs may have one or two vertical partitions which divide the ovary into compartments (Fig. 26.4, 10, 11) and the sacs are open posteriorly. During early development, the ovary is spindle-shaped but becomes quite oblong and enlarged as the larvae increase in size (Fig. 26.4, 2-9). Mature eggs are ~.3mm in diameter, spherical and contain very little yolk.

The fertilized eggs and larvae are not directly connected with any part of the ovary during their development (Fig. 26.4, 15-18). The

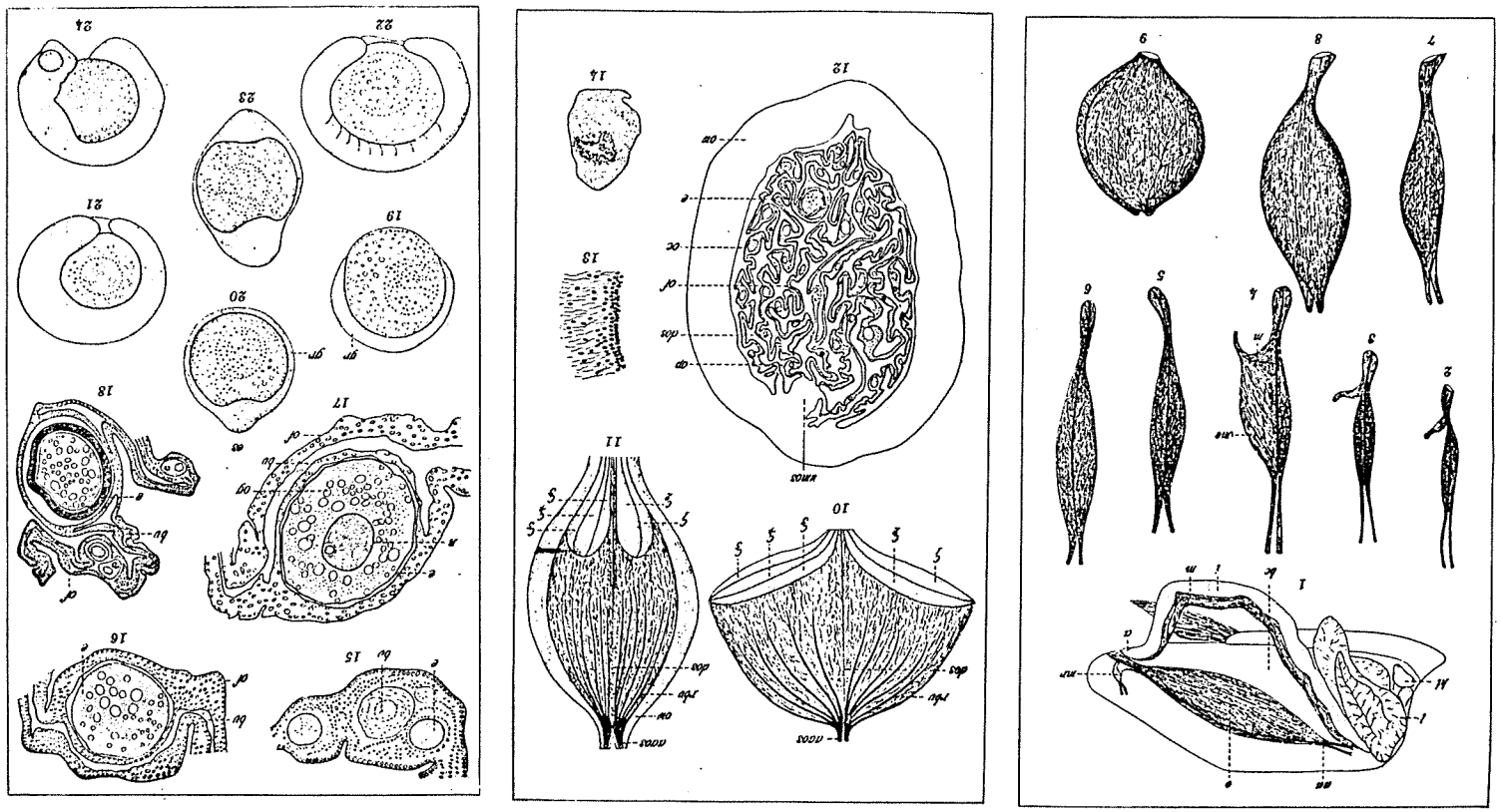


Fig. 26.4. Characteristics of the ovary and ovarian development of striped seaperch - Embiotoca lateralis: 1) position of ovary in the body cavity; 2-9) change in ovary shape due to embryonic development during October to July; 10-11) arrangement of two sacs and five compartments of the ovary; 12) cross section through an ovary; 13) cross section through a portion of the inner lining of an ovarian wall; 14) cross-section through a posterior region of the ovary; 15) cross section through an ovarian follicle; 17) cross-section through an early stage egg; 18) cross section through a late stage egg; 19-20) gastrula stage egg; 21-22) early embryos; 23) ventral view of embryo; 24) advanced embryo. Abbreviations: a, Anus; aaos, anterior arm of ovarian sac; ab, air bladder; au, auditory capsule; bc, body cavity; br, branchial gill slit; bv, blood vessel; c_1, c_2, c_3, c_4, c_5, compartments 1, 2, 3, 4, and 5; csc, coracoscapular cartilage; dos, division of ovarian sac; e, egg; es, embryonic shield; gr, germ ring; ht, heart; hg, hind gut; i, intestine; l, liver; m, mesentery; me, mesovarium; mr, mesorectum; n, nuculeus; o, ovary; oc, ovarian cavity; of, ovarian follicle; og, oil globule; op, ovarian partition; ow, ovarian wall; rbv, radial blood vessel; umos, upper margin of ovarian sac; v, villi; ys, yolk sac. (Source: Eigenmann 1892).

embryos are found tightly packed against the ovarian walls and between the ovarian folds. There is no definite arrangement of the larvae within the ovary and the larvae are able to change position even when nearing extrusion (Blanco 1938). The sequence of larval development has been illustrated (Fig. 26.5).

The largest and oldest females produce the largest number of embryos per season (Fig. 26.6). Embryos range in number from 10-25 in youngest fish to over 40 in larger females (Swedberg 1965; Gnose 1967; Blanco 1938).

The food absorbed and digested by the growing larvae consists of ovarian fluid and solid cell-like particles which are products of the epithelial lining of the ovarian folds. O_2 is provided to the embryos by the ovarian fluid which is oxygenated by circulation within the ovarian follicles. With development, larvae develop highly vascularized fins which aid in exchange of gases and are always in contact with the vascular ovarian folds. The larval gills become well-developed and may become functional in the later stages while young are still in the ovary (Blanco 1938).

At birth, young are golden in color and have little resemblance to the adult.

During late stages of pregnancy, the females become dull, drab, and faded in color, but regain their color after giving birth. Some males may also become drab during this time (Gnose 1967).

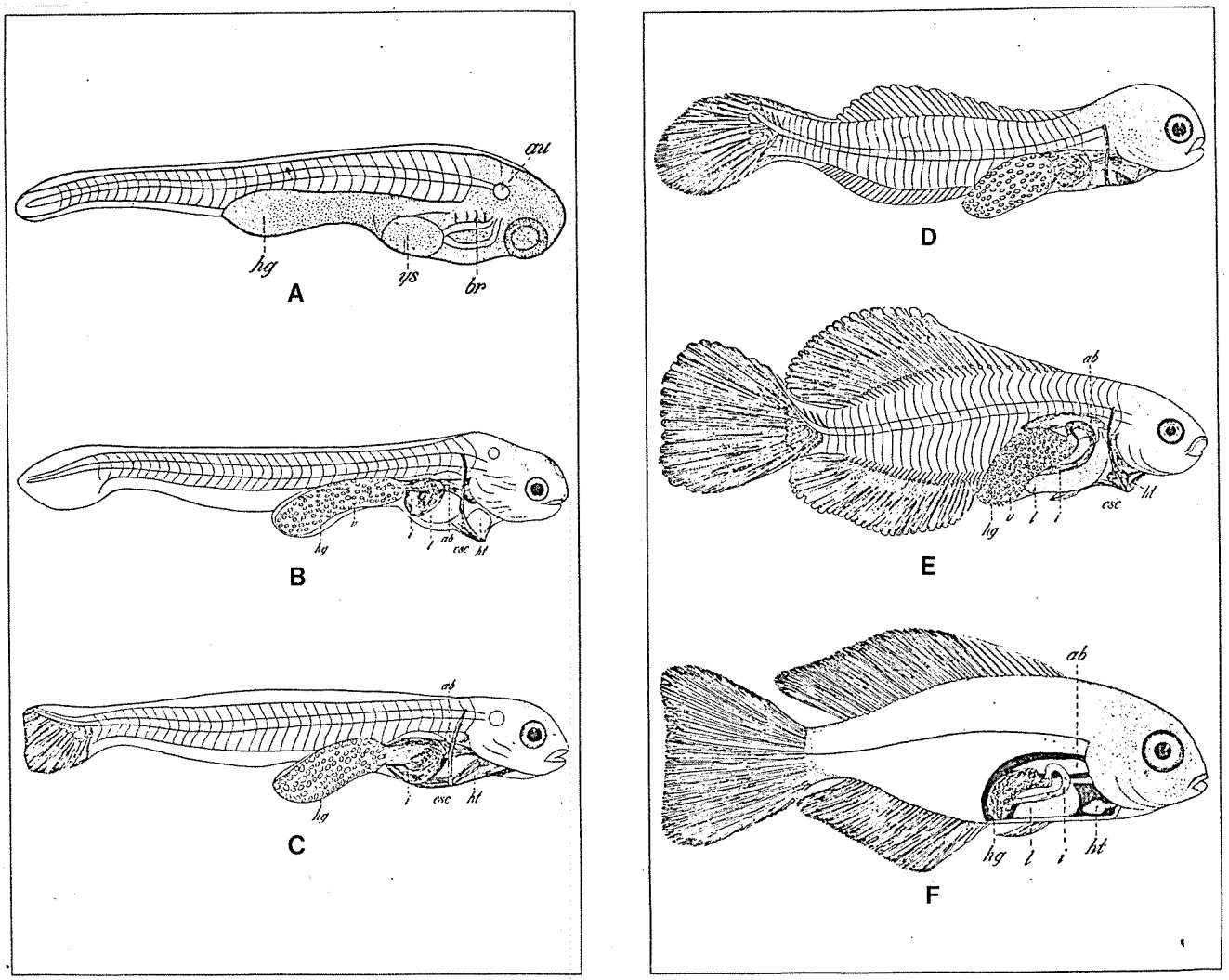
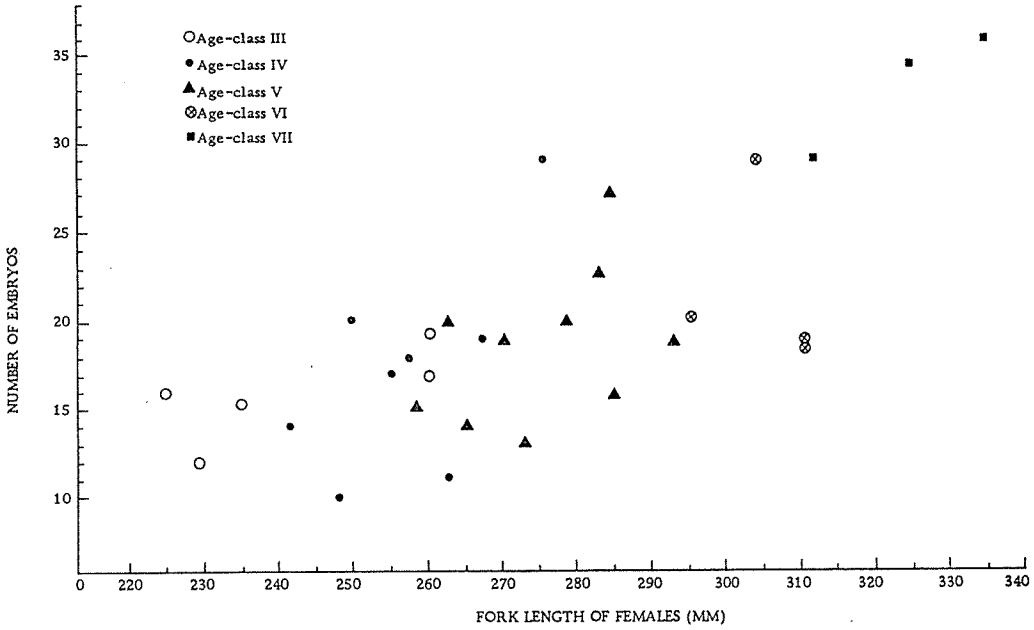


Fig. 26.5. Development sequence of striped seaperch, Embiotoca lateralis: A) 3 mm; B) 7 mm; C) 12 mm; D) 16 mm; E) 21 mm; F) 41 mm. Abbreviations: hg, hind gut; ys, yolk sac; br, branchial gill slit; au, auditory capsule; v, villi; i, intestine; l, liver; ab, air bladder; ht, heart; scs, coracoscapular cartilage. (Source: Blanco 1938).



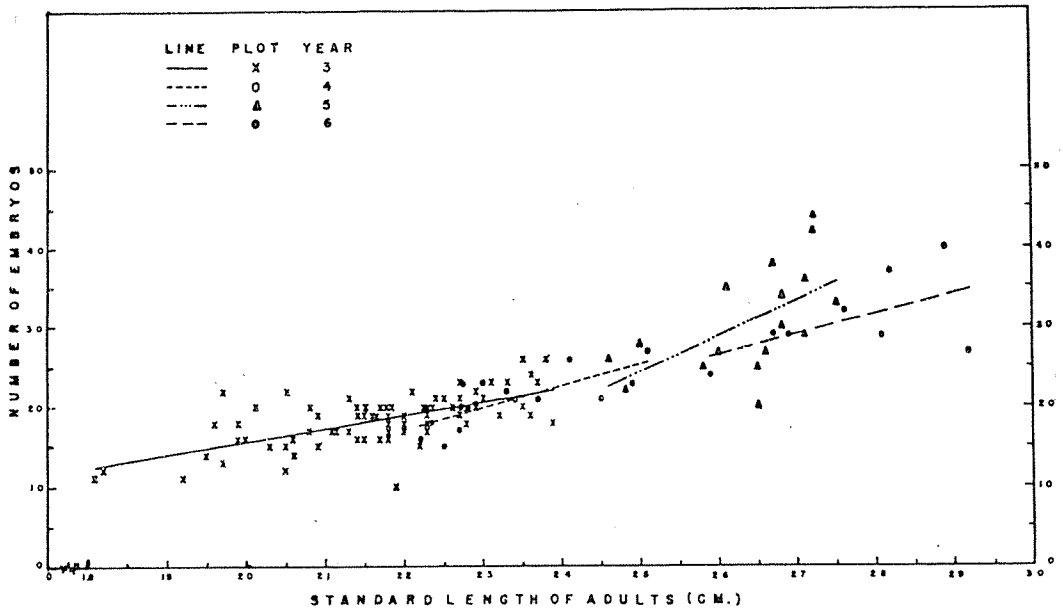


Fig. 26.6. Fecundity-length relationship by age for striped seaperch, Embiotoca lateralis, from Yaquina Bay, Oregon. (Sources: Gnose 1967, top; Swedberg 1965, bottom).

Hyperprosopon ellipticum - Silver surfperch

Range: southern California to Vancouver Island, B. C.

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic

Spawning habitat: pelagic

Spawning season: mating in fall, parturition in summer (Oregon)

Mode of reproduction: ovoviviparous

Larvae: born as pelagic young

Silver surfperch range from southern California to Vancouver Island, but are rarely encountered in Puget Sound (Hart 1973; Miller and Borton 1980). Adults abound in the sandy surf zone of the exposed coasts and are also found around old piers, or other submerged structures, around rocky outcroppings, jetties, and sometimes in the mouth of estuaries (DeMartini 1969; Wyodoski and Bennett 1973).

Males may become mature by age class I and at lengths of 141 mm and greater, but females are not mature until age class II and about 170 mm or more. All fish $\geq$ 3 years are mature (Table 26.2). In Oregon, mating occurs in fall and young are born the following June - August (Wyodoski and Bennett 1973).

The young are retained by the female until they are about 40-45 mm SL and the number of larvae brooded tends to increase with increasing size of the female (Table 26.3).

Additional information on reproduction in silver surfperch is lacking.

Table 26.2. Relationship of size and age of female silver surfperch, Hyperprosopon ellipticum, to size of their embryos. (Source: Wyodoski and Bennett 1973).

	Female			Embryos		
Date collected	Total length (mm)	Weight (g)	Age	Number	Mean standard length (mm)	Standard deviation
6-27-67	174	77	II+	4	31.3	--
6-28-67	175	95	II+	10	32.8	0.63
6-28-67	189	120	III+	7	36.1	0.63
5- 5-68	190	102	III+	9	18.3	0.26
6-27-67	198	116	III+	5	39.8	0.84
6-27-67	203	134	III+	5	37.2	0.84
6-28-67	203	138	III+	12	36.6	0.38
1- 2-69	210	136	III+	9	6.8	0.09
6-27-67	215	165	III+	14	36.2	0.67
6-25-68	218	182	III+	11	44.7	0.61
6-21-68	219	172	III+	16	36.2	0.81
6-25-68	221	184	III+	17	41.7	0.71

Table 26.3. The relationship between size and age of sexual maturity for silver surfperch, Hyperprosopon ellipticum, from Oregon. (Source: Wyodoski and Bennett 1973).

Total length (mm)	Age group I		II		III		IV		V		VI		VII		Total	
	N*	%M**	N	%M	N	%M	N	%M	N	%M	N	%M	N	%M		
(Males)																
121-130	1	0													1	0
131-140	1	0													1	0
141-150	4	100													4	100
151-160			1	0											1	0
161-170			6	67											6	67
171-180			8	62											8	62
181-190			1	100	8	100	2	100							11	100
191-200					3	100	9	100	2	100					14	100
201-210							12	100	16	100	1	100			29	100
211-220									8	100	7	100			15	100
221-230									1	100	2	100	5	100	8	100
Total	6	66	16	62	11	100	23	100	27	100	10	100	5	100		
(Females)																
121-130	1	0													1	0
131-140	--	--													--	--
141-150	1	0													1	0
151-160	1	0													1	0
161-170			2	0											2	0
171-180			5	40											5	40
181-190			--	--	2	100									2	100
191-200			2	50	2	100									4	75
201-210			--	--	5	100	1	100							6	100
211-220			1	100	5	100	--	--							6	100
221-230					2	100	1	100							3	100
231-240															--	--
241-250									1	100					1	100
Total	3	0	10	40	16	100	2	100	1	100						

*N = number examined

**%M = percent mature

Phanerodon furcatus - White seaperch

Range: northern Baja California to Vancouver Island, B.C.

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic

Spawning habitat: pelagic

Spawning season: parturition in spring-summer (California)

Mode of reproduction: ovoviviparous

Larvae: born as pelagic young

White seaperch are not frequently encountered in Puget Sound (Miller and Borton 1980), but range from Vancouver Island to northern Baja California (Hart (1973). Adults are found near piers, docks, or reefs, at stream entrances, in kelp beds and occasionally over sandy areas or at the interfaces of sand and rock areas (Bray and Ebeling 1975; DeMartini 1969). They are basically bottom oriented, although they occasionally are seen schooling in mid-water or singly in the kelp canopy (Bray and Ebeling 1975). White seaperch seem to prefer sheltered bays, but are also found along rocky open coasts (DeMartini 1969).

In California, young are born in May through August. The embryos develop between 11-12 ovarian sheets which provide nourishment and oxygen to the embryos. In the ovary, some embryos are oriented anteriorly and others posteriorly, which may be an important space-conserving technique. In March in California, embryos are about 15 mm and when they reach 16.2 mm, they have pigmented eyes, and scales are formed along the lateral line around the eyes and below the pectoral fin. At birth, the young average about 43.5 mm and may be born head-first or tail-first. The young are active at birth and immediately form schools in bays (Banerjee 1971).

Females produce from 8 to 33 young, depending on their size. The average number of young produced by fish 165-215 mm is 12.1; 20.5 embryos for fish 216-252 mm; and 24.6 for parents greater than 252 mm (Banerjee 1971).

Rhacochilus vacca - Pile perch

Range: northern Baja California to southeast Alaska

Occurrence in Puget Sound: common

Adult habitat: pelagic

Spawning habitat: pelagic

Spawning season: mating in winter, parturition in summer (Oregon)

Mode of reproduction: ovoviviparous

Larvae: born as pelagic young

Pile perch are found along rocky shores, near submerged objects such as old piers and reefs, and in kelp beds (DeMartini 1969; Alevizon 1975). They forage and feed close to the substrate, but are also observed in the water column hovering near fronds of kelp (Alevizon 1975).

In Yaquina Bay, Oregon, fertilization occurs between late December and early February, with mating occurring possibly 2 1/2 months prior to fertilization. Gestation lasts about 6 months and the young are born between late June and early August (Wares 1968).

Females reach maturity and deliver their first brood at 3 years of age, and by 5 years, almost all female pile perch are mature (Wares 1968). Although the ovaries contain numerous oocytes, only a few become swollen and supplied with blood and develop into embryos. These mature eggs measure 792 μ in diameter and weigh .00016 g. The growth rate of embryos prior to birth is believed to be linear with an instantaneous daily growth rate of 0.0606 which declines dramatically after birth. During the first two months after birth, the instantaneous daily growth rate is .0093. At birth, the young pile perch are 76.0-85.7 mm TL and 4.5-8.9 g (Wares 1968).

Fecundity of pile perch is positively correlated with size of the female (Fig. 26.7) and ranges from ~15 to 50 or more embryos per female. Prenatal mortality of ovulated eggs and embryos is estimated at 3.7% and 1.1%, respectively (Wares 1968).

In Yaquina Bay, juvenile pile perch, as well as adults, are benthic feeders, consuming molluscs, barnacles, and decapod crustaceans. Juveniles feed less on these organisms compared to adults and more on Corophium (Ware 1968).

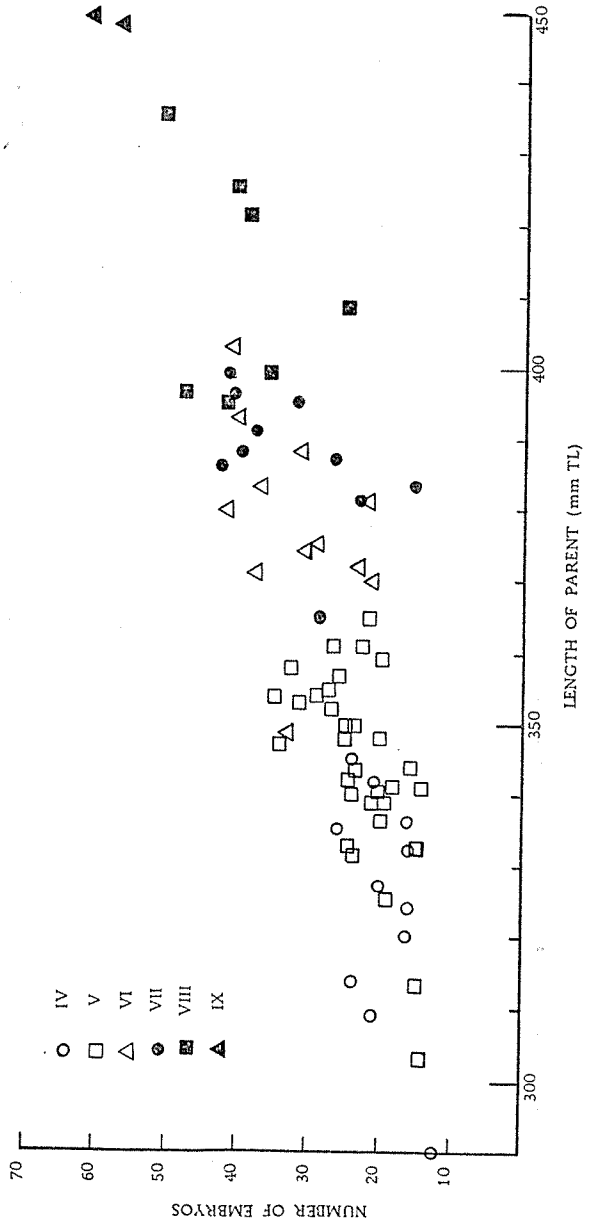


Fig. 26.7. Fecundity-length relationships by age of 74 pile perch, Rhacochilus vacca, from Yaquina Bay, Oregon, based on females whose embryos were less than 32 mm SL. (Source: Wares 1968).

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27. SPHYRAENIDAE

Sphyraena argentea - Pacific barracuda

Range: Gulf of California to Gulf of Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic, schooling nearshore

Spawning habitat: pelagic

Spawning season: spring-summer (California)

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Pacific barracuda form pelagic schools close to shore and are primarily found in warm seas (Hart 1973), although they have been known to migrate as far north as Kodiak Island, Alaska during warm water periods. They are also known on a few occasions from Puget Sound (Miller and Borton 1980).

Information on early life history has been obtained for Pacific barracuda in California. All males are mature by 48 cm and two years of age, but only 50-75% of the females are mature. By three years of age or $\geq$ 55 cm in length, all females are mature. The sex ratio during spawning varies from day to day, but tends to favor males (Walford 1932).

In California, the spawning season begins in April, peaks in May-June, and is over by late September. Females may spawn more than once per season as ripe ovaries tend to contain both mature and a large proportion of immature eggs (Walford 1932).

The immature ovary is pinkish in color, gelatinous and narrow. Eggs appear as small yellow granules and as maturity approaches, eggs increase in size and number and the pinkish color is obscured. As they reach maturity, the eggs lose their yellow color an becomes translucent gray. Mature eggs become detached and fill the lumen and spent ovaries are flaccid and pink in color. Immature males have firm, slender, pale brown or greenish testes. As they mature, the gonads become white, less firm in texture and increase in size (Walford 1932).

Mature eggs are 1.2-1.6 mm in diameter and a female may produce between 51,000 and 484,000 eggs (Table 27.1). The planktonic eggs are transparent, have a small perivitelline space, and contain a single oil globule (~.2 mm in diameter) (Barnhart 1927). In live eggs, there is no

Table 27.1. Fecundity of Pacific barracuda, Sphyraena argentea, from California. (Source: Walford 1932).

Total length (cm)	Age (years)	Weight of fish (g)	Weight of ovary (g)	Number of mature ova
50	2	414	28	51,000
53	2	506	30	48,000
56	3	590	50	71,000
63	4	900	110	163,000
70	4	1131	104	172,000
72	4	1339	229	247,000
79	5	1572	134	170,000
86	7	1998	173	294,000
91	7	2867	480	340,000
93	7	3106	261	309,000
94	6	3226	340	484,000

obvious texturing on the shell, but after preservation, eggs show a minutely striated surface. The yolk is colorless and distinctly alveolate (Orton 1955).

During embryonic development, the embryos acquire melanophores and yellow chromatophores, the latter fading with preservation. By the time a small tail bud has formed, melanophores are abundant on the dorsal and dorsolateral surface of the embryo. Anteriorly, the pigmented area divides into two dorsolateral bands which rejoin across the posterior part of the midbrain. This pattern is retained through the larval stage. There are also a few melanophores over the ventrolateral surface of the tail and a few which extend down the posterior surface of the yolk sac toward the level of the oil globule (Fig. 27.1 A, B).

With further development, pigmentation increases over the sides of the embryo and extends back along both the dorsal and ventral surfaces of the tail bud (Fig. 27.1 B). At this stage, yellow chromatophores are present (in unpreserved specimens) and located behind each eye, scattered irregularly along the dorsal and dorsolateral body surfaces, along the ventrolateral body surface in the pectoral region, ventrolateral to the base of the tail bud, and on the posteroventral surface of the yolk sac near the oil globule. In addition to the above, melanophores begin to form in a sharply defined middorsal line along the base of the developing dorsal finfold and along the midventral surface at the base of the ventral finfold (Fig. 27.1 B). As the finfold enlarges, the median lines of melanophores move out into the finfolds and retain their linear alignment (Fig. 27.1 C), but begin to aggregate into a series of disconnected blotches (Fig. 27.1 D). The larva hatches at about 2.25 mm, has a large globular, segmented yolk sac, and pigment spots along the body, in the finfolds, and on the posterior end of the yolk sac (Fig. 27.2 A). The eyes and ear capsules are conspicuous, but the jaws are unformed and the pectoral fin buds are very small. The moderately long gut extends well past the end of the yolk sac. Twenty-four or 25 myomeres are visible. Pigmentation is similar to late-embryonic stages. After one day, the yolk sac is reduced, the head is larger and jaws are forming, and the pectoral fin buds have enlarged (Fig. 27.2 B). At two days, the yolk sac is reduced to a small mass and the pectoral fins are functional. Jaws are formed and the eyes are pigmented. The embryonic pattern of melanophores on the neck persists, but is less distinct. A double row of large, closely spaced melanophores extends along the top of the gut. Melanophores are scattered along the dorsal and dorsolateral surface of the body and begin to form a lateral patch on the body above the anus. At three days, the jaws are observed to snap occasionally and the larva may bend into an S-shape and then dart forward, probably a feeding response. Pigmentation is intensified (Fig. 27.2 C), and may take on a coppery-greenish or bluish hue.

Larvae at four days are capable of feeding. By the time larvae are only 7 mm, they begin to take on juvenile characters, especially in the head which has narrow, beak-like jaws. Basal elements of the dorsal and anal fin are forming although the finfolds are still intact and rudiment

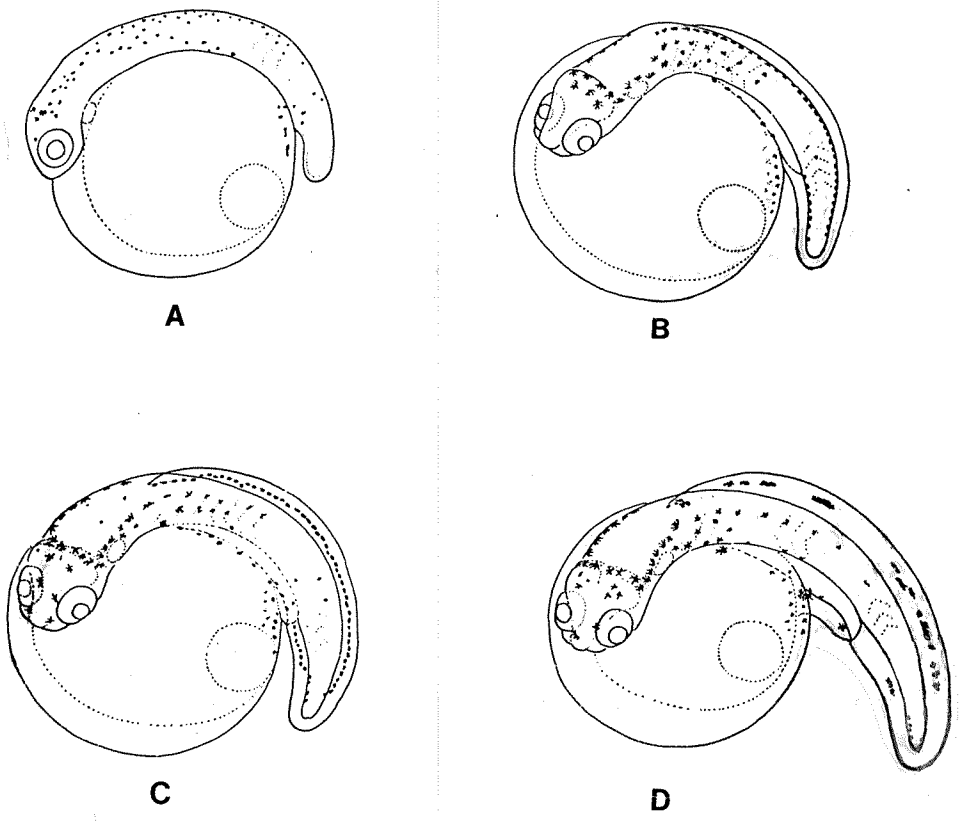

Fig. 27.1. Embryonic stages of Pacific barracuda, Sphyraena argentea. Egg capsules are omitted. (Source: Orton 1955).

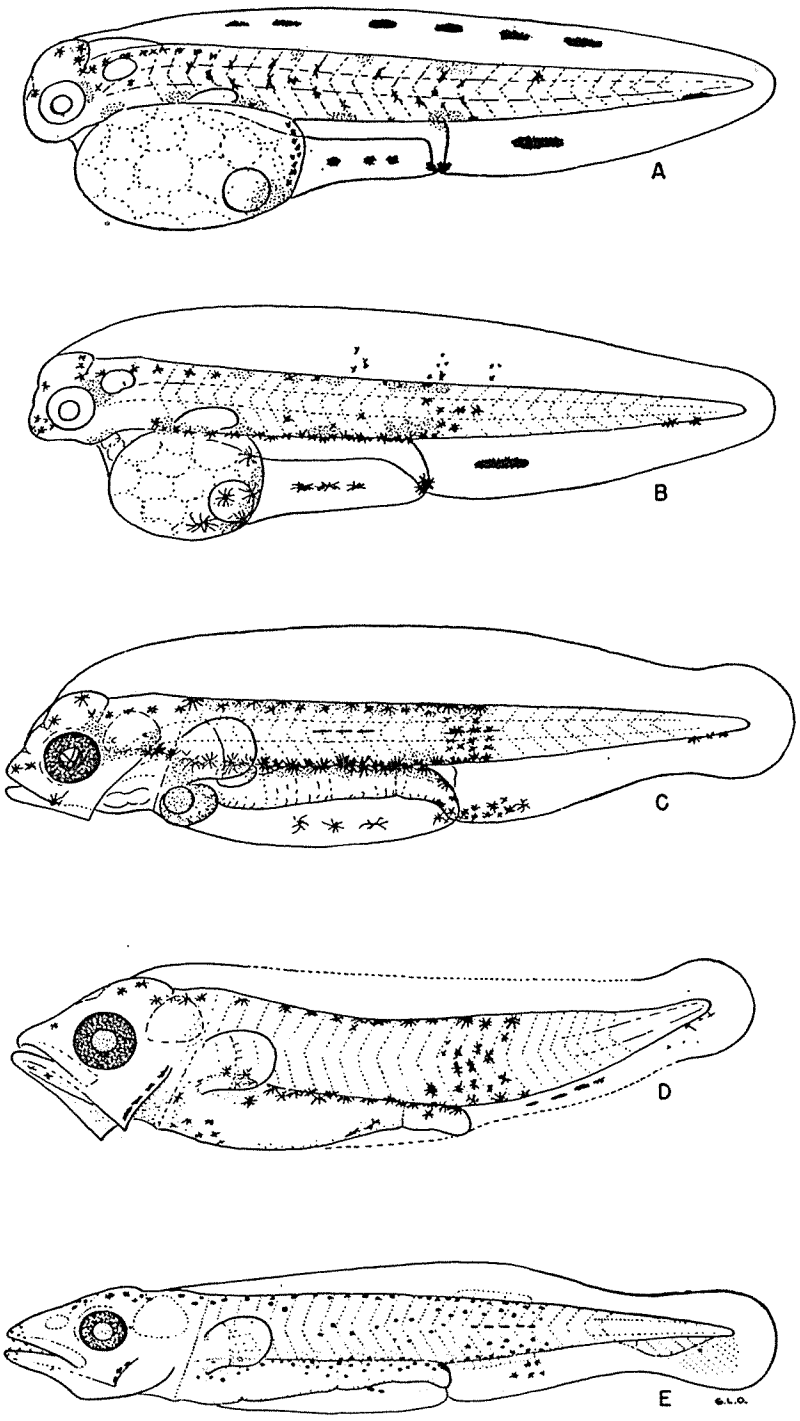

Fig. 27.2. Larval development of Pacific barracuda, Sphyraena argentea: A) Recently hatched - 2.5 mm; B) one day after hatching; C) three days after hatching; D) 4 mm larva; E) 7 mm larva. (Source: Orton 1955).

of the caudal fin are evident (Fig. 27.2 E). Later larval stages and juveniles are undescribed.

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28. TRICHODONTIDAE

Trichodon trichodon - Pacific sandfish

Range: San Francisco Bay, California to Aleutian Islands and Bering Sea; Medniji Island, Kamchatka.

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, on sand-gravel substrates

Spawning habitat: rocky intertidal

Spawning season: winter-spring (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached

Larvae: pelagic

Little is known about the biology of the Pacific sandfish which ranges from California to the Bering Sea and Kamchatka (Hart 1973). Adults are characteristic of inshore, sand-gravel communities (Isakson et al. 1971) where they are reported to bury themselves in sand (Clemens and Wilby 1946). In Puget Sound, Pacific sandfish have been reported from the San Juan Islands and Bellingham Bay (Miller and Borton 1980).

The first recorded discovery of natural spawn of Pacific sandfish was made during June, 1976 (Marliave 1981). The egg mass, which contained about 1,000 amber colored eggs of mean diameter 3.52 mm, was irregularly shaped and firmly adhered to the rocky substrate. Although adults are known to inhabit sandy beaches, the egg mass was located in a surge channel along a rocky shoreline between the 0.6 and 1.0 m tide levels. This particular spawning site was reported to be about 8 km from the nearest sandy intertidal area, indicating that a limited spawning movement along the shoreline may occur.

At the time of collection, these sandfish eggs contained embryos with pigmented eyes and when incubated in the aquarium, continued to develop for over 8 more months. Marliave postulated an incubation period of 1 year may be required. The larvae hatched in February at a size of 14.5 mm SL (16 mm TL) and grew to 40-43 mm SL (45-50 mm TL) in 70 days.

Pacific sandfish larvae are distinct from other fish larvae and morphometrics, myomere count, and fin development can aid in their identification (Table 28.1). An outstanding feature of late embryos is the presence of caudal fin rays and the beginning of notochord flexion. Late embryos and early larvae are further characterized by a large diameter eye, short snout to anus length, elongate body form, a large

Table 28.1. Morphometric and meristic statistics for larval Pacific sandfish, Trichodon trichodon. Fresh length, immediately after killing; preserved lengths 1 year later. (Source: Marliave 1981).

Hatched age (d)	Fresh length (mm SL)	Preserved length (mm SL)	SL, percent shrinkage	Preserved snout-anus length (mm)	Ratio snout-anus ÷ SL	Preserved body depth (mm)	Ratio body depth ÷ SL	Myomeres		Fin ray counts					Melanophore count	
								Preanal	Postanal	D-1	D-2	Anal	Pectoral	Pelvic	PVM[1]	Hypural
Embryo	—	11.0	—	—	—	—	—	12	36	0	0	0	—	0	16	3
0	14.5	13.0	10.3	4.5	0.35	2.5	0.19	12	38	0	0	0	—	0	18	3
0	14.5	13.0	10.3	4.5	0.35	2.7	0.21	12	38	0	0	0	—	0	16	1
0	14.5	13.0	10.3	4.5	0.35	2.7	0.21	12	40	0	0	0	—	0	20	2
9	—	14.5	—	5.0	0.34	3.0	0.21	12	37	0	0	0	—	0	16	4
18	19.5	17.2	11.8	7.0	0.41	3.3	0.19	12	37	0	0	0	21	0	20	6
25	21.0	20.0	4.8	8.7	0.43	4.2	0.21	14	34	VIII	15	28	21	0	18	Bands
29	24.5	22.0	6.1	9.3	0.42	5.0	0.23	15	34	X	19	27	21	0	[2]19 + 19	Bands
35	27.5	27.0	1.8	12.0	0.44	5.5	0.20	14	32	XII	18	I,28	21	3	19 + 21	Bands
43	29.0	28.0	3.4	12.7	0.45	6.8	0.24	15	34	XIII	18	I,28	21	I,3	25	Brackets
56	31.5	30.0	4.8	14.0	0.47	7.0	0.23	13	35	XIV	19	I,29	23	I,5	19	Brackets
56	32.5	32.0	1.5	15.0	0.47	7.0	0.22	14	36	XIII	18	I,28	21	I,5	20	Brackets
70	40.0	38.0	5.0	18.0	0.47	9.3	0.24	14	36	XIV	I,19	I,29	22	I,5	15	Brackets
70	43.0	40.5	5.8	20.5	0.51	11.0	0.27	14	34	XIV	I,17	I,27	22	I,5	12	Brackets

[1]Postanal ventral midline melanophores versus hypural melanophores.
[2]Internal and superficial melanophore counts.

oil droplet in the anterior part of the yolk sac, three preopercular spines, and presence of pectoral fin rays. Early larval pigmentation consists of about 40 large stellate melanophores on the abdomen and other melanophores on the crown, snout, postanal midventral body surface, lower jaw angle, and at the base of the hypural plate (Fig. 28.1 A). With development, a row of pigment spots appears and spreads along the dorsal body surface on each side of the dorsal finfold. Also, melanophores begin to appear internally along the notochord. Additional melanophores appear on the head and jaws. Small teeth are visible at 14.5 mm SL, but become progressively reduced and less noticeable (Fig. 28.1 B). At about 17 mm SL, pectoral fin ray development is complete at 21 rays, and four preopercular spines are present (Fig. 28.1 C). By 20 mm SL, a row of superficial melanophores appears on the mediolateral body surface and a small "bracket" of melanophores appears over the flexed notochord tip. A fifth preopercular spine appears and the dorsal and anal fin ray development has started. Pelvic fin buds are also visible (Fig. 28.1 D). By the time larvae are 27 mm SL, a ring of small melanophores circles each eye, dorsal body pigment has developed into two rows on each side of the dorsal finfold, and melanophores have appeared on the dorsal, pectoral, and caudal fins. A slight upturning of the jaw is also observable (Fig. 28.1 E). At 32 mm SL, the young fish is easily recognized as a young sandfish (Fig. 28.1 F).

In the aquarium, larvae begin to school at the surface immediately upon hatching. Active swimming is probably aided by their large size at hatching and the precocious development of caudal and pectoral fin elements. After 48 h, the neustonic behavior is replaced by subsurface schooling within 10 cm of the surface, and feeding is observed. Schooling behavior decreases during metamorphosis (from 30 to 50 mm SL) and juveniles do not exhibit true schooling behavior in captivity. At about 50-60 mm SL, the young sandfish possesses the fringed lips, elongate nostrils, steep jaw angle, and eye positioning of the adult, and burrowing behavior appears (Marliave 1981).

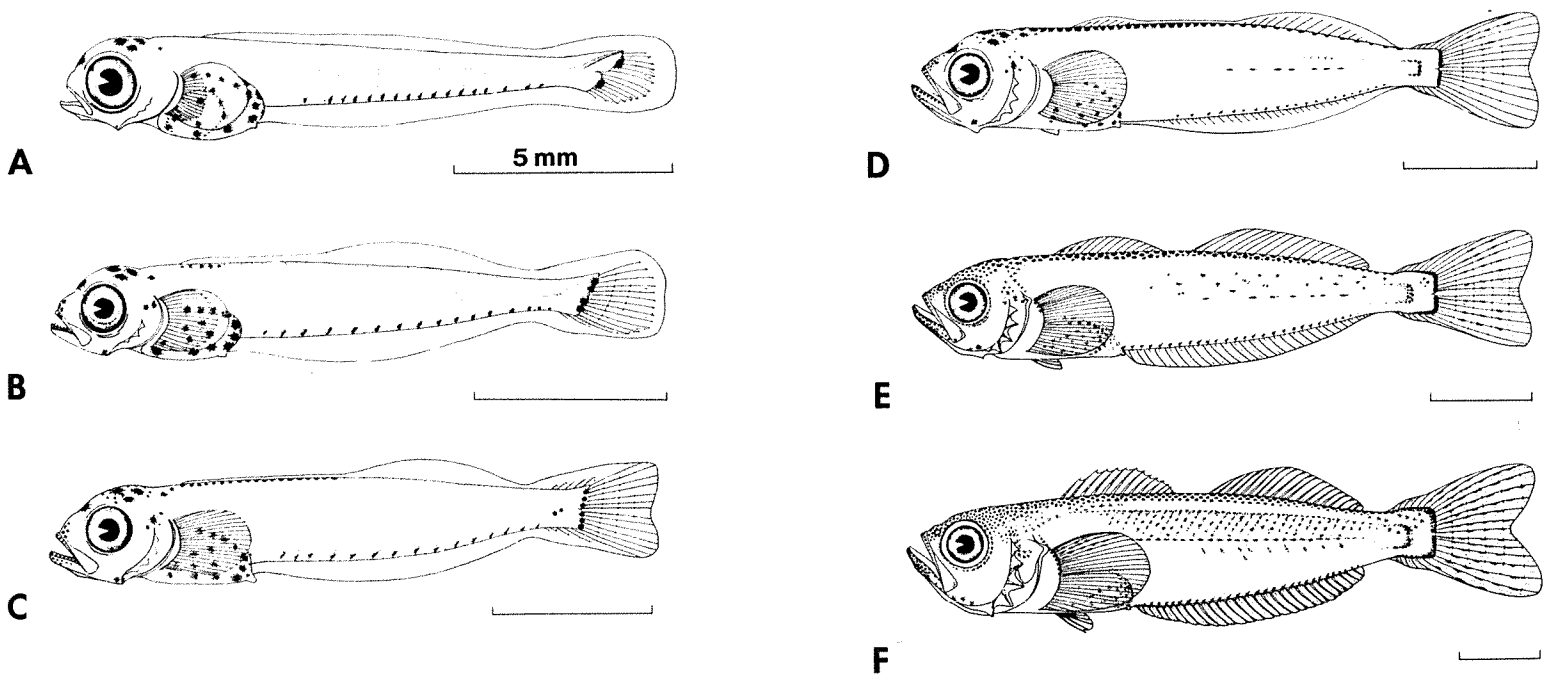

Fig. 28.1. Larvae and juveniles of Pacific sandfish, Trichodon trichodon: A) 0 d, 13 mm SL; B) 9 d, 14.5 mm SL; C) 18 d, 17.2 mm SL; D) 25 d, 20 mm SL; E) 35 d, 27 mm SL; F) 56 d, 32 mm SL. (Source: Marliave 1981).

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29. BATHYMASTERIDAE

Ronquilus jordani - Northern ronquil

Range: Monterey Bay, California to Aleutians and Bering Sea

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: later winter-spring

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: undescribed, pelagic

Northern ronquil are widely distributed throughout Puget Sound (Miller and Borton 1980) and range from central California to the Bering Sea (Hart 1973). They are taken at depths of 18-165 m in British Columbia where females with fully developed salmon-colored eggs have been found in March. Ripening individuals have been observed in Puget Sound in February (Hart 1973).

Northern ronquil eggs are probably demersal and spawned in masses (Breder and Rosen 1966), but have not been described. Larvae have also not been described in the literature, but are reported to be planktonic. Small larvae 5-11 mm were collected in surface waters near the Fraser River mouth and in Saanich Inlet, B.C. during June and were found to have eaten Cladocera, copepods eggs and nauplii, clam larvae, phytoplankton and barnacle larvae (Robinson et al. 1968). In the northern part of its range, ronquil larvae are caught in the upper mixed layer (0-28 m) during summer (Kendall et al. 1980).

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30. STICHAEIDAE

Anoplarchus insignis - Slender cockscomb

Range: Puget Sound, Washington to Attu Island, Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Known from Puget Sound to Attu Island, slender cockscomb are a demersal, nearshore fish found in the intertidal zone and to depths of 30 m (Hart 1973).

No information is available on the reproductive biology of slender cockscomb.

Anoplarchus purpurescens - High cockscomb

Range: Santa Rosa Island, California to Pribilof Islands, Bering Sea.

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal

Spawning habitat: demersal, under rocks

Spawning season: later winter-early spring

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached, guarded

Larvae: pelagic

High cockscomb are found in the North Pacific from California to the Bering Sea (Miller and Lea 1972). As adults they are primarily an intertidal species living between the upper low intertidal and midintertidal levels. They are found throughout Puget Sound (Miller and Borton 1980), and along the Straits of Juan de Fuca they are the most abundant and widely distributed eel-blenny found in tidepools and beneath rocks. Small high cockscomb are more abundant in tidepools, and large individuals are more numerous under rocks (Cross 1981).

Adults exhibit sexual dimorphism in color and morphology which becomes enhanced during the breeding season. While color differences exist at other times of the year, differences in spawning coloration are more obvious. The breeding male develops bright orange anal and pectoral fins, and the caudal and dorsal fins become reddish, with color in the caudal fin more pronounced. Similar coloring appears in non-spawning males, but is less intense and usually confined to the anal and pectoral fins. In contrast, the fins of the female are highly speckled, lack bright coloration, and the dorsal fin has grayish to white blotches which extend onto the dorsal part of the back. Morphologically, the males are smaller in body size and have a higher and wider cockscomb than females (Peppar 1965).

When high cockscomb are not breeding, they may be found in small groups of 6 or more individuals under the same rock. During the breeding season, however, there is conflicting opinion about the nesting territoriality of this species. Peppar (1965) found pairs of breeding cockscombs limited to usually one pair per rock. Marliave (1975a) however, reported often finding 2 females tending eggs under the same rock and occasionally found males nearby. It is possible that territoriality breaks down under conditions of higher abundances of individuals and limited nesting sites.

The spawning season of high cockscomb begins in January in British Columbia (Peppar 1965; Marliave 1975a), and eggs have been found in late February to late March in Puget Sound (Schultz and DeLacy 1932). The first signs of sexual maturing begin at ages of 2-3 years and lengths of about 80-90 mm for both sexes (Peppar 1965).

At maturity, the partially bilobed ovary ranges from 18.4 to 28 m by 7.1 to 12.3 mm and contains from 2,000 - 3,000 eggs (Fig. 30.1). These unfertilized eggs measure .79-.96 mm in diameter and are all spawned at once (Peppar 1965). Spawning takes place in the mid to low intertidal zones where the tightly adhering eggs are deposited under rocks or on large bivalve shells (Marliave 1975a; Schultz and DeLacy 1932). Egg masses are only loosely attached to the substrate (Schultz and DeLacy 1932).

Fertilized eggs range from 1.27-1.45 mm in diameter (Peppar 1965), and are lime-green to white becoming silver-gray with development (Marliave 1975a). Freshly laid eggs contain 1-3 oil globules and older eggs contain a large globule (.33-.41 mm diameter) and one smaller one (Schultz and DeLacy 1932). Schultz and DeLacy (1932) reported the dimensions of an egg mass to be 14 mm high, 20 mm diameter at the top, 17 mm diameter at the middle, and 27 mm diameter at the bottom.

Parental care of the developing embryos is provided by the female which coils around the eggs creating a groove around the outermost edge of the mass. In the laboratory, a female was observed coiled in a U-shape around the egg mass with dorsal and anal fins erect and caudal fin expanded, and rhythmically fanned the eggs with the posterior half of her body (Peppar 1965). The female remains with the eggs until hatching, which occurs in 16 days at 7-9^{o}C and 13 days at 10-12^{o}C (Peppar 1965).

Larvae are about 7.5 mm at hatching and contain an oil globule in the yolk sac. They are translucent and elongate, with a snout to anus length of about 2/5 of total length. Newly hatched larvae described by Peppar (1965) contained the following pigment pattern: a pair of large melanophores on the anterolateral surface of the yolk sac, two to three widely spaced chromatophores lateral to the gut, a row of 10-14 large melanophores on the ventral gut surface from the yolk sac to the anal opening, two large chromatophores on the lateral surfaces of the anal pipe and a pair of equal size median to them at the base of the pipe, 36-47 small postanal midventral melanophores, and 4-6 pigment spots on the caudal peduncle (Fig. 30.2 A, B).

Anoplarchus sp. larvae (6, 8, 15, 17, 23 mm) described by Blackburn (1973), differ slightly in the numbers of ventral melanophores present. Marliave (1975a) also briefly described and illutrated newly hatched high cockscomb (Fig. 30.2 C).

The larvae are positively phototactic at hatching (Marliave 1975a; Peppar 1965) and young of the year enter the intertidal area at ~25-30 mm during June-August. They are first located in the low intertidal zone

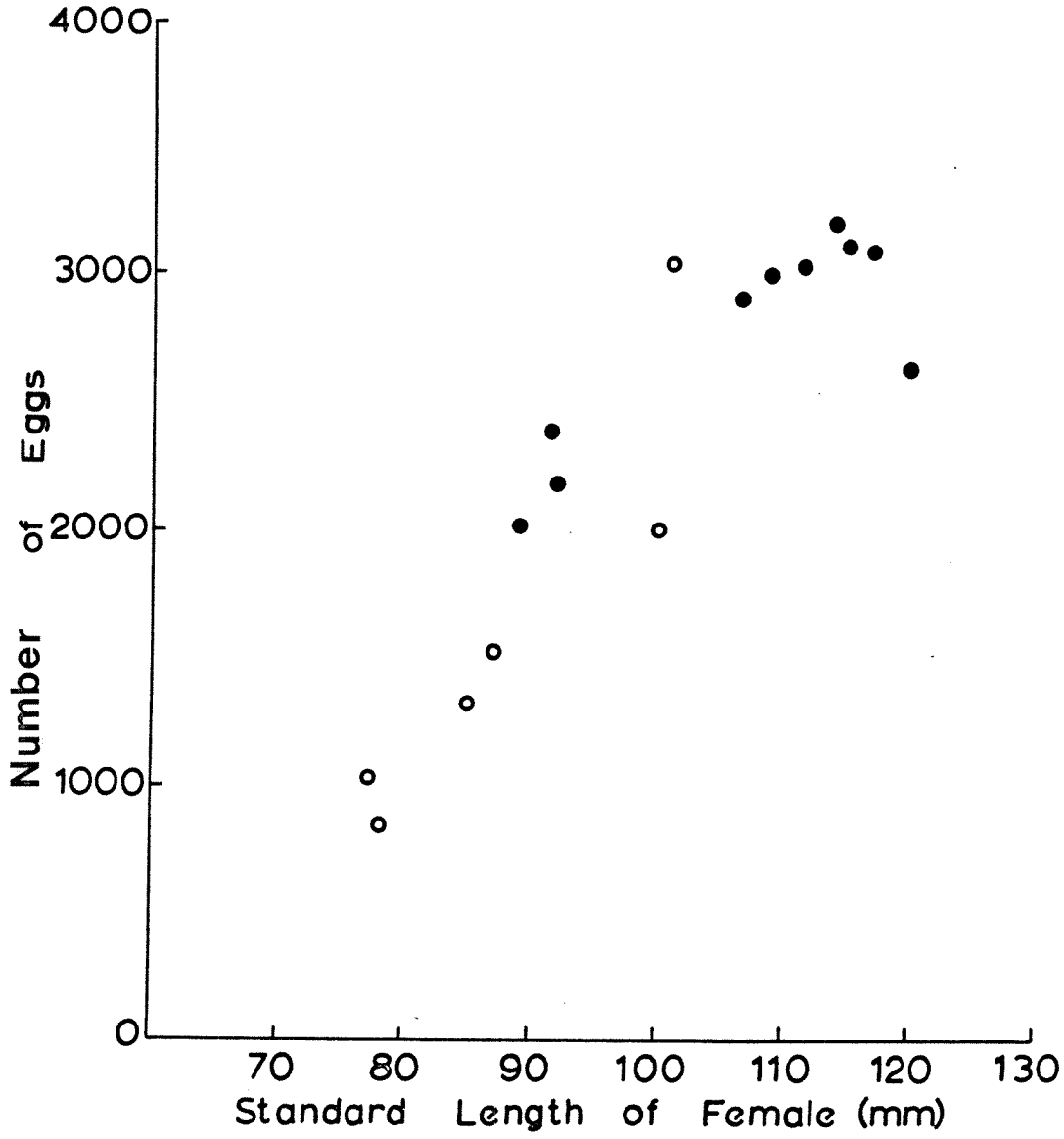

Fig. 30.1. Relationship of number of eggs produced to length of female for high cockscomb, Anoplarchus purpurescens. Unenclosed points from Schultz and DeLacy (1932). (Source: Peppar 1965).

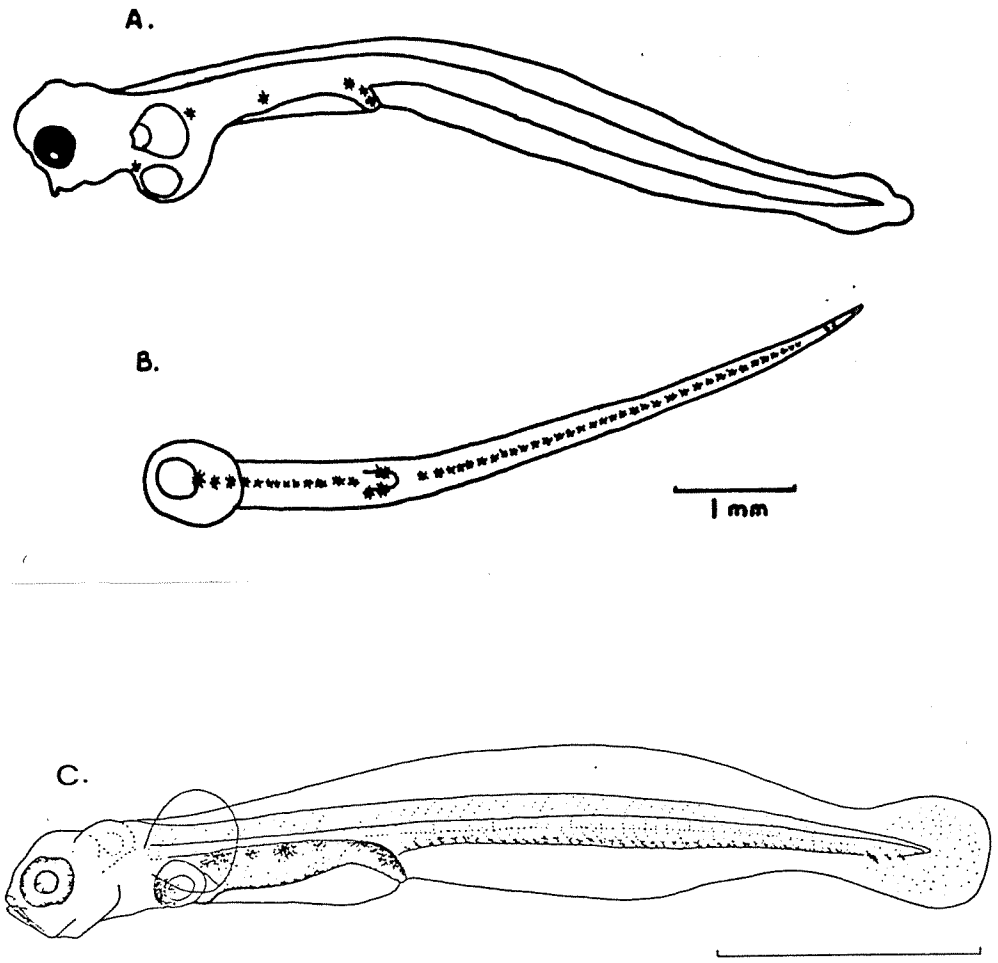

Fig. 30.2. Larvae of high cockscomb, Anoplarchus purpurescens: A) Newly hatched larva, 7.4 mm TL; B) same larva, ventral view from anterior tip of yolk sac to tail; C) 2 mm scale, 7.5 mm TL. (Sources: A,B- Peppar 1965; C- Marliave 1975a).

and later, move to midintertidal levels (Peppar 1965). Food of the planktonic larvae includes eggs, nauplii, and adult copepods (Barraclough and Fulton 1968; Barraclough et al. 1968).

Chirolophis nugator - Mosshead warbonnet

Range: northern California to Umnak, Aleutian Islands

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, subtidal to intertidal

Spawning habitat: unknown

Spawning season: winter (British Columbia)

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Adults are mainly subtidal, but are also found under rocks at low tide in the intertidal zones. They range from California to the Aleutian Islands (Hart 1973). Sitings of this species in Puget Sound have occurred from the Tacoma area to the San Juans (Miller and Borton 1980).

Life history and reproduction of mosshead warbonnet are unstudied. Hart (1973) mentioned finding a gravid female with 2 mm diameter eggs during January on southern Vancouver Island.

Larvae identified as "Chirolophus sp." were measured and described by Blackburn (1973). For larvae 10-30 mm, snout to anus length ranges from 35-40% of total length, and the anterior portion of the gut forms a single coil to the right. In 10.5 mm larvae, there are 1-3 small melanophores on the posterior part of the crown and usually 3 on the dorsal midline of the "medulla of the spine chord." There are 6-9, often square, melanophores along the dorsolateral surface of the peritoneum on each side of the body. In addition, there is a single row of 33-42, or more, melanophores on the ventral postanal midline which begin on the 4th or 5th myomere posterior to the anus. Finally, on small thin specimens, a row of 27-40 internal melanophores are present dorsal to the spinal chord which extends from just posterior to the anus to the caudal peduncle. At sizes of 15.5 mm, a few dermal melanophores appear on the dorsal body surface just anterior to the caudal peduncle forming a row on either side of the dorsal fin.

Chirolophis polyactocephalus - Decorated warbonnet

Range:

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

No early life history or reproductive information is presently available for decorated warbonnet. Adults are known from only a few records in Puget Sound (Miller and Borton 1980).

Lumpenus maculatus - Daubed shanny

Range: Puget Sound, Washington to Arctic Alaska; also in north Atlantic to Spitzbergen Island

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, subtidal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Populations of daubed shanny occur in both the Pacific and Atlantic oceans. In the Pacific, Puget Sound marks the southern range limit, with the species extending north to Arctic Alaska (Hart 1973).

Habits of the adults are largely unknown although Hart (1973) reported they are taken to depths of 55 to 91 m on hard sand bottoms in British Columbia. Aspects of their spawning biology are also unknown.

Larvae from the Atlantic, were briefly described by Faber (1976). They are distinguished by an elongate body form and a tubular gut which reaches to the middle of the body. No gas bladder is present. Pigmentation of a 13.5 mm larva consists of large stellate melanophores along each side of the gut, a pair of melanophores ventral to the pectoral fins, several melanophores on the anal pipe, and < 45 (usually 30-40) postanal midventral melanophores, which correspond closely to the number of postanal myomeres and developing anal fin rays (Fig. 30.3). During the larval period, no melanophores are present on the head. Illustrations of daubed shanny have occurred in other references, but were often misidentified (see Faber 1976).

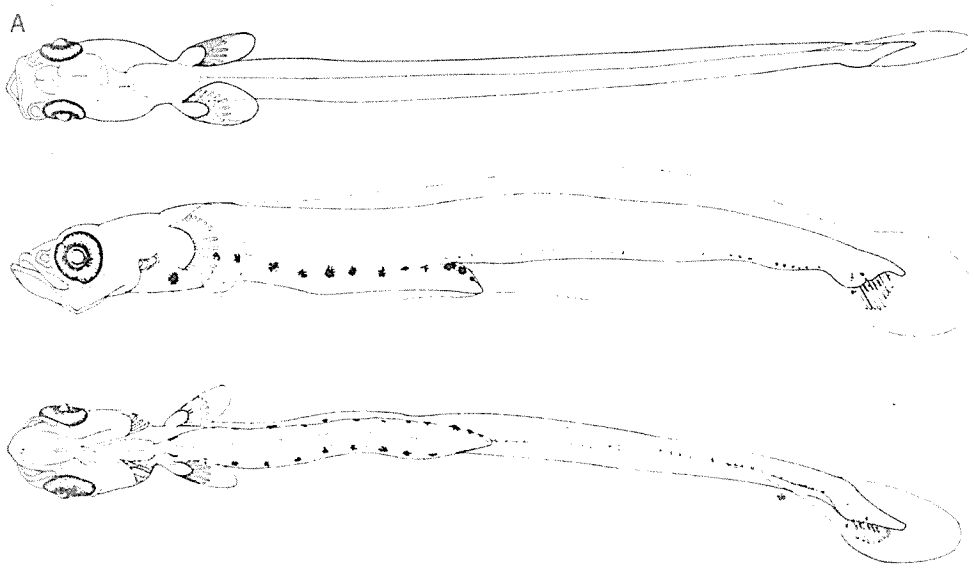

Fig. 30.3. Larvae of daubed shanny, Lumpenus maculatus, 13.5 mm; dorsal, lateral, and ventral views. (Source: Faber 1976).

Lumpenus sagitta - Snake prickleback

Range: northern California to Aleutians and Bering Sea

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: unknown

Larvae: undescribed

Snake prickleback are common and widespread throughout Puget Sound and the San Juan Islands (Miller and Borton 1980). They are taken to depths of 200 m in British Columbia and range from northern California to the Bering Sea (Hart 1973).

Information on spawning biology is currently unavailable. Larvae are pelagic and at lengths of 5-52 mm occur in the Strait of Georgia in April and May, and consume primarily copepods (Barraclough 1967; Robinson et al. 1968).

Blackburn (1973) briefly described snake prickleback larvae from Skagit Bay, Washington, which were collected only during February to April. Pigmentation consisted of a row of 4-7 melanophores on either side of the gut in line with its dorsal margin, one melanophore on either side immediately below the pectoral fin base, one row of up to four melanophores on the midventral line of the isthmus (in larvae larger than 34 mm), and one or two melanophores on the dorsal surface of the downward projecting anal pipe. The presence of adult coloration occurred on some individuals as small as 35 mm and not in others as large as 40-42 mm. Blackburn also included morphometrics for 15, 21, 25, 33.5, and 36.8 mm larvae.

Phytichthys chirus - Ribbon prickleback

Range: southern California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, in tidepools

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Ribbon prickleback are frequently reported from the San Juans (Miller and Borton 1980) and Strait of Juan de Fuca where they occur as adults primarily in tidepools above the +0.30 m tide height on rocky headlands. They occur rarely beneath rocks and prefer pools with surfgrass, mussels, coralline algae, or bedrock (Cross 1981).

No early life history information is available.

Plectobranchus evides - Bluebarred prickleback

Range: southern California to central British Columbia

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Probably subtidal as adults, bluebarred prickleback range from southern California to central British Columbia (Hart 1973). In Puget Sound they are known from south Sound (Eld Inlet), Hood Canal, and north to Skagit Bay (Miller and Borton 1980).

No information on their spawning habits is available.

Poroclinus rothrocki - Whitebarred prickleback

Range: southern California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Whitebarred prickleback are reported throughout Puget Sound and are known on a number of occasions from Port Susan and northern Saratoga Passage areas (Miller and Borton 1980). This species ranges from southern California to the Bering Sea (Hart 1973).

Spawning biology and early life history remain unstudied.

Xiphister atropurpureus - Black prickleback

Range: Baja California to Kodiak Island

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, intertidal

Spawning habitat: demersal, under rocks in intertidal areas

Spawning season: late winter - spring (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: pelagic

Black prickleback is a demersal, nearshore species ranging from Baja California to southeast Alaska and Kodiak Island (Hart 1973). Along the Strait of Juan de Fuca, it is a primary intertidal resident, spending all its life (except larval stages) in the intertidal zone. Adults are found in tidepools or under rocks on pebbles, shells, or sand substrates (Wourms and Evans 1974a; Cross 1981).

In British Columbia, the spawning season of black prickleback extends from late winter to spring with earlier spawning occurring in more protected sites. That is, during winter, spawning takes place on rocky beaches protected from wave action beginning in December and continuing to March. At the more exposed sites spawning does not begin until early April and ends in early May. Marliave (1975b) suggested that spawning began when a decrease in wave action permitted breeding and probably ceased when water temperatures became too high. Most evidence indicates that only one spawning per female per year takes place (Wingert 1974; Wourms and Evans 1974a; Marliave and DeMartini 1977).

In the females, the ovary is fusiform in shape and united posteriorly forming a common ovarian duct. The testes are paired, elongate, fusiform and united posteriorly to form a common sperm duct that leads directly to the genital opening (Wingert 1974).

Black prickleback reach sexual maturity at 120-125 mm TL or about 2-3 years of age (Wingert 1974), and spawning takes place under boulders on moderately exposed shores with a pebble or shell substrate (Marliave 1975a). In the lab, a male black prickleback was observed to coil around the female and fertilized the eggs as they were extruded. After fertilization, both individuals worked the eggs into a spherical egg mass (Wourms and Evans 1974a). Marliave and DeMartini (1977) found that the male guards the egg mass and in some cases one male guarded several egg masses simultaneously. These masses were at different stages of development, suggesting repeated spawnings.

Egg masses range in size from 20-50 mm in diameter and contain 2 mm adhesive eggs. The number of eggs produced per female ranges from ~500 to over 4,000 (Table 30.1) and the number of eggs increases with length of the female (Fig. 30.4). Ovarian eggs and newly spawned, unfertilized eggs are orange, but become opaque white several hours after fertilization. When first spawned, the outer egg covering is soft and glutenous and becomes deformed into flat surfaces at the points of contact with adjacent eggs. When the eggs are hardened, they are securely bound at these points of contact. Black prickleback eggs contain several central oil globules (Wourms and Evans 1974b).

Embyonic development of black prickleback requires about 21 days at 13°C and is similar to development of most teleost fishes (Table 30.2 and Fig. 30.5).

Larvae hatch at 7 to 10 mm TL depending on the size of the parent or the egg, and maturity of the hatch. They are elongate with a snout to anus length of about 2/5 of their total length. The yolk sac is small and contains a single oil globule. Larval pigmentation consists of about seven melanophores on each side of the dorsal gut surface, about 12 small melanophores on the dorsal surface of the tail, about 25 postanal midventral melanophores, and from the illustrations, numerous melanophores on the ventral surface of the yolk sac and gut (Fig. 30.6). With development, melanophores appear on the head and nape and along the lateral posterior body surface. Larvae up through 17 mm TL appear to possess a preanal finfold in addition to the continuous dorsal and anal finfolds.

In Barkley Sound, larval black prickleback begin schooling inshore around kelp beds and rocky prominences during late May to early June (Marliave 1975b). They transform at about 21 mm TL and demonstrate a preference to settle on gravel as opposed to sand, pebbles, or rocks (Marliave 1977).

Table 30.1. Fecundity estimates for black prickleback, Xiphister atropurpureus, based on examinations of ovaries and egg masses.

Reference	Location	Fecundity* 1	2
Wourms and Evans 1974(a)	California	-	500
Marliave and DeMartini 1977	B.C.-California	1234±656 (n=9)	1314±419
Marliave 1975(a)	B.C.	-	500-2,000(8,000)
Wingert 1974	California	∿600-∿4000 (n=18)	-

*1 = number of eggs per ovary
2 = number of eggs per egg mass
n = sample number

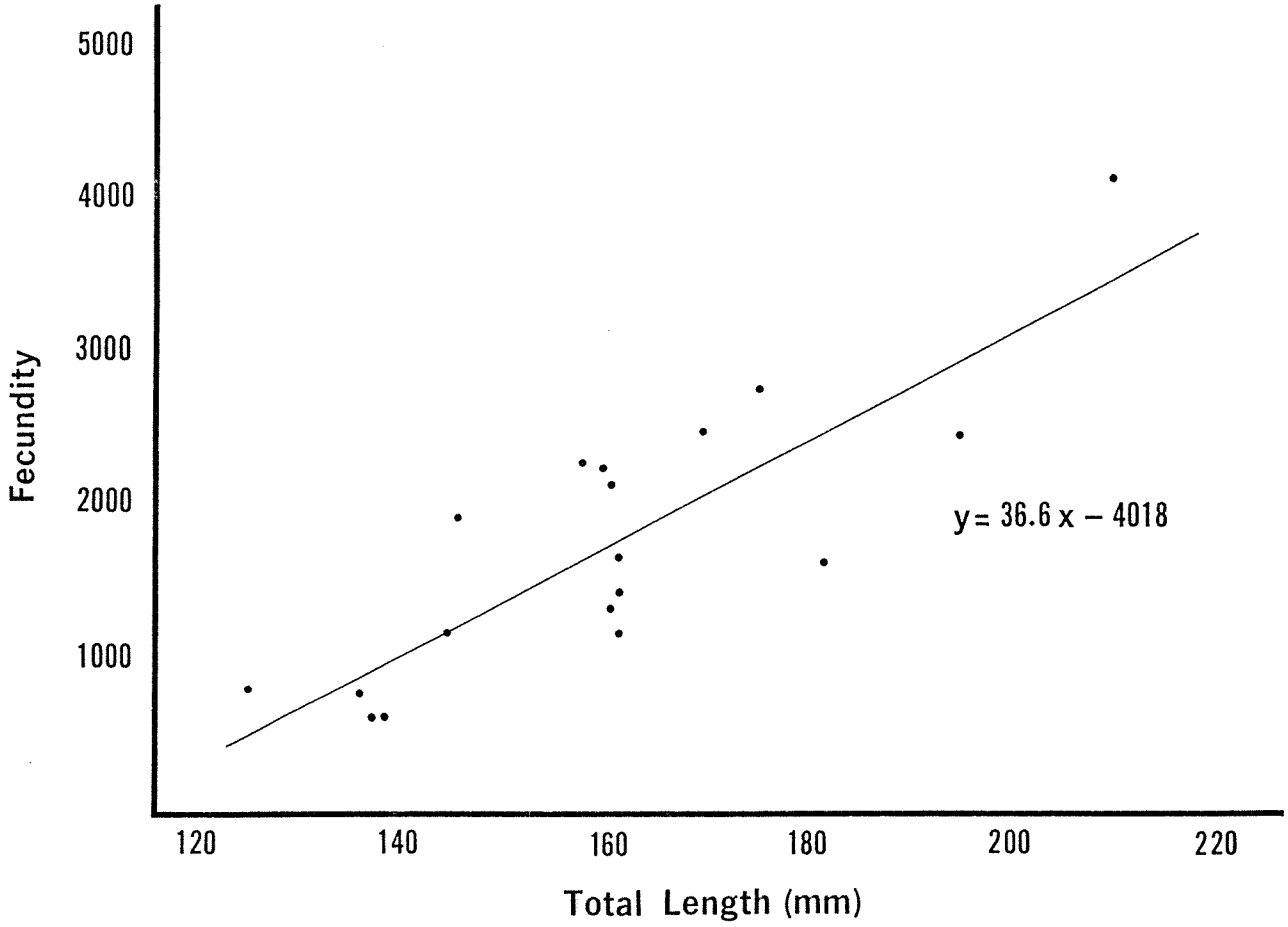

Fig. 30.4. Fecundity-length relationship for black prickleback, Xiphister atropurpureus, r = +.825. (Source: Wingert 1974).

Table 30.2. Embryonic development of black prickleback, Xiphister atropurpureus. (Source: Wourms and Evans 1974b).

Time (from fertilization)	Developmental event
1-2 h	1-cell stage (Fig. 30.5).
2-3 h	2-cell stage.
4 h	4-cell stage.
6 h	8-cell stage.
8 h	16-cell stage.
10 h	32-cell stage.
12 h	64-cell stage.
14 h	Early blastula (Fig. 30.5).
22 h	Mid blastula.
38 h	Late blastula (Fig. 30.5).
40 h	Early epiboly, gastrula (Fig. 30.5).
48 h	Mid epiboly, gastrula (Fig. 30.5).
72 h	Embryonic axis.
84 h	Early somite. Embryo with 1-15 pairs of somites, optic vesicles appear (Fig. 30.5).
120 h	Midsomite. Embryo with 15-25 pairs of somites. Embryo extends over 1/2 the circumference of yolk, regionalization of brain begins, Kupffer's vesicle appears.
6 d	Late somite. Embryo with 25-50 somites, and extends 3/4 of way around yolk. Well defined head, trunk, and tail, Optic cup and lens have formed (Fig. 30.5).
7 d	Early tail bud. Embryo is about 1.5 mm, tail lifts from yolk, heart beat (Fig. 30.5).
8 d	Mid tail bud. Embryo moves, hindgut forming, head massive and dome-shaped, nasal placodes present, otic vesicles formed.
9 d	Late tail bud. Embryo is 2.75-3.0 mm dorsal and ventral finfolds evident (Fig. 30.5).
10 d	Finfold 1. Embryo is about 3.5 mm, eyes becoming pigmented, anus formed.

Table 30.2. (Cont.) Embryonic development of black prickleback, Xiphister atropurpureus. (Source: Wourms and Evans 1974b).

Time (from fertilization)	Developmental event
11 d	Finfold 2. Length about 4.0-4.5 mm, embryo is motile, retina pigmented.
12 d	Finfold 3. Length about 5.0 mm, operculum visible, otoliths appear, liver and viscera forming, pigment cells appear on the ventral surface of the tail.
13 d	Finfold 4. Length about 5.25 mm, eye is heavily pigmented, pectoral fins free. (Fig. 30.5).
14 d	Mouth and gills 1. Length 5.5 mm, lower jaw formed, pectoral fins contain fin rays, liver well formed.
15 d	Mouth and gills 2. Length 6.0 mm, well-developed pericardial sinus.
16 d	Mouth and gills 3. Length about 6.5 mm, gill operculum well developed with free access to gill cavity.
17 d	Mouth and gills 4. Length about 7.0 mm, branchial arches prominent, presence of large melanopheres along ventral body surface at base of finfold.
18 d	Circulation 1. Length about 7.0 mm. Erythrocytes present but confined to pericardial cavity and yolk mass.
19 d	Circulation 2. Length about 7.5 mm circulation becomes more extensive (Fig. 30.5).
20 d	Circulation 3. Length about 8.0 mm, gill arches more developed, circulation extends to tail.
21 d	Hatching. Larva is $\sim$ 8.5 mm (Fig. 30.5).

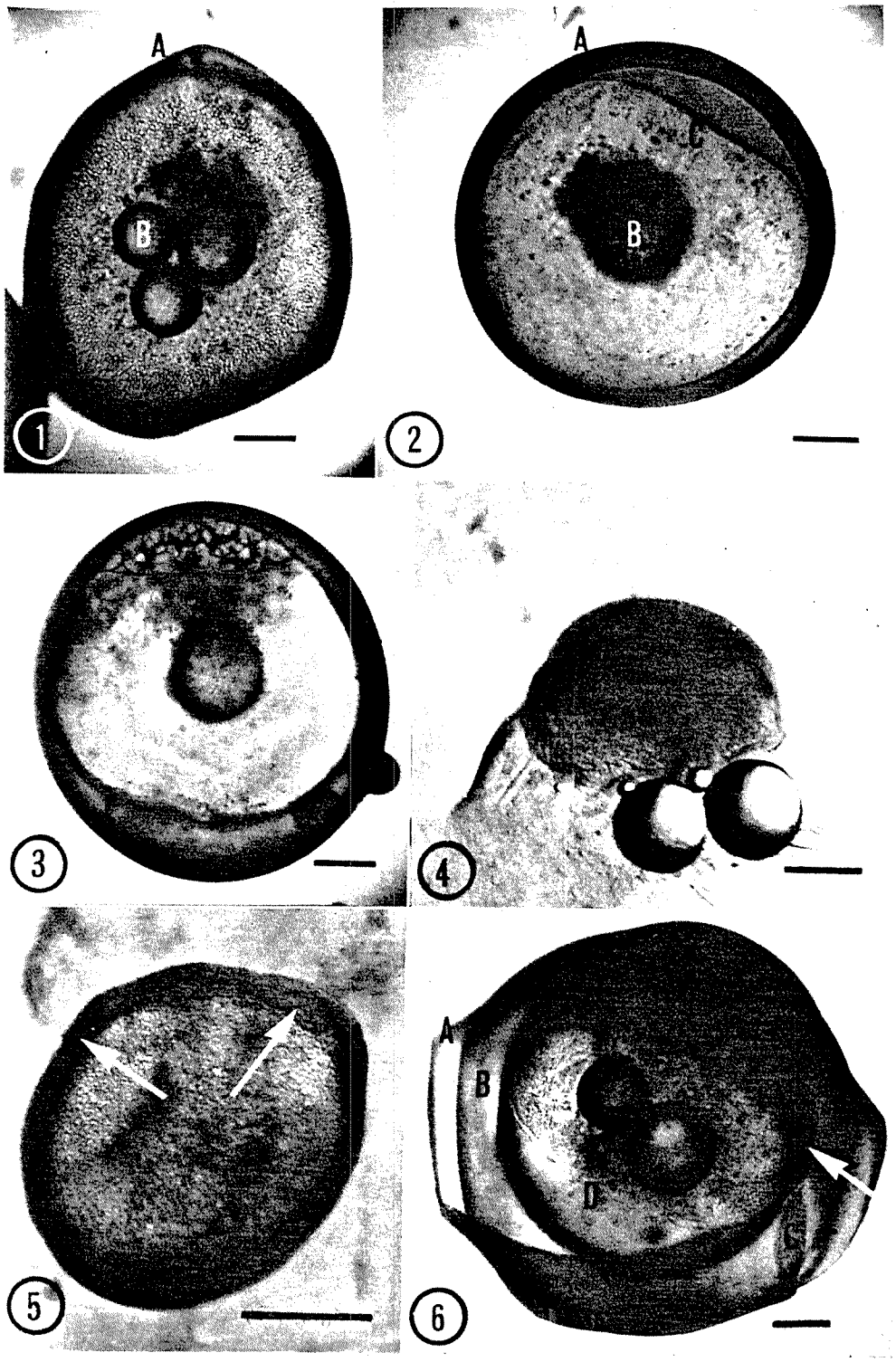

Fig. 30.5. Development of eggs of black prickleback, Xiphister atropurpureus. 1) Unfertilized ovum, newly spawned, B = oil droplets; 2) One-cell stage, C = blastodisc, A = egg envelope, B = oil droplet; 3) Early blastula; 4) Late blastula; 5) Early epiboly, gastrula, partially dechorionated, A = outer envelope, B = inner envelope, C = point of contact, D = germ ring, arrow indicates site of embryonic shield. (Source: Wourms and Evans 1974b).

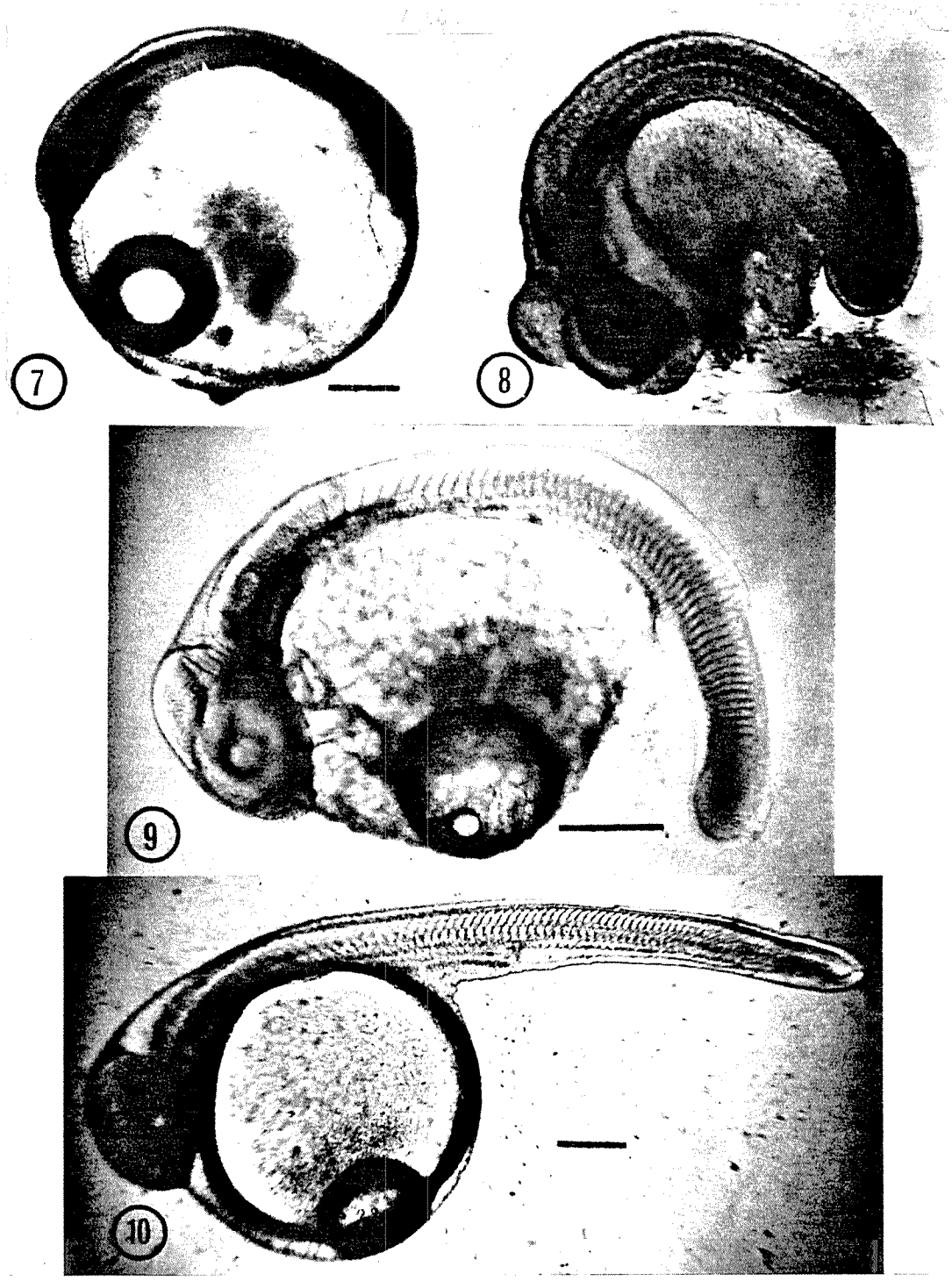

Fig. 30.5. (cont.) Development of eggs of black prickleback, Xiphister atropurpureus. 7) Early somite; 8) Late somite, about 30-40 pairs of somites; 9) Early tail bud. Figs. 7-10 are dechorionated eggs. (Source: Wourms and Evans 1974b).

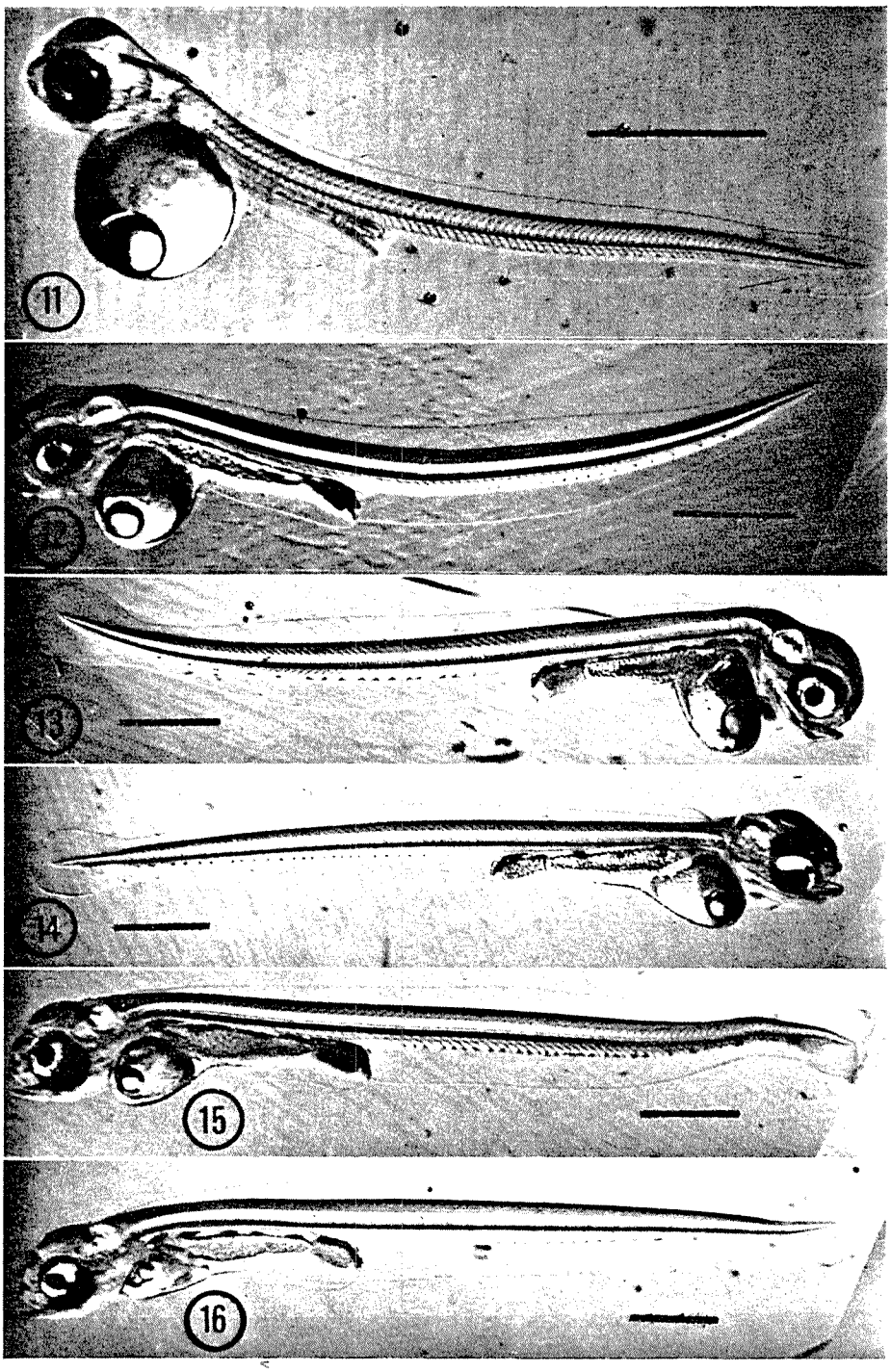

Fig. 30.5. (cont.) Development of black prickleback, Xiphister atropurpureus. 11) Finfold 4, length about 5.25 mm; 12) Circulation 2, length about 7.5 mm; 13) Hatching, length about 8.5 mm; 14) Posthatching 1, about 1 d; 15) Posthatching 2, about 4 d; 16) Posthatching 3, about 8 d. Figs. 11-12 are dechorionated. (Source: Wourms and Evans 1974b).

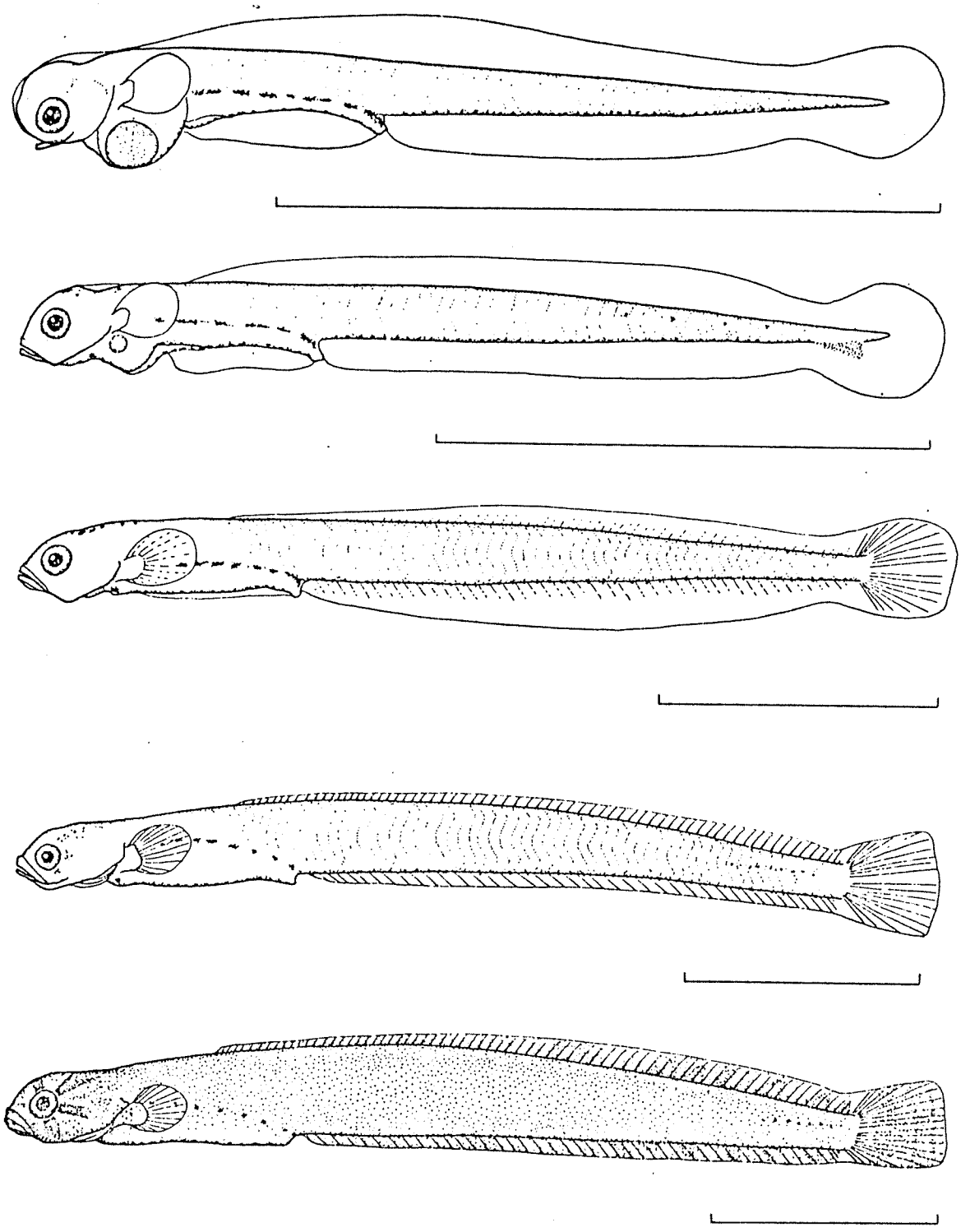

Fig. 30.6. Larval development of black prickleback, Xiphister atropurpureus. (5 mm scale) 0-day, 7 mm TL; 6-day, 9 mm TL; 32-day, 17 mm TL; 60-day, 20 mm TL; 60-day, settled, 21 mm TL. (Source: Marliave 1975a).

Xiphister mucosus - Rock prickleback

Range: southern California to southeast Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, intertidal and subtidal

Spawning habitat: demersal, under rocks

Spawning season: late winter-spring (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: pelagic, undescribed

Rock prickleback are found subtidally and in the intertidal zone from southern California to southeast Alaska (Hart 1973). Intertidally, they are found in tidepools with green algae, cobbles or pebbles and beneath rocks (Cross 1981).

In British Columbia, rock prickleback demonstrate a similar spawning ecology to that of black prickleback. For example, spawning occurs at about the same time, late winter to spring, for both species and eggs are deposited under boulders in the low intertidal zone. Eggs are spawned in a mass which the male coils around. Like black prickleback, rock prickleback females spawn only once per season and release all the mature eggs in one batch (Marliave and DeMartini 1977; Marliave 1975a).

In California, rock prickleback are reported to spawn several months earlier and at deeper depths than black prickleback (Wingert 1974; Wourms and Evans 1974a).

Adult rock prickleback are larger than black prickleback and produce larger eggs (2.5 mm in diameter) and more of them. Marliave (1975a) found rock prickleback egg masses to contain between 2,000 and 15,000 eggs and the average fecundity of 8 rock prickleback females was 7,276 $\pm$ 2,552 (s.d.) eggs (Marliave and DeMartini 1977). Rock prickleback also reach sexual maturity at a greater size (280-300 mm TL) and older age (~5 years) than black prickleback (Wingert 1974).

Marliave (1975a) described larval rock pricklebacks as being identical to larval black prickleback, except they are larger, hatching at ~11 mm TL.

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31. PHOLIDAE

Apodichthys flavidus - Penpoint gunnel

Range: southern California to Kodiak Island

Occurrence in Puget Sound: common

Adult habitat: demersal, near rocks and algae

Spawning habitat: demersal, under rocks

Spawning season: winter (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: pelagic

Penpoint gunnel, which range from southern California to Kodiak Island (Hart 1973), are common in the lower intertidal and upper subtidal zones where they may seek cover under rocks or in algae (Wilkie 1965).

Clemens and Wilby (1961) observed pairs of penpoint gunnels coiled around white eggs near low tide in Burrard Inlet in January. Marliave (1975), however, found a penpoint gunnel egg mass tended by a lone male. Eggs were about 3 mm in diameter and under a boulder.

Larvae hatch at a length of 13 mm (Marliave 1975), are pelagic, and settle after 50 days or at about 25 mm TL (Wilkie 1965). Newly hatched larvae are thin, transparent, and elongate with a snout to anus length approximatley 3/5 of the total length. Pigmentation consists of about 10 prominent dorsal gut melanophores, which are especially large over the anus, a similar number of smaller melanophores on the ventral tail musculature, several melanophores on the dorsal musculature near the caudal peduncle, and a row of numerous fine melanophores on the ventral gut surface (Marliave 1975)(Fig. 31.1).

Other aspects of the reproductive biology of penpoint gunnel are unstudied.

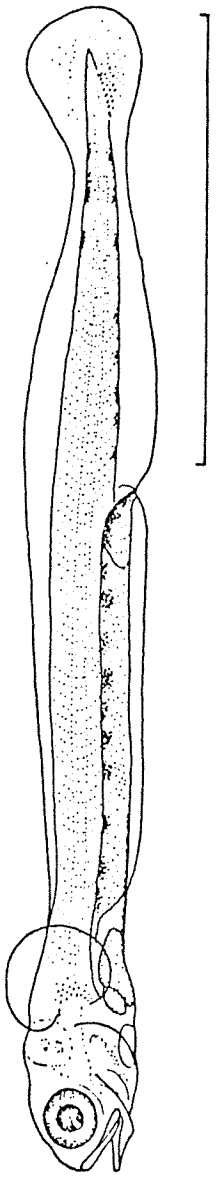

Fig. 31.1. Larval penpoint gunnel, Apodichthys flavidus. 5 mm scale, 0-day, 13 mm TL. (Source: Marliave 1975).

Pholis clemensi - Longfin gunnel

Range: Strait of Juan de Fuca and Strait of Georgia

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, near rocks

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Longfin gunnel are found only in northern Puget Sound, Strait of Georgia, and Juan de Fuca Strait (Hart 1973; Miller and Borton 1980), and have been collected among rocks from 12-28 m (Rosenblatt 1964).

No information on reproductive ecology or early life history is presently available.

Pholis laeta - Crescent gunnel

Range: northern California to Bering Sea

Occurrence in Puget Sound: common

Adult habitat: demersal, near rocks or algae

Spawning habitat: demersal

Spawning season: winter (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: pelagic

Crescent gunnel have been reported throughout Puget Sound (Miller and Borton 1980) and range along the Pacific coast from northern California to the Bering Sea and Aleutian Islands (Hart 1973). In British Columbia they reside beneath rocks and in tidepools with algal cover in the midintertidal zone (Peppar 1966) and at depths down to 73 m (Hart 1973).

An egg mass was reported by Marliave (1975) from the lower intertidal zone in early February and was protected by a pair of crescent gunnels coiled around it. After transport to the laboratory, the eggs hatched in late February and released 9 mm larvae. In contrast to penpoint gunnel, early stages of crescent gunnel do not have dorsal gut melanophores. Three large melanophores are located on the anal pipe and both the ventral gut surface and postanal ventral midline have rows of numerous fine melanophores. At about the time fin ray formation begins, a fine row of melanophores becomes visible on the dorsal gut surface. Snout to anus length is about 1/2 the total length (Fig. 31.2) (Marliave 1975). At metamorphosis, settling larvae show a preference for Phyllospadix where they entwine themselves in the blades (Marliave 1977).

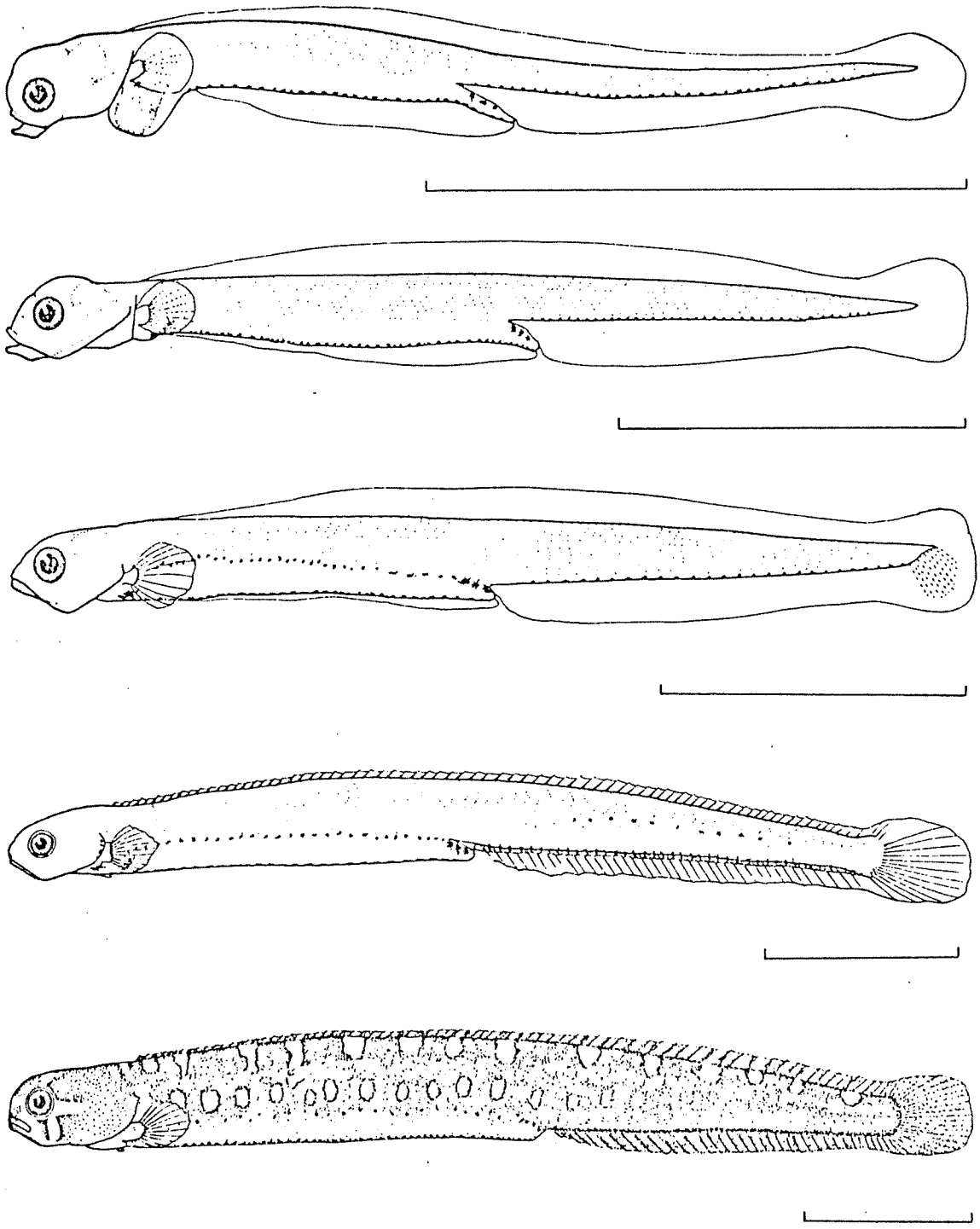

Fig. 31.2 Development of larval crescent gunnel, Pholis laeta. (5 mm scale) 0-day, 9 mm TL; 10-day, 14 mm TL; 27-day, 16 mm TL; 39-day, 25.5 mm TL; 52-day, settled, 29 mm TL. (Source: Marliave 1975).

Pholis ornata - Saddleback gunnel

Range: northern California to Bering Sea; Sea of Japan, Peter the Great Bay

Occurrence in Puget Sound: common

Adult habitat: demersal, near rocks and in tidepools

Spawning habitat: unknown

Spawning season: winter (British Columbia)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: undescribed

Saddleback gunnel are known from tidepools and beneath rocks in the midintertidal zone and lower (Peppar 1965) and are also found near the outlets of streams on muddy bottoms at depths between 18 and 37 m (Hart 1973). They range from northern California to the Bering Sea and in the western Pacific in the Sea of Japan and Peter the Great Bay (Hart 1973). They are frequently reported and widely distributed in appropriate habitats in Puget Sound (Miller and Borton 1980).

Except for one report of saddleback gunnel spawning demersal, guarded eggs during January and February in the low intertidal zone (Peppar 1965), no information on early life history or reproductive biology is available.

Pholis schultzi - Red gunnel

Range: Diablo Cove, California to southern British Columbia

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Ranging from Diablo Cove, California (Burge and Schultz 1973) to southern British Columbia (Hart 1973), red gunnel are recorded from areas exposed to ocean surge at depths down to 15 ft below the intertidal zone (Hart 1973). In Puget Sound they have been collected from the San Juan Islands and Admiralty Inlet (Miller and Borton 1980).

Reproduction and early life history of red gunnel remain unstudied.

Xererpes fucorum - Rockweed gunnel

Range: Baja California to central British Columbia

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, intertidal

Spawning habitat: demersal, under rocks

Spawning season: fall-winter (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: undescribed

Rockweed gunnel range from Baja California to central British Columbia, but only a few occurrences are reported from Puget Sound (Miller and Borton 1980). In California, they are concentrated in the lower intertidal zone where they usually associate with dense patches of brown and red algae or eelgrass (Barton 1974), or in moist crevices under rocks, or in shallow tidepools (Burgess 1976). In Canada, adults associate closely with masses of rockweed (Fucus)(Hart 1973).

Marliave (1975) found a rockweed gunnel nest with eyed embryos in the lower intertidal zone in early December, implying a fall-winter spawning period. An adult male was found coiled around the egg mass which contained eggs that were probably white when spawned, but had become silver gray with development of the embryos.

Larvae hatch at about 11 mm TL and have a melanophore color pattern and snout to anus length similar to penpoint gunnel (Marliave 1975).

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32. ANARHICHADIDAE

Anarrhichthys ocellatus - Wolf-eel

Range: Southern California to Gulf of Alaska, Krenitzen Islands in the Aleutians

Occurrence in Puget Sound: common

Adult habitat: demersal, in caves

Spawning habitat: same

Spawning season: probably winter-spring

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: pelagic

Wolf-eels are distributed from Southern California to the Gulf of Alaska and among the Krenitzen Islands in the Aleutians (Hart 1973). They are widely distributed throughout Puget Sound (Miller and Borton 1980) and are commonly found between 12-30 m, although smaller individuals ($\leq$ 30 cm) are sometimes found shallower (Friese 1966). They prefer rocky areas or cliffs and lead a secluded life in large rocky caves and crevices (Friese 1966).

Male wolf-eels can be distinguished from females by a larger size, more powerful head, and jaws with extremely thick lips. Spawning has been observed in the aquarium and in one case, the same female and male within a group of wolf-eels were observed spawning together during successive breeding seasons. It is not known if long-term pairing of the sexes occurs naturally (Friese 1966).

The eggs are laid demersally within a rocky crevice and in a cluster which the parents coil around (Hart 1973; Friese 1966; Cruys and Contera 1980). The white eggs are adhesive to each other, although not to the substrate. Both parents wrap their bodies around the gelatinous mass to keep the current from carrying it away (Fig. 32.1). The mass is gently rotated to insure a good flow of water throughout the eggs. The egg masses consist of 3,500 - 5,000 "pea-sized" eggs and have been observed in February in the wild (Cruys and Cantera 1980) and in December (Friese 1966) and February (Cruys and Cantera 1980) in aquaria. Development requires 3 to 4-1/2 months and hatching from an egg mass may continue over a two-week period (Cruys and Cantera 1980; Friese 1966).

Larvae hatch at about 30-35 mm and are characterized by a highly elongate body form, a short snout to anus length, and about 223 myomeres (Fig. 32.2)(Marliave 1975).

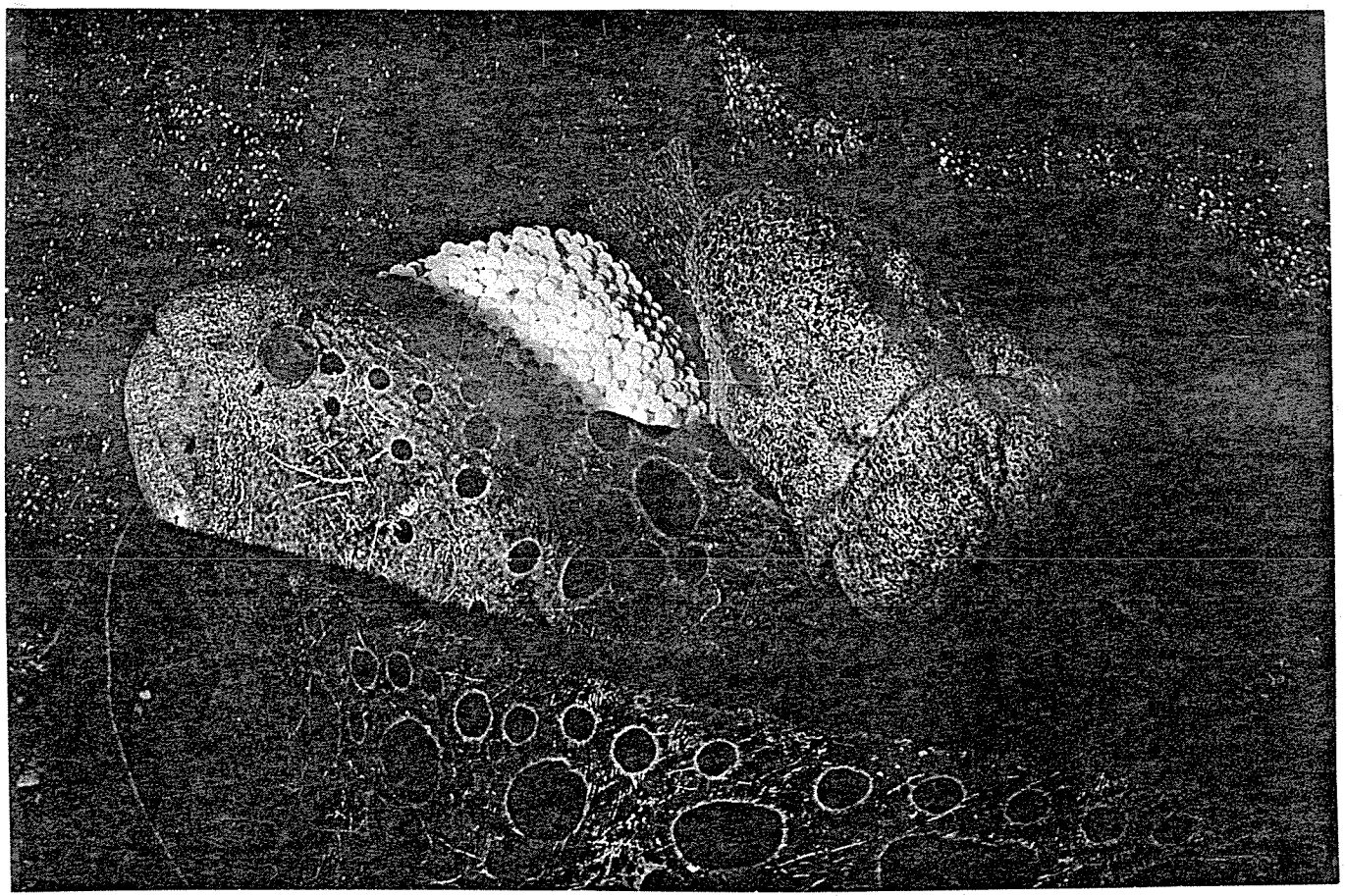

Fig. 32.1. Male and female wolf-eels, Anarrhichthys ocellatus, guarding their egg mass. The male (right) can be identified from the female (left) by a more powerful head and jaws with thick lips (Source: Cruys and Cantera 1980).

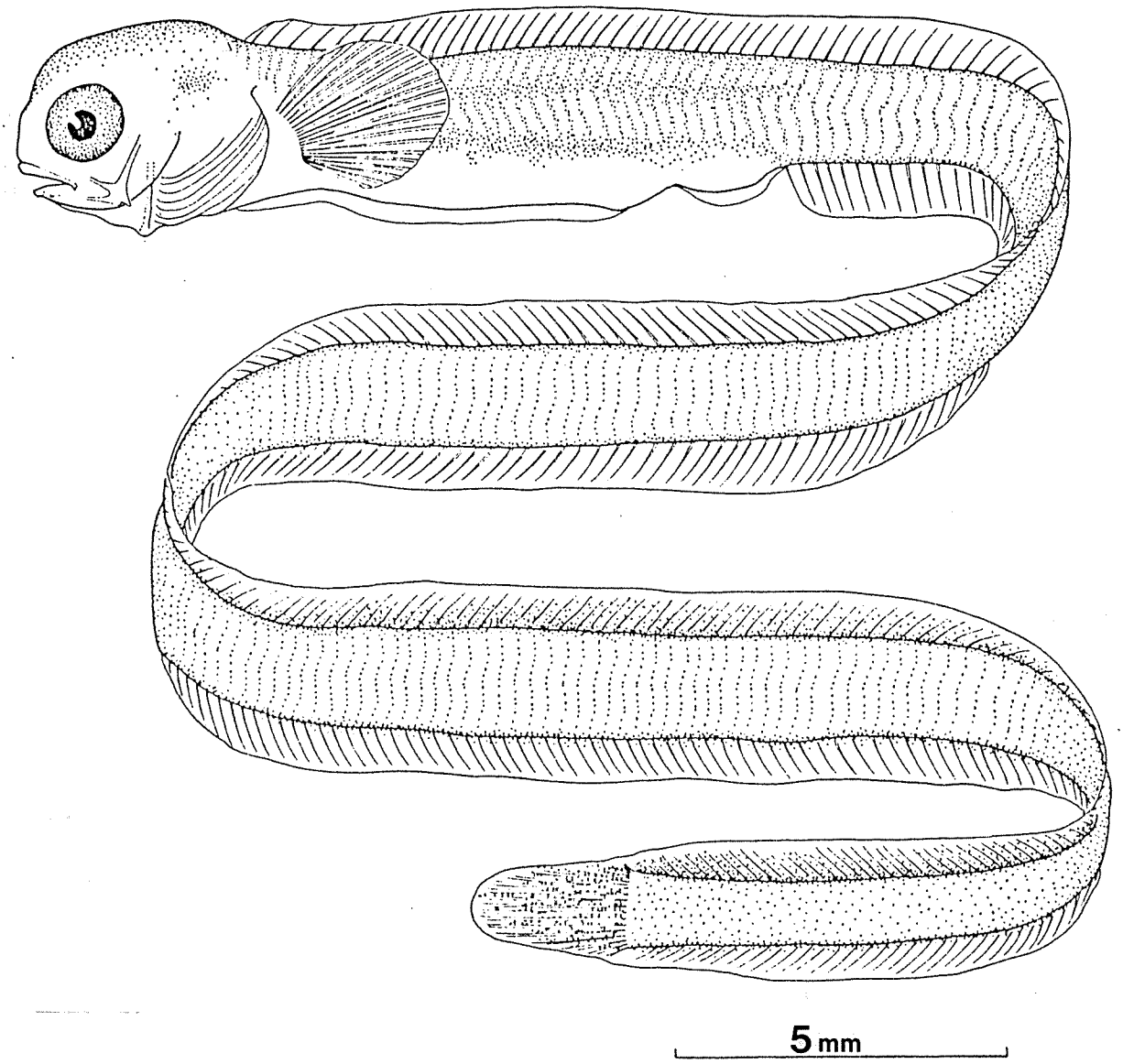

Fig. 32.2. Larval wolf-eel, Anarrhichthys ocellatus, 65 mm TL, collected from the plankton. (Source: Marliave 1975).

At hatching, wolf-eel larvae are pelagic and can feed on their own immediately, although they are born with a week's supply of yolk. In the aquarium, they have been observed to coil like snakes and strike at their prey, and have been successfuly reared on herring larvae and copepods (Cruys and Cantera 1980). Barraclough (1967) reported that two large larvae, 82 and 84 mm FL, from the Strait of Georgia during April had eaten larval walleye pollock.

Wolf-eel young remain pelagic for about two months after which they settle to the bottom. In the aquarium settled juveniles become highly territorial, seeking a rock crevice and defending it. Little is known about their behavior in the wild at this stage. After settling they begin to feed about once per day and their larval transparency is replaced by two bright orange stripes on the tail. At 7 months, aquarium reared wolf-eels feed once every 48 hours and are almost a year old before they are able to catch and eat crab (Cruys and Cantera 1980).

Wolf-eels pass through a definite change in dentition, body form, and coloration as they change from juvenile to adult form (Kanazawa 1952).

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33. PTILICHTHYIDAE

Ptilichthys goodei - Quillfish

Range: Oregon to the Bering Sea; Kanchatka, Kuril Islands, Okhotsk Sea

Occurrence in Puget Sound: uncommon

Adult habitat: probably demersal

Spawning habitat: unknown

Spawning season: spring (Oregon; Kodiak, Alaska)

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

This unusually shaped, long and slender fish ranges from Oregon (Richardson and DeHart 1975) through the Strait of Juan de Fuca to the San Juan Islands (Miller and Borton 1980) and north to Unalaska Island and the Bering Sea. In the western Pacific it is found off Kamchatka, in the Kurile Islands and in the Okhotsk Sea (Hart 1973).

Spawning behavior and eggs of the quillfish are unknown. Larvae are pelagic and have been taken up to 18 km off the central Oregon coast during March-May (Table 33.1) and in bays off Kodiak Island during May and July (Garrison and Rogers 1980). Larvae have also been taken in the western Pacific at about the same time (Kobayashi 1961).

The larvae of P. goodei are readily recognized by their slender, elongate form, a gut length of 34-40% SL, 225-229 myomeres, and a characteristic pigment pattern (Fig. 33.1). The pigmentation of larvae between 20 and 40 mm remains relatively unchanged and consists of: 1) head pigment which includes spots on the lower jaw, anterior part of the upper jaw, throat, and internal spots at the base of the hindbrain; 2) gut pigment which is mostly restricted to the dorsal and ventral surfaces with some additional spots over the anterior region. (Melanophores on the ventral surface of the gut form a single row on the anterior one-fourth to one-half of the gut and a double row along the rest of the gut); and 3) body pigment which is concentrated on the dorsal and ventral body surfaces (Richardson and DeHart 1975).

By the time larvae are 36 mm, the spines of the first dorsal fin and the rays of the second dorsal fin begin to form at the posterior and anterior ends of the fins, respectively. Development then proceeds anteriorly in the first dorsal fin and posteriorly in the second dorsal. The anal fin rays begin to form slightly anterior to the center of the

Table 33.1. Collection data for larval, transforming, and adult quillfish, Ptilichthys goodei, off Oregon. (Source: Richardson and DeHart 1975).

SL (mm)	Date	Location Lat. N	Location Long. W	Km from coast	Coastal reference	Time	Bottom depth (m)	Tow depth (m)	Gear	Bottom type[1]	Surface temp. (°C)
Larvae:											
20.3	25 Mar. 1973	44°00′	124°22.1′	18	Siuslaw River	1526-1542	117	100-0	Bongos	Gray sand-green mud	11.0
24.7	20 Apr. 1973	44°00′	124°22.1′	18	Siuslaw River	0235-0300	109	75-0	Bongos	Gray sand-green mud	10.4
36.0	14 May 1971	44°39.1′	124°17.7′	18	Newport	1621-1641	80	75-0	Bongos	Gray sand	11.2
Transforming:											
114	29 June 1971	44°39.1′	124°52.7′	65	Newport	1128-1153	340	150-0	Bongos	(Slope)	14.5
Adults:											
272	7 Aug. 1973	44°42′	124°7′	5	Moolach Beach	0945-1007	52	52	Otter trawl	Gray sand	9
309	3 July 1973	44°45′	124°14′	13	Cape Foulweather	1010-1028	80	80	Otter trawl	Gray sand	10

[1]From USC&GS Charts No. 5702 and No. 5802.

Table 33.2. Morphometrics (mm) and meristics of larval, transforming and adult quillfish, Ptilichthys goodei, off Oregon. (Source: Richardson and DeHart 1975).

		Morphometrics								Meristics								
													P_1			Myomeres		
SL	TL[1]	Snout length	Eye diameter	Head length	Upper jaw length	Lower jaw length	Snout to anus	Depth at pectoral base	Depth at anus	DI	DII[2]	A[2]	Left	Right	Branchiostegals	Preanal	Postanal	Total
Larvae:																		
20.3	21.0	0.4	0.7	2.3	0.8	1.1	8.0	0.9	0.9	—	—	—	—	—	—	55	174	229
24.7	25.5	0.4	0.6	2.2	0.7	1.1	9.3	1.1	1.1	—	—	—	—	—	—	55	170	225
36.0	36.9	0.5	0.7	2.7	0.9	1.1	12.5	1.1	1.1	40	~80	~113	—	—	5	57	170	227
Transforming:																		
114	117	1.6	1.1	6.1	1.8	2.6	32.2	2.0	2.0	83	148	179	13	13	5	55	172	227
																	Vertebrae	
Adults:																Abdominal	Caudal[3]	Total
272	276	5.2	2.8	17.0	3.8	5.0	81	5.5	7.0	83	144	180	13	13	5	53	174	227
309	313	6.3	3.0	19.0	4.2	6.0	91	6.0	7.7	88	142	181	13	13	5	53	174	227

[1]Total length is given for comparison with other publications, although the long caudal filament was not intact.
[2]Dorsal and anal fin ray counts include possible caudal fin elements dorsal and ventral to the fleshy caudal extension respectively.
[3]One fused caudal vertebra found in each adult specimen was counted as one vertebra.

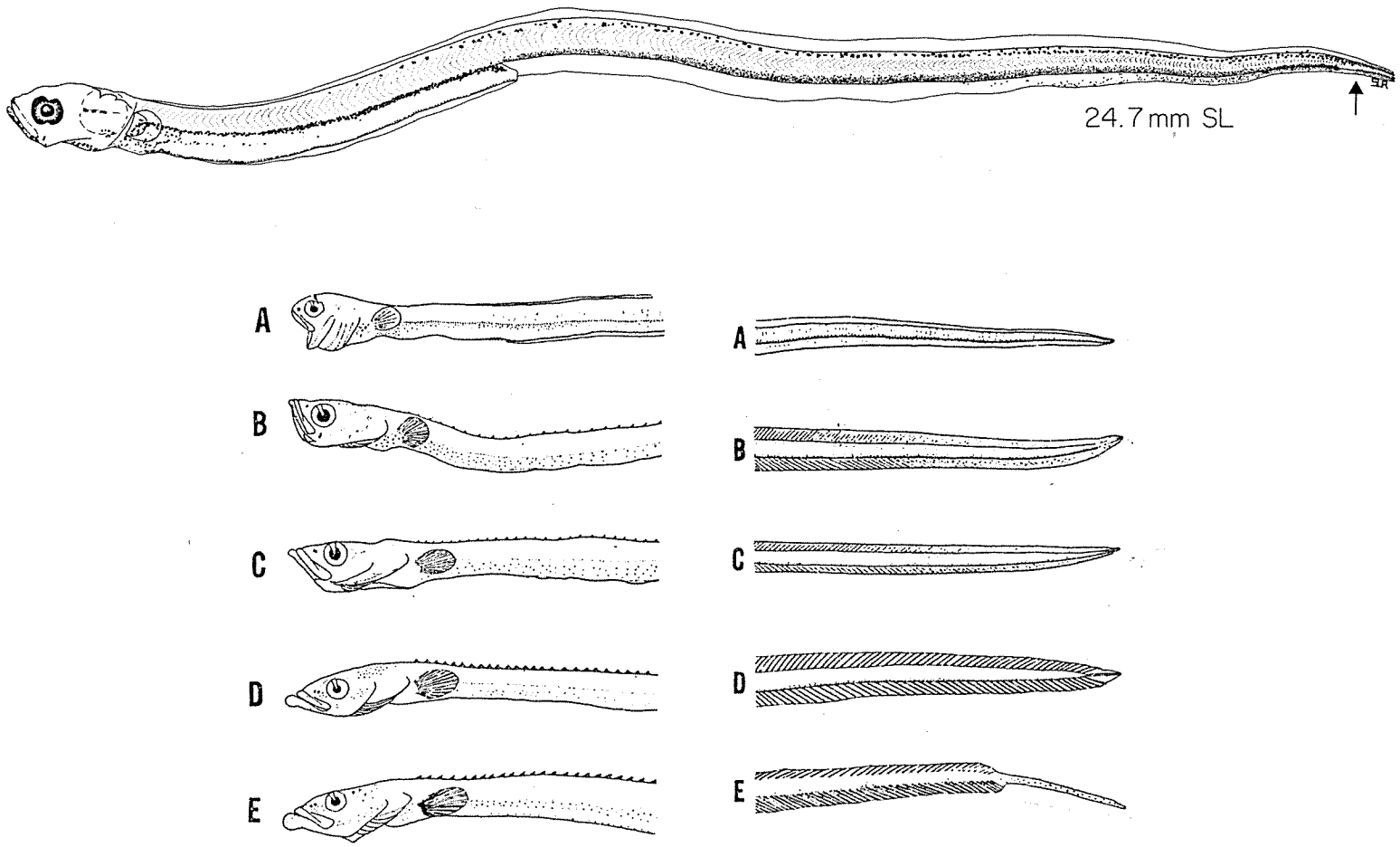

Fig. 33.1. Larval quillfish, Ptilichthys goodei: Top) 25 mm larva collected from the plankton off Oregon - arrow indicated point of reference for SL. (Source: Richardson and DeHart 1975); bottom) A - E, left - formation of fleshy tip of lower jaw of the quillfish; A - E, right - formation of the tip of caudal region of quillfish. A - 47 mm TL, B - 66.0 mm TL, C - 86.5 mm TL, D - 135.4 mm TL, E - 144.6 mm TL. (Source: Kobayashi 1961).

fin and develop anteriorly and posteriorly. At 36 mm, no pectoral fin rays are formed and pelvic fins are absent. The full number of adult fin rays are not developed in 86.5 mm larvae (Kobayashi 1961) but are present by 114 mm and the dorsal spines have the hooked character of the adults (Richardson and DeHart 1975).

Quillfish are also characterized by a fleshy protuberance on the anterior tip of the lower jaw and a fleshy extension in the caudal region. The lip feature begins to appear in larvae between 66 and 86.5 mm (Kobayashi 1961) and is distinct by 114 mm (Richardson and DeHart 1975). The caudal extension does not become apparent until sometime between 135 and 145 mm (Fig. 33.1).

Morphometrics and meristics for planktonic larvae collected off Oregon are provided in Table 33.2.

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34. CRYPTACANTHODIDAE

Delolepis gigantea - Giant wrymouth

Lyconectes aleutensis - Dwarf wrymouth

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35. SCYTALINIDAE

Scytalina cerdale - Graveldiver

Range: central California to the Aleutian Islands and Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, intertidal to subtidal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Aptly named for its ability to burrow in sand and gravel, the graveldiver inhabits the inshore area and may be found in tidepools left by the receding water. It ranges from central California through British Columbia and southeastern Alaska to the Aleutian Islands and Bering Sea (Hart 1973). From Puget Sound, specimens have been collected from the San Juan Islands area (Miller and Borton 1980).

At present, no information is available on the reproductive biology or early life history of this unusual fish.

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36. AMMODYTIDAE

Ammodytes hexapterus - Pacific sand lance

Range: southern California to Chukchi Sea; Sea of Okhotsk

Occurrence in Puget Sound: common

Adult habitat: pelagic, schooling, but becoming demersal at times

Spawning habitat: demersal, on sand

Spawning season: winter

Mode of reproduction: oviparous

Eggs: demersal, adhesive

Larvae: pelagic

Sand lance (sandlance or sand launce) or sand eels are small, schooling fish which are widely distributed in shallow seas throughout the higher latitudes of both the Pacific and Atlantic oceans. Currently, the systematics of the genus Ammodytes are confused with little agreement among authors (see Andriyashev 1954; Richards et al. 1963; Macer 1966; Reay 1970). One common point, at least among Atlantic species, is that there appears to be an inshore groups of species which is separate from an offshore group, although speciation within the groups is unresolved (Trumble 1973). In the Pacific Ocean, most investigators agree that sand lances are represented as a single species, Ammodytes hexapterus, which ranges along the west coast of North America and also occurs in the Chukchi, Bering, and Okhotsk Seas. However, some scientists (Kasahara 1961) feel that a different species, A. personatus, inhabits the area around Japan (Macy et al., 1978).

Despite the taxonomic confusion, life styles of sand lances are similar (Trumble 1973). Although widely distributed, sand lance populations form localized schools which usually associate with clean sand bottoms in areas rarely exceeding 100 m depths. Because they have no swim bladder, they must remain actively swimming to maintain position. When not swimming, they have been observed resting on the bottom or burrowing into sandy sediments at night or when threatened (see also Reay 1970; Meyer et al. 1979; Winslade 1974a, b, c; and Girsa and Danilov 1978).

Most of the literature available on sand lance reproductive biology comes from studies of species found in the Atlantic Ocean and North Sea. Summaries of literature from these areas are given by Reay (1970), Macer (1966), Fritzsche (1978), and Russel (1976). Descriptions and/or illustrations of eggs and larvae of Atlantic species are included in Macer (1967), Fritzsche (1978), Russel (1976), Williams et al. (1964), and

Richards (1965). Spawning biology and early life history of sand lance from the western Pacific near Japan (Ammodytes personatus) have also been studied somewhat (Hamada 1966 a, b, c, 1967, 1968; Inoue et al. 1967).

Limited information is available on the reproductive biology and early life history of Pacific sand lance (Ammodytes hexapterus), which according to Hart (197), ranges in the eastern Pacific from southern California to the Chukchi Sea. In Puget Sound, adults are common and widely distributed throughout the Sound (Miller and Borton 1980). Larvae appear in the plankton in January and remain accessible to plankton nets through April. Larger larvae are collected by surface tow nets through May. Sand lance larvae are numerically abundant in parts of the Sound during the spring and may be more common in Puget Sound during April than off the coast (Blackburn 1973; Waldron 1972). Larvae are also commonly taken in plankton tows during early spring in the Gulf of Alaska and Bering Sea (e.g., Waldron and Vinter 1978; Kashkina 1970; Musienko 1963; Dunn and Naplin 1974; Rogers et al. 1979; Kendall et al. 1980; English 1977, 1978; Favorite et al. 1975). Despite the numerous sources reporting on larval sand lance distributions, most aspects of spawning biology of Pacific sand lance remain unstudied.

In the following sections, most information was derived from studies on Atlantic Ammodytes species and similarities to the Pacific species, A. hexapterus, can only be inferred.

In the Atlantic, most sand lance species spawn during winter, although for at least one species, two spawning periods, spring and autumn, are reported (Reay 1970). According to Trumble (1973), sand lance in the Northeast Pacific probably spawn during winter, November-February, which agrees well with most catches of small larvae from this area. Atlantic sand lances reach sexual maturity at 1 to 2 (usually 2) years of age (Reay 1970), and in the western Pacific near Japan, sand lance ranging in ages from 1 to 3 years participate in spawning activity (Hamada 1966). Hamada (1967) considered the sex ratio to be 1:1, but ratios deviating from unity are known from other areas (and for other species)(Macer 1966).

Fecundity of sand lance females from the Murman coast ranges from 3,300 to 22,100 with an average of 6,800 eggs per female (Nikol'skii 1954, cited by Macy et al. 1978). A smaller Novaya Zemlya sand lance averages 4,350 eggs per female (Andriyashev 1954, cited by Trumble 1973) and the small (7-12 cm) Japanese sand lance has a fecundity of 1,000-8,000 eggs (Inoue et al. 1967). In the southern North Sea, the fecundity of A. tobianus ranges from 2,500 to 16,300 for females between 10.5 and 18.1 cm (Reay 1970). According to Macer (1966), North Sea sand lance have a unimodal or bimodal egg distribution and fecundity of lances with a unimodal egg distribution can be expressed by the equation:

$$\text{Fecundity} = 2.046\ (\text{length, cm})^{3.055}$$

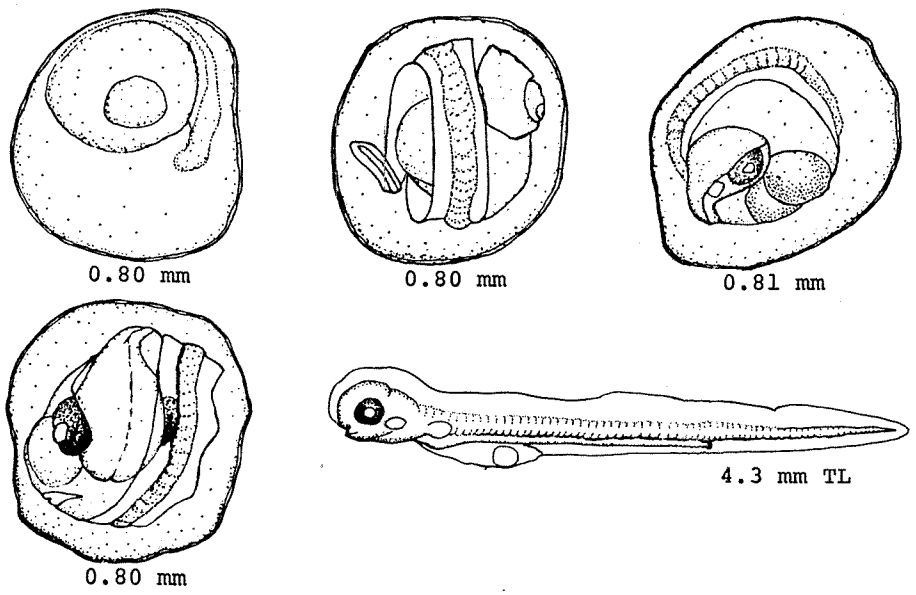
Japanese sand lance, according to Inoue et al. (1967), may spawn once or twice per season.

Sand lance spawning has been reported to occur at depths of 5-10, 20-40, and 25-100 m for Atlantic species (Reay 1970) and may take place in areas with strong currents (Andriyashev 1954, cited by Trumble 1973). Along the Atlantic coast, the eggs are not quite spherical and are demersal and slightly adhesive to sand grains. The egg membrane is pitted, the perivitelline space is small and the yolk is pale dull yellow or white. One bright yellow oil globule is located near the edge of the yolk but sometimes 0, 2, or 3 oil globule are present (Fig. 36.1). Fertilized, developing eggs are 0.67-0.91 mm ($\bar{X}$ = 0.825 mm) with the oil globule measuring 0.17-0.33 mm ($\bar{X}$ 0.22)(Williams et al. 1964). Similarly sized eggs are reported for sand lances from the Murman coast and the southwest North Sea (Macer 1966; Trumble 1973).

Near Japan, development of sand lance eggs requires 33 days at 6.19°C and 13 days at 15.74°C, with optimal hatching occurring at 8.2°C and poor development at 15.74°C (Inoue et al. 1967). During development, the embryo remains unpigmented until myomere formation at which times the eyes become brownish in color. The eyes darken later to black at about the same time that pigment appears along the ventral surface of the embryo (Fig. 36.1)(Williams et al. 1964).

In Japan waters, sand lance yolk larvae are about 3.81 mm (Inoue et al. 1967). According to Reay (1970), newly hatched larval sand lances undergo a period of quiescence within the sand not emerging until lengths of 4-5 mm. At this size, they appear near the bottom and remain there until they are about 10 mm, after which they become planktonic. Larger larvae undergo vertical migrations, being concentrated at 6-10 m during the day and deeper and occupying a wider range of depths at night (Inoue et al. 1967; Reay 1970).

Pacific sand lance (Ammodytes hexapterus) from the North Pacific (Okhotsk and Bering Seas) have been described (briefly) and illustrated (Kobayashi 1961). They are elongate, slender and relatively unpigmented. The anus is located slightly posterior to midbody and the head length is 15% of total length. Both these characters are reported to stay the same through all larval stages. Fin rays first appear in all fins in a 16.6 mm TL larva and attain the full number of rays in the pectoral fin at 21.1 mm TL, in the anal fin at 26.7 mm TL, and in the dorsal fin at 31.0 mm TL. Larval sand lance possess about 70-71 myomeres. Throughout most of the larval period, pigment is restricted to the lower portion of the body. A series of melanophores is present along the dorsal margin of the gut from near the pectoral fin to the anus and at the base of the anal fin (or finfold). Scattered melanophores are located on other parts of the body and increase in number with development (Fig. 36.1). References to descriptions and/or illustrations for other species of sand lance from other areas were given at the beginning of this section. A larval series (5.2 to 46.5 mm TL) of Ammodytes sp. was compiled from the literature by Fritzsche (1978)(Fig. 36.2).



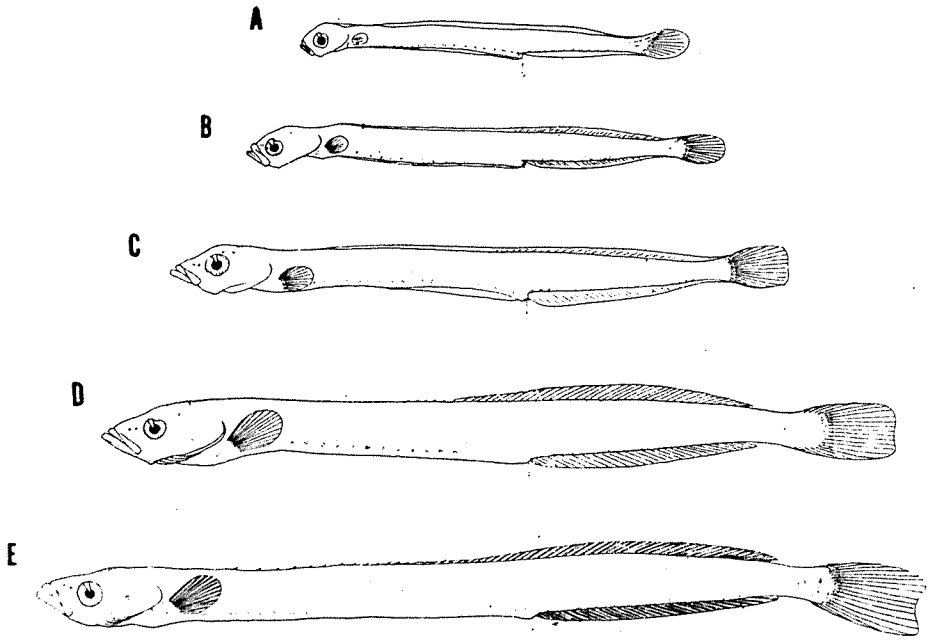


Fig. 36.1. Eggs and yolk sac larva of Ammodytes sp. from the Atlantic, top, (Source: Williams et al. 1964), and larval series of Ammodytes hexapterus from Bering Sea and Sea of Okhotsk: A) 12.6 mm TL; B) 16.6 mm TL; C) 21.1 mm TL; D) 26.7 mm TL; E) 31.0 mm. (Source: Kobayashi 1961).

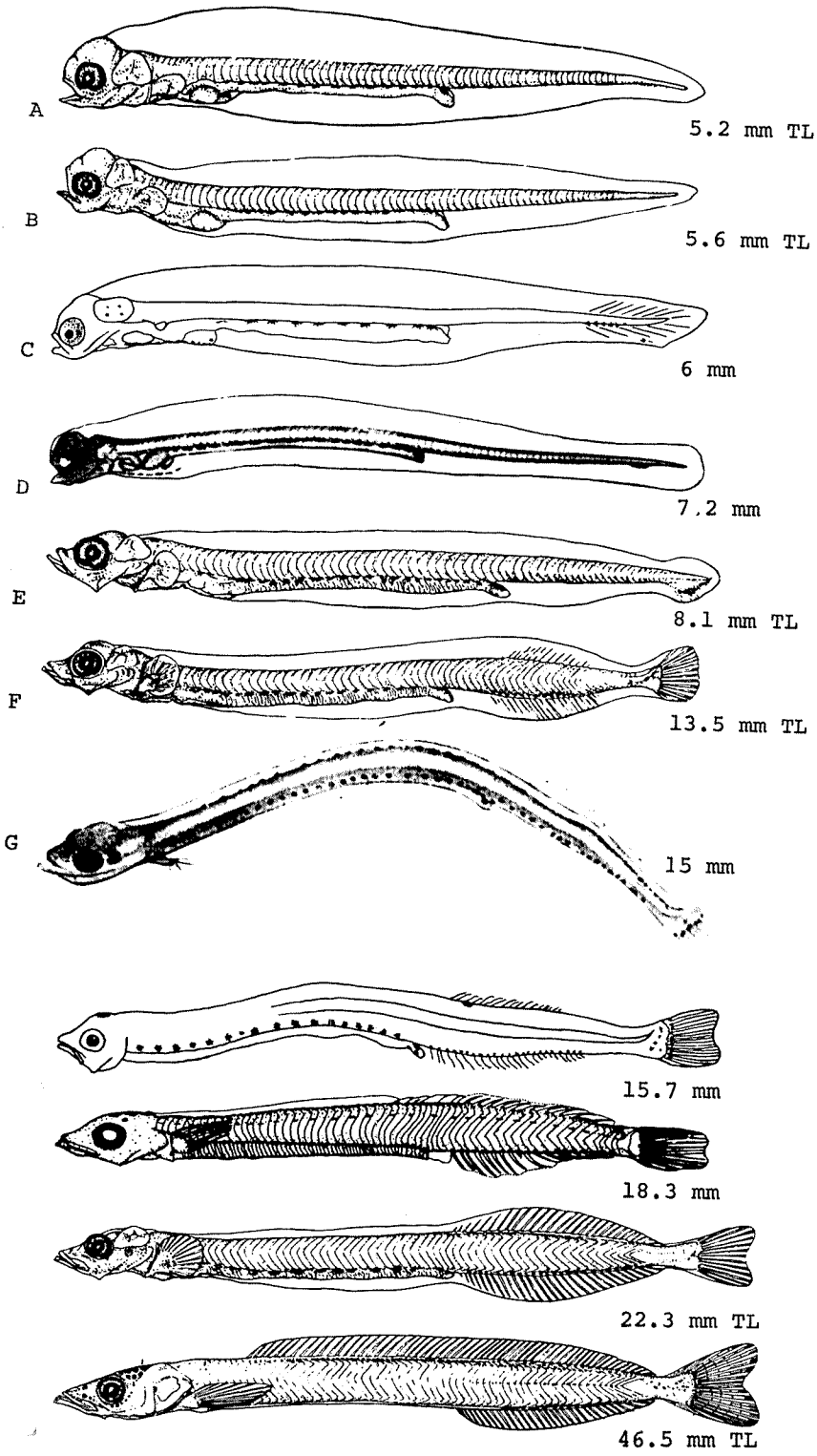


Fig. 36.2. Larval series of sand lance, Ammodytes spp., compiled from the literature by Fritzsche (1978) and probably representing several species. (Original sources: A, B, E, F, J, K - Norcross et al. 1961; C - O. Sette, original drawing; D - G. Dannevig 1918; H - Miller 1958; I - Richards 1965).

Metamorphosis from the larval to the adult form takes place between 30 and 40 mm. Larvae spawned in winter in the Atlantic may metamorphose within a month of hatching, but autumn-spawned larvae may overwinter in a pelagic larval phase lasting 3-5 months (Reay 1970).

Small sand lance larvae consume diatoms and dinoflagellates, but switch to copepods and their nauplii with growth. In turn, larval sand lance are eaten by a variety of predators, such as North Sea herring which feed primarily on larval sand lances during spring (Reay 1970).

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37. GOBIIDAE

Clevelandia ios - Arrow goby

Range: southern California to Strait of Georgia, B.C.

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, in shallow water

Spawning habitat: demersal, on sand

Mode of reproduction: oviparous

Eggs: demersal, attached

Larvae: pelagic

Ranging from southern California to southern British Columbia (Hart 1973), arrow goby are found over sand and mud substrates from middle to low intertidal to subtidal depth. They live freely or in burrows with Upogebia or Callionassa, retreating into burrows during low tide (Prasad 1958a; MacDonald 1975). In Puget Sound they are found from near Olympia to the San Juans and in Bellingham Bay (Miller and Borton 1980).

In California, the breeding season is prolonged and ovarian development is not synchronous as ovaries of breeding females are found to be at various stages of maturation during the spawning season. The peak months of spawning activity are March-June, although mature fish are also found in December, January, February, July, and August (Prasad 1958b).

Maturity is reached for some fish at 29 mm SL with 50% maturity level at 31 mm and all arrow gobies over 34 mm are mature (Prasad 1958b).

Males (> 19 mm) can be distinguished from females by a straight and tubular genital papilla as opposed to a fleshy, bulbous tubercle with a short spout-like opening of the female. There is no size difference in standard length between the sexes; however, males possess a significantly longer head and maxillary (Prasad 1958b).

During the onset of the breeding season, changes in body coloration are apparent. A few days prior to spawning, females possess a bright yellow abdomen, and a black streak of pigment may develop on the anal fin. There is also an increase in melanophores on the two dorsal fins and an increase in xanthophores all over the body. In the males, a black streak appears on the anal fin and yellow pigment also develops on the ventral surface. Two streaks of melanophores appear on the lower jaw and melanophores increase on the dorsal fins and on the upper part of the pectoral fin. These color changes are temporary and disappear after spawning (Prasad 1958b).

Courtship behavior has been observed to include fighting, chasing, nipping, and a belly-flashing display by males (MacDonald 1975).

Prasad (1958b) reported that mature females possess three size categories of eggs, but was unsure if the intermediate size group developed into a second batch or was resorbed. Unfertilized, ripe eggs are honey colored, translucent, almost spherical and measure about .7 μ mm in diameter. Spawning consists of the release of 750-1,000 eggs (Prasad 1958b), which in the laboratory are shed singly in groups of 15-25 eggs and settled to the bottom where they attach to the sand (MacGinitie 1935). Eggs contain numerous oil globules (Fig. 37.1).

As soon as the egg contacts water, the outermost, transparent net-like covering consisting of thread-like filaments breaks at one pole and gradually falls around the opposite pole forming a circlet of adhesive threads (Fig. 37.1, 10). These threads firmly attach the eggs to the substrate (Prasad 1958b). No parental care of the eggs has been observed.

In the aquarium, egg development required 10-12 days at 15-15.5°C (Table 37.1). Newly hatched arrow goby larvae are pelagic and vary in size from 2.75 to 3.25 mm TL. They are slender, delicate, and transparent with a rounded head, well-developed mouth, and prominent eyes. The anus is located about midbody and a single oil drop is present in the round yolk sac. The finfold is continuous from the dorsum to the vent and a short preanal finfold is present. Early larval pigment consists of three dorsal body melanophores which disappear by 9.5 mm, and pigment spots along the ventral surface of the gut (6 melanophores) and on the postanal midventral surface (11 melanophores). Seven to eight melanophores are present on each side of the yolk sac and the upper part of the air bladder is covered with melanophores creating a characteristic crescent-shaped area. At 7.0 mm, pigmentation remains basically unchanged except that the ventral postanal melanophores have fused to form a continuous line, and a pigment spot has appeared on the lower jaw. Caudal fin pigment is also well defined at this size. At 9.5 mm, pigmentation is present only along the ventral surface, and consists of two melanophores on the lower jaw, about nine melanophores from the base of the operculum to the anus, and six spots along the base of the anal fin (Prasad 1958b).

At 7.0 mm SL, all fins except the first dorsal and the pelvic fins are developing and become well-formed by 9.5 mm. The pectoral fin rays are also developing and pelvic fin buds are evident. The spinous dorsal fin is the last to appear and is found developing in 10.75 mm larvae (Fig. 37.1, 36). All the adult external characteristics are present in the 14.0 mm juvenile (Fig. 37.1, 37) and the pelvic fins have fused to form a single fin (Prasad 1958b).

Pelagic arrow goby larvae < 11 mm reportedly consume copepod nauplii, copepodites, barnacle cypris, euphausiid eggs and calyptoris (Barraclough and Fulton 1968) and the copepod Acartia clausii (MacDonald 1975).

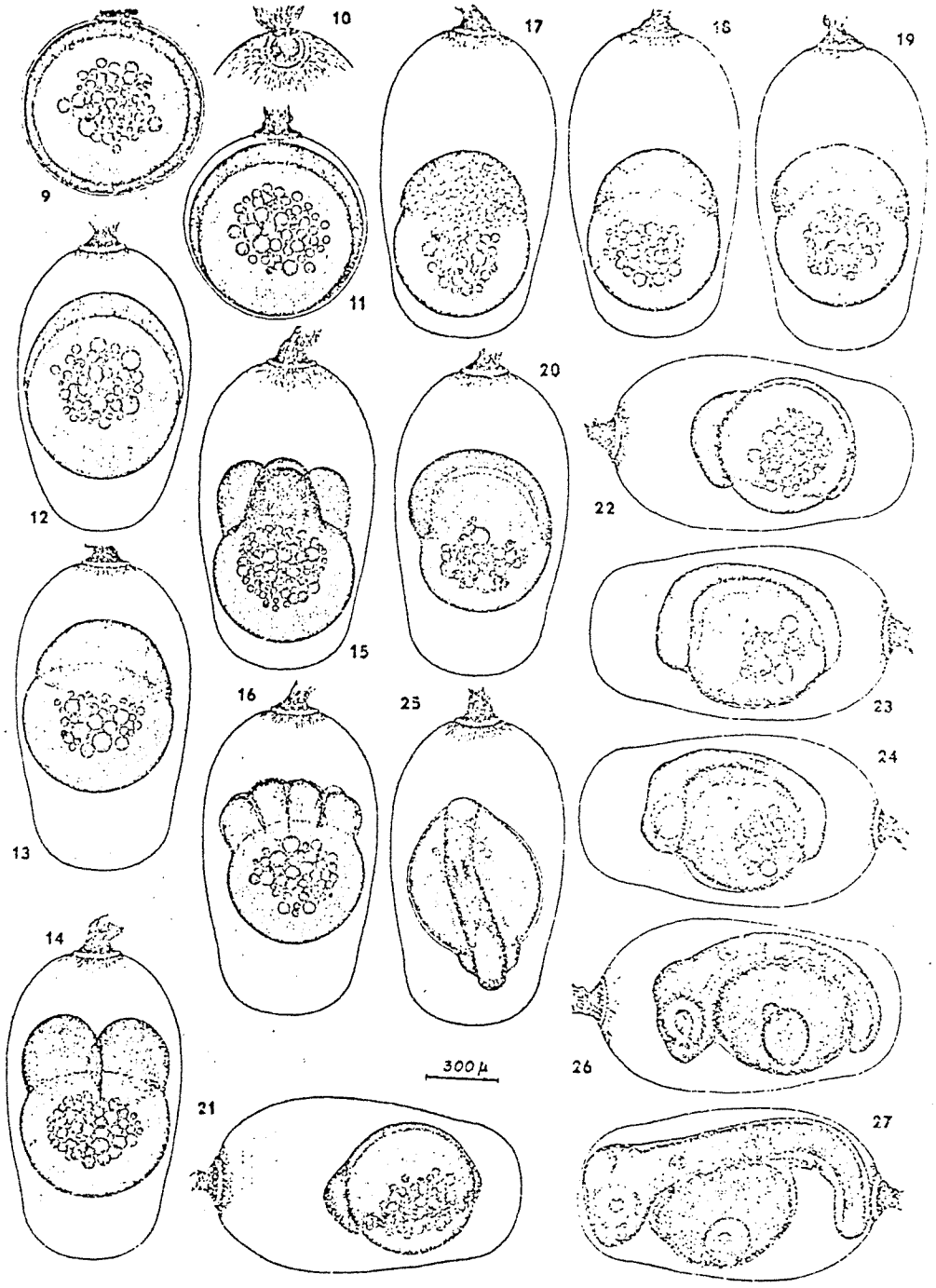

Fig. 37.1. Development of eggs of arrow goby, Clevelandia ios: 9) Unfertilized egg after formation of adhesive threads; 10) adhesive threads; 11) an egg 5 mins. after fertilization; 12) elongated egg capsule; 13) fully developed blastodisc; 14) 2-cell stage; 15) 4-cell stage; 16) 8-cell stage; 17) blastoderm with many cells; 18) blastoderm resembling blastodisc; 19) segmentation cavity; 20) segmentation cavity increased; 21) embryonic axis; 22) differentiation of embryonic axis; 23) Kupffer's vesicle appears; 24) optic vesicle and mesoderm somites appear; 25) dorsal view of 24; 26) advanced embryo; 27) tail lifts from yolk. (Source: Prasad 1958b).

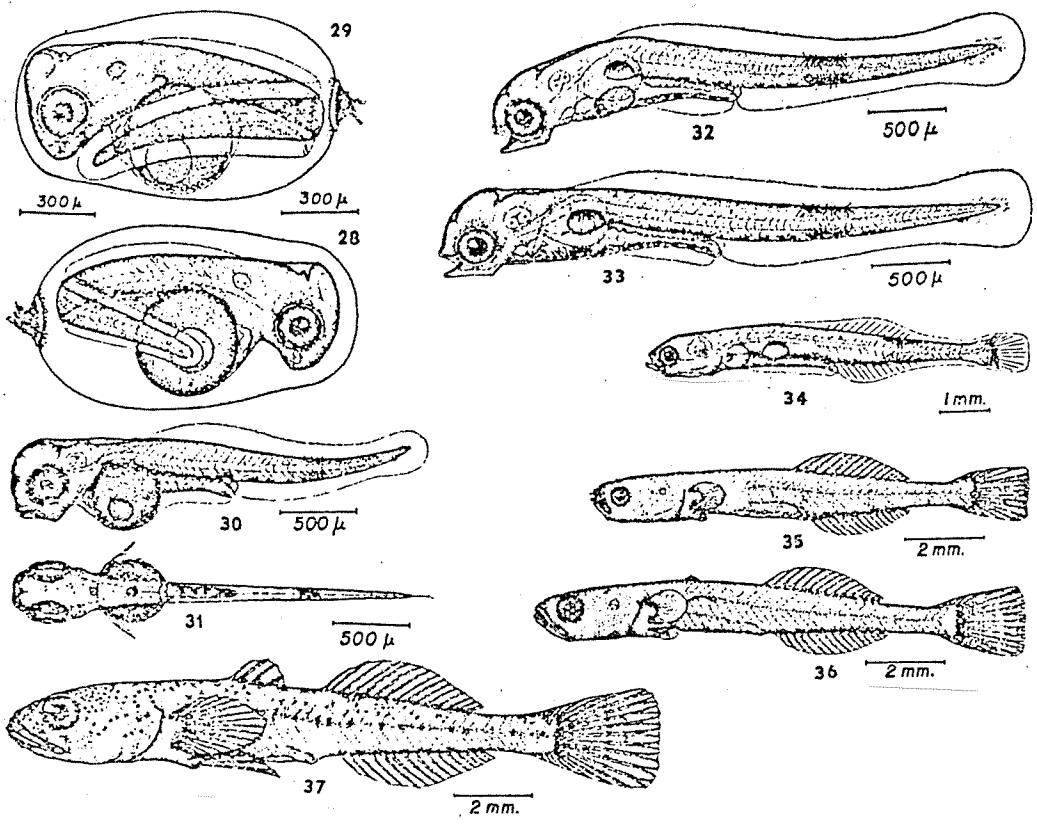

Fig. 37.1. (cont.) Development of arrow goby, Clevelandia ios: 28) well developed embryo with finfold; 29) rudiment of pectoral fin and melanophores in tail appear; 30) newly hatched larva; 31) dorsal view; 32) 6-day old larva; 33) 10-day old larva; 34) 7.0 mm; 35) 9.75 mm; 36) 10.75 mm; 37) 14.0 mm. (Source: Prasad 1958b).

Table 37.1. Summary of developmental events in eggs of arrow goby, Clevelandia ios. (Source: Prasad 1958b).

Time (from fertilization)	Developmental event
.1 h	Protoplasm begins to concentrate at animal pole to form the blastodisc (Fig. 37.1, 11); egg takes on an elliptical form (Fig. 37.1, 12).
2 h	Egg reaches maximal size (1300 μ x 790 μ), blastodisc is fully developed and is located toward the attached end of the egg (Fig. 37.1, 13).
2.5 h	First sign of cleavage.
3 h	First cleavage complete (Fig. 37.1, 14); subsequent cleavage take place at hourly intervals; second cleavage (Fig. 37.1, 15); third cleavage (Fig. 37.1, 16).
9 h	Blastoderm forms a thick dome shaped cap with sharply defined edges (Fig. 37.1, 17).
21.5 h	Individual cells of blastoderm not distinquishable (Fig. 37.1, 18).
22 h	Appearance of segmentation cavity which becomes visible as a narrow central area beneath the blastoderm.
24 h	Segmentation cavity well formed (Fig. 37.1, 19-20).
∿25-40 h	Germ ring, embryonic shield (Fig. 37.1, 21); early embryo (Fig. 37.1, 22).
42 h	Blastopore closure, embryo extends 3/4 of the way around the yolk mass, appearance of Kupffer's vesicle (Fig. 37.1, 23).
46 h	Formation of optic vesicle, appearance of first pair of somites near the middle of the embryo, oil globules decrease in number, those remaining increase in size (Fig. 37.1, 24-25).

Table 37.1. (cont.) Summary of developmental events in eggs of arrow goby, Clevelandia ios. (Source: Prasad 1958b).

Time (from fertilization)	Developmental event
59 h	Optic cup well developed with a prominent choroid fissure, auditory capsules appear, notochord and 10 fully formed somites are present Kupffer's vesicle reduced in size, yolk reduced, 3 primary divisions of the brain distinguishable, 2 or 3 oil globules present. (Fig. 37.1, 26).
63 h	Kupffer's vesicle disappears, eyes with lenses, tail lifts from yolk.
71 h	Embryo completely fills egg-capsule, anal pit and olfactory capsules appear.
80 h	Heart beat.
5 d	Embryo moves and finfold develops (Fig. 37.1, 28).
6 d	Eyes become pigmented and melanophores appear on dorsal and ventral sides of the posterior body (Fig. 37.1, 29).
7 d	Stomodaeum apparent
8 d	Air bladder visible
9 d	Pectoral fins well developed, pigmentation increases on yolk mass, mouth well developed.
10-12 d	Embryos active and hatching.

Coryphopterus nicholsi - Blackeye goby

Range: Baja California to Queen Charlotte Islands, B.C.

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, near rocks in shallow water

Spawning habitat: demersal, under rocks

Spawning season: spring-summer (California)

Mode of reproduction: oviparous

Eggs: demersal, attached, guarded

Larvae: pelagic

Blackeye gobies are found along the west coast of North America from Baja California to the Queen Charlotte Islands in British Columbia (Hart 1973). Adults inhabit shallow water (from 6 m to 60 m or more) where rocky reefs or rocks on open sand are found. They prefer the periphery of the reefs where they seek shelter in holes and crevises and the open area in front of the hole serves as a feeding and display area (Wiley 1973).

Like other members of the family Gobiidae, sexual dimorphism of the genital papilla between males and females is evident. In specimens over 25 mm, the male possesses an elongate and pointed papilla and the female papilla is broad and truncated. During the breeding season, males can also be distinguished from females by their black pelvic fins. The pelvic fins of the female remain grey throughout the year. Size differences between the sexes also occur, males attaining a greater maximum length (90.0 mm) than females (76.0 mm). The length of the second dorsal and anal fins is also longer in males than in females (Wiley 1973).

Males may reach sexual maturity at 55 mm or larger which corresponds to ages III to V and females are found to be mature at 47.3 mm or larger and ages II to V (Wiley 1973).

Blackeye gobies are spring through summer spawners in the southern part of their range as ripe fish have been collected from Laguna Beach, California from February to late August (Wiley 1973). Ebert and Turner (1962) also reported finding nests of blackeye gobies from April through October in southern California waters.

During the breeding season, the male goby selects a rock for a nest site and begins to hollow out a small depression beneath it. He attempts to clear the underside of the rock where the female will later deposit her eggs.

Courting behavior is distinct among species of the family Gobiidae, and behavior of the blackeye goby was described by Wiley (1973):

> "When courting, each male rose a few centimeters off the bottom, spread his fins fully and settled back to the substrate. After one to several of these displays, he swam back to his nest, where he continued nest contruction for a short time, and then resumed courting.
>
> Intermittently, the male swam swiftly toward the female and then quickly returned to his starting place, apparently in an attempt to stimulate the female and to attract her to his nest site. If the female reacted negatively, the male followed and continued courting, often nipping and chasing her. Early in courtship the female simply darted away into other shelter. Prior to spawning the female often took shelter in the male's nest, from which she was chased. However, the male upon seeing the female within the nest, approached with courting movements before entry and chasing . . . Occasionally a female approached a male that was courting her. The female then slowly undulated the body, gaped, and spread the fins."

When spawning commences, the female enters the nest and deposits her eggs on the underside of the rock. The male is intermittently present and fertilizes the eggs during and after oviposition. After spawning, males remain in the nest area to guard and fan the eggs (Wiley 1973; Ebert and Turner 1962).

Blackeye goby eggs are oblong, orange, laid in a monolayer and attached to the substrate, but have no adhesive threads (Fig. 37.2A) (Marliave 1975; Ebert and Turner 1962). Roughly circular, the egg mass is about 10 cm in diameter and mature eggs average 2.10 mm by 0.48 mm (Ebert and Turner 1962). During the breeding season, Wiley (1973) found females with two size classes of ovarian eggs, but could not determine how many times a female spawned per season. Fecundity ranged from 3,274-4,788 eggs (both ovaries) from four females examined. Ebert and Turner (1962) estimated nests to contain only about 1,700 eggs and believed only one female contributed to a nest.

The embryo develops with its head directed opposite the pole of attachment (downwards), and the eggs turn gray-silver as the embryos develop (Marliave 1975). The larvae are released when the egg cases split in a median plane, and newly hatched larvae are about 2.97 mm with prominent eyes and transparent bodies (Ebert and Turner 1962)(Fig. 37.2). The anus is located anterior to midbody and the swim bladder is well-developed and covered with melanin. Large melanophores are located on the ventral trunk musculature and on the dorsal body surface at the caudal peduncle. Larvae also have a row of small ventral gut melanophores. There are no melanophores on the dorsal gut surface at the anus (Marliave 1975).

Prejuvenile blackeye gobies are pelagic and oceanic (off California), and juveniles are found to assume a benthic habit at about 20 mm

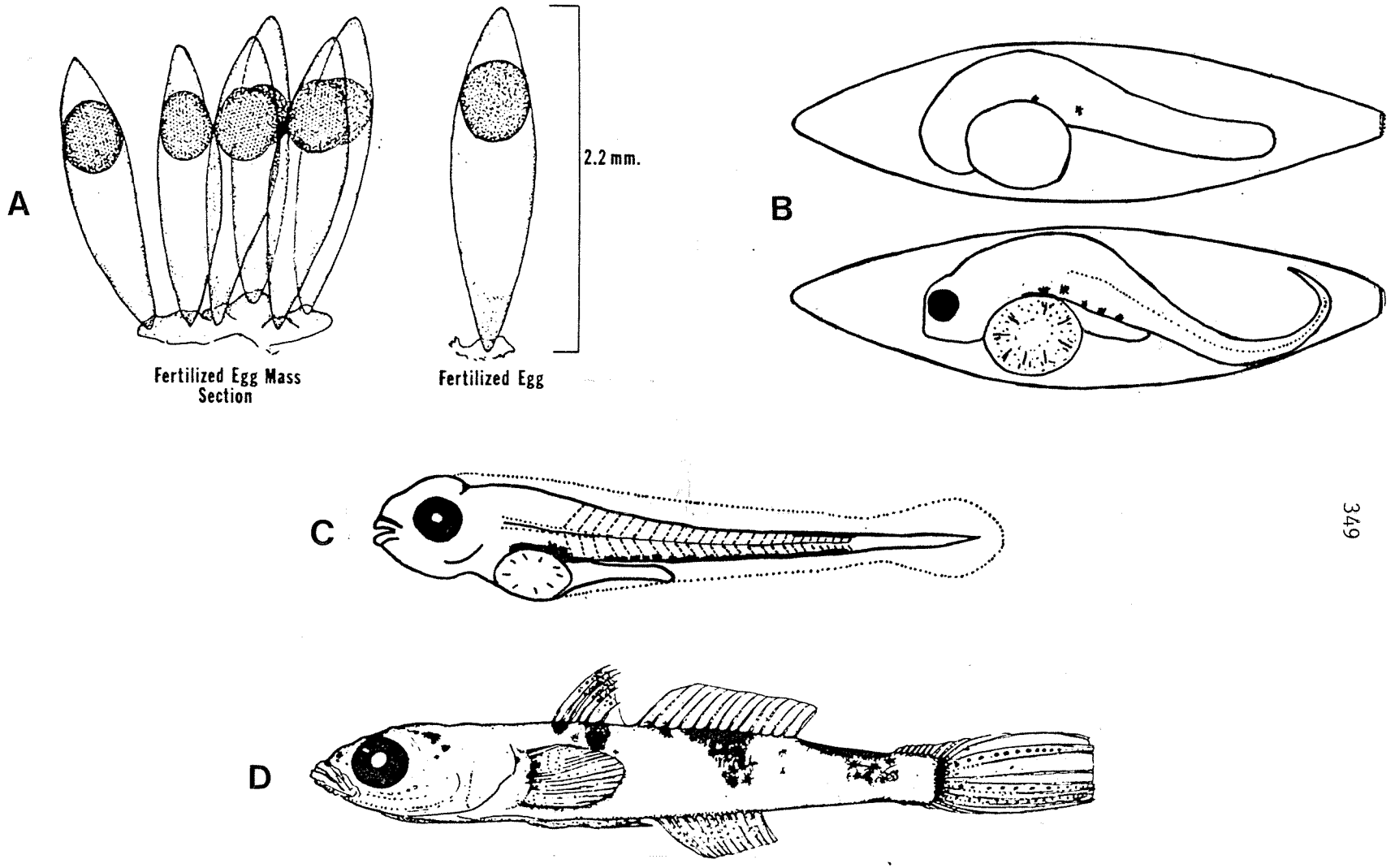

Fig. 37.2. Eggs, larva, and pre-juvenile of blackeye goby, Coryphopterus nicholsi: A) fertilized eggs; B) developing embryos-egg case is 2.10 mm by 0.48 mm, yolk is 0.30 mm by 0.42 mm. Note black eye and developing melanophores on mature embryo; C) newly hatched larva, 2.97 mm TL; D) pelagic pre-juvenile, 19.4 mm SL. (Sources: A,D-Wiley 1973; B,C-Ebert and Turner 1962).

SL (Wiley 1973). Barraclough and Fulton (1967, 1968) reported the food of larval blackeye goby to include small planktonic crustaceans.

Lepidogobius lepidus - Bay goby

Range: Baja California to southern British Columbia

Occurrence in Puget Sound: common

Adult habitat: demersal, on mud bottoms

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Bay goby inhabit muddy bottoms from shallow water down to 30 fm (Clemens and Wilby 1961) and range from Baja California to British Columbia (Hart 1973). Their occurrence in Puget Sound is common and they are distributed throughout the Sound (Miller and Borton 1980).

No early life history information is available.

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38. TRICHIURIDAE

Benthodesmus simonyi - Frostfish

(Available literature not reviewed)

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39. SCOMBRIDAE

Sarda chiliensis - Pacific bonita

Range: Subtropical eastern Pacific off northern Chile to Copper River, Alaska; off Japan

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic, primarily forms oceanic schools

Spawning habitat: pelagic

Spawning season: summer (California)

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Pacific bonita are largely an open ocean, pelagic schooling fish, but are not uncommon inshore and have been recorded on a few occasions from Puget Sound and the Strait of Georgia. They are known to occur in the subtropical Pacific off South America and extend north along California to the Gulf of Alaska, and are also taken off Japan (Hart 1973).

No spawning activity is known from northern regions but is believed to take place during summer off California and northern Baja California (Klawe 1961).

Spawning behavior has been observed in a large oval tank (Magnuson and Prescott 1966):

> "Courtship included temporary pairing, aggressive defense of females by males, and a sequence of behavior leading to the simultaneous and adjacent release of gametes. A wobbling swimming motion by a female released a following by males, and likewise, if a male swam immediately behind a female, she began a wobbling type of swimming. Sexual discrimination was mediated by the wobbling and following movements. If more than one male was in the following position, agonistic behavior occurred which included the transient vertically barred coloration observed in both sexes at feeding time. During courtship, only males assumed the coloration. Gametes were released during a circle swimming behavior in which the female with the male in tandom swam in a circular path about three body lengths in diameter. If aggression occurred during the wobbling - following portion of the sequence, the sequence usually terminated and did not result in circle swimming and spawning."

Pacific bonita eggs are pelagic, transparent, and about 1.5 mm in diameter with a single yellow-brown oil globule of .28 mm in diameter. Eggs have a small perivitelline space and a homogeneous yolk. The surface of the egg is covered with fine wavey striations (Barnhart 1927). In California waters, development requires only 3 days (Frey 1971) and results in newly hatched larvae which are about 3.75 mm in length (Barnhart 1927). Orton (1953) described the development of pigmentation in embryos and early larvae. Both black and yellow pigments develop early in embryology, with light-gray pigment cells appearing before the development of a definite tail bud. Most black cells are initially concentrated along the dorsolateral surface and on the yolk sac and as the embryo develops, migrate toward the ventral half of the somites and on top of the body cavity. Small yellow chromatophores appear at the bases of both dorsal and ventral finfolds and later move out into the finfold and become concentrated near the finfold margins. These chromatophores persist in 5 day old larvae.

Small larvae have not been described in any detail. Klawe (1961) illustrated a 3.5 mm larval Sarda spp. which may be either S. chiliensis or S. orientalis (Fig. 39.1A). This planktonic specimen had between 43 and 45 myomeres, a large mouth with teeth and three preopercular spines. Pigmentation was present on the crown, snout, lower jaw, ventral surface of the gut, dorsal gut surface, and along the postanal midventral line of the tail.

Postlarval and juvenile Pacific bonita were described and illustrated by Pinkas (1961). Postlarvae (16.7, 19.0 mm FL) are characterized by a fusiform body shape formed by large tapering jaws anteriorly and a tapering body posteriorly. The head is relatively large, almost 40% FL at 16.7 mm FL, with a conspicuous eye, and the jaws contain conical, curved teeth. Head spines are present and include 4-5 small blunt spines over the eye, 8 preopercular spines, (the three largest spines are in the center of the series and each possess a small blunt spine anterior to its base), and 3-4 relatively short posttemporal spines. At these stages, the dorsal fin is a single uninterrupted fin, but spines, rays, and 8 finlets are distinguishable. The pectoral and pelvic fins are discernible. At 16.7 mm, Pacific bonita possess well pigmented pelvic and first dorsal fins with the other fins remaining unpigmented and translucent. The head is moderately covered with melanophores and melanophores occur on the crown, nape, tip of the snout and lower jaw, and below the eye. Pigment also occurs at the base of the caudal rays (Fig. 39.1). With development, 7-12 vertical dusky bars appear along the lateral body surface.

Also with development, the head is reduced to 31.7% body length at 41.0 mm and decreases to 27.6% of body length for subadults. The number of teeth in the lower jaw increases slightly as the fish grows. At the end of the postlarval period, the preopercular spines are engulfed except for the three largest spines. By 60 mm FL, these spines are completely overgrown and the posttemporal spines also completely disappear (Klawe 1961).

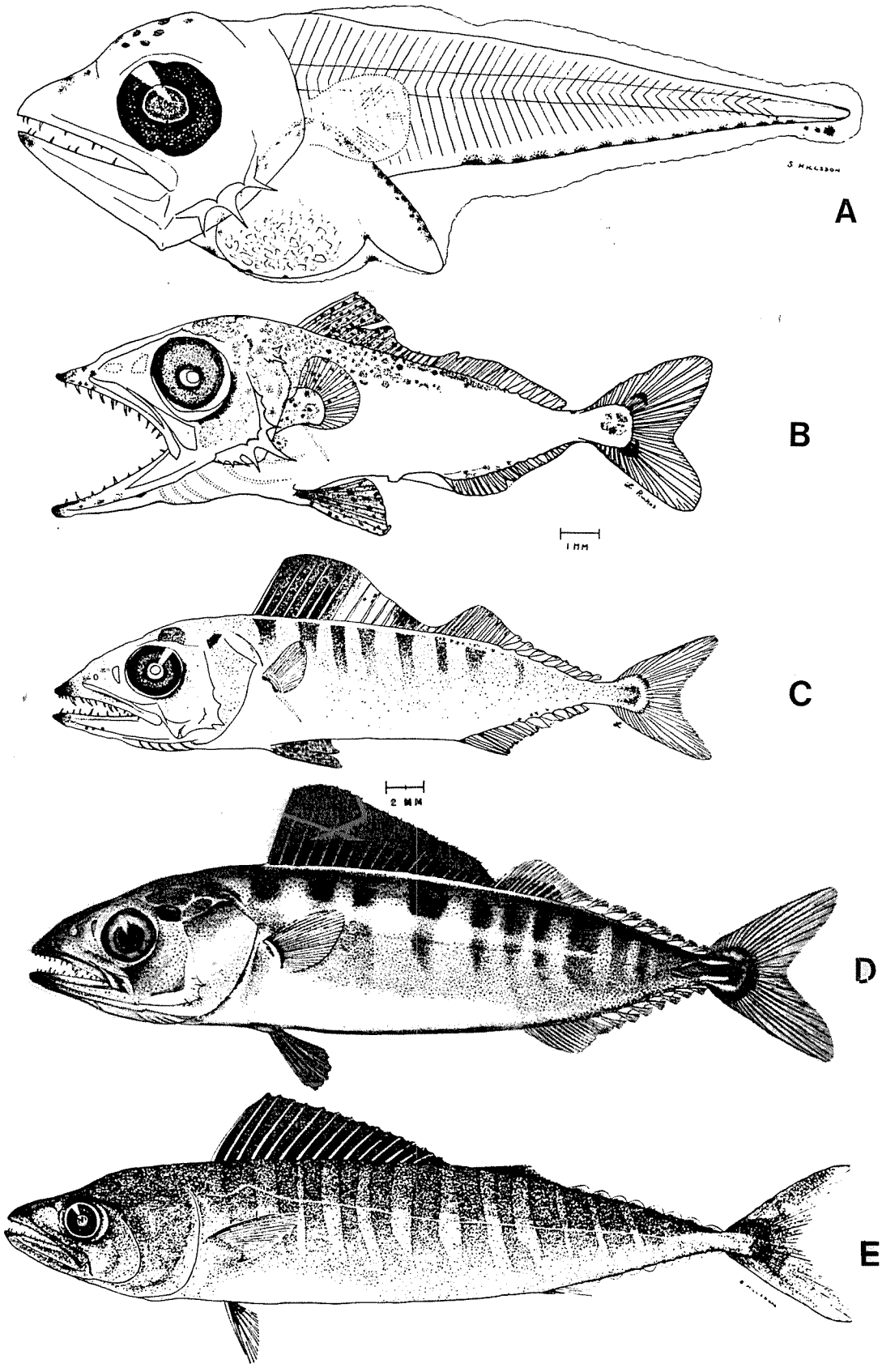

Fig. 39.1. Larvae and juveniles of Pacific bonita, Sarda chiliensis: A) 3.5 mm Sarda spp.; B) 16.7 mm FL; C) 33.0 mm FL; D) 42 mm; E) 160 mm (Sources: A,D,E, - Klawe 1961; B,C - Pinkas 1961).

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Scomber japonicus - Chub mackeral

(Available literature not reviewed.)

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40. STROMATEIDAE

Peprilus simillimus - Pacific pompano

Range: Baja California to British Columbia

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic, nearshore to edge of shelf

Spawning habitat: same

Spawning season: spring-early summer (California)

Mode of reproduction: oviparous

Eggs: probably pelagic, undescribed

Larvae: pelagic

Pacific pompano are frequently found associated with nearshore soft-bottom habitats (D'Vincent et al. 1980) from Baja California to Queen Charlotte Sound, British Columbia (Hart 1973) and have been taken on several occasions throughout Puget Sound (Miller and Borton 1980).

Spawning behavior of Pacific pompano is unknown, but larvae of these silvery, laterally compressed fish occur in surface waters (50 m or less) over the continental shelf. Horn (1970) studied the distribution of larval pompano off California and concluded that they may be spawned offshore, but move into bays or other nearshore protected areas where the majority of larvae are usually found. At present it is not known if a separate breeding population of Pacific pompano exists north of California or if fish occurring in northern waters are migrants from the California stocks. Eggs and larvae of this species have apparently not been found in northern waters (Horn 1970).

Eggs of other species of Peprilus are buoyant, transparent, spherical, and contain one or more oil globules and Pacific pompano are probably similar although they have not been described.

Although it is unknown if Pacific pompano spawn in Puget Sound, the larvae will be described here for completeness. P. simillimus hatch at 1.8-2.0 mm, undergo notochord flexion at 4.8-6.2 mm, and begin to transform into juveniles at 20 mm, and are fully transformed juveniles at 28 mm (D'Vincent et al. 1980).

Yolk sac larvae are similar in appearance to Genyonemus lineatus (Sciaenidae), white croaker, both possessing scattered melanophores along the lateral and ventral region of the head and body. Pacific pompano are distinguishable from white croaker however, by a prominent median dorsal melanophore located slightly posterior to a vertical from the anus which

persists through larval development and may be composed of 1-6 pigment spots (Fig. 40.1). Newly hatched Pacific pompano have a robust body form, a large yolk sac with a posteriorly located oil globule, an incomplete mouth, and unpigmented eyes.

At the completion of yolk absorption, about 2.2 mm, the mouth is formed, eyes become pigmented and the gut begins to coil. At this size, pigment consists of a prominent zone of large melanophores on the trunk above the gut and a median ventral series of spots from the cleithrum to the anus (Fig. 40.2A). At about 6.5 mm SL small preopercular spines (up to 12 in number) begin to appear, but become incorporated into the preopercular bone by about 14 mm SL. Also, at about 6.5 mm, the caudal, pectoral, dorsal, and anal fins begin to ossify and the full complements of these fins are all ossifying at about 10.0 mm (Fig. 40.2A′). The vertebral column begins to ossify after completion of notochord flexion and the full complement is ossifying by 10.0 mm.

As development continues, the lateral melanophores spread posteriorly, and the nape and the dorsum become covered (Fig. 40.2B′). Seventy percent of the body is covered with melanophores by 12 mm and 90% is covered by 15 mm. At 19 mm, scales appear on the lateral line marking the beginning of transformation to juvenile characters. At 20 mm, the caudal peduncle is completely covered and melanophores are present in the hypural region and at the base of the caudal fin rays (Fig. 40.2C′). Pigment also forms on the anterior part of the dorsal and anal fins and spreads posteriorly and increases in width in the juveniles (D′Vincent et al. 1980).

Morphometrics of larvae between 2.0 and 47.0 mm are provided by D′Vincent et al. (1980) and the most conspicuous feature is the two-fold increase in relative body depth with development. Less conspicuous ontogenetic trends are a relative shortening of snout-to-anus length, an increase in head length, and a decrease in relative eye size.

Fish smaller than 100 mm SL are reported to associate with jellyfish medusae of several genera. This association may be important during the early critical growth phase of the fish (Horn 1970).

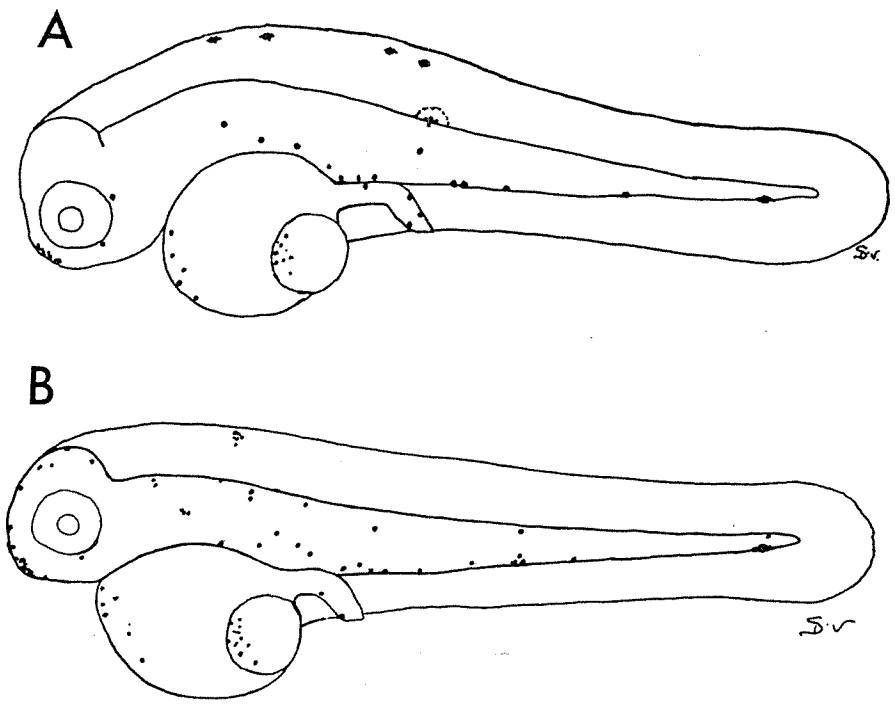

Fig. 40.1. Yolk-sac larvae of Pacific pompano, Peprilus simillimus (2.0 mm) and white croaker, Genyonemus lineatus (2.1 mm). (Source: D'Vincent et al. 1980).

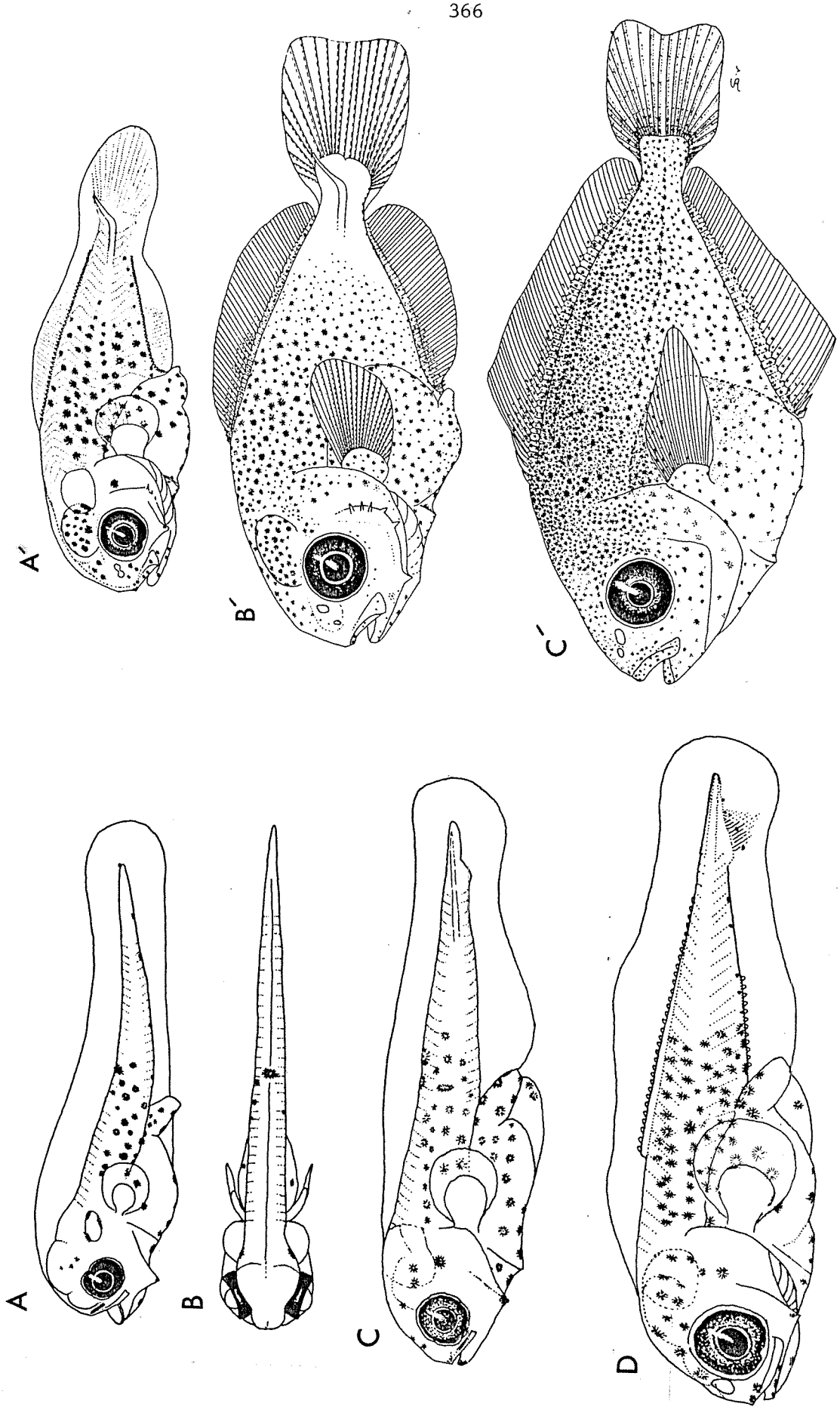

Fig. 40.2. Larval development of Pacific pompano, Peprilus simillimus: A) 2.4 mm; B) 2.4 mm, dorsal view; C) 4.1 mm; D) 4.7 mm; A') 6.5 mm; B') 10.8 mm; C') transforming specimen, 21.3 mm. (Source: D. Vincent et al. 1980).

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41. ICOSTEIDAE

Icosteus aenigmaticus - Ragfish

Range: southern California to southeastern Alaska; Japan

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic or bathypelagic

Spawning habitat: pelagic

Spawning season: summer and winter (California)

Mode of reproduction: oviparous

Eggs: pelagic, undescribed

Larvae: undescribed

Ragfish are distributed in the North Pacific from California to Alaska and in Japan. Adults are pelagic and may inhabit deep ocean water to 730 m (Hart 1973). They have also been reported on a few occasions from within Puget Sound (Miller and Borton 1980). Juveniles may be found in relatively shallow water nearshore and in offshore surface waters (Fitch and Lavenberg 1968). Ragfish are reported to form a large part of the diet of sperm whales taken in deep water off Queen Charlotte Islands (Cowan 1938). Adults may attain a length of 2 m (Hart 1973).

Spawning times for ragfish in California have been reported as summer (Fitch and Lavenberg 1968) and winter (Allen 1968) and spawning occurs when ragfish are 3 or 4 years old. Mature females are frequently taken in coastal California fishing grounds implying a shoreward migration during the spawning season (Fitch and Lavenberg 1968).

The mature ovaries of ragfish are bilobed and occupy almost the entire body cavity, or about one-third of the standard length. Out of four fish examined, the right ovaries were longer and more slender than the left. Both ovaries were J-shaped posteriorly where they connected to a complicated folding of mesenteries that form channels which fuse into a common passage leading to the vent. Underlying the external tissue layer which surrounds the ovary there is a thick layer of connective tissue which is called the ovarian case. The ovarian tissue which contains the developing eggs is only loosely attached to the ovarian case except dorsally near the midline where it is very securely held (Allen 1968).

Females may mature up to 400,000 3.0 mm eggs with two other size classes of eggs present (Table 41.1). The large, clear amber colored eggs appear to develop simultaneously at all points in the ovary with no

Table 41.1. Fecundity estimate, weight of ovaries and size class of ovarian eggs of ragfish, Icosteus aenigmaticus, from northern California. (Source: Allen 1968).

Specimen number	Month collected	Weight of fish (lb)	Length		Weight of Ovaries[1]		Category and Size of Eggs, mm			Estimated number of large eggs in both ovaries
			Total (cm)	Standard (cm)	Right (g)	Left (g)	large	medium	small	
1	July	-	150	135	927	894	1.5-1.0	.75-.5	<.1	430,000
4	July	-	119	106	541	-	-	-	-	293,000
5	November	51	129	124	1564	1775	3.0-2.0	1.0-.5	< .5	392,000
3	January	66	150	127	1488	1569	3.0-2.5	2.5-1.0	<1.0	230,000

[1]Includes entire ovarian structure plus eggs.

relationship of size distribution of eggs to position in the ovary (Allen 1968).

The increase of sizes of eggs in all size categories from summer to winter indicates this period as a time of maturation (Table 41.1). It is unclear if ragfish spawning is restricted in time or if spawning occurs several times per year (Allen 1968).

Descriptions of egg and larval development and larval behavior are lacking.

Juvenile ragfish are morphologically distinct from the adult form (Fig. 41.1) and undergo a striking metamorphosis during their first year (Fitch and Lavenberg 1968). As juveniles, they are relatively elongated in the dorsal-ventral plane becoming more dorsal-ventrally flattened with age. Another dramatic change is the encroachment of limp skin over the anterior ends of the dorsal and anal fins, giving lower counts of rays in the adults except under dissection. Other changes include the rounded pectoral fins become pointed, rounded caudal fin becomes broadly emarginate, and the yellow color and purplish spots of the juvenile changes to the more somber brown adult coloration (Clemens and Wilby 1961). Juveniles also move offshore during this time (Fitch and Lavenberg 1968).

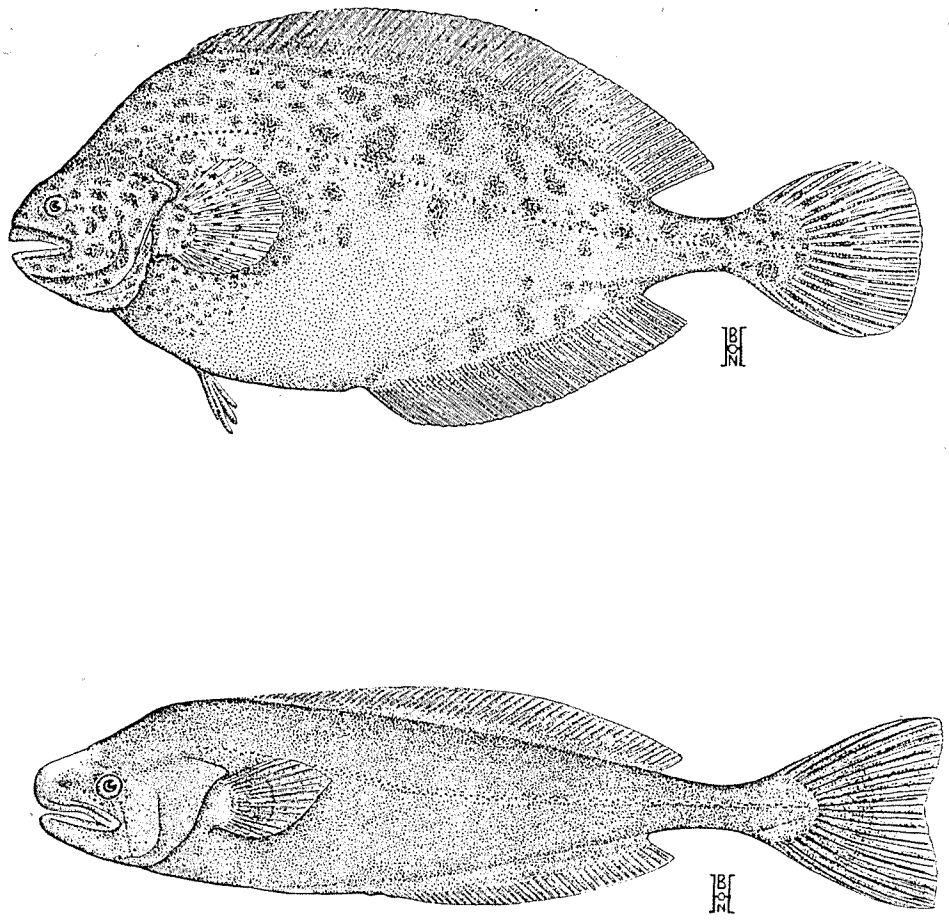

Fig. 41.1. Juvenile (top) and adult (bottom) ragfish, Icosteus aenigmaticus. (Source: Hart 1973).

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42. SCORPAENIDAE

General

The family Scorpaenidae, rockfishes or scorpionfishes, contains about 100 species in the eastern Pacific Ocean which are divided into eight genera (Moser et al. 1977). The majority of species belong to the genus Sebastes, which includes 69 species that occur between the Gulf of California and the Gulf of Alaska (Richardson and Laroche 1979). Twenty-six of these also occur in Puget Sound, along with one species of the genus Sebastolobus (Table 42.1). The species of Sebastes which are commonly caught by sport and commercial fisheries in Puget Sound include S. auriculatus, S. caurinus, S. flavidus, S. maliger, S. melanops, S. paucispinis, S. pinniger, and S. ruberrimus (Washington et al. 1978). Less frequently encountered are S. alutus, S. babcocki, S. brevispinis, S. entomelas, S. helvomaculatus, S. mystinus, and S. rosaceus (Miller and Borton 1980).

Most rockfish of the species Sebastes are demersal or at least associated with bottom waters. They may occur singly, in loose groups of several individuals, or in larger schools which may undergo seasonal migrations between spawning and feeding areas. The more truly demersal species can be observed in crevices or caves formed by rocks, or swimming slowly along the bottom.

All Sebastes are ovoviviparous. Transfer of sperm to the female may occur before ovulation and sperm are stored in the ovary until eggs are matured. The developing embryos lack placenta-like connections to the female which are found in some groups of live-bearing teleosts. After ovulation and fertilization, the developing embryos simply lie free in the ovarian cavity surrounded by ovarian fluid. They are in close proximity to the empty ovarian follicles whose capillary beds remain intact and functional and through which carbon dioxide, oxygen, and nitrogenous wastes are exchanged. Moser (1967) described the unusual and somewhat unique vascular system of the female which is necessary to provide a large and even supply of arterial blood to the gonads. This system is a striking departure from the typical situation in most teleosts and consists of an "arterial loop" which provides an even distribution of oxygen along the gonads.

The ovaries enlarge significantly as the eggs develop and are yellow or cream in color. As the embryos become pigmented, the ovaries take on a grayish color. Following the release of the larvae the ovaries are small and range in color from pale pink to grayish red. In most cases, females carry only one brood per season and development of the embryos requires 1-2 months. Larvae are released (or extruded in an event referred to as parturition) in a relatively undeveloped state. Debate continues as to whether or not they hatch from the eggs before or after release from the parent (Moser 1967).

Table 42.1. Species of the family Scorpaenidae reported to occur in Puget Sound, Washington. (Source: Miller and Borton 1980).

Species	Common name
Sebastes aleutianus	Rougheye rockfish
Sebastes alutus	Pacific ocean perch
Sebastes auriculatus	Brown rockfish
Sebastes babcocki	Redbanded rockfish
Sebastes brevispinis	Silvergray rockfish
Sebastes caurinus	Copper rockfish
Sebastes crameri	Darkblotched rockfish
Sebastes diploproa	Splitnose rockfish
Sebastes elongatus	Greenstriped rockfish
Sebastes emphaeus	Puget Sound rockfish
Sebastes entomelas	Widow rockfish
Sebastes flavidus	Yellowtail rockfish
Sebastes helvomaculatus	Rosethorn rockfish
Sebastes maliger	Quillback rockfish
Sebastes melanops	Black rockfish
Sebastes miniatus	Vermilion rockfish
Sebastes mystinus	Blue rockfish
Sebastes nebulosus	China rockfish
Sebastes nigrocinctus	Tiger rockfish
Sebastes paucispinis	Bocaccio
Sebastes pinniger	Canary rockfish
Sebastes proriger	Redstripe rockfish
Sebastes rosaceus	Rosy rockfish
Sebastes ruberrimus	Yelloweye rockfish
Sebastes saxicola	Stripetail rockfish
Sebastes zacentrus	Sharpchin rockfish
Sebastolobus alascanus	Shortspine thornyhead

In the male reproductive system, the elongated paired testes consist of numerous tubules radiating from a single sperm duct that extends along the surface of each testis. The paired sperm ducts converge at the posterior ends of the testes to form a single median duct which continues into the urogenital papilla, a probable intromittent organ. The testes are small during the early stages of spermatogenesis but become enlarged and pale white with maturity (Moser 1967).

Large broods are characteristic of Sebastes, but information on the number of broods produced per species per year remains somewhat sketchy. It would appear, that for most species encountered in Puget Sound, only one brood is matured and released annually. However, for at least two species, there is some evidence that two broods a year may be produced (Table 42.2).

Sufficient information to identify most rockfish larvae to species does not exist. A number of authors have described and illustrated well developed embryos which were removed from identified pregnant females (Table 42.3). Problems remain in that preextrusion larvae frequently are similar in morphology and pigmentation (Figs. 42.1-4). In addition, these early pigmentation patterns may change considerably by the time the yolk is absorbed making identification difficult (Westrheim 1975; Moser et al. 1977). Preextrusion larvae have been described for 20 out of 27 of the Puget Sound rockfish species and newborn or larvae reared to yolk sac absorption for eight species. Complete larval series of development have been done for only nine of the species.

While difficulties exist for distinguishing between species of larval rockfish, several characters can be used to identify larvae to Sebastes level:

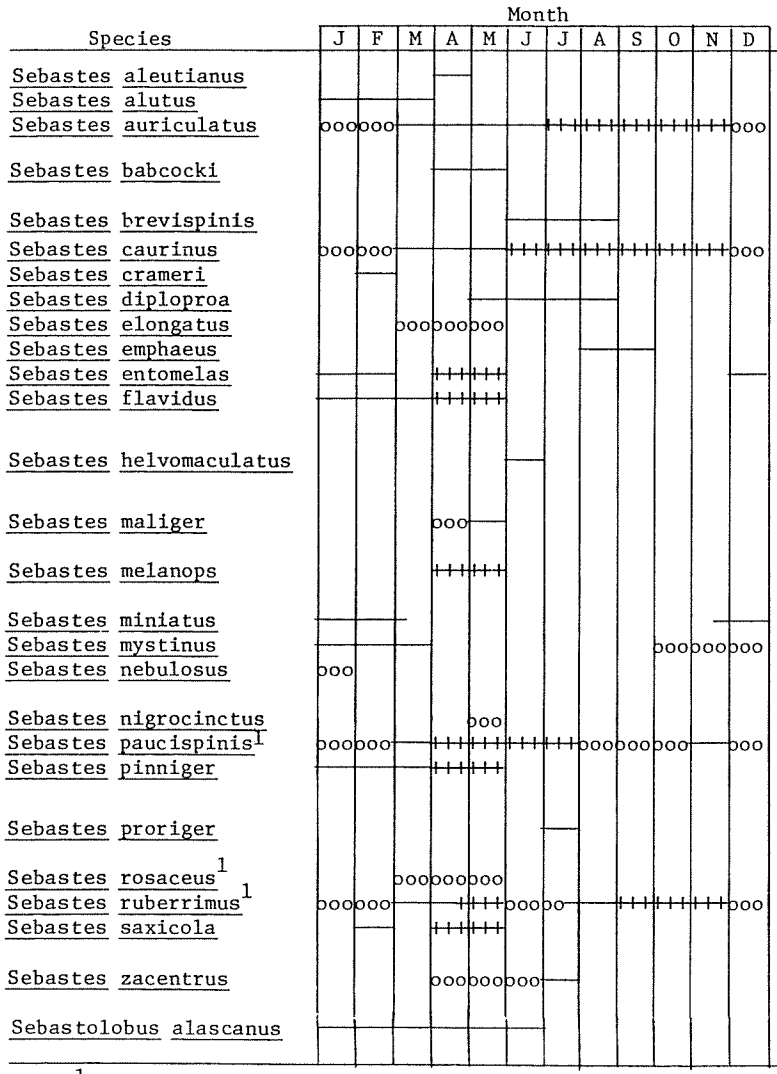
Myomeres: Members of the genus Sebastes have approximately 26 myomeres, with yolk sac larva showing slightly more (English 1976).

Spination: Rockfish and sculpins (Cottidae) are the two primary groups of fishes in Puget Sound which produce larvae with head spines. The spination found in larval rockfish is often more elaborate than that encountered in larval sculpins. In the rockfish, difficulties exist in naming the head spines found in larvae and juveniles because some of the spines disappear in the adult and the names used do not always reflect the bone from which the spines originate, leading to some confusion. Richardson and LaRoche (1979) have attempted to standardize the terminology of head spination in larvae and juveniles and their methods will be used (Fig. 42.5).

Head spines may develop in larvae as small as 7.0 mm in some species.

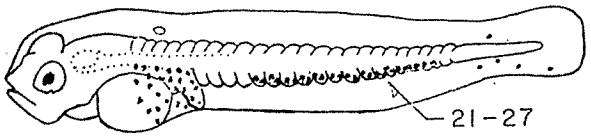
Pigmentation: Preextrusion larval Sebastes are relatively unpigmented and melanophores exist in all species along the ventral postanal midline and in varying degrees on the dorsal gut surface and anal

Table 42.2. Timing of reproductive events for species of the family Scorpaenidae occurring in Puget Sound, Washington (ooo - maturing eggs or embryos; ——— - extrusion of larvae; +++ - transitional or spent; blank - unknown).

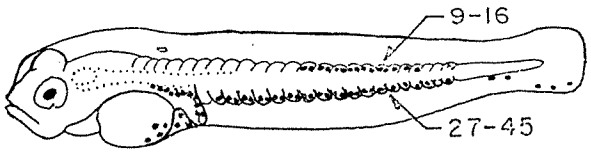


Species	Area	References
Sebastes aleutianus	British Columbia	Westrheim 1975
Sebastes alutus	Washington-Oregon	Snytko 1968
Sebastes auriculatus	Puget Sound	DeLacy et al. 1964; Washington et al. 1978
Sebastes babcocki	Oregon, British Columbia	Hitz 1962; Westrheim et al. 1968a, b
Sebastes brevispinis	Oregon	Hitz 1962
Sebastes caurinus	Puget Sound	DeLacy et al. 1964
Sebastes crameri	Oregon	Hitz 1962
Sebastes diploproa	Oregon	Hitz 1962
Sebastes elongatus	Oregon	Hitz 1962
Sebastes emphaeus	San Juan Islands, WA	Moulton 1975
Sebastes entomelas	Oregon	Hitz 1962
Sebastes flavidus	Oregon, British Columbia	Hitz 1962; Westrheim 1975
Sebastes helvomaculatus	Oregon, British Columbia	Westrheim 1975
Sebastes maliger	Puget Sound and San Juan Is., WA	Moulton 1977; Washington et al. 1978
Sebastes melanops	San Juan Is., WA Central North Pacific	Dunn and Hitz 1969; Moulton 1975
Sebastes miniatus	California	Phillips 1964
Sebastes mystinus	California	Miller and Geibel 1973
Sebastes nebulosus	California	Burge and Schultz 1973 (based on one gravid female)
Sebastes nigrocinctus	San Juan Is., WA	Moulton 1977
Sebastes paucispinis[1]	California	Moser 1967
Sebastes pinniger	Oregon-British Columbia	Hitz 1962; Westrheim 1975
Sebastes proriger	W. Vancouver Is., British Columbia	Westrheim 1975
Sebastes rosaceus[1]	California	Moser 1967
Sebastes ruberrimus[1]	Puget Sound	Washington et al. 1978
Sebastes saxicola	Oregon-British Columbia	Westrheim 1975; Hitz 1962
Sebastes zacentrus	Oregon-British Columbia	Hitz 1962; Westrheim 1975
Sebastolobus alascanus	California	Moser 1974

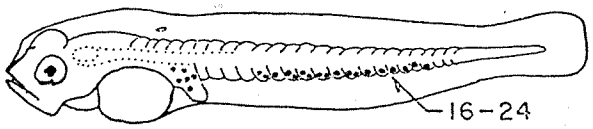
[1] Two broods may be developed.



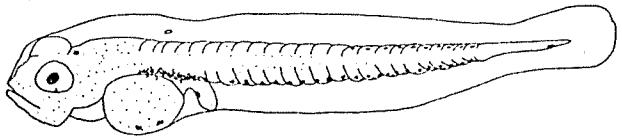
A. Sebastes aleutianus
preextrusion



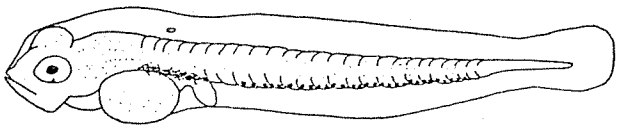
F. Sebastes babcocki
preextrusion



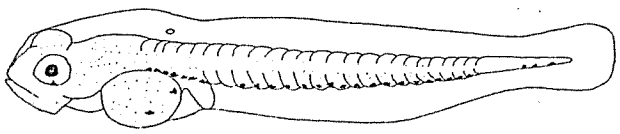
B. Sebastes alutus
preextrusion



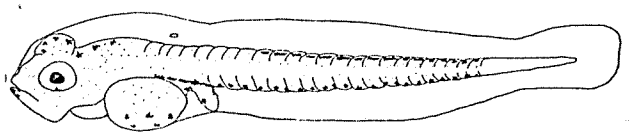
G. Sebastes babcocki
preextrusion



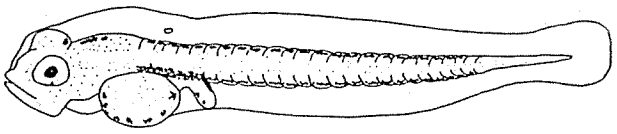
C. Sebastes alutus
preextrusion



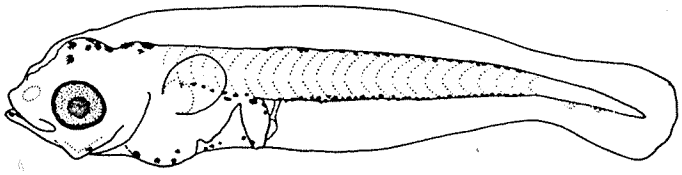
H. Sebastes brevispinis
preextrusion



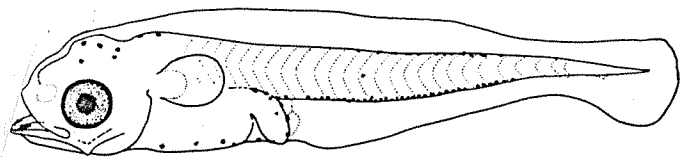
D. Sebastes auriculatus
preextrusion



I. Sebastes caurinus
preextrusion

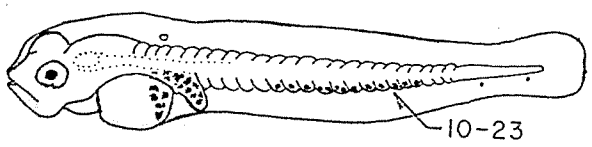


E. Sebastes auriculatus
at yolk exhaustion, 5.2 mm

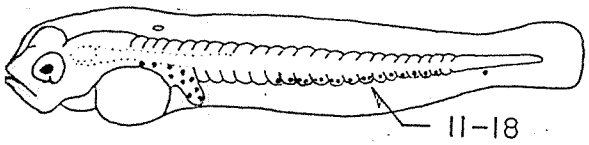


J. Sebastes caurinus
at yolk exhaustion, 5.5 mm

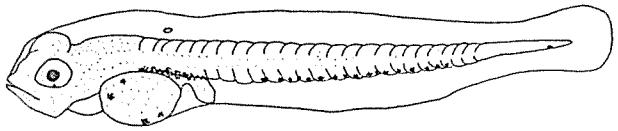
Fig. 42.1. Early larvae of Sebastes found in Puget Sound, Washington. (Sources: A, B, F - Westrheim et al. 1968a; C, D, G, H, I - DeLacy et al. 1964; E, J - Moser et al. 1977).



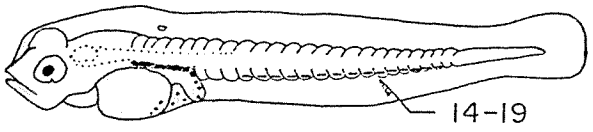
A. Sebastes crameri
preextrusion



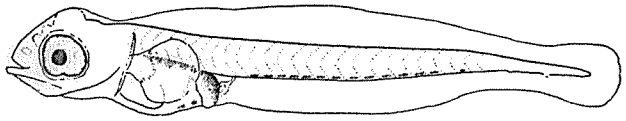
B. Sebastes diploproa
preextrusion



C. Sebastes diploproa
preextrusion



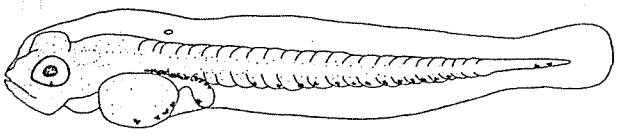
D. Sebastes elongatus
preextrusion



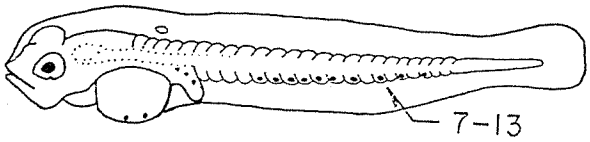
E. Sebastes elongatus
at yolk exhaustion, 4.9 mm

F. Sebastes emphaeus
undescribed

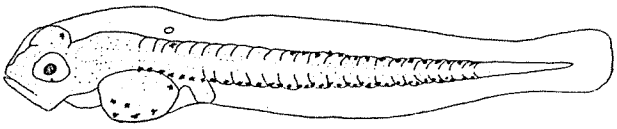
G. Sebastes entomelas
preextrusion
(See Hailing et al. 1971)



H. Sebastes flavidus
preextrusion

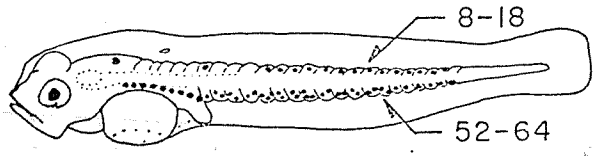


I. Sebastes helvomaculatus
preextrusion



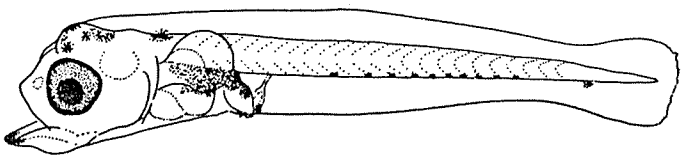
J. Sebastes maliger
preextrusion

Fig. 42.2. Early larvae of Sebastes found in Puget Sound, Washington. (Sources: A - Westrheim et al. 1968a; B, D, I - Westrheim et al. 1968b; C, H, J - DeLacy et al. 1964; E - Moser et al. 1977).

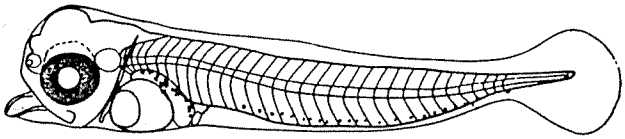


A. Sebastes maliger
preextrusion

B. Sebastes melanops
preextrusion undescribed



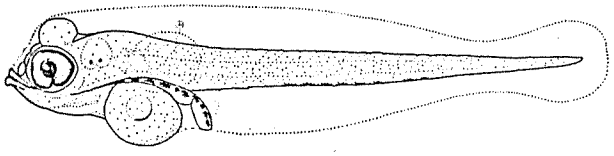
C. Sebastes miniatus
at yolk exhaustion, 4.3 mm



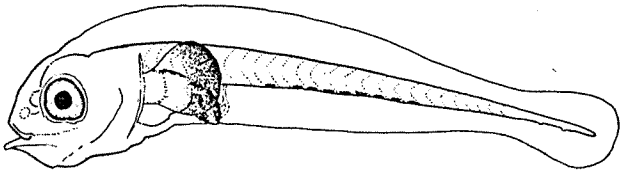
D. Sebastes mystinus
preextrusion

E. Sebastes nebulosus
undescribed

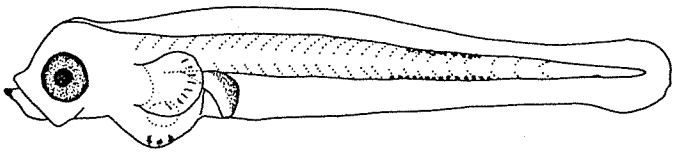
F. Sebastes nigrocinctus
undescribed



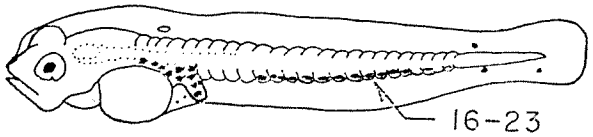
G. Sebastes paucispinis
newly hatched, 6.0 mm



H. Sebastes paucispinis
at yolk exhaustion, 4.7 mm

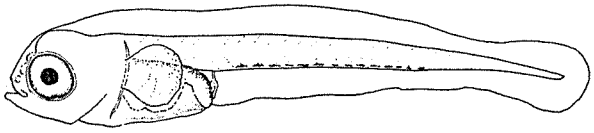


I. Sebastes pinniger
at yolk exhaustion, 4.0 mm

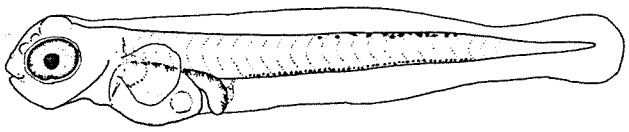


J. Sebastes proriger
preextrusion

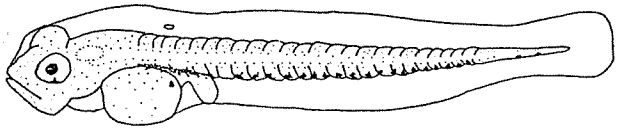
Fig. 42.3. Early larvae of Sebastes found in Puget Sound, Washington. (Sources: A, J - Westrheim 1968b; C, H, I - Moser et al. 1977; G - Morris 1956; D - Efremenko and Lisovenko 1970).



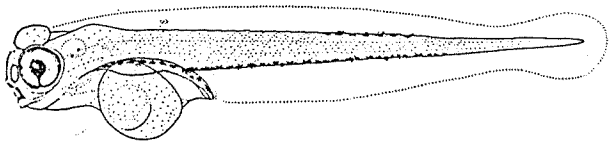
A. Sebastes rosaceus
at yolk exhaustion



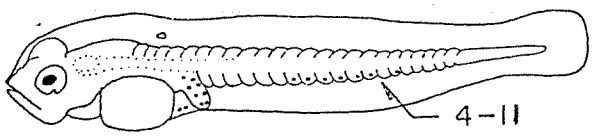
E. Sebastes saxicola
at yolk exhaustion, 4.7 mm



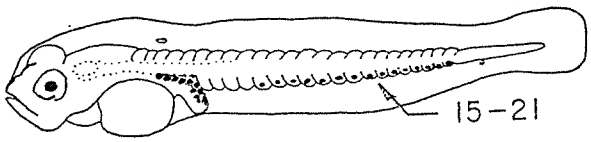
B. Sebastes ruberrimus
preextrusion



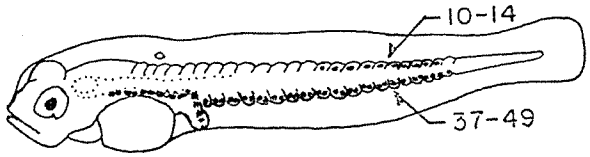
F. Sebastes saxicola
newly hatched, 4.3 mm



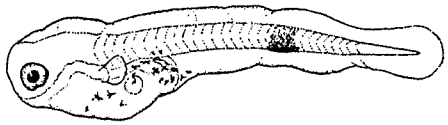
C. Sebastes ruberrimus
preextrusion



G. Sebastes zacentrus
preextrusion



D. Sebastes saxicola
preextrusion



H. Sebastolobus spp.
planktonic, 3.0 mm

Fig. 42.4. Early larvae of Sebastes and Sebastolobus found in Puget Sound, Washington. (Sources: A, E - Moser et al. 1977; B - DeLacy et al. 1964; C, G - Westrheim et al. 1968b; D - Westrheim et al. 1968a; F - Morris 1956; Moser 1974).

Table 42.3. Summary of sources of descriptions and/or illustrations of species of rockfish (Scorpaenidae) found in Puget Sound, Washington (P - preextrusion larva; L - newborn or larva reared to yolk sac absorption; S - larval series) (updated and modified from Richardson and Laroche 1979).

Species	Wales 1952	Morris 1956	DeLacy et al. 1964	Moser 1967	Waldron 1968	Westrheim et al. 1968a	Westrheim et al. 1968b	Efremenko and Lisovenko 1970	Harling et al. 1971	Moser 1974	Westrheim 1975	Moser et al. 1977	Richardson and Laroche 1979	Laroche and Richardson 1980	Laroche and Richardson 1981
Sebastes aleutianus						P*		P*			P				
S. alutus			P*			P*		P*			P				
S. auriculatus			[1]P*			[1]P*		[1]P*			P	L*			
S. babcocki			P*			P*		P*			P				
S. brevispinis			P*					P*			P	P			
S. caurinus			P*								P	L*			
S. crameri						P*					P		S*		
S. diploproa			P*				P*				P	P			
S. elongatus				L*			P*				P	L*			
S. emphaeus															
S. entomelas									P*		P				S*
S. flavidus			P*								P	P		S*	
S. helvomaculatus							P*				P	P	S*		
S. maliger			P*				P*				P				
S. melanops														S*	
S. miniatus												L*			
S. mystinus	P*							P*							
S. nebulosus															
S. nigrocinctus															
S. paucispinis		L*		S*							P	S*			
S. pinniger					L*						P	L*	S*		
S. proriger							P*				P				
S. rosaceus				L*								L*			
S. ruberrimus			P*				P*		P*		P				
S. saxicola		L*				P*					P	L*			
S. zacentrus							P*	P*	P*		P				
Sebastolobus alascanus										S*		S*			

*Illustrated.

[1]Described as S. rubrivinctus, but are probably S. babcocki (Richardson and LaRoche 1979).

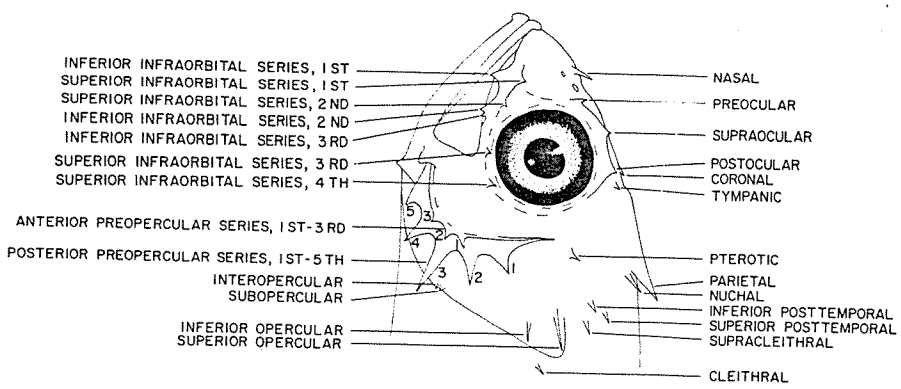


Fig. 42.5. Composite diagram of head spines found in larval and juvenile Sebastes species. (Terminology and illustration after Richardson and Laroche 1979.)

pipe. In some species, melanophores also exist on the head and nape, on the dorsal surface of the body and/or on the pectoral fin margin. The remainder of the body of the larvae is unpigmented (Fig. 42.1-4). With development, melanophores may be added to some areas and lost in others. Major changes in pigmentation occur with the development of juvenile characteristics.

Sebastes aleutianus - Rougheye rockfish

Range: central California to Aleutian Islands

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for preextrusion larvae

Rougheye rockfish are most commonly caught in offshore waters at moderate depths between 90 and 730 m. They are rare inshore (Hart 1973) and recorded sitings in Puget Sound have occurred on only four occasions (Miller and Borton 1980).

Early life history information is lacking, but the principal spawning time off British Columbia is reported as April and lengths of 50% maturity for rougheye rockfish are 43 cm for males and 45 cm for females (Westrheim 1975). Preextrusion larvae have a ventral postanal row of 21 to 27 pigment spots and several spots in the finfold below the hypural region. Melanophores are also located on the dorsal surface of the gut, but are absent on the head, nape, and dorsal body surface (Fig. 42.1A). Later stage larvae remain undescribed.

Sebastes alutus - Pacific ocean perch

Range: southern California to Bering Sea; parts of western Pacific

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic, schooling offshore

Spawning habitat: pelagic

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: pelagic, largely undescribed

Pacific ocean perch have been well known for their commercial importance in the North Pacific and Bering Sea. Ranging from southern California to the Bering Sea and along the northwestern Pacific coast to Japan (Hart 1973), Pacific ocean perch are found in large schools along the outer continental shelf and upper slope at depths of 150-460 m, and usually near the 180 m contour. They also exhibit an affinity for gullies, canyons, and submarine depressions along the upper continental slope (Major and Shippen 1970).

Pacific ocean perch are not common in Puget Sound (Miller and Borton 1980), but are more abundant off the coast of Washington.

The early life history and reproductive characteristics of Pacific ocean perch have been well studied compared to the other species of rockfish found in Puget Sound. Work has targeted on stocks in the Bering Sea, Gulf of Alaska, and off the coast of British Columbia, Washington and Oregon.

Pacific ocean perch are late winter to early spring spawners off Washington and Oregon (Table 42.4) with insemination occurring in October (Westrheim 1975). There is some conflict in the literature as to whether or not mating occurs simultaneously with fertilization (Paraketsov 1963; Sorokin 1967) or if sperm are stored for several months before fertilization takes place (Lyubimova 1963, 1965; Westrheim 1975).

Pacific ocean perch are relatively slow maturing fish, not reaching 50% maturity level until age 6-13 for males and 9-15 for females, depending on the stock (Table 42.5).

The number of ova produced per Pacific ocean perch has been studied by several different authors (Table 42.6). Differences in the fecundity-length relationships calculated, may be due to different techniques of estimating egg abundances, as well as due to differences between stocks of Pacific ocean perch. In general, the fecundity of Pacific

Table 42.4. Spawning season, by area, of Pacific ocean perch, Sebastes alutus.

Area	Spawning Season[1]	Reference
Bering Sea	March-May	Paraketsov 1963
Northern Gulf of Alaska	March-April	Lyubimova 1963
Southern Gulf of Alaska	May-June	Lyubimova 1963
SE Alaska	April-May	Westrheim 1975
Vancouver Island, B.C.	March	Westrheim et al. 1968a
Washington-Oregon	January-March	Snytko 1968
Oregon	January-February	Hitz 1962

[1]Time of release of larvae

Table 42.5. Lengths and ages at maturity, by area, of Pacific ocean perch, *Sebastes alutus*.

Length at maturity, cm		Age at maturity, yrs		Area	Reference
Males	Females	Males	Females		
-	22-25	-	6-7	Bering Sea	Paraketsov (1963)
-	-	4-8[2]	5-8[2]	Gulf of Alaska	Lyubimova 1965
-	26-48[3]	-	6-21[3]	Oregon	Westrheim 1958
29[1]	28[1]	10[1]	10[1]	W. Gulf of Alaska	Westrheim 1975
33[1]	34[1]	13[1]	15[1]	S.E. Gulf of Alaska	"
34[1]	35[1]	11[1]	12[1]	Vancouver Isl., B.C.	"
-	-	6-7[1]	9-11[1]	Washington- Queen Charlotte Sound, B.C.	Gunderson 1977

[1] 50% maturity level.
[2] All fish 8 yrs and older were mature.
[3] All fish within these ranges were mature.

Table 42.6. Fecundity-length relationships for Pacific ocean perch, Sebastes alutus.

Fecundity-length relationship	Area	Reference
$^{1}F = (4.8556 \times 10^{-15})L^{6.33454}$	Washington-Oregon	Westrheim (1958)
$^{2}F = (0.19295 \times 10^{-9})L^{7.32506}$	Washington-Oregon	Gunderson (1977)
$^{2}F = (0.12240 \times 10^{-6})L^{5.51258}$	Queen Charlotte Sound	Gunderson (1977)
$^{3}F = (2.2 \times 10^{-4})L^{5.3}$	Gulf of Alaska	Lisovenko (1965)
$^{4}F = (2.075P^{1.56})$	Gulf of Alaska	Lisovenko (1965)

^{1}F = number of eggs in thousands, L = fork length, mm.
^{2}F = number oocytes in thousands, L = fork length, cm.
^{3}F = fecundity, L = length, cm.
^{4}F = fecundity, P = weight of fish in g.

ocean perch off Washington-Oregon between 35 and 45 cm, ranges between about 35,000 and 300,000 (Gunderson 1977).

Migrations of rockfish during the spawning season have been noted for many areas. In general, Pacific ocean perch move into deeper water spawning areas to release their embryos and return to shallower water to feed and mature (Paraketsov 1963; Lyubimova 1963, 1965; Gunderson 1971, 1977; Westrheim 1958).

Observations of Pacific ocean perch in the Bering Sea showed spawning groups consisted of females whose embryos were all at the same stage of development and although the spawning season extended from March to May, individual schools spawned all at once and all members were spawned out within 3 to 3 1/2 hours (Paraketsov 1963).

Release of larvae was described by Moiseev and Paraketsov (1961) and cited by Major and Shippen (1970): "The activities occurred over bottom depths of 390 to 400 m. What the authors assumed to be spawning females were concentrated in a layer 25 to 30 m off the bottom. A massive liberation of larvae began at twilight (1730 hours) and was visible on the echogram as a foglike trace above the concentration of adult females. During the ensuing 1.5 to 2 hours, the number of larvae increased and ascended to 125 to 150 m off the bottom. By 2010 hours an accumulation of larvae was recorded in a layer between 120 and 175 m off the bottom. These observations were substantiated by catches of ocean perch larvae in egg nets."

The horizontal distributions of Pacific ocean perch larvae in the Bering Sea and Gulf of Alaska have been documented (Paraketsov 1963; Lisovenko 1964), but due to identification problems, it is possible, these distributions include other species of rockfish as well.

A developmental series of Pacific ocean perch has not been described, making identification of larvae from the plankton difficult. At present, the pigmentation patterns of the preextrusion larvae have been described and illustrated by several authors but with some differences. Westrheim et al. (1968a) did not find the multiple or irregular row of melanophores on the ventral surface of their specimens that DeLacy et al. (1964) found. Westrheim et al. (1968a) also reported that the ventral row of melanophores stopped short of the anus by four myomeres, and DeLacy et al. (1964) reported it stopped short by two myomeres. In each case, however, no melanophores existed on the dorsal body surface, head, nape, or yolk sac (Fig. 42.1 b, c). The lengths of larvae at emergence range from 5-8 mm (Paraketsov 1963; Lisovenko 1964; Westrheim 1975).

Laroche and Richardson (unpublished data) examined six planktonic specimens of larval and juvenile Pacific ocean perch and noted a development similar to Sebastes flavidus and Sebastes melanops. The

major differences were a lack of a black pigment blotch on the posterior portion of the spinous dorsal fin and the lack of melanophores at the articulation of the anal rays until near the beginning of transformation. Pacific ocean perch juveniles are also characterized by blotches of pigment along the distal margin of the spinous dorsal membrane immediately posterior to each dorsal spine (Fig. 42.6). In addition, a flat to convex interorbital space, presence of preopercular, postocular, supraocular, and tympanic spines, along with meristics, help distinguish Sebastes alutus juveniles from other Sebastes species.

The behavior of juvenile Pacific ocean perch is not well known. Some authors believe they remain pelagic until their second or third year. These conclusions have been based on back-calculated growth rates, or the presence of juvenile Pacific ocean perch in the stomachs of albacore located several hundred of miles offshore. However, based on sampling four coastal fjords in southeastern Alaska, Carlson and Haight (1976) concluded:

> "Our own idea of Pacific ocean perch early life history is this: The larvae are released in spring and ascend to upper layers of the water where they become part of the plankton. Drifting with the currents, they feed at first on the smallest zooplankters. In a matter of several weeks-- by early summer-- they assume the adult form and by fall take up a demersal existence in subtidal shallows inshore, locating over the roughest, most broken, often vertical substrate where shelter and intricate cover are most extensive. The young fish spend their first fall and winter months here and move deeper in spring. In their second summer (Age I+) we know that at least some have taken up residence in a fjord and believe that others are along the coast in a similar environment, where they remain through their third summer (Age II+). By the following spring when the perch are age III, we believe that ours leave, presumably to take up residence with juveniles ages III-V in another location where they remain for another 2 to 3 years. At around age VI they obtain maturity and most join adult stocks offshore."

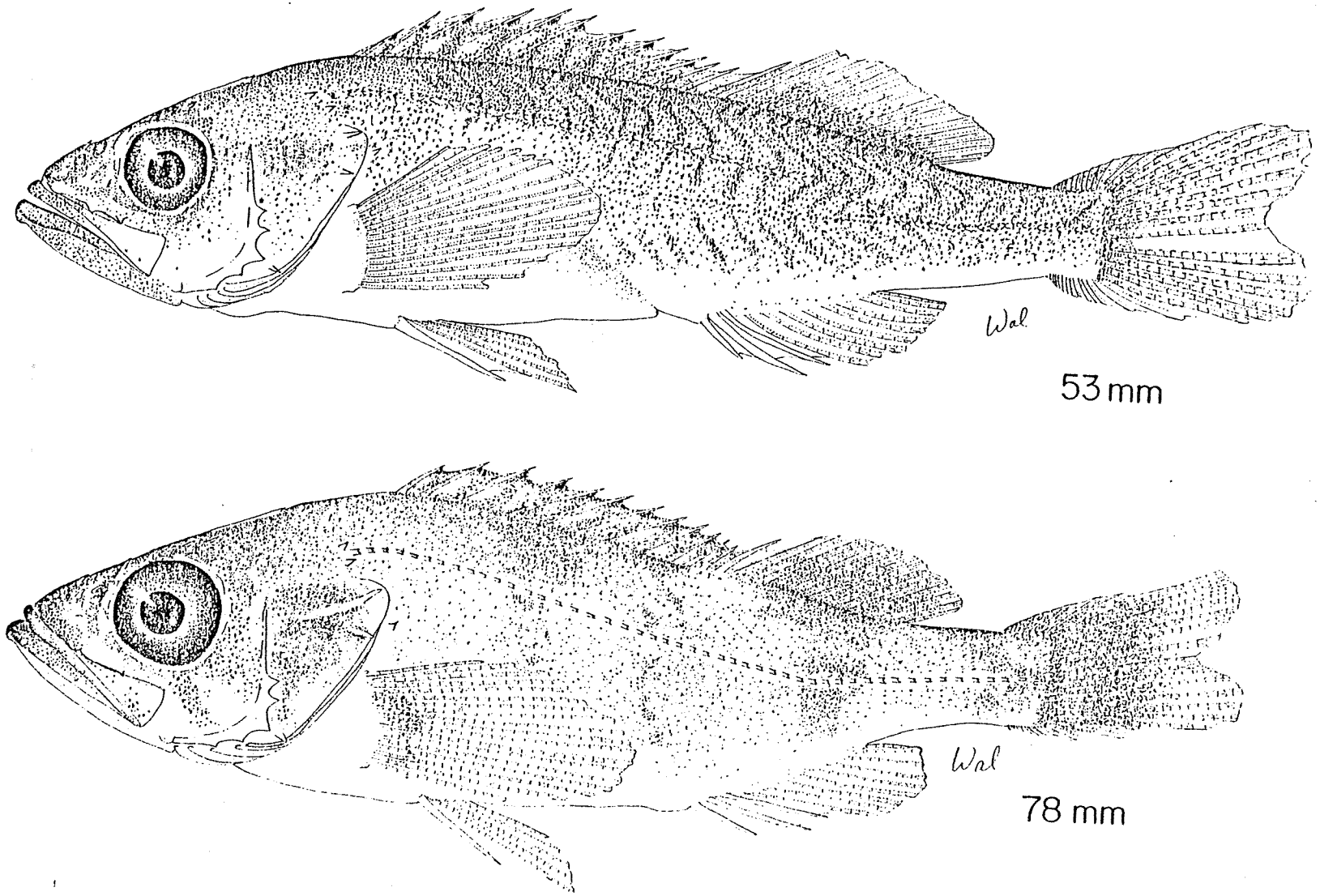


Fig. 42.6. Pelagic juvenile (53 mm) and benthic juvenile of Pacific ocean perch, Sebastes alutus. (Source: Laroche and Richardson, unpublished data).

Sebastes auriculatus - Brown rockfish

Range: Baja California to southeastern Alaska

Occurrence in Puget Sound: common

Adult habitat: unknown

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for preextrusion larvae and larvae at yolk exhaustion

Common in Puget Sound, this species also occurs along the coast from Baja California to southeastern Alaska and is frequently encountered at shallow to moderate depths (Hart 1973).

Reproductive events are not well documented; however, it is thought that ova mature during winter and larvae are born in spring followed by a transitional stage of the ovaries from late summer through fall (DeLacy et al. 1964).

Fecundity of a 47.7 cm total length fish was 338,540 eggs and the smallest mature fish was reported by DeLacy et al. (1964) to be 22.5 cm. A fecundity-length relationship is given in Fig. 42.7.

Pigmentation of preextrusion larvae (~ 5.8 mm) includes both dorsal and ventral postanal midline melanophores and melanophores on the head, nape, and ventral surface of the gut (Fig. 42.1 D, E).

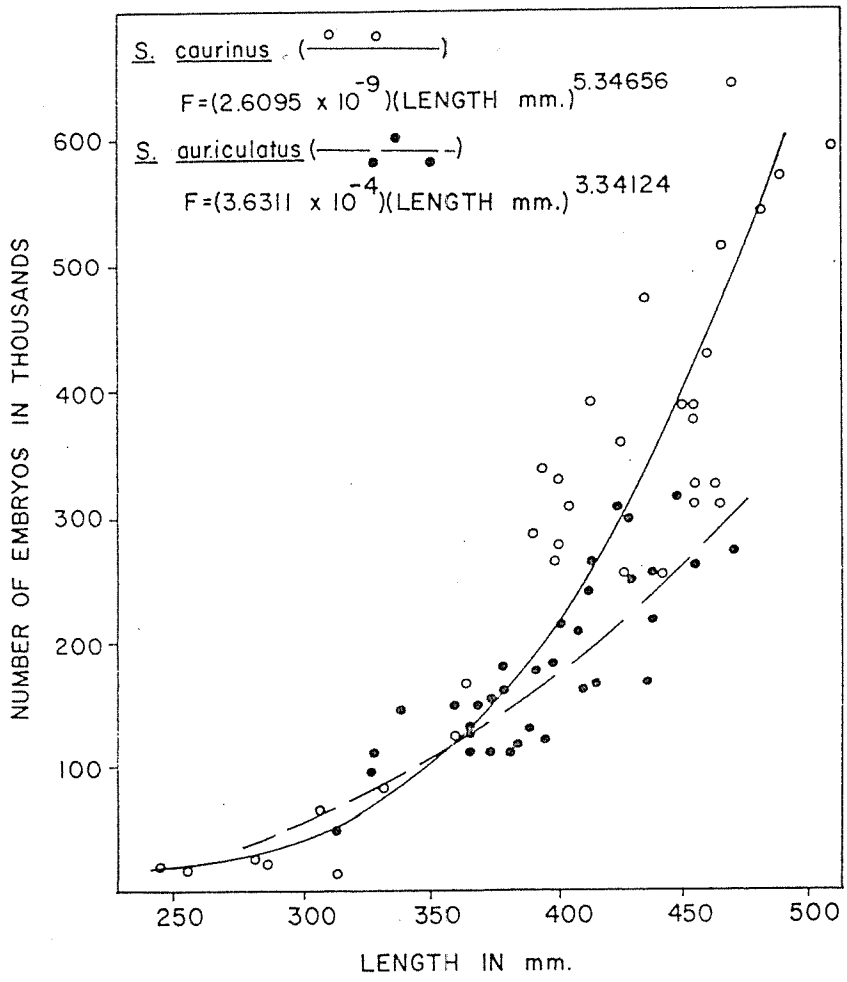


Fig. 42.7. Fecundity-length relationship for brown rockfish, Sebastes auriculatus, from Puget Sound. (Source: DeLacy et al. 1964).

Sebastes babcocki - Redbanded rockfish

Range: southern California to Kodiak, Alaska and Aleutians

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal, open water

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for preextrusion larvae

Redbanded rockfish are infrequently found in Puget Sound although they range from San Diego, California to Kodiak, Alaska. Off British Columbia, they occur in open waters and at depths of 90 to 460 m (Hart 1973). Several authors have confused this species with S. rubrivinctus (Table 42.3) which has been shown to be a different species, and so far, not recorded north of San Francisco (Hart 1973).

Off Oregon, larval redbanded rockfish are born in April and May, and off British Columbia in April (Hitz 1962; Westrheim 1975). Females are mature (50% level) at 42 cm and males at 38 cm (Westrheim 1975).

The only larval stages described are preextrusion larvae (~ 5.0 mm). These larvae have, in addition to the postanal midventral row of melanophores, a shorter dorsal midline row plus some pigmentation on the ventral surface of the posterior part of the gut. A few melanophores may also appear in the anal finfold near the tip of the tail (Fig. 42.1 F, G). After a few days, melanophores begin to appear on the head, nape and/or lower jaw (Westrheim 1975). Larval development beyond these stages remains undescribed.

Sebastes brevispinis - Silvergray rockfish

Range: Santa Barbara Island, California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal, both open and inside water

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed, except for preextrusion larvae

Silvergray rockfish are found from southern California to the Bering Sea and occur in both open coast and inshore waters of British Columbia and occasionally in Puget Sound (Hart 1973; Miller and Borton 1980).

Off Oregon, young are released in late spring or summer (Hitz 1962) and the 50% maturity levels for males and females are 43 cm and 45 cm, respectively (Westrheim 1975).

Preextrusion larvae are lightly pigmented with pigment present along the ventral midline posterior to the anus and sparsely distributed on the dorsal surface of the gut and on the yolk sac. A few spots are also present in the hypural region (Fig. 42.1 H).

Other information on reproductive biology is lacking.

Sebastes caurinus - Copper rockfish

Range: Monterey, California to Gulf of Alaska

Occurrence in Puget Sound: common

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for preextrusion larvae and larvae at yolk exhaustion

Copper rockfish are one of the most common rockfishes in Puget Sound and are distributed throughout the Sound (Miller and Borton 1980). Ranging from Monterey, California to the Gulf of Alaska, they are typically solitary bottom dwellers that associate with objects which provide cover in shallow water such as reefs or rock piles. Young of the year are seen in October in Puget Sound and are associated with the base of rock piles or under objects on the bottom. Coppers are infrequently seen over sandy areas, although they do occur occasionally in trawl gear over sandy bottoms. During winter and spring most copper rockfish are within caves and are inactive. In July-October a few fish remain in rock crevices, but the majority are outside although within one meter of the rocks (Patten 1973).

Females extrude larvae in spring followed by a resting stage during late summer and fall. Maturing of ovaries begins again during winter. Two groups of ova (based on ova diameters) are seen in the ovaries during the resting stage (fall) and over winter. The smaller group consists of eggs 0.01-0.17 mm in diameter which are not matured that season, and a larger diameter group of eggs that continues to increase over winter and becomes fertilized (DeLacy et al. 1964). The mature female gonads may represent up to 9% of the individual's body weight (Patten 1973).

The majority of fish of both sexes are mature for the first time at the end of their fourth year but some females may mature at three years (Patten 1973). Fecundity studies of copper rockfish have revealed over 500,000 ova for the largest fish examined. Washington et al. (1975), and DeLacy et al. (1964), arrived at similar length-fecundity relationships and fecundity appeared to increase at a rate proportional to about the fifth power of the total body length (Fig. 42.8).

In addition to the postanal midventral melanophores, preextrusion and recently hatched larvae have dorsal midline melanophores and pig-

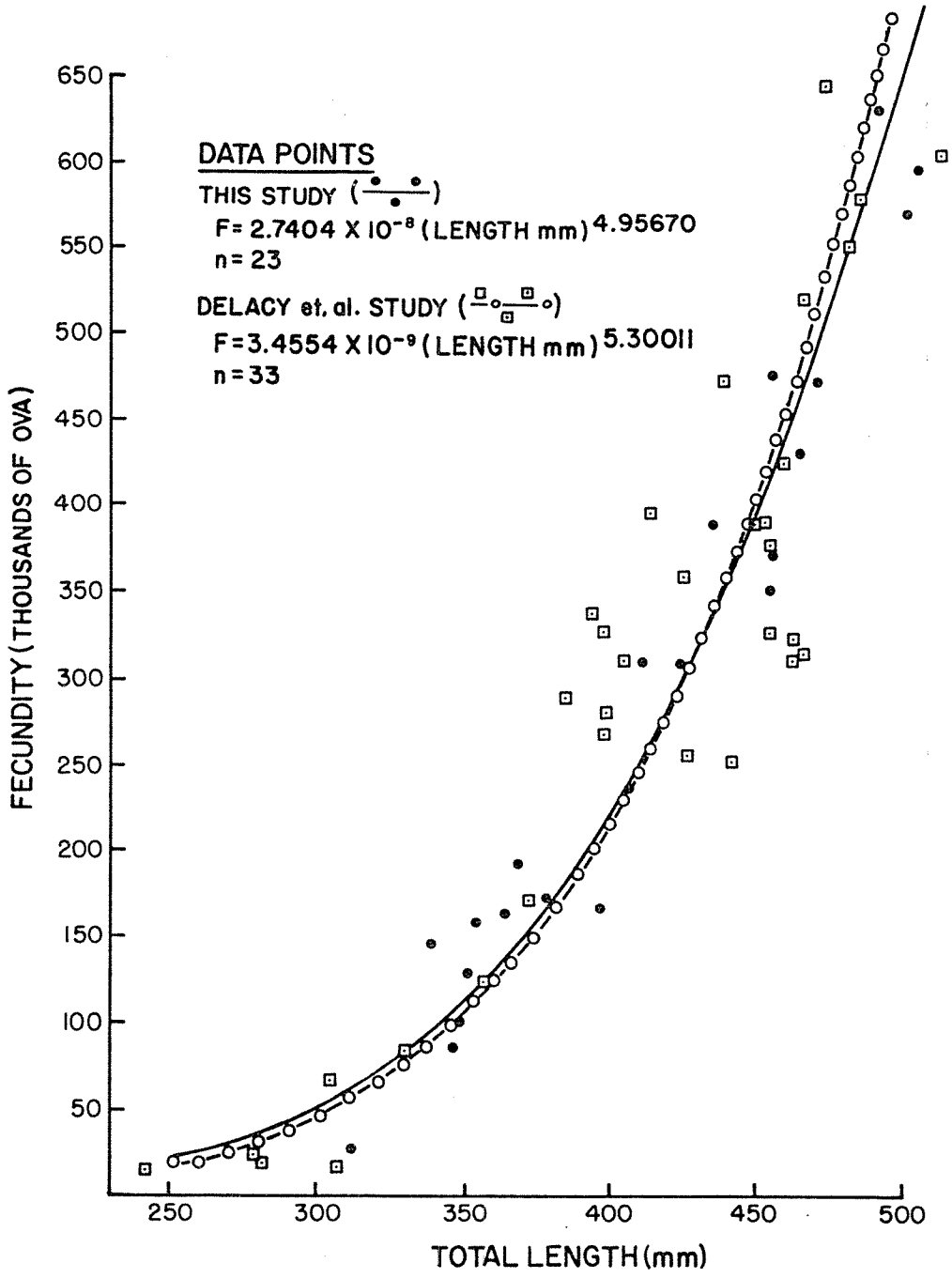


Fig. 42.8. Fecundity-length relationship for copper rockfish, Sebastes caurinus, in Puget Sound. (Source: Washington et al. 1978).

ment spots on the head, nape, dorsal gut surfaces, and on the ventral surface of the yolk sac (Fig. 42.1 I, J). Later larval stages are undescribed at present.

Sebastes crameri - Darkblotched rockfish

Range: southern California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal, primarily offshore

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for preextrusion larvae

This species occurs primarily offshore from southern California to the Bering Sea and at depths from 30 m to 550 m with greater abundances in the deeper part of its depth range (Hart 1973). It is known on only a few occasions from the Puget Sound area and has been reported from the Strait of Juan de Fuca (Miller and Borton 1980).

Young are released in February off British Columbia to Oregon (Hitz 1962; Westrheim 1975) and the spawning season runs from mid-November to mid-March in the southern part of its range (Phillips 1964). In California, a few darkblotched rockfish may mature at 5 years of age and 28 cm, but the 50% maturity level is 6 years and about 30.5 cm. They may attain a maximum age of 30 years (Phillips 1964). Westrheim (1975) reported lengths of 50% maturity for British Columbia fish to be 34 cm for males and 37 cm for females. Fecundity ranges from 50,000 eggs in 33.5 cm females to over 600,000 eggs in 57.5 cm females (Table 42.7).

Pigment patterns of preextrusion larvae (~ 5.7 mm) are described (Westrheim 1975) and illustrated (Westrheim 1968a) and consist of a relatively short row of ventral postanal midline melanophores which stop short of the anus by 4 or 5 myomeres. Pigment spots are also usually present on the ventral finfold in the hypural region and the gut is pigmented (Fig. 42.2 A). No pigment occurs on the head, nape, or dorsal body surface of preextrusion larvae; however, larvae reared for several days after birth developed additional pigment spots on the head, nape, and lower jaw (Westrheim 1975).

A planktonic larval series (8.0-130.5 mm) identified as S. crameri has been described and illustrated by Richardson and Laroche 1979).

Characters used to identify the smallest larvae (8.0 mm) are:

1) heavily pigmented pectoral and pelvic fins;

2) a heavy nape pigment patch from which some melanophores

Table 42.7. Fecundity of darkblotched rockfish, Sebastes crameri. (Source: Phillips 1964).

Date	Total length (mm)	Fecundity (Number of eggs)
10-59	335	52,500
10-60	352	36,600
10-60	392	169,600
10-60	420	173,600
10-60	425	190,100
10-60	440	313,800
10-60	473	331,700
10-60	475	251,600
10-60	483	384,200
10-60	500	478,900
10-60	513	347,200
10-59	575	609,800

extend down and over the gut externally on the body wall;

3) absence of dorsal midline pigment other than at the nape;

4) about eleven distinct melanophores on the postanal ventral midline (anterior ones are embedded and only the posterior-most ones remain on the ventral body surface); and

5) pigment at the tip of the lower jaw.

The presence of pigment on the first dorsal fin in larvae as small as 11 mm is also a useful character (Fig. 42.9).

Juveniles can be distinguished by a combination of meristics, presence of supraocular spine, flat to convex shape of the interorbital space, heavily pigmented pelvic and pectoral fins and a pigment-banding pattern on the body (Fig. 42.10).

In larvae as small as 8.0 mm, about 13 spines are visible on each side of the head region and by the time notochord flexion is complete, eight additional spines are visible. Some head spines (primarily the first through third spines in the anterior preopercular series) which are visible in the smaller larvae are no longer visible in pelagic juveniles (Table 42.8). Scales are first visible on specimens about 20 mm in length, appearing on the posterior dorsal region of the head and anterior dorsal region of the trunk above the gut. By 29 mm, scales cover the remainder of the body.

Detailed morphometrics and meristics on the larval series are given by Richardon and Laroche (1979).

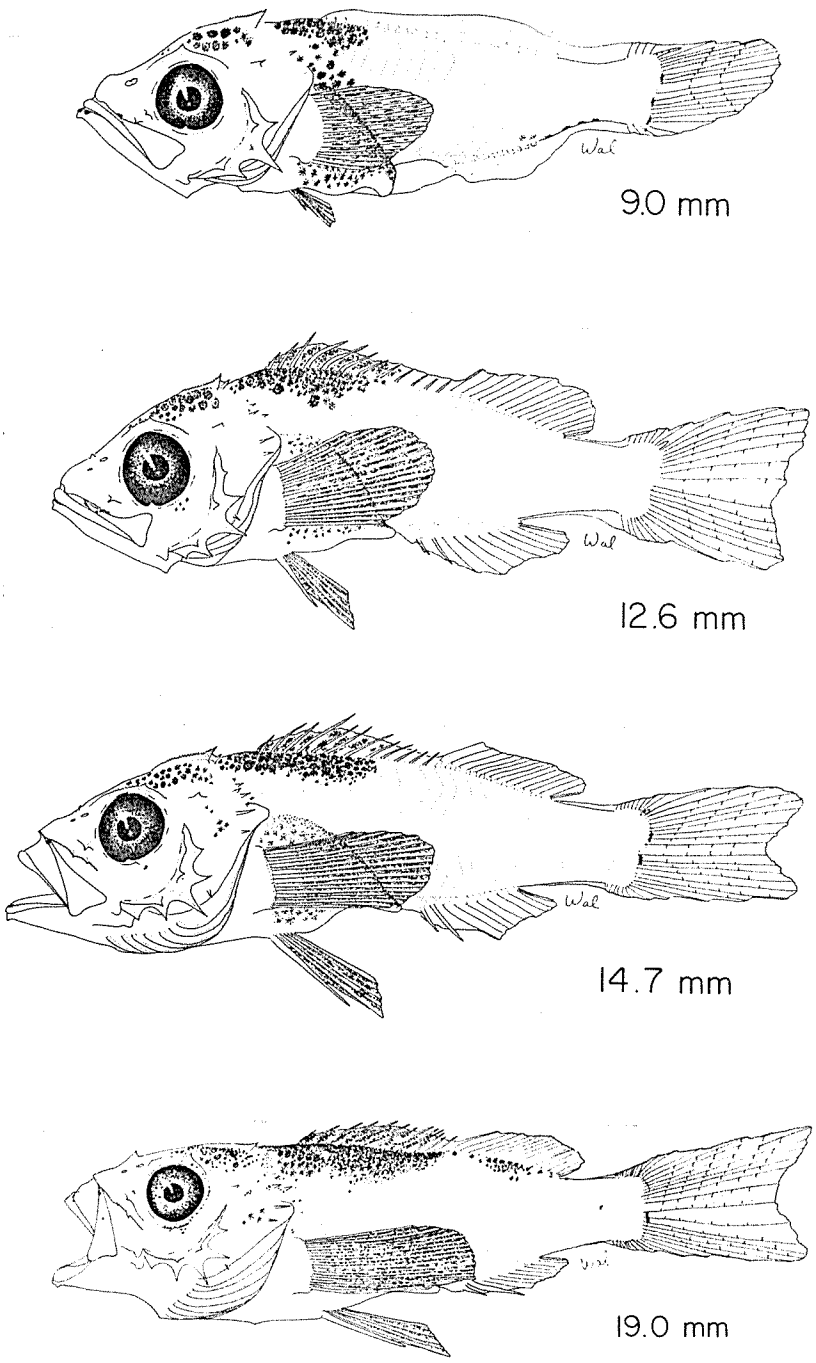


Fig. 42.9. Planktonic larvae of darkblotched rockfish, Sebastes crameri. (Source: Richardson and Laroche 1979).

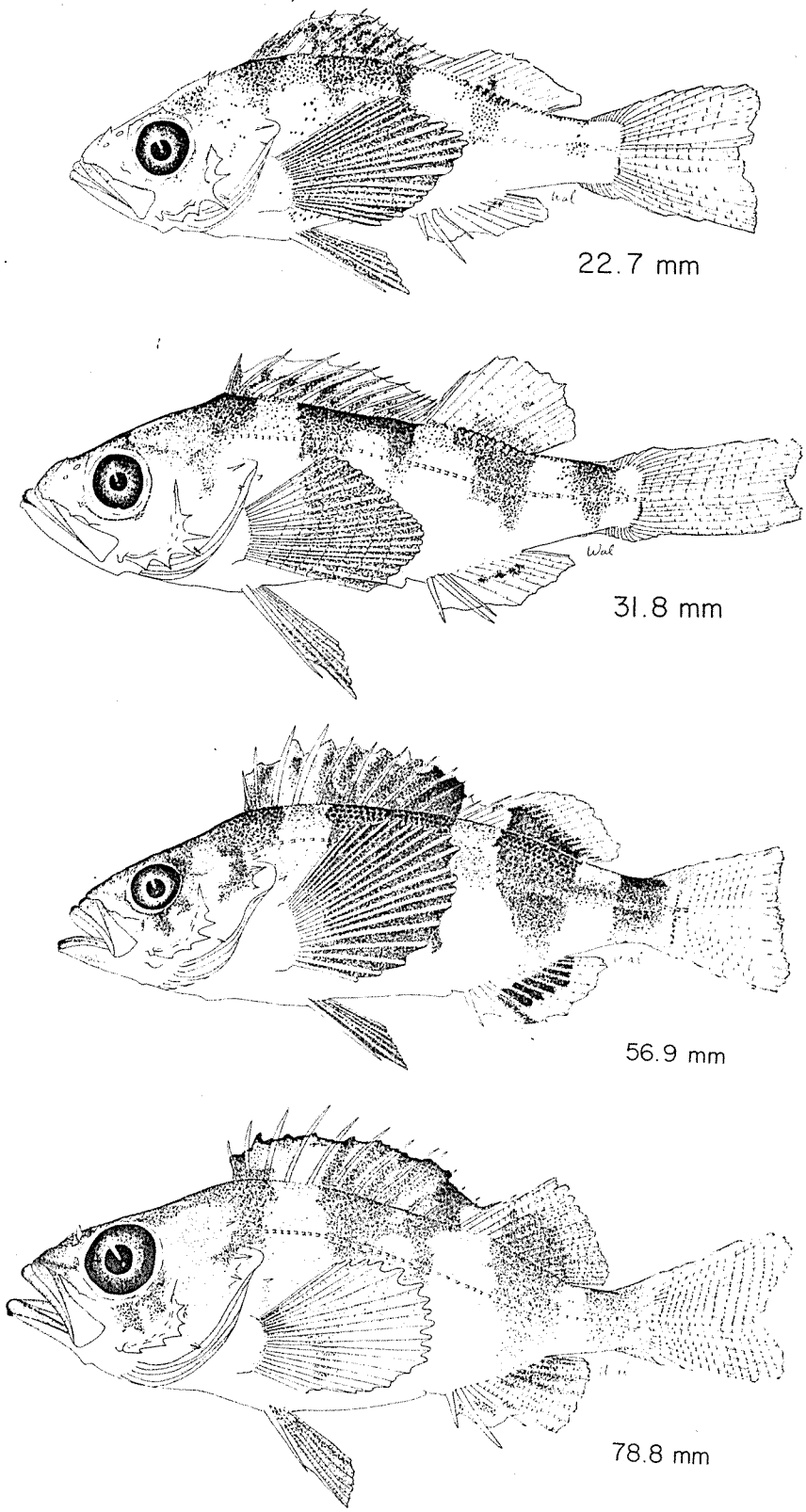


Fig. 42.10. Pelagic (22.7, 31.8, 56.9 mm) and benthic (78.8 mm) juveniles of darkblotched rockfish, Sebastes crameri. (Source: Richardson and Laroche 1979).

Table 42.8. Development of head spines in larval and juvenile dark-blotched rockfish, Sebastes crameri. Ranges given are lengths of specimens which possess a particular spine. (Source: Richardson and Laroche 1979).

Spine	Length (mm)[1]
Parietal	8.0-130.5[2]
Nuchal	8.0-130.5[2]
Preopercular (anterior series)	
1st	8.0-23.5
2nd	8.0-9.3
3rd	8.0-23.5
Preopercular (posterior series)	
1st	10.6-130.5
2nd	8.0-130.5
3rd	8.0-130.5
4th	8.0-130.5
5th	10.6-130.5
Opercular	
Superior	9.3-130.5
Inferior	10.6-130.5
Interopercular	12.2-130.5
Subopercular	78.8-130.5
Preopercular	16.3[3]-130.5
Supraocular	21.0[3]-130.5
Postocular	8.0-130.5
Infraorbitals	
Inferior	
1st	8.0-130.5
2nd	10.6-130.5
3rd	Absent in all sizes examined
Superior	
1st	8.0-49.2
2nd	Absent in all sizes examined
3rd	Absent in all sizes examined
4th	13.8[3]-130.5
Nasal	10.6-130.5
Coronal	Absent in all sizes examined
Tympanic	24.2-130.5
Pterotic	8.0-49.2
Posttemporal	
Superior	18.4-130.5
Inferior	8.0-130.5
Supracleithral	10.6-130.5
Cleithral	31.8-130.5

[1]Specimens examined ranged from 8.0 to 130.5 mm.
[2]Parietal and nuchal spines fused in 125.7 and 130.5 mm specimens.
[3]First appears as a bump.

Sebastes diploproa - Splitnose rockfish

Range: Baja California to Gulf of Alaska and Alaska Peninsula

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed, except for preextrusion larvae

Ranging from Baja California to Gulf of Alaska, splitnose rockfish are found at depths of 90 to 580 m (Hart 1973). In Puget Sound they have been reported in Hood Canal, central Puget Sound, and in the San Juan Islands (Miller and Borton 1980).

Splitnose rockfish release their young primarily in late spring-summer off Oregon (Hitz 1962), although some evidence exists which indicates they release larvae throughout the year as females with fertilized eggs have been present in February through September (representing 2-53% of the mature fish)(Westrheim 1975).

A few fish of this species are mature at 19 cm and four years of age, but the 50% maturity level is 5 years and 21 cm for California fish (Phillips 1964) and off British Columbia, 50% maturity is reached at about 27 cm for both sexes (Westrheim 1975). Fecundity ranges from about 14,000 eggs at 19 cm to 256,000 eggs at 36 cm (Table 42.9). Moser (1967) noted that S. diploproa females had one ovary which was smaller than the other and both ovaries were enclosed in the same ovarian sac over most of their length.

Prior to extrusion, larvae have a postanal ventral row of 11-20 melanophores as well as melanophores on the posterior dorsal surface of the gut (Fig. 42.2 B, C).

Table 42.9. Fecundity of splitnose rockfish, Sebastes diploproa, from California. (Source: Phillips 1964).

Date	Total length (mm)	Fecundity (Number of eggs)
4-10	195	14,400
12-59	249	50,500
4-59	265	56,000
4-59	265	63,800
12-59	270	83,200
12-59	295	145,800
10-59	307	232,500
1-61	320	189,100
10-59	325	238,500
10-59	335	184,200
10-59	345	218,900
10-59	346	303,700
10-59	355	225,700
10-59	365	234,500
10-59	365	256,500

Sebastes elongatus - Greenstriped rockfish

Range: Baja California to Gulf of Alaska

Occurrence in Puget Sound: common

Adult habitat: semi-demersal, inshore and offshore

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed, except for preextrusion larvae and larvae at yolk exhaustion

This species is found in both inshore and offshore waters at 90-365 m and is fairly common in the Strait of Georgia and Puget Sound (Hart 1973; Miller and Borton 1980).

Embryos are developing during April-May and are probably born in late spring or early summer off Oregon and British Columbia (Hitz 1962; Westrheim 1975). Sexual maturity is reached at lengths of 23 cm for both sexes (Westrheim 1975).

Preextrusion larvae have a postanal midventral row of 14-19 melanophores, pigment on the dorsal surface of the gut and on the yolk sac and are about 4.8 mm (Fig. 42.2D). Larvae reared to yolk sac absorption differ little (Fig. 42.2E), although Westrheim (1975) reported that additional melanophores appeared on the head, nape, and lower jaw regions.

Additional information on early life history is lacking.

Sebastes emphaeus - Puget Sound rockfish

Range: Puget Sound and San Juan Islands

Occurrence in Puget Sound: common

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed

This species occurs mainly in the deep water of Puget Sound and in the San Juan Islands area. It is common in areas of strong current, along steep slopes, and in crevices and caves formed by rocks. The behavior of adults observed by divers indicated they spend some time in relatively shallow water (10-25 m), particularly during June-October. These fish are found in small groups of 3 to 10 members which rest in contact with rocks or hover motionless in crevices or small caves, but when disturbed, will squeeze tightly into the crevice. Some Puget Sound rockfish are also seen swimming away from the rocks individually or in loosely associated groups. In the aquarium, these rockfish rest with the tips of the pectoral fins in contact with solid objects and they do not show aggression or territoriality (Moulton 1975).

Spawning reportedly occurs in August and September which is later than most other Sebastes species in this area, and the minimum recorded size at maturity is 130 mm TL (Moulton 1975). Males are generally mature at 2 years and possibly at one year (Moulton 1977). Fecundity of fish collected in the San Juans ranges from 20,177 to 57,103 eggs for fish between 150 and 179 mm (Table 42.10).

Larval stages of Puget Sound rockfish are undescribed.

Table 42.10. Fecundity of Puget Sound rockfish, Sebastes emphaeus, caught in the San Juan Islands, 1974. (Source: Moulton 1975).

Date	Age (yr)	Length (mm)	Weight (g)	Fecundity (Number of eggs)
8-13	2	148	40	20,437
8-11	2	150	46	20,117
8-13	3	160	58	24,435
8-13	3	169	68	43,984
8-13	3	179	79	57,103

Sebastes entomelas - Widow rockfish

Range: Baja California to southeast Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: pelagic

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: pelagic

Widow rockfish have been reported from the San Juan Islands area, but remain unrecorded from other parts of Puget Sound (Miller and Borton 1980). In addition to occurring in Washington, they are found from Baja California to southeastern Alaska and at depths of 90-365 m (Hart 1973).

Females examined off Oregon during April and May by Hitz (1962), had ovaries in the transitional or spent stage, indicating larvae were released in winter. For widow rockfish found in British Columbia, Westrheim (1975) reported the principal month of parturition to be April.

In California, widow rockfish reach sexual maturity at three years of age or about 30.5 cm, with the 50% maturity level at four years of age and 30.4 cm in length (Phillips 1964). Fifty percent maturity levels for B.C. widow rockfish appear to be at larger lengths, 37 cm for males and 38 cm for females (Westrheim 1975).

When mature, females are reported to carry between 55,000 and 915,000 eggs (Table 42.11).

Preextrusion larvae have been described and illustrated (Table 42.3). Pigment of 4.8-5.0 mm larvae consists of a ventral postanal midline of less than 16 melanophores which stops short of the anus by at least 4 myomeres and gut pigment near the anus. No pigment is present on the dorsum, head, or hypural region. However, with reared larvae, the number of postanal midventral melanophores increases to more than 16 (Harling et al. 1971; Westrheim 1975).

Later stage larvae and juveniles of widow rockfish have been described by Laroche and Richardson (1981) from plankton-caught specimens off Oregon. Characters which were used to separate 9.9 - 18 mm larvae (Fig. 42.11) from other rockfish larvae included:

1) fin element counts of 17-19 (usually 18) pectoral rays, 7-9 (usually 8) soft anal rays, and 14-16 (usually 15) soft dorsal rays;

Table 42.11. Fecundity of widow rockfish, Sebastes entomelas, from California. (Source: Phillips 1964).

Date mo.-yr	Total length (mm)	Fecundity (Number of eggs)
12-58	324	55,600
10-59	349	66,000
12-58	350	135,100
12-58	353	91,800
10-57	387	165,000
10-59	395	274,900
10-59	404	247,800
10-59	410	248,300
11-58	428	282,300
12-58	434	234,700
11-58	448	495,600
12-58	470	239,200
12-58	475	250,000
11-58	476	845,800
11-58	478	915,200
10-59	495	470,700
10-59	496	659,200
10-59	503	739,500
10-59	525	802,800
10-59	533	386,300

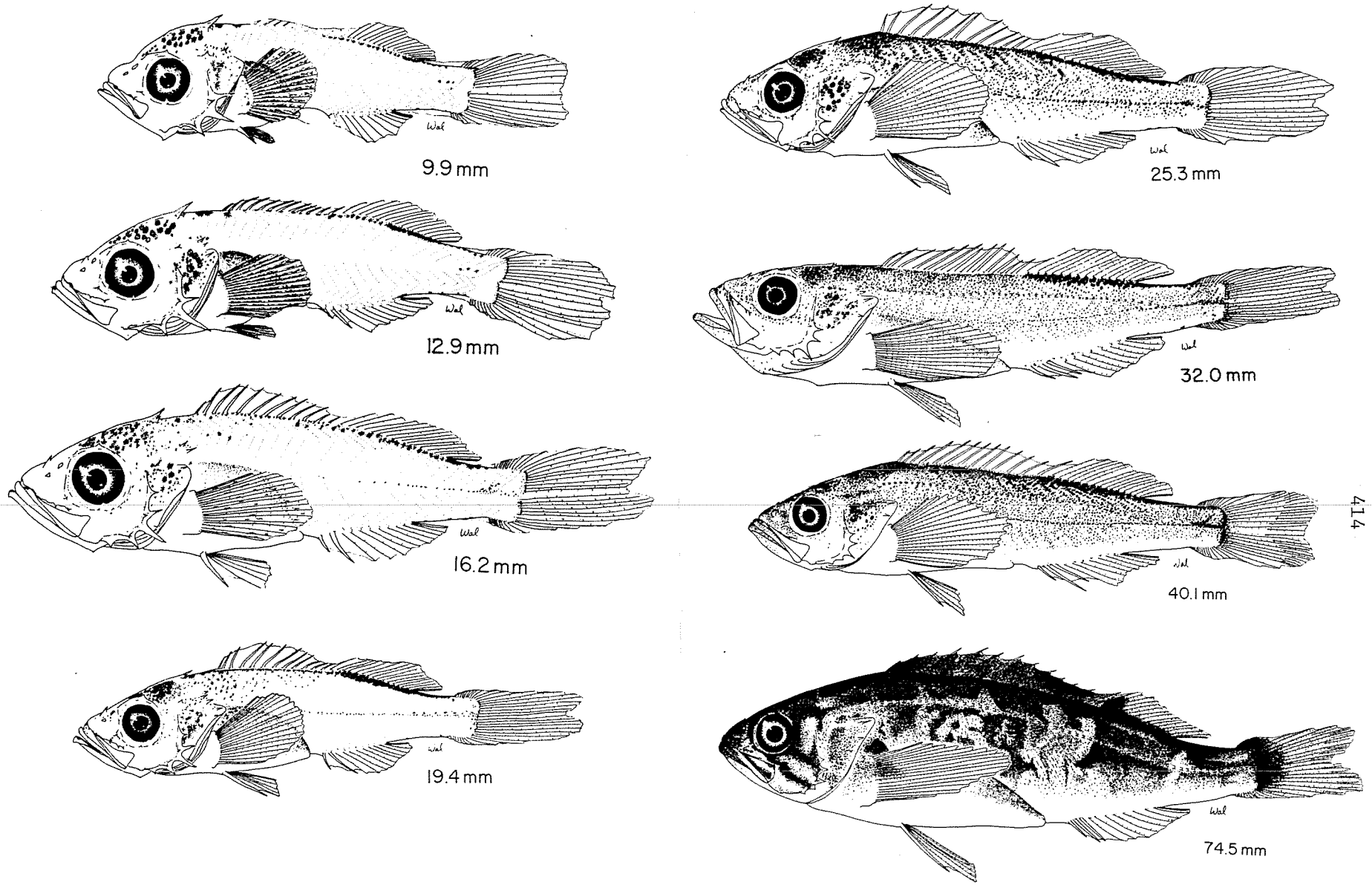


Fig. 42.11. Pelagic larvae (9.9, 12.9, 16.2, 19.4, 25.3 mm), pelagic juveniles (32.0, 40.1 mm), and benthic juvenile (74.5 mm) of widow rockfish, Sebastes entomelas. (Source: Laroche and Richardson 1981).

2) 34-39 gillraker counts;

3) morphometrics, especially the smaller caudal peduncle depth to caudal peduncle length ratio and presence of 18 pectoral fin rays which helps distinguish entomelas from melanops; and

4) pigmentation which includes moderate pigment on the pelvic and pectoral fins, melanophores along the dorsal and ventral margins of the caudal peduncle, melanophores along the dorsal body surface beneath the dorsal fin, and internal and/or external melanophores above the notochord near the point of flexion. (The lack of melanophores at the articulation of anal fin rays helps distinguish entomelas from flavidus and melanops larvae).

Meristics, spines (presence of preocular spines in specimens > 22 mm and supraocular spines in specimens > 18 mm), flat to convex interorbital space, body and fin pigmentation and morphology can be used to separate larvae > 18 mm (Laroche and Richardson 1981)(Fig. 42.11).

Details of pigmentation and morphological development were presented by Laroche and Richardson and are summarized below.

Larval widow rockfish complete flexion by about 14 mm and transform from the larval stage to the pelagic juvenile stage at 22-31 mm. Pelagic juveniles take up a benthic existence between 55 and 75 mm.

The most distinctive morphological feature of larval and juvenile widow rockfish is the relatively slender body form. Body depth decreases from about 29% to 24% of standard length (SL) through the pelagic juvenile stage after which it increases to ~ 28% SL.

Fin development, as outlined by Laroche and Richardson (1981), consists of the adult compliment of 17-19 (usually 18) pectoral rays, I, 5 pelvic fin spines and rays, and 8+7 principal caudal fin rays being present at 9.9-10.0 mm. The adult arrangement of dorsal and anal fin spines can be counted by 11 mm and the prespines in these fins become true spines by 27 and 30 mm, respectively.

As in other rockfish larvae, head spines of widow rockfish are numerous and well-developed (Table 42.12). Lateral line organs are visible in larvae as small as 9.9 mm and appear as light colored spots. Development of scales begins at about 22 mm and scales first appear above the pectoral fin. The body is covered with scales by ~ 26 mm.

According to Laroche and Richardson (1981), widow rockfish larvae occurred from 9 to 306 km off the coast of Oregon and small larvae (< 15 mm) have been taken in March through June with greatest abundance during April and May. Pelagic juveniles (> 15 mm) have been found at similar distances from shore during April and June. The benthic juveniles were found only in June (may be due to inadequate sampling) and at depths of 9-37 m.

Table 42.12. Summary of formation of head spines in larval and juvenile rockfish, Sebastes entomelas, between 9.9 and 74.5 mm. (Source: Laroche and Richardson 1981).

Spine		Size of specimen with spines
Parietal		9.9 - 74.5[1] mm SL
Nuchal		9.9[2]- 74.5[1]
Preopercular		
Anterior:	1st	9.9 - 29.7[3]
	2nd	12.0[4]
	3rd	9.9[2]- 27.9[3]
Posterior:	1st	9.9[2]- 74.5[5]
	2nd	9.9 - 74.5
	3rd	9.9 - 74.5
	4th	9.9[2]- 74.5
	5th	11.0[2]- 74.5
Opercular		
Superior		9.9[2]- 74.5
Inferior		15.2[2]- 74.5
Interopercular		10.9[2]- 74.5[3]
Subopercular		65.0[2]- 74.5[3]
Preocular		22.3[2]- 74.5
Supraocular		18.4[2]- 74.5
Postocular		9.9 - 74.5
Infraorbital		
Inferior:	1st	9.9[2]- 55.7[3]
	2nd	10.9 - 55.7[3]
	3rd	14.9 - 65.0[3],[6]
Superior:	1st	9.9 - 32.0[3]
	2nd	16.8 - 29.7
	3rd	13.7 - 30.8, 36.8[3]
	4th	9.9 - 55.5[3]
Nasal		11.0[2]-74.5
Coronal		Absent at all sizes examined
Tympanic		29.9[2]- 74.5
Pterotic		9.9 - 36.8[3]
Posttemporal		
Superior		16.2[2]- 74.5
Inferior		9.9 - 74.5
Supracheithral		11.9 - 74.5
Cheithral		40.1[2]- 71.1

[1]Parietals and nuchals spines fuse, only one tip visible at ≥ 45.0 mm.
[2]May appear as a bump at smaller sizes.
[3]May be present as a bump before being overgrown at larger sizes.
[4]Present on right side in one individual.
[5]Spine tip directed posteriorly at ≥ 40.1 mm.
[6]Spine is bifid at 24.5, 29.1, 30.8 mm.

Sebastes flavidus - Yellowtail rockfish

Range: southern California to Gulf of Alaska

Occurrence in Puget Sound: common

Adult habitat: schooling, semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: pelagic

Distributed off the coast from southern California to the Gulf of Alaska (Hart 1973), yellowtail rockfish are also frequently found in Puget Sound and inside waters of British Columbia. They are primarily a schooling species, forming large groups off the bottom. Schools near the San Juans have been observed between 12-13 m during the summer and slightly deeper (22-24 m) during winter and spring and fish are frequently seen schooling around rocky points, or along vertical rock walls (Moulton 1977). Juveniles reportedly live n small groups in crevices in the rocks and during the evening form large schools (hundreds of individuals) along or above the reef. At night, juveniles remain active, but adults may settle down among the rocks and become inactive (Moulton 1977).

In Puget Sound, spawning, spent, or ripe fish have not been seen (Moulton 1977; Washington et al. 1978), but the spawning season is November-March off California (Phillips 1964), and young are released in January-February off Oregon (Hitz 1962) and in March off British Columbia (Westrheim 1975). Length of 50% maturity for British Columbia fish is 40 cm for males and 42 for females (Westrheim 1975). Off California, a few fish are mature as small as 28 cm and 3 years of age, with 50% mature at 5 years and 33 cm (Phillips 1964). When mature, females may brood between 48,000 and 632,000 eggs per season (Table 42.13). Gunderson et al. (1980) determined the relationship of fecundity (F) to length (L) for yellowtail rockfish to be $F = 82721.8L-323516$.

Preextrusion larvae have a row of usually less than 16 (range 8 - 12) postanal midventral melanophores. The gut is pigmented and melanophores are usually present on the ventral body surface near the tip of the notochord (Fig. 42.2H).

Larvae and juveniles have been described by Laroche and Richardson (1980). Characters useful to distinguish the smallest (10-11 mm) planktonic larvae identified are (Fig. 42.12):

1) Moderately pigmented pectoral and pelvic fins;

Table 42.13. Fecundity of yellowtail rockfish Sebastes flavidus from California (Source: Phillips 1964).

Date mo.-yr.	Total length (mm)	Fecundity (Number of eggs)
12-58	297	66,100
10-59	330	48,400
12-58	345	80,800
12-58	381	242,600
12-58	430	295,400
12-58	433	591,700
12-58	440	266,000
1-61	445	621,200
12-58	455	611,900
1-61	475	632,800
12-58	478	394,400
10-59	484	578,600
12-58	487	579,000
12-58	514	472,200
12-58	535	575,000

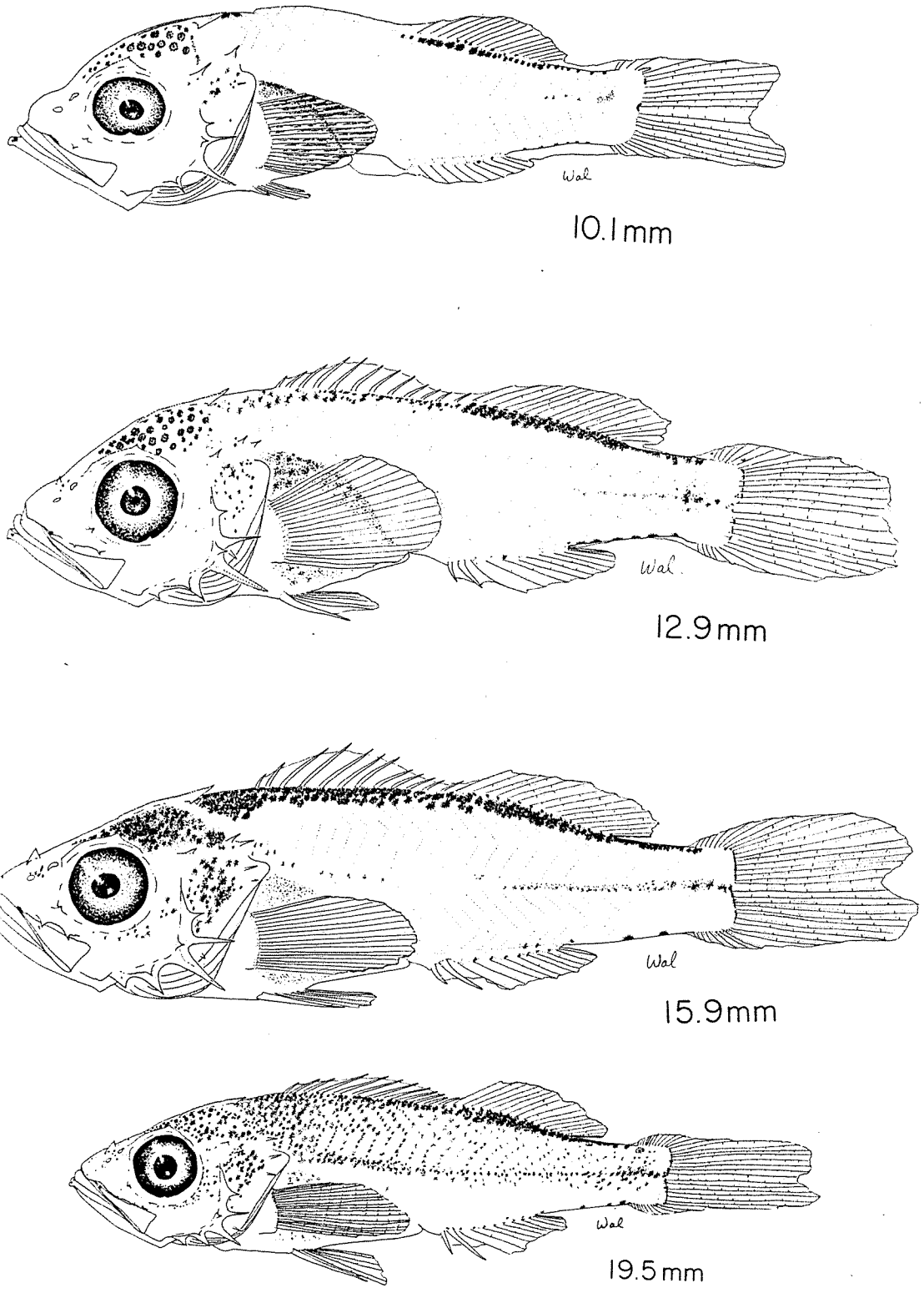


Fig. 42.12. Planktonic larvae of yellowtail rockfish, Sebastes flavidus. (Source: Laroche and Richardson 1980).

2) presence of pigment along the dorsal body surface under the dorsal fin;

3) internal and external melanophores above the notochord at and anterior to the point of notochord flexion;

4) melanophores along the dorsal and ventral margins of the caudal peduncle;

5) melanophores at the articulation of some dorsal and anal rays;

6) relatively long and narrow caudal peduncle; and

7) presence of 18 pectoral rays.

Meristics, lack of preocular and supraocular spines, flat to convex interorbital space, body and fin pigmentation, and body morphology, combine to distinguish larger larvae and juveniles (Fig. 42.13).

During larval development, notochord flexion is complete by 10.1 mm. Transformation from postflexion larvae to pelagic juveniles takes place between 23 and 27 mm and is accompanied by the structural change of the "prespines" in the dorsal and anal fins to sharp, hard spines. Melanistic pigmentation gradually increases over the body through the larval and transformation periods. Transition from pelagic to benthic habitat occurs when fish are between 40 and 50 mm.

Pectoral fins are formed and have 17-19 (usually 18) fin rays by the time larvae are 10-11 mm, the adult pelvic fin complement (I, 5) is also present at this time. Adult complements of dorsal and anal fin spines and rays can be counted by about 11-12 mm, and the transition of the 13th dorsal and 3rd anal fin "prespines" to spines is complete by ~ 27 mm.

At 10 mm, larvae of yellowtail rockfish possess at least 13 head spines (Table 42.14). Lateral line organs are visible on specimens > 14.8 mm and scales are first visible in 23-24 mm specimens and are located above the pectoral fin, near the posttemporal and supracleithral spines, and over the upper two-thirds of the body in the postanal region. Scale coverage is complete by 28 mm.

Detailed morphometrics and development of pigmentation are given by Laroche and Richardson (1980).

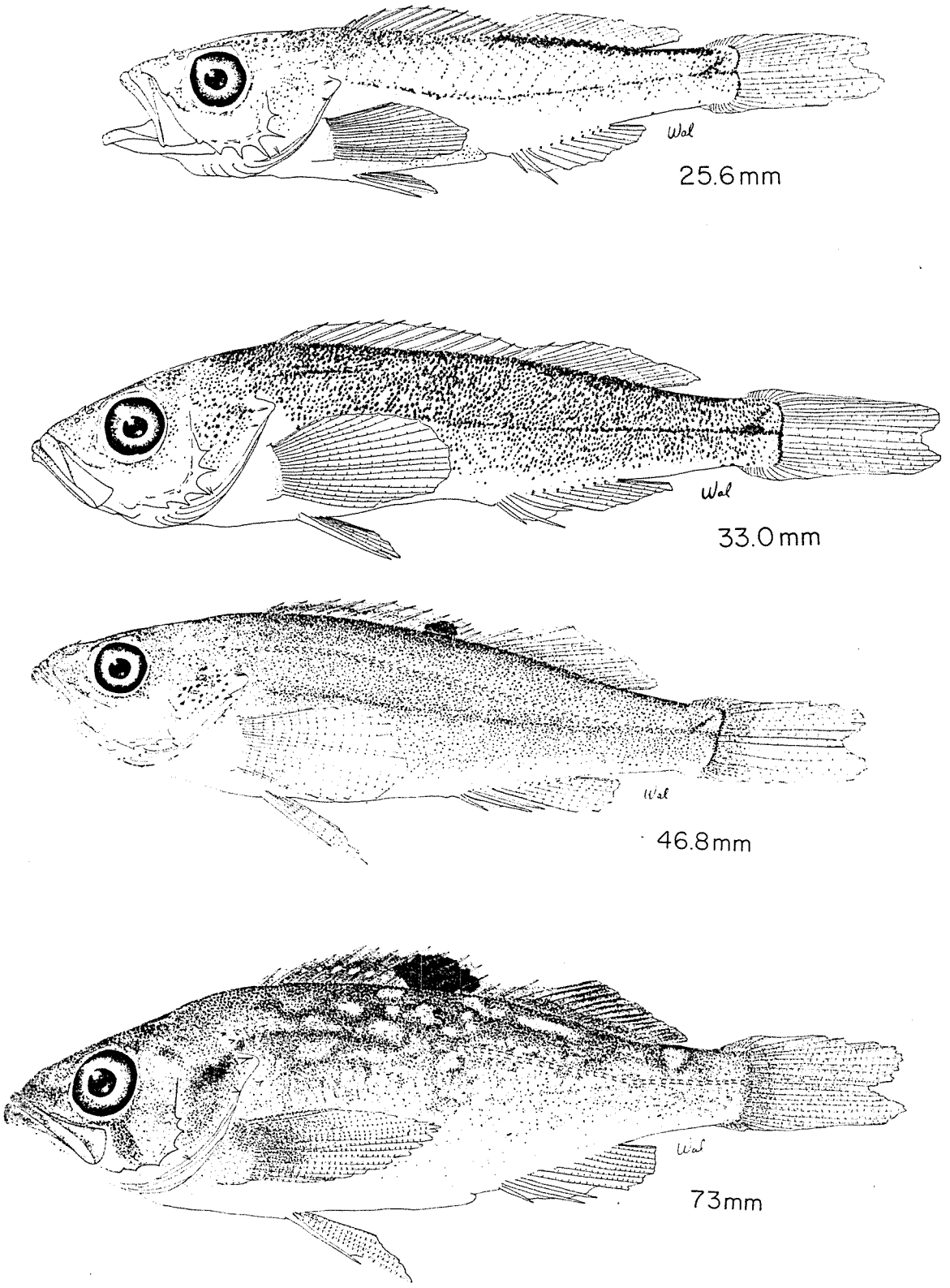


Fig. 42.13. Transforming specimen (25.6 mm), pelagic juveniles (33.0, 46.8 mm), and benthic juvenile (73 mm) of yellowtail rockfish, Sebastes flavidus. (Source: Laroche and Richardson 1980).

Table 42.14. Development of head spines in larval and juvenile yellowtail rockfish, Sebastes flavidus . Ranges given are lengths of specimens which possess a particular spine (Laroche and Richardson 1980).

Spine	Length (mm)[1]
Parietal	10.1-105.0[2]
Nuchal	10.1-105.0[2]
Preopercular-anterior series	
1st	10.1-30.4[3]
2nd	10.7, 11.4, 11.9, 12.0, 12.8, 19.8
3rd	10.1-29.6[3]
Preopercular-posterior series	
1st	10.1-105.0[3]
2nd	10.1-105.0
3rd	10.1-105.0
4th	10.1-105.0
5th	10.3[4]-105.0
Opercular	
Superior	10.1-105.0
Inferior	11.9[4]-105.0
Interopercular	10.1[4]-105.0[5]
Subopercular	absent on all sizes examined
Preocular	absent on all sizes examined
Supraocular	absent on all sizes examined
Postocular	10.1-105.0
Infraorbital	
Inferior	
1st	10.1-105.0[6]
2nd	10.3[4]-105.0[3,6]
3rd	12.9[4]-105.0[3,6]
Superior	
1st	10.1-43.6[3]
2nd	absent on all sizes examined
3rd	13.7[4]-33.1
4th	10.3-43.6
Nasal	11.4[4]-105.0
Coronal	absent on all sizes examined
Tympanic	30.4[4]-105.0
Pterotic	10.1-45.2[3]
Posttemporal	
Superior	20.5[4]-105.0
Inferior	10.1-72.5[3]
Supracleithral	10.3[4]-105.0
Cleithral	23.7-105.0[7]

[1] Lengths of specimens examined ranged from 10.1-105.0 mm.
[2] Parietals and nuchals fused and begin to regress at 35-37 mm.
[3] Bony overgrowth of spine in larger sizes.
[4] First appears as a bump.
[5] Covered by a fleshy lobe at 81 and 105 mm.
[6] Covered by a fleshy lobe at 67.6-105.0 mm.
[7] Spine becomes covered by scales at larger sizes.

Sebastes helvomaculatus - Rosethorn rockfish

Range: Baja California to Gulf of Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: pelagic

In Puget Sound, the only known recording of this species is from the San Juan Islands (Miller and Borton 1980), although it ranges along the entire coastline from Baja California to the Gulf of Alaska (Hart 1973). It is primarily a deep water species judging by some of the older common names given to it "deep-water scacciatale" and "deep-water scratch-tail" (Phillips 1957, cited by Richardson and Laroche 1979).

From examination of female gonads, Westrheim (1975) reported that parturition of rosethorn rockfish larvae occurred primarily in June off Oregon-British Columbia and 50% maturity level for females was at 20 cm and for males at 22 cm. Other aspects of the spawning biology have been little studied.

Preextrusion larvae (~ 4.1 mm) have the typical postanal ventral row of melanophores with usually less than 16 melanophores. A few spots occur on the hind gut and ventral yolk sac surface (Fig. 42.2I). Melanophores are lacking in all other areas, but reportedly begin to appear on the head, nape, or lower jaw after extrusion (Westrheim 1975). Newly extruded larvae have not been identified fom the plankton, but larvae as small as 7.7 mm have been included in a series describing larval and juvenile rosethorn rockfish (Richardson and Laroche 1979). The characters most useful in distinguishing the smallest larvae (7.7-11.0 mm; Fig. 42.14) are:

1) pigmentation on the fringes of the pectoral and pelvic fins;

2) general lack of body pigment;

3) melanophores inside the tip of the lower jaw;

4) a narrow interorbital distance (about 31% of the head length);

5) a long, deeply serrated parietal spine (about 27% of the head length); and

6) relatively long pectoral fins (about 24% of the standard length).

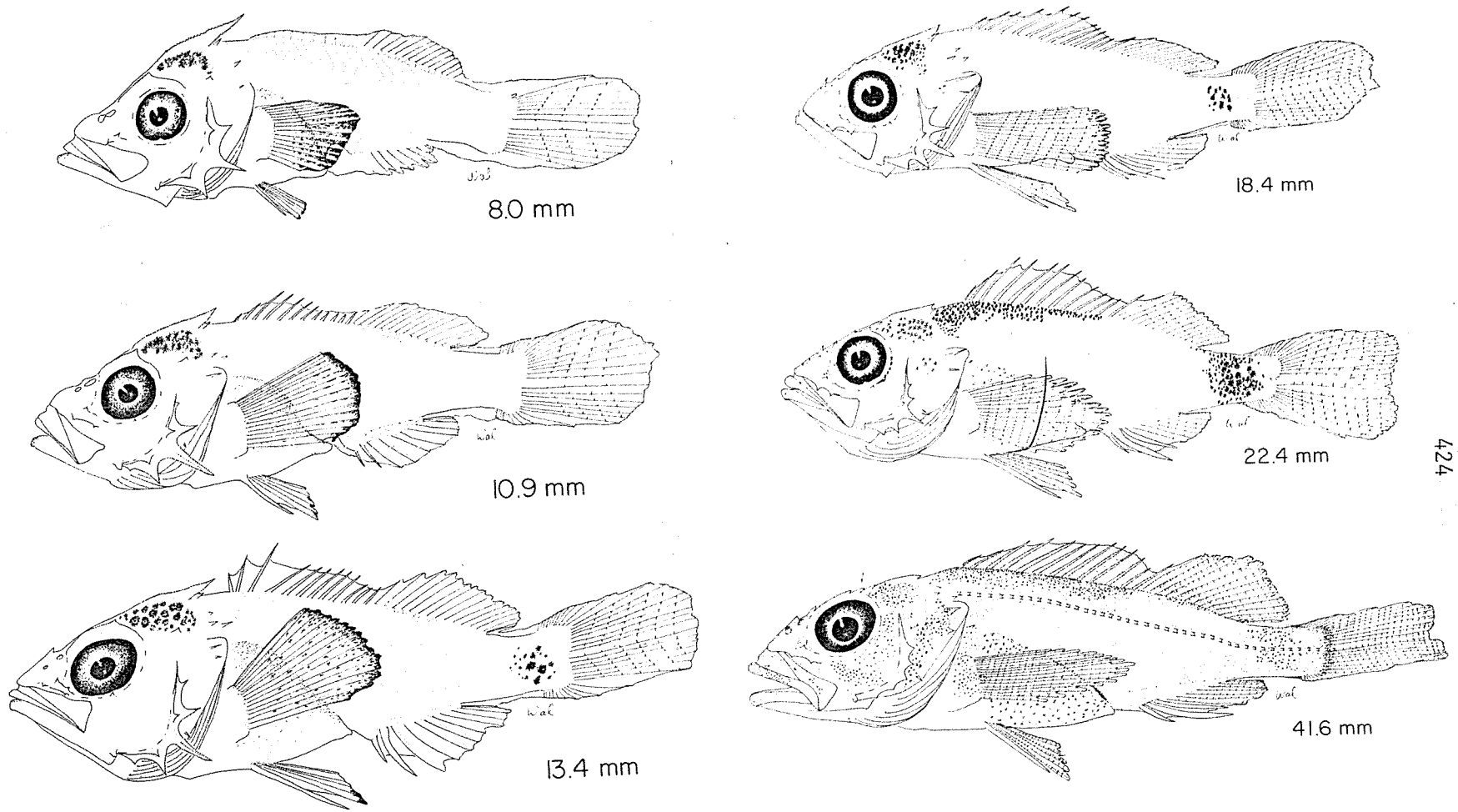


Fig. 42.14. Planktonic larvae (8.0, 10.9 mm) transforming specimens (13.4, 18.4 mm) and pelagic juveniles (22.4, 41.6 mm) of rosethorn rockfish, Sebastes helvomaculatus. (Source: Richardson and Laroche 1979).

Later stage larvae (13.4-18.4 mm) change little in appearance except for an increase of dorsolateral internal gut pigment and a distinctive pigment patch which appears on the caudal peduncle during transformation (Fig. 42.14). Meristics, presence of a supraocular spine, concave and narrow interorbital space, melanophores on the caudal peduncle, and the single melanistic pigment saddle which extends from the nape to the dorsal spine XI and ventrally about one-half the distance to the lateral line, are all key juvenile characteristics (Fig. 42.14).

Eleven head spines are present on larvae which have not completed notochord flexion (i.e., 7.7 and 8.8 mm). After flexion, an additional 9 spines can be seen. Head spines which become obscured with development include first and third anterior preopercular spines, and first through fourth superior infraorbitals (Table 42.15). Lateral line pores first appear anteriorly and are present on specimens > 17 mm and scales are forming on pelagic juveniles greater than 23 mm.

Detailed morphometrics and meristics of rosethorn rockfish larvae and juveniles (7.7-183 mm) are given by Richardson and Laroche (1979).

Table 42.15. Development of head spines in larval and juvenile rosethorn rockfish, Sebastes helvomaculatus. Ranges given are lengths of specimens which possess a particular spine. (Source: Richardson and Laroche 1979).

Spine	Length (mm)[1]
Parietal	7.7-183
Nuchal	8.0-183
Preopercular - anterior series	
1st	7.7-22.4
2nd	absent in all sizes examined
3rd	7.7-22.4
Preopercular - posterior series	
1st	8.8-183
2nd	7.7-183
3rd	7.7-183
4th	7.7-183
5th	8.8-183
Opercular	
Superior	8.8-183
Inferior	8.8-183
Interopercular	8.8-183
Subopercular	183
Preocular	13.4[2]-183
Supraocular	13.4-183
Postocular	7.7-183
Infraorbitals	
Inferior	
1st	8.8-183
2nd	8.8-183
3rd	absent in all sizes examined
Superior	
1st	7.7-22.4
2nd	12.0-22.4
3rd	13.4-22.4
4th	8.8-22.4
Nasal	9.9[2]-183
Coronal	absent in all sizes examined
Tympanic	41.6-183
Pterotic	7.7-23.8
Posttemporal	
Superior	13.4-183
Inferior	7.7-183
Supracleithral	8.8-183
Cleithral	18.4-136.4

[1] Specimens examined ranged from 7.7-183 mm.

[2] First appears as a bump.

Sebastes maliger - Quillback rockfish

Range: central California to Gulf of Alaska (Hart 1973)

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed, except for preextrusion and early postextrusion larvae

Quillback rockfish are common and widely distributed in Puget Sound (Miller and Borton 1980). Notable for its high, deeply incised spinous dorsal fin and brown and yellow body color, this species exists as a solitary bottom dweller, although it may hover in areas of strong current. Surprisingly, little early life history information is available on this seemingly abundant resident in Puget Sound. In Puget Sound, ripe females have been reported in April (Moulton 1977) and parturition of larvae is thought to occur in May (Washington et al. 1978). The preextrusion larvae (~ 5.0 mm) have, in addition to a long row of postanal midventral melanophores (52-64), a shorter dorsal row of 8-18 melanophores. A few pigment spots are present on the yolk sac (Fig. 42.2J; 42.3A). With development, postextrusion larvae acquire additional spots on the head, nape or lower jaw (Westrheim 1975).

Sebastes melanops - Black rockfish

Range: southern California to Gulf of Alaska (Hart 1973)

Occurrence in Puget Sound: common

Adult habitat: semi-demersal, schooling near rocks

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: pelagic

This species is also frequently found and widely distributed in Puget Sound. As a schooling species, it is common in shallow water, around rocky points or vertical rock walls (Moulton 1977), and in kelp beds (Leaman 1976). Dunn and Hitz (1969) believed that black rockfish, at some stage of its life or in some races, maintains a pelagic existence off the continental shelf over deeper ocean waters, with offshore migrations possibly relating to spawning behavior.

Spawning time has not been pinpointed but occurs prior to April (Moulton 1977; Westrheim 1975; Dunn and Hitz 1969) and possibly prior to January (Washington et al. 1980).

Preextrusion larvae have not been described, but recently Laroche and Richardson (1980) described planktonic larvae and juveniles from off Oregon. Characters useful in distinguishing Sebastes melanops larvae are (Fig. 42.15):

1) moderately pigmented pectoral and pelvic fins;

2) presence of pigment along the dorsal body surface under the dorsal fin;

3) internal and external melanophores above the notochord at and anterior to the point of notochord flexion;

4) melanophores along the dorsal and ventral margins of the caudal peduncle;

5) melanophores at the articulation of some dorsal and anal rays;

6) relatively deep and short caudal peduncle; and

7) presence of 19 pectoral rays.

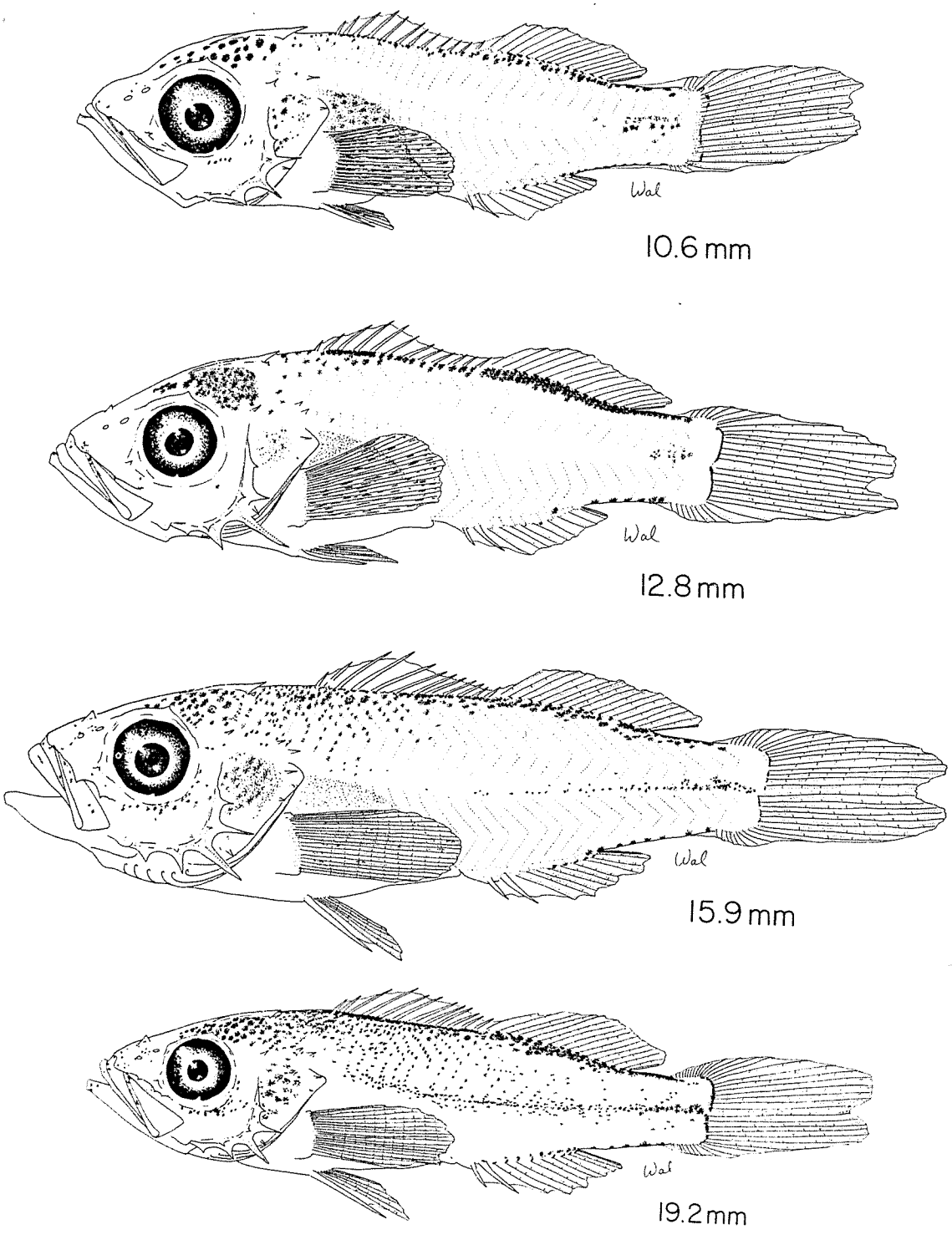


Fig. 42.15. Planktonic larvae of black rockfish, Sebastes melanops. (Source: Laroche and Richardson 1980).

A combination of several characters can distinguish larger larvae and juveniles (Fig. 42.16) and include meristics, lack of preocular and supraocular spines, flat to convex interorbital space, body and fin pigmentation, and body morphology.

During larval development, larvae complete notochord flexion by 10.6 mm. Transformation from postflexion larvae to pelagic juveniles occurs at 24-33 mm as indicated by dorsal and anal "prespines" becoming hard, sharp spines. Pigmentation gradually increases during development, with no marked change during transformation. Juveniles descend to the benthic habitat at about 40-50 mm (Fig. 42.16).

By about 12 mm, larval black rockfish possess the full adult complement of pectoral fin rays, pelvic fin rays, and dorsal and anal fin spines and rays.

The smallest black rockfish larvae, collected from the plankton (10.6 mm) had 17 head spines and benthic juveniles possess or have traces of 15 remaining head spines (Table 42.16).

Detailed morphometrics and meristics of black rockfish larvae and juveniles are provided by Laroche and Richardson (1980).

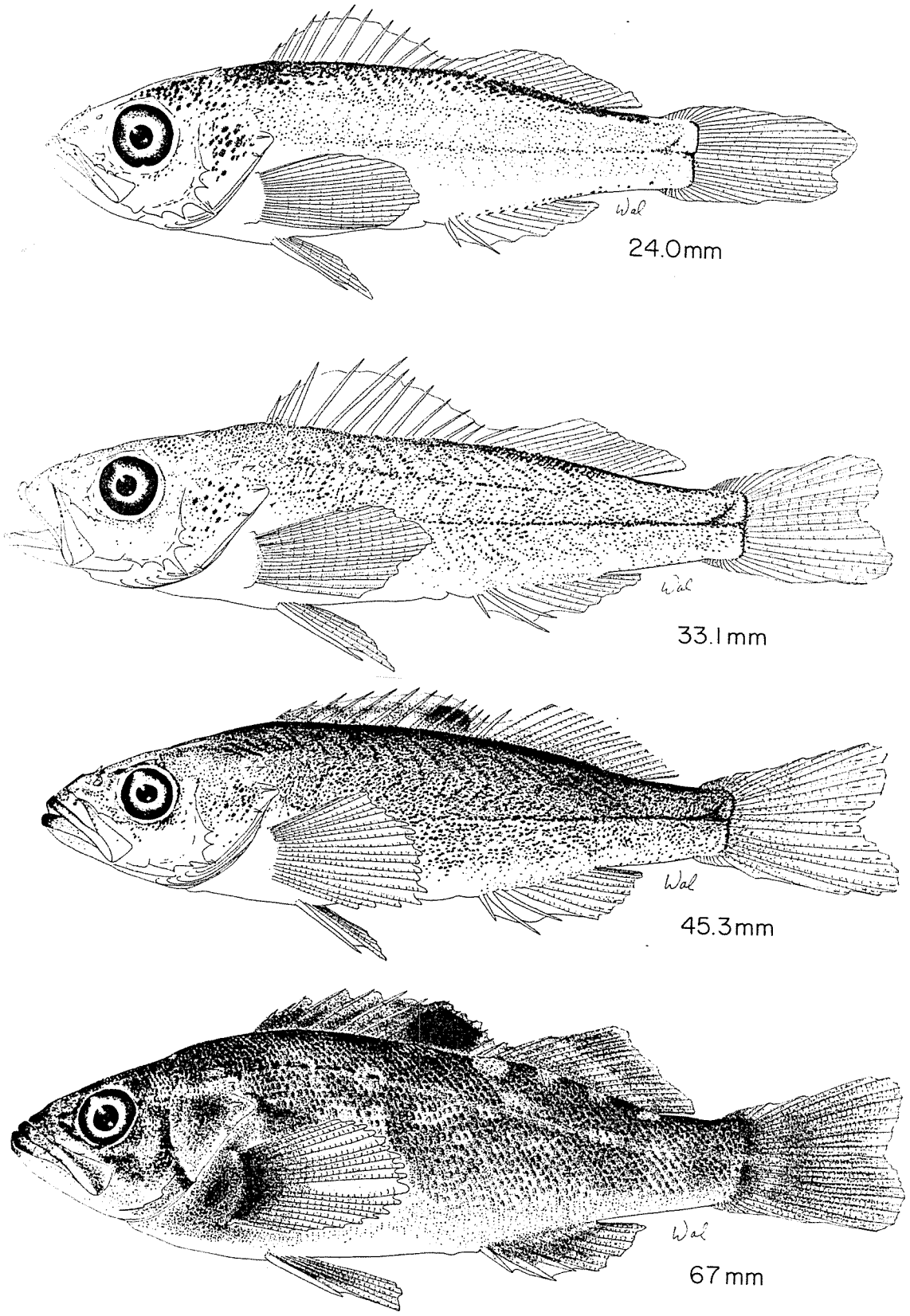


Fig. 42.16. Pelagic larvae (24.0, 33.1 mm), pelagic juvenile (45.3 mm), and benthic juvenile (67 mm) of black rockfish, Sebastes melanops. (Source: Laroche and Richardson 1980).

Table 42.16. Development of head spines in larval and juvenile black rockfish, Sebastes melanops. Ranges given are lengths of specimens which possess a particular spine. (Source: Laroche and Richardson 1980).

Spine	Length (mm)[1]
Parietal	10.6-97.7[2,3]
Nuchal	10.6[4]-97.7[2,3]
Preopercular - anterior series	
1st	10.6-27.9[3]
2nd	present in 11.9, 17.4 mm specimens
3rd	10.6-24.6[3]
Preopercular - posterior series	
1st	10.6-67.0[3]
2nd	10.6-111.6[3]
3rd	10.6-111.6
4th	10.6-111.6
5th	11.7[4]-111.6
Opercular	
Superior	10.6[4]-111.6[5]
Inferior	12.8[4]-111.6[3,6]
Interopercular	10.6[4]-111.6[3,6]
Subopercular	absent on all sizes examined
Preocular	absent on all sizes examined
Supraocular	absent on all sizes examined
Postocular	10.6-111.6
Infraorbital	
Inferior	
1st	10.6-111.6[6]
2nd	11.7[4]-111.6[3,6,7]
3rd	13.6[4]-111.6[3,6,7]
Superior	
1st	10.6-35.8[3]
2nd	absent on all sizes examined
3rd	19.2-33.1[3]
4th	10.6-48.4[3]
Nasal	11.7[4]-111.6
Coronal	absent on all sizes examined
Tympanic	24[4]-67[3]
Pterotic	10.6-41.0[3]
Posttemporal	
Superior	19.0-111.6[8]
Inferior	10.6-43.8[2]
Supracleithral	10.6[4]-111.6[8]
Cleithral	30.6[4]-111.6[8]

[1] Lengths of specimens examined ranged from 10.6-111.6 mm.
[2] Parietal and nuchals become fused at ≥ 27.9 mm.
[3] Bony overgrowth of spine at some sizes.
[4] First appears as a bump.
[5] Spine is bifid at some sizes.
[6] Spine covered by fleshy lobe at larger sizes.
[7] Adjacent spines fused at larger sizes.
[8] Spine has become scale-covered at larger sizes.

Sebastes miniatus - Vermilion rockfish

Range: Baja California to central Vancouver Island

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for early larvae

From Baja California to Vancouver Island, vermilion rockfish occur mainly at depths of 180-275 m (Hart 1973). In Puget Sound, they have been recorded from Discovery Bay and the San Juan Islands (Miller and Borton 1980).

Spawning season in California is November (Moser 1967) and may extend to mid-March (Phillips 1964). An occasional female may mature at 23 cm and 3 years of age, but the 50% maturity level is at 6 years of age and 33 cm; vermilion rockfish may live as long as 22 years (Phillips 1964). During the spawning season, over a million eggs may be matured (Table 42.17). Other aspects of the spawning biology remain unstudied.

A 4.3 mm larvae illustrated by Moser et al. (1977) showed a short row (~ 10 spots) of postanal midventral melanophores, rather heavy dorsal gut pigment, spots on the head, nape and lower jaw, and a spot in the ventral finfold below the hypural region (Fig. 42.3C). Larval development remains unstudied.

Table 42.17. Fecundity of vermilion rockfish, Sebastes miniatus, from California. (Source: Phillips 1964).

Date mo.-yr.	Total Length (mm)	Fecundity (Number of eggs)
11-59	315	63,300
11-59	358	129,300
11-59	388	158,800
11-59	440	383,600
11-60	466	527,300
12-59	476	226,500
12-58	500	1,070,700
11-59	512	501,700
11-59	520	1,189,500
12-59	528	1,048,800
11-59	530	1,388,400
11-59	550	1,625,600

Sebastes mystinus - Blue rockfish

Range: Baja California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: pelagic, undescribed except for preextrusion larvae

Blue rockfish occur from Baja California to the Bering Sea, but are probably infrequently encountered in Puget Sound (Hart 1973; Miller and Borton 1980). Off the coast, their common depth range is between 180-550 m (Hart 1973). This species is gregarious, although it does not form tight schools (Wales 1952).

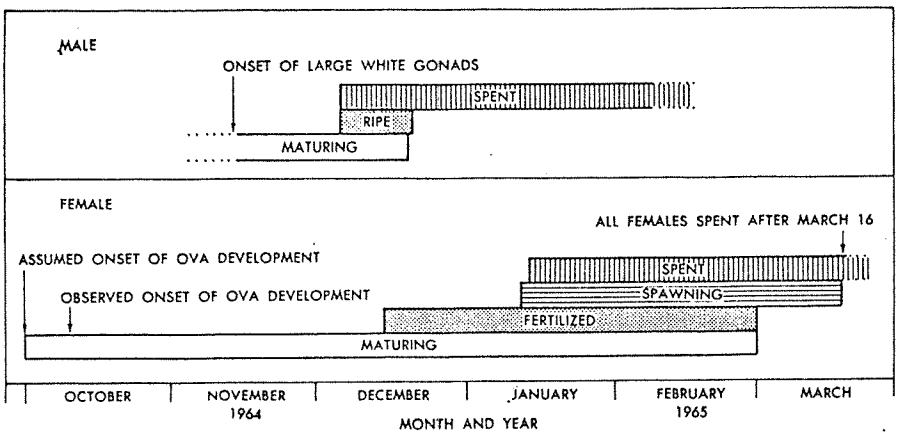
Based on studies in California, ovaries of blue rockfish are maturing, but ova are unfertilized, in October. The first signs of fertilized ova or developing embryos appear in mid-December and release of larvae occurs from mid-January to mid-March (Fig. 42.17).

Size and age of maturity varies considerably. Some males and females mature at age 3 and lengths of 190-200 mm for males and 210-220 mm for females. However, some females are 8-10 years old before spawning and some males are immature at 8 years. Most fish are mature, however, by their sixth or seventh year (Fig. 42.18).

When mature, females between 250-325 mm can carry 50,000-300,000 eggs per year (Fig. 42.17). One female, 405 mm, reportedly carried 524,000 nearly mature embryos (Wales 1952).

During October, the immature eggs are from .03 to .24 mm in diameter and their oil globules are colorless (Fig. 42.19 A, B). With advancement, the globules become better developed and are pale yellow (Fig. 42.19 C, D), but when near maturity (Fig. 42.19 E), are colorless. Mature eggs are ~.35 mm and probably break from the follicles at this point (Wales 1952). Interovarian larvae possess a large yolk sac with a single large oil globule (Fig. 42.19 G). The yolk sac is much reduced prior to hatching.

Preextrusion larvae have a ventral row of 22-28 postanal melanophores, a concentration of melanophores on the dorsal surface of the peritoneum, a few melanophores near the tip of the tail, and a concentration of small melanophores near the tip of the tail, and a concentration of small melanophores either in front of or behind the eye (Fig. 42.3 D).



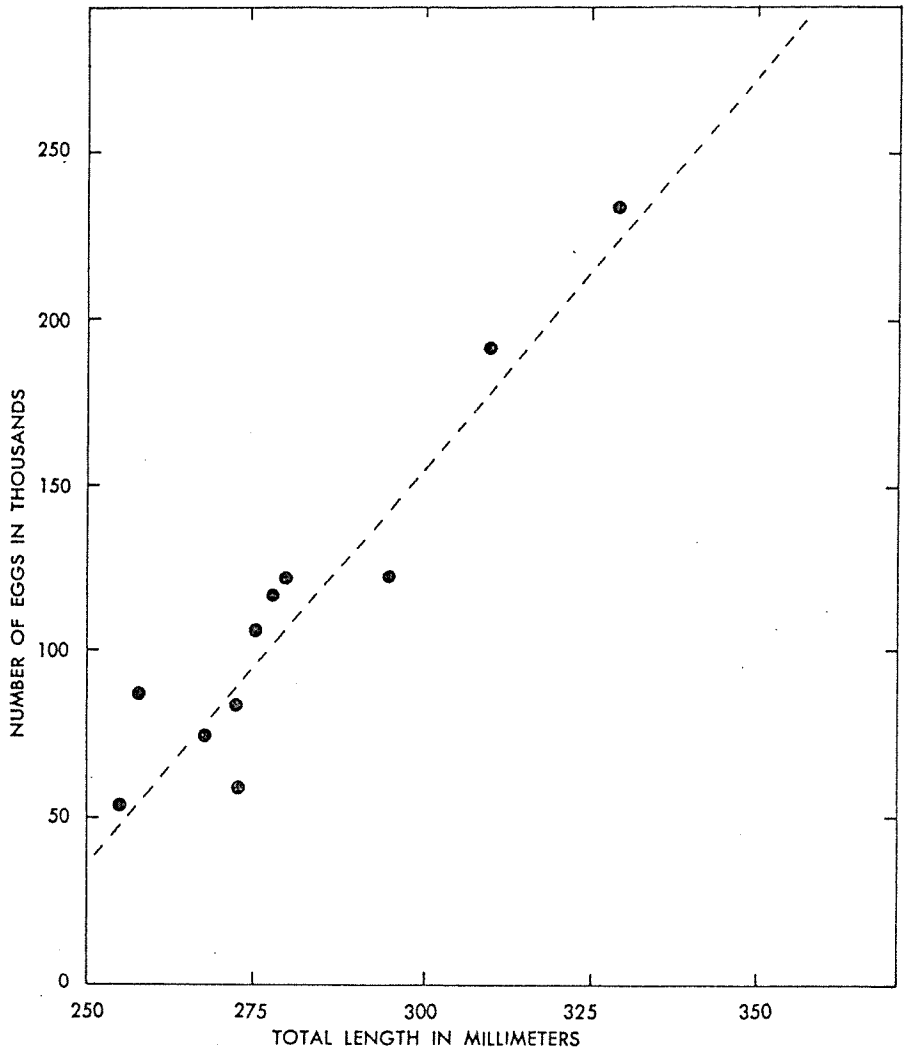


Fig. 42.17. Sexual development, by month, of mature male and female blue rockfish, Sebastes mystinus, from California (top) and number of eggs in ovaries of eleven blue rockfish, 256-330 mm TL (bottom). (Source: Miller and Geibel 1973).

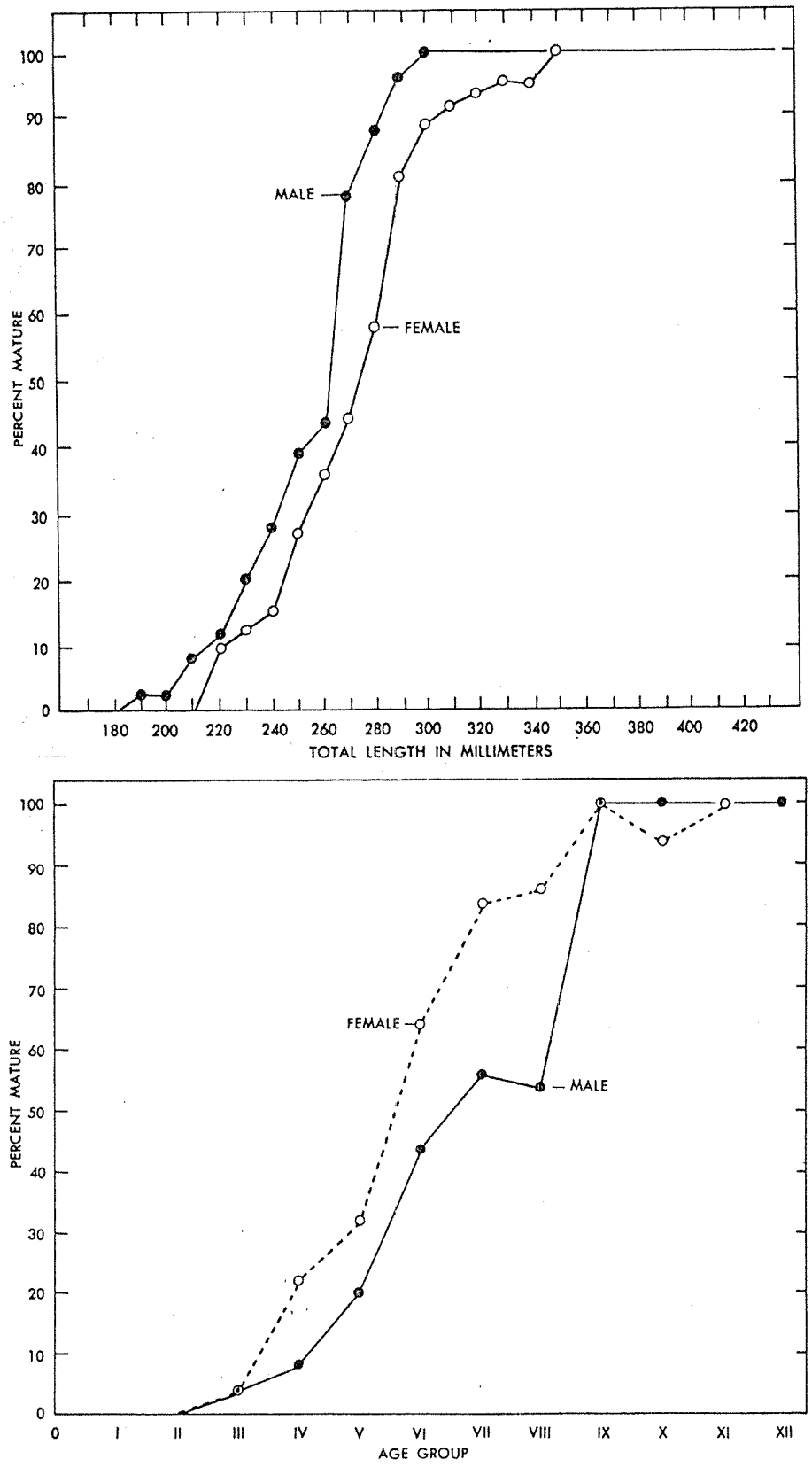


Fig. 42.18. Sexual maturity of 648 female and 343 male blue rockfish, Sebastes mystinus, by length (top), and sexual maturity of 399 females and 170 males by age (bottom). (Source: Miller and Geibel 1973).

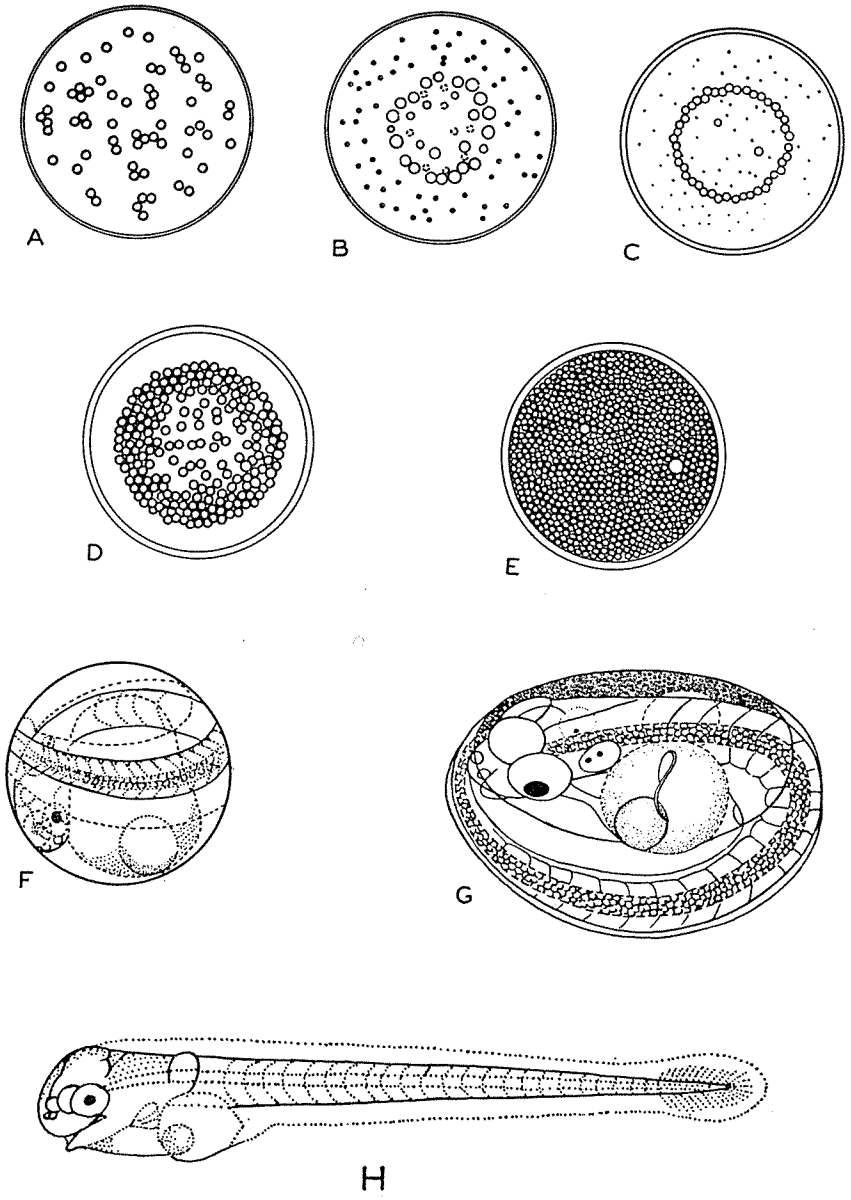


Fig. 42.19. Embryonic development of blue rockfish, Sebastes mystinus: A) oil globules colorless; B) spheres of colorless globules starting to form; C) globules growing; E) nearly mature, globules colorless; F) embryo with large yolk sac; G) embryo just prior to hatching; H) larva just hatched. (Source: Wales 1952).

Larvae are born at about 3.5 mm and it is not known for sure if they hatch prior to or after extrusion from the female. They are pelagic at birth and remain so for several months. In April, juvenile blue rockfish 45-50 mm concentrate in protected shallow rocky areas and in kelp canopies. By June, there are large concentrations of juveniles in protected inshore areas of central California and by October, juveniles are 65-90 mm TL (Miller and Geibel 1973).

Sebastes nebulosus - China rockfish

Range: central California to southeastern Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: demersal in caves

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed

China rockfish are commonly found in shallow water (less than 50 fm) from central California to southeastern Alaska (Hart 1973). They seem to prefer crevices and remain in close proximity, returning to a "home" crevice when disturbed (Hart 1973; Moulton 1977). Information on reproduction consists of a report of the collection of a gravid female, 322 mm TL and 908 g taken during January in Diablo Cove, California (Burge and Schultz 1973).

Sebastes nigrocinctus - Tiger rockfish

Range: central California to southeastern Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, in crevices

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed

Ranging from central California to southeastern Alaska, the tiger rockfish is a solitary bottom dweller which inhabits caves and crevices where it sometimes lies on its side. They are commonly observed in the Strait of Georgia at depths down to 275 m (Hart 1973) and are also reported from the San Juan Islands and central Puget Sound (Miller and Borton 1980). Its preference for caves may account for its rare occurrence in moving gear and it may be more abundant than evident. Based on aquarium observations, territorial behavior is marked and tiger rockfish are aggressive in defending a home crevice. They also exhibit rapid color changes when disturbed or in response to changes in light intensity (Hart 1973).

Spawning characteristics are little known. Moulton (1977) reported finding ripe females in May in the San Juan Islands and Westrheim (1975) lists the principal month of parturition as also occurring in May.

Juveniles are pelagic as evidenced by 4 individuals (42, 43, 45, 52 mm) that were found associated with a barnacle covered glass float off the coast of British Columbia (Hitz 1961).

Sebastes paucispinis - Bocaccio

Range: Baja California to Gulf of Alaska

Occurrence in Puget Sound: common in some areas

Adult habitat: semi-demersal

Spawning habitat: same

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: pelagic

Bocaccio are present from Baja California to the Gulf of Alaska (Hart 1973) and are found in Puget Sound from Tacoma to Bellingham Bay (Miller and Borton 1980).

Off California, adult bocaccio have been taken at a wide range of depths (25-305 m) during the spawning season and do not show any evidence of an upward spawning migration. It is assumed that larvae are born in the normal adult rockfish habitat and since rockfish larvae (Sebastes spp.) inhabit surface waters (Ahlstrom 1959, cited in Moser 1967), young may have to travel a considerable distance upward to reach the larval habitat. Newborn larvae have been observed swimming rapidly with lateral flexions of the tail and beating of the pectoral fins. In addition, they exhibit positive phototaxis in aquaria and are buoyant, thus aiding upward migrations (Moser 1967).

According to Phillips (1964), bocaccio reach maturity at 3 years and 35 cm, but 50% are not mature until 4 years and about 41 cm in total length. Off Washington-Oregon, Gunderson et al. (1980) found 50% of males mature at 44.8 cm forklength and females at 48.2 cm fork length.

Bocaccio are one of the few rockfish which may mature more than one brood per year. In the females, ovaries are small during the postextrusion period of March to June and the diameter of unyolked eggs is less than .2 mm. Vitellogenesis begins in July and continues through the summer, and by October the mature eggs are .55 mm. Large females may mature up to 2 million eggs (Table 42.18). Embryos appear and develop during October and the first brood is released in November. Gestation of the second batch takes place immediately and larvae are released in March (Moser 1967). MacGregor (1970) also encountered females which contained a few intact hatched larvae from a previous spawning along with early embryos or unfertilized eggs. In more northern waters the spawning season of bocaccio is not as well known: Washington et al. (1978) examined only a few male bocaccio during mid-late January in Puget Sound and all were ripe and Westrheim (1975) reported the principal month of parturition off British Columbia as prior to February.

Table 42.18. Fecundity of bocaccio, Sebastes paucispinis, in California. (Source: Phillips 1964).

Date mo.-yr.	Total Length (mm)	Fecundity (Number of eggs)
2-59	380	20,000
12-58	420	143,700
12-59	423	300,000
2-59	445	105,000
12-58	455	255,200
11-59	485	343,800
12-58	525	432,400
10-59	525	434,100
12-58	550	316,400
11-59	574	618,300
10-59	586	549,800
12-58	628	596,400
11-58	648	1,371,200
2-59	650	1,057,000
11-58	650	1,266,600
1-59	660	839,100
10-59	666	888,700
11-58	678	1,306,600
12-58	690	1,138,000
12-59	695	1,271,600
2-59	720	2,107,900
12-60	745	1,196,000
12-60	747	1,629,400
10-59	771	2,297,900

The development of embryos, larvae, and juveniles of bocaccio has been described. The youngest brood examined during October from females taken off California consisted of larvae that were .85-1.0 mm. Each had a translucent yolk mass with a single large oil globule ranging from 0.3 to 0.4 mm in diameter and were in the early high blastula stage (Fig. 42.20 A), according to stages described by Oppenheimer (1937). Melanophores began to form at about stage 27 (Fig. 42.20 G) and first appeared along the dorsolateral surface of the gut, followed by a single median series of melanophores along the ventral margin of the tail. Melanophores develop on the posterior margins of the pectoral fins in the most advanced intra-ovarian embryos (Fig. 42.20 H). At parturition, the embryos have functional jaws, eyes, and pectoral fins, and range in length from 4-5 mm. Most of the yolk is depleted, but the oil globule persists even after the yolk is absorbed and is often seen in larvae collected from the plankton. In the most advanced broods examined, embryos appeared to be hatched or were in the process of hatching before birth (Moser 1967).

One of the most striking morphological features of bocaccio larvae are the paired fins. At birth, the pectorals are large and fan-shaped (Fig. 42.21 A). The dorsal part of the fin grows faster than the ventral part, giving the fin an aliform shape which is retained in larvae up to 10 mm SL (Fig. 42.21 B, C). The pelvic fins also undergo spectacular development. They first appear in 5 mm larvae, lengthen quickly and reach the greatest relative length (to body length) in 13-14 mm SL larvae (Fig. 42.21 D).

Another prominent morphological feature of larvae of this species is the presence of numerous head spines which are nearly all lacking in juveniles and adults. The third preopercular spine (posterior series) which forms first, becomes the largest larval head spine. It appears in larvae at 5-6 mm and reaches its greatest relative length (to head length) in 10-13 mm larvae. It is also serrated at this time. The first and fifth preopercular spies do not develop until late in the larval period (Fig. 42.21 D, E). The anterior series of preopercular spines develops by 8.7 mm. Other spines which develop and regress during the larval period are parietals, tympanics, cleithrals, supracleithrals, nuchals, postoculars, supraoculars, preoculars, suborbitals, and nasals. Only the opercular and preopercular spines persist in juveniles and adults (Moser 1967).

The pigmentation pattern exhibited by larval bocaccio is another diagnostic character. At birth, larvae have a series of 6-14 melanophores between the third-fourth and fourteenth-seventeenth postanal myomeres on the ventral surface of the tail. Newborn larvae also have pigment on the margin of the pectoral fin. With development, a pair of melanophores appears above the optic lobes of the brain. These melanophores and a single median melanophore above the medulla first appear in 5-6 mm larvae (Fig. 42.21 B). Melanophores are rapidly added in this region and cover all lobes of the brain in 10 mm larvae. The only other major head pigment formed during the larval period is on the posterior

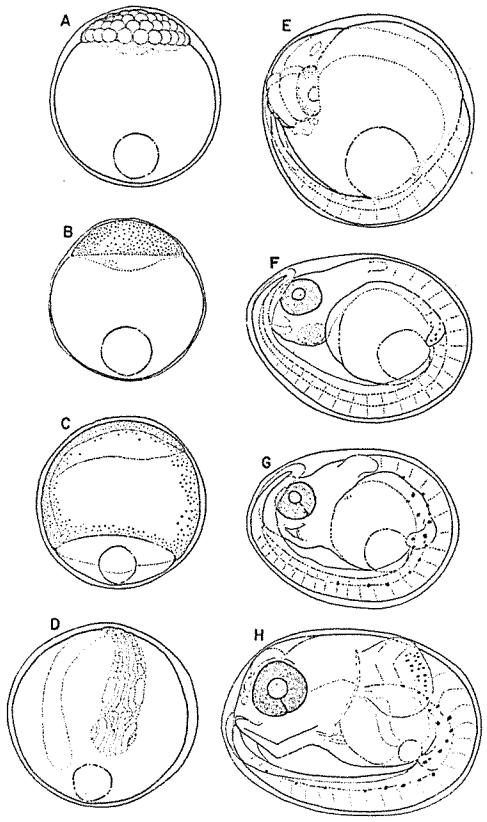


Fig. 42.20. Intra-ovarian embryos of Sebastes paucispinis taken from different females at various stages of gestation and staged according to Oppenheimer (1937): A) Stage 8, 0.94 mm diameter; B) stage 9, 0.90 mm; C) stage 14, 1.0 mm; D) stage 19, 1.0 mm; E) stage 22, 1.0 mm; F) stage 26, 1.6 mm at long axis; G) stage 27, 1.5 mm at long axis; H) stage 32, 2.0 mm at long axis. (Source: Moser 1967).

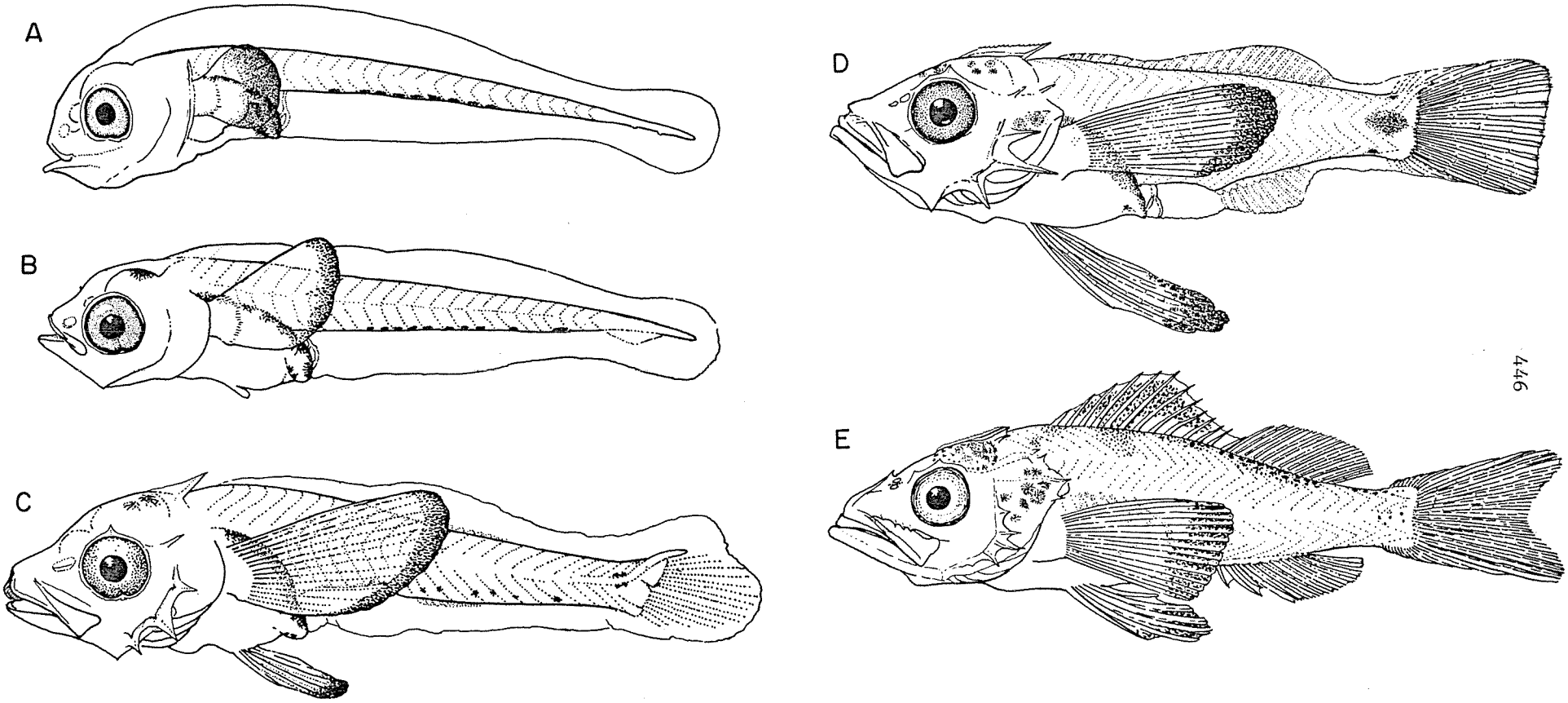


Fig. 42.21. Developmental series of larval bocaccio, Sebastes paucispinis: A) 4.7 mm; B) 6.1 mm; C) 8.7 mm; D) 14.0 mm; E) 24.2 mm. (Source: Moser et al. 1977).

part of the operculum (Fig. 42.21 D, E). Melanophores begin to form on the posterior margin of the pelvic fins at about 7 mm and also on the caudal fin at an early stage. Each side of the developing hypural element has several melanophores which develop into a characteristic blotch at the base of the hypurals (Fig. 42.21 D). After formation of the caudal fin, pigment appears near and on the dorsal fin (Fig. 42.21 D, E).

Transformation of the larvae into juveniles occurs at about 30 mm SL and is accompanied by reduction in cranial spines, appearance of scales, and more intensive pigmentation. Transforming individuals and juveniles inhabit shallow coastal waters over rocky bottoms in association with algae or over sandy bottom in association with eel grass, but may also be found in offshore surface waters within floating patches of kelp. They spend approximately one year in shallow water and move into deeper water with age (Moser 1967).

Sebastes pinniger - Canary rockfish

Range: Baja California to southeastern Alaska

Occurrence in Puget Sound: common in some areas

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: pelagic

Canary rockfish range from Baja California to southeastern Alaska and occur mainly between 90 and 180 m, but have been taken as deep as 365 m (Hart 1973). They are also fairly widely distributed in Puget Sound (Miller and Borton 1980).

Spawning season in California takes place between November and March (Phillips 1964) and from British Columbia to Oregon, spawning probably occurs from January to March (Waldron 1968; Hitz 1962; Westrheim 1975). Fifty percent maturity for California fish is at 35.5 cm and 5-6 years of age, with some fish mature at 3 years and 24 cm. Off British Columbia, 50% maturity occurs at 41 cm for males and 48 cm for females (Westrheim 1975). Gunderson et al. (1980) reported that off Washington-Oregon 50% maturity level corresponds to 39.5 cm fork length for males and 49.2 cm fork length for females. Fecundity of mature fish ranges from 260,600 to 1,600,000 eggs for fish between 478 and 665 mm in length (Table 42.19). Gunderson et al. (1980) determined the fecundity (F) - length (L) over relationship for Washington-Oregon canary rockfish to have the form F = 64221.3L - 2330029.

The preextrusion larvae described by Westrheim (1975) have a relatively short row of postanal melanophores (located between the 18th and 22nd myomeres according to Waldron 1968) and some pigment above the yolk sac near the anus (Fig. 42.3 I). After two weeks, additional melanophores are present at the tip of the lower jaw, on the ventral part of the yolk sac, on the pectoral fins, along the dorsal midline in an irregular double row between the 19th and 21st myomeres, and in the hypural region. When larvae are about 7-8 mm (Fig. 42.22), the characters useful in distinguishing them are:

1) presence of traces of both dorsal and ventral midline melanophores, anterior ones are internal;

2) lightly pigmented pectoral fins;

Table 42.19. Fecundity of canary rockfish, Sebastes pinniger, from California. (Source: Phillips 1964).

Date mo.-yr.	Total length (mm)	Fecundity (Number of eggs)
11-58	478	260,000
10-59	490	946,700
12-58	498	827,400
10-59	515	815,300
10-59	528	655,500
12-58	535	1,353,100
12-58	535	1,897,600
12-58	548	1,366,900
10-59	575	1,515,000
10-60	665	1,597,000

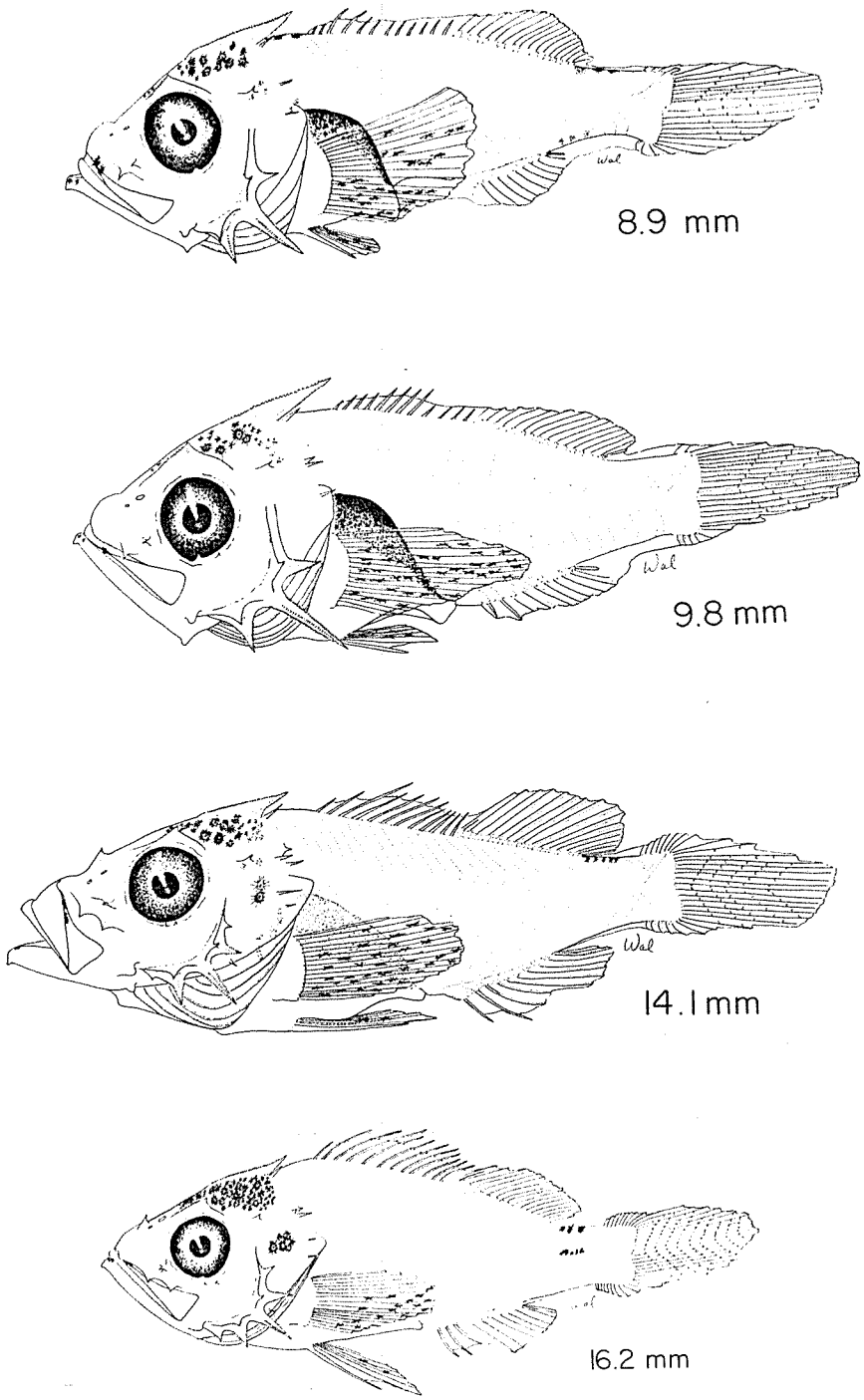


Fig. 42.22. Planktonic larvae (8.9, 9.8, mm) and transforming specimens (14.1, 16.2 mm) of canary rockfish, Sebastes pinniger. (Source: Richardson and Laroche 1979).

3) melanophores at the tip of the lower jaw and on the anteroventral margin of the maxillary;

4) presence of one or two large external stellate melanophores on the dorsum just posterior to the parietal spines;

5) relatively deep body (about 40% of standard length);

6) long parietal spines (about 24% of head length); and

7) long pectoral fins (about 25% of standard length).

Later stage larvae (Fig. 42.22) can be recognized by their relative lack of pigment on the trunk except over the gut, a relatively deep body, and long parietal and third posterior series preopercular spines. Juveniles can be recognized by a combination of meristics, including flat to convex interorbital space, presence of the supraocular spine, and a dark pigment patch at the base of the spinous dorsal fin (Fig. 42.23) (Richardson and Laroche 1979).

Twelve head spines appear on larvae by the time they are 7.8 mm and after flexion (~ 8.8 mm) about 13 additional spines appear, some of which disappear with development (Table 42.20).

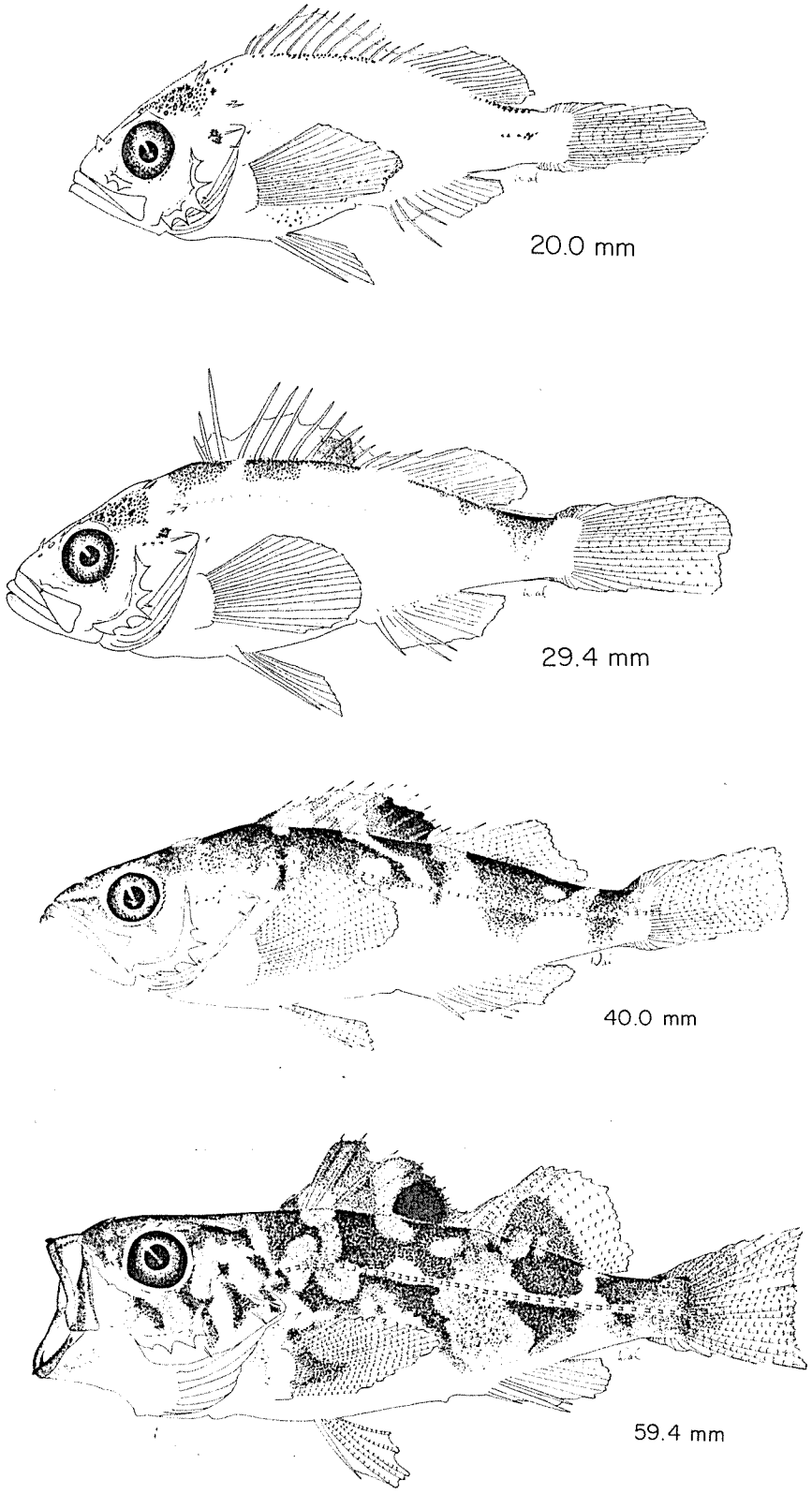


Fig. 42.23. Pelagic (20.0, 29.4, 40.0 mm) and benthic (59.4 mm) juveniles of canary rockfish, Sebastes pinniger. (Source: Richardson and Laroche 1979).

Table 42.20. Development of head spines in larval and juvenile canary rockfish, Sebastes pinniger. Ranges given are lengths of specimens which possess a particular spine. (Source: Richardson and Laroche 1979).

Spine	Length (mm)[1]
Parietal	7.8-181[2]
Nuchal	7.8-181[2]
Preopercular - anterior series	
1st	7.8-26.4
2nd	absent in all sizes examined
3rd	7.8-23.4
Preopercular - posterior series	
1st	9.3-181[3]
2nd	7.8-181
3rd	7.8-181
4th	7.8-181
5th	10.7-181
Opercular	
Superior	8.8-181
Inferior	12.3-181
Interopercular	10.7-181
Subopercular	absent in all sizes examined
Preocular	16.0-181[4]
Supraocular	12.8-181
Postocular	7.8-181
Infraorbitals	
Inferior	
1st	7.8-181[5]
2nd	10.7-181
3rd	absent in all sizes examined
Superior	
1st	7.8-29.4
2nd	absent in all sizes examined
3rd	10.7-29.4
4th	9.3-28.8
Nasal	9.3-181[4]
Coronal	absent in all sizes examined
Tympanic	38.0-181
Pterotic	7.8-117.7
Posttemporal	
Superior	14.1-59.4[3]
Inferior	7.8-181
Supracleithral	9.8-181
Cleithral	19.5-181

[1] Specimens ranged from 7.8-181 mm

[2] Parietal and nuchal spines become fused at 41.0 mm

[3] Spine is bifid in some specimens.

[4] First appears as a bump.

[5] Spine becomes rounded, no sharp tip at 117.7 mm.

Sebastes proriger - Redstripe rockfish

Range: southern California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for preextrusion and early postextrusion larvae.

Widely distributed, but uncommon, throughout Puget Sound (Miller and Borton 1980), redstripe rockfish also occur from southern California to the Bering Sea and at depths ranging from 90 to 375 m (Hart 1973).

Early life history information is sparse: Westrheim (1975) reported the principal parturition month as July and lengths of 50% maturity are reached at 28-29 cm for fish occurring in British Columbia. Preextrusion larvae have 16-23 postanal midventral melanophores, a few spots near the tip of the tail in both the anal and dorsal finfold, and pigment spots on the dorsal and posterior portion of the gut (Fig. 42.3 J). With development, melanophores appear on the head, nape, and lower jaw (Westrheim 1975).

Sebastes rosaceus - Rosy rockfish

Range: Baja California to Puget Sound

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for early larvae at yolk exhaustion

Little early life history information exists for this species which has been reported off Marrowstone Island in Puget Sound (Miller and Borton 1980) - the northern limit of its range (Miller and Lea 1972). In California, Moser (1967) found some evidence of more than one brood being developed per season, although MacGregor (1970) found no indication of multiple spawning. In either case, the primary months of gestation appear to be March-May and females may produce up to 1,355,838 ova (MacGregor 1970). Pigment of the 3.9 mm larvae consists of 12 (range 8-14) postanal midventral melanophores, no dorsal body melanophores, and pigment along the dorsal surface of the gut (Fig. 42.4 A).

Sebastes ruberrimus - Yelloweye rockfish

Range: Baja California to Gulf of Alaska

Occurrence in Puget Sound: common in some areas

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for preextrusion and early postextrusion larvae

Yelloweye are widespread in Puget Sound and are common around reefs in both inside and coastal waters. Spawning time is not well known. Off Oregon to British Columbia, fish had ovaries with developing embryos in April-May (Hitz 1962) and DeLacy et al. (1964) reported July as the principal month of parturition. However, Washington et al. (1978) thought that two periods of insemination (July and December) were possible with maturation during winter and summer and spawning in early spring and mid to late summer. Fecundity is also not well known. One report of a 8.9 kg female containing 2,700,000 eggs is available (Hart 1942, cited by Hart 1973), and two other fish 3.2 and 5 kg produced 271 and 324 eggs per gram of fish weight (MacGregor 1970). Late stage embryos have a short row (4-11) of postanal midventral pigment spots, melanophores on the gut (Fig. 42.4 B, C) and acquired additional pigmentation on the head, nape, and lower jaw with development (Westrheim 1975).

Sebastes saxicola - Stripetail rockfish

Range: Baja California to southeastern Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: undescribed except for preextrusion larvae and larvae at yolk exhaustion

Stripetail rockfish range from Baja California to southeastern Alaska and occur in both inside and outside waters of British Columbia and Washington (Hart 1973).

Young are released in February in British Columbia (Westrheim 1975) and probably about the same time off Oregon as spent individuals have been observed in April-May (Hitz 1962). Spawning season off California ranges from mid-November to mid-March (Phillips 1964). Lengths at 50% maturity appear to be at sizes less than 20 cm for females and less than 17 cm for males (Westrheim 1975; Phillips 1964). Age of 50% maturity for females is 4 years and the youngest reported mature fish was 2 years old. Number of eggs per female ranges from 13,000-200,000 (Table 42.21).

At birth, larvae are about 4.3 mm and have a postanal midventral row of melanophores that blends with the dorsal gut pigment and is composed of 37-49 melanophores. Stripetail larvae also have a short dorsal row of 10-14 melanophores. Up through yolk absorption, no melanophores appear on the head, nape, or lower jaw (Fig. 42.4 E, F, G) (Morris 1956; Westrheim 1975).

Table 42.21. Fecundity of stripetail rockfish, Sebastes saxicola, from California. (Source: Phillips 1964).

Date mo.-yr.	Total Length (mm)	Fecundity (Number of eggs)
10-59	176	39,100
10-59	180	13,500
3-59	185	17,900
10-59	201	101,500
11-58	294	175,700
11-60	295	153,800
12-58	300	79,300
10-59	300	178,600
12-58	302	65,300
11-60	308	191,600
10-59	311	185,600
10-59	324	166,200
10-59	326	230,000

Sebastes zacentrus - Sharpchin rockfish

Range: southern California to Gulf of Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: ovoviviparous

Larvae: pelagic

Ranging from southern California to the Gulf of Alaska, sharpchin rockfish mature their young during spring off Oregon-British Columbia, and young are primarily released in July off B.C. (Hitz 1964; Westrheim 1975). Fifth percent of males and females are mature at about 24-25 cm (Westrheim 1975). Other aspects of reproductive biology and behavior are unstudied.

However, development of the larval stages has been studied to a greater extent. Preextrusion larvae have been described and/or illustrated by a number of authors (Table 42.3). According to Laroche and Richardson (1981), Efremenko and Lisovenko (1970), Westrheim (1975), and Westrheim et al. (1971), described preextrusion larvae (4.2-4.5 mm TL) of sharpchin rockfish which have a ventral postanal midline row of melanophores consisting of 15-21 (usually 16) melanophores which stop short of the anus by at least 4 myomeres, and with at least one melanophore in the pre-hypural region. No dorsal body surface melanophore are present (Fig. 42.4 G). Harling et al. (1971) described a different form of preextrusion larvae, which Laroche and Richardson (1981) believed may have been from a misidentified adult female.

A larval series (7.4 to 65.3 mm) of sharpchin rockfish was assembled from the plankton by Laroche and Richardson (1981). The characters used to identify the smallest larvae in the series, 7.4 mm (Fig. 42.24) were:

1) fin counts which included 16-18 (usually 17) pectoral rays, 6 or 7 (usually 7) soft anal rays, and 13 to 16 (usually 14) soft dorsal rays;

2) moderately pigmented pectoral and pelvic fins, a general lack of body pigment, and melanophores on the inside tip of the lower jaw;

3) a narrow interorbital distance equal to about 27.7% of the head length; and

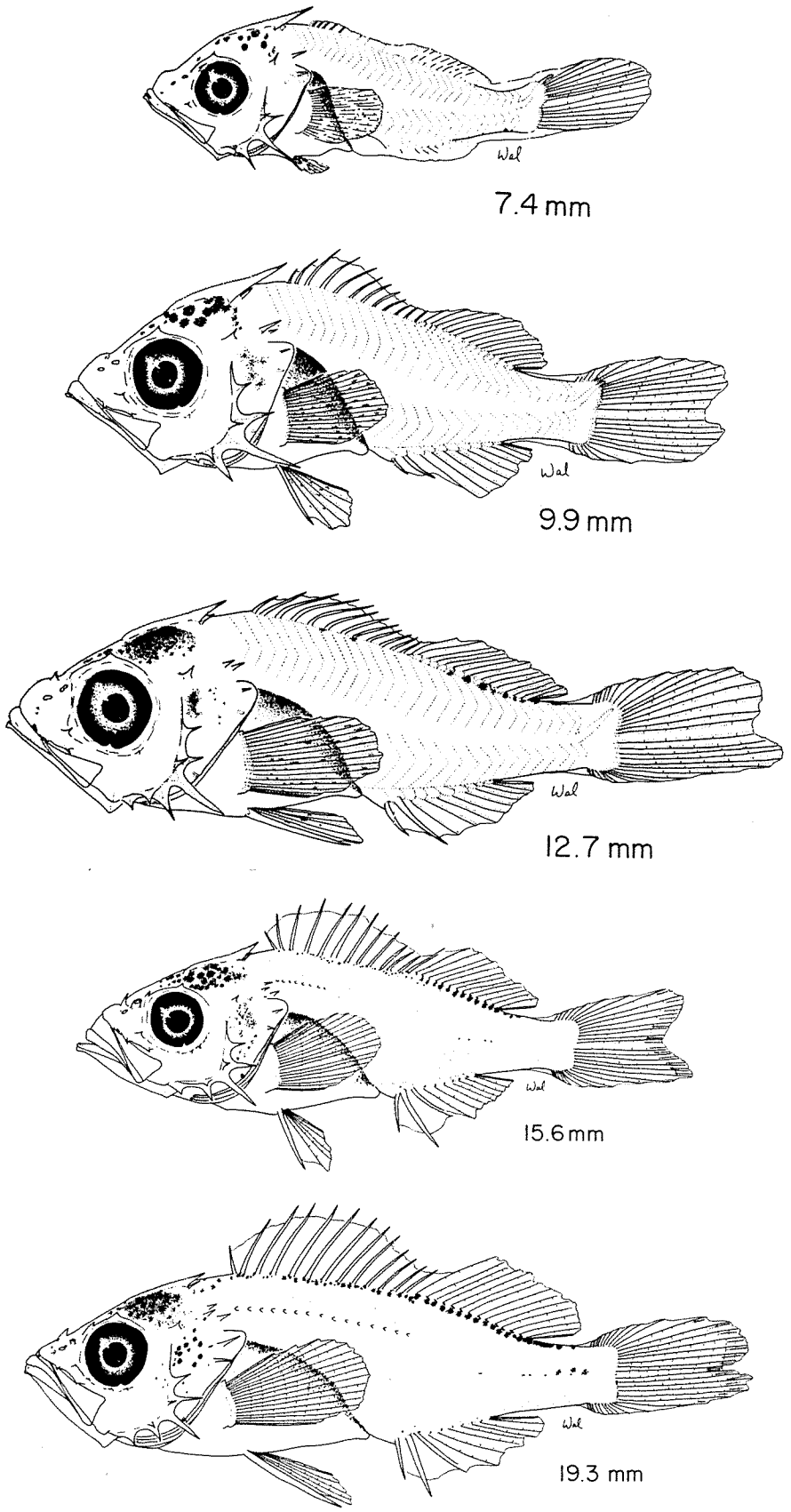


Fig. 42.24. Pelagic larvae (7.4, 9.9, 12.7 mm) and transforming larvae (15.6, 19.3 mm) of sharpchin rockfish, Sebastes zacentrus. (Source: Laroche and Richardson 1981).

4) a long, deeply serrated parietal spine equal to about 26.5% of the head length.

Later stage larvae (Fig. 42.24) were identified by the addition of melanophores along the dorsal body surface beneath the spinous and soft dorsal fins, along the dorsal surface of the caudal peduncle, and at the articulation of some dorsal soft fin rays in specimens > 12.5 mm. In addition, a row of melanophores develops along the lateral midline and a strong, sharp preocular spine develops during transformation. Meristics, presence of a preocular spine and lack of a supraocular spine, a flat to convex and narrow interorbital space, and a stout, relatively long second anal spine were used to identify pelagic and benthic juveniles of sharpchin rockfish (Fig. 42.25).

Details of morphology and pigmentation of larval and juvenile sharpchin rockfish were presented by Laroche and Richardson (1981) and are summarized below.

Specimens between 7.4-8.5 mm undergo the final stages of notochord flexion which is complete by 9.0 mm. Transformation from the larval stage to the pelagic juvenile is marked by the structural change of the dorsal and anal fin prespines to sharp, hard spines and occurs when the rockfish are between 13.5 and 20 mm in length. At 35 to 65 mm, the pelagic young make a transition to the benthic habitat.

Morpholopgically, sharpchin rockfish are a relatively deep-bodied form with a body depth of 35% standard length (SL) in flexion larvae decreasing to 30% SL in pelagic juveniles. They also are characterized by a relatively large head which averages 40-43% SL during larval and transforming periods.

Development of rays is completed in most fins at a small size. The adult complement of 16-18 (usually 17) pectoral rays is complete at 7.4 mm; I, 5 pelvic fin spines and rays are present at 7.4 mm; and the adult arrangement of 8+7 principal caudal rays is also present by 7.4 mm. Developing elements of the dorsal fin are present in 7.4 mm larvae and spines, rays and prespines are completely formed by 8.0 mm. The dorsal and anal prespines become true spines by ~ 15.5 mm and 20 mm, respectively, and as mentioned earlier, mark the beginning of the pelagic juvenile phase.

Development of head spination is summarized in Table 42.22. the smallest larvae have parietal, nuchal, first and third anterior preopercular, five posterior preopercular (the fifth is present as a bump), superior opercular (present as a bump), postocular, first inferior infraorbital, first superior infraorbital, pterotic, and inferior posttemporal spines. All five of the posterior preopercular spines are present as sharp spines by 8.5 mm and persist into the adult stage.

The lateral line organs are visible as rows of light colored spots in the smallest larvae and in the larger larvae before scale formation.

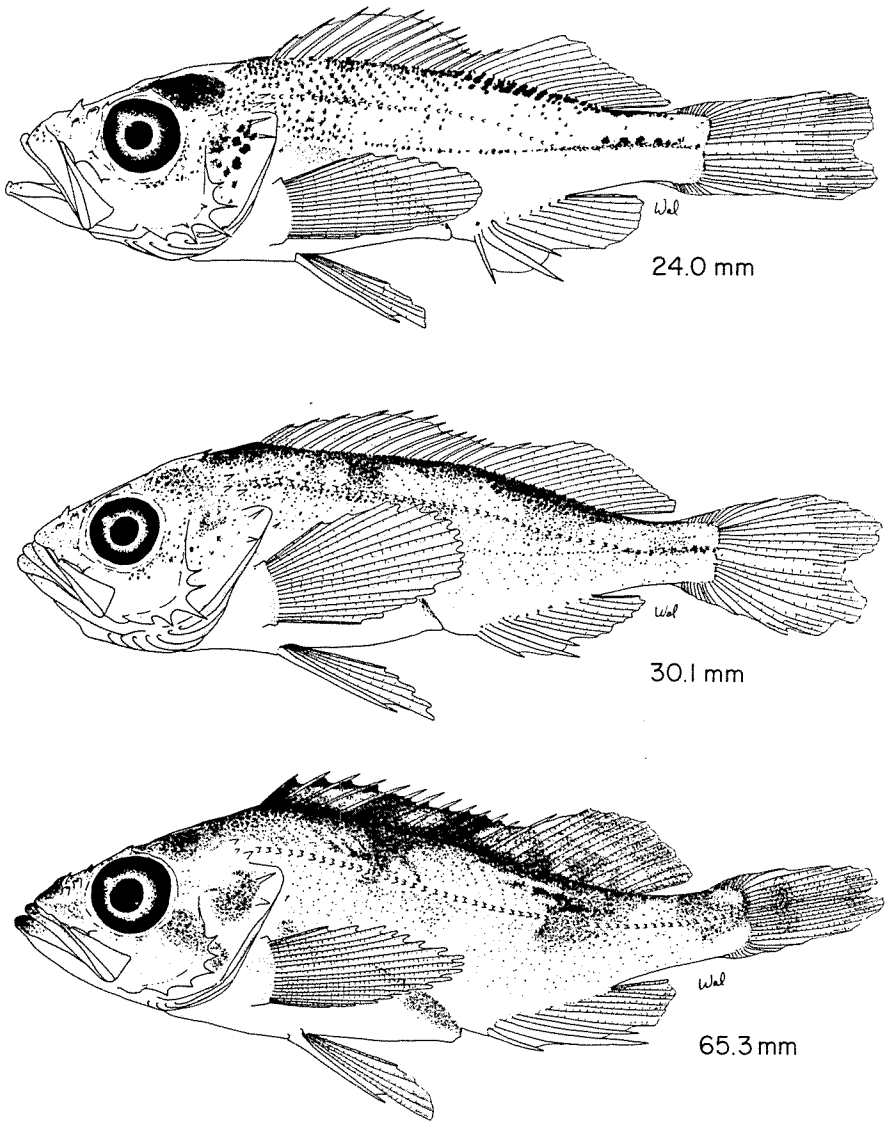


Fig. 42.25. Pelagic juveniles (24.0, 30.1 mm) and benthic juvenile (65.3 mm) of sharpchin rockfish, Sebastes zacentrus. (Source: Laroche and Richardson 1981).

Table 42.22. Summary of formation of headspines in larval and juvenile sharpchin rockfish, Sebastes zacentrus, between 7.4 and 74.8 mm. (Source: Laroche and Richardson 1981).

Spine		Sizes of specimens with spine
Parietal		7.4[2] - 74.8[1]
Nuchal		7.4[2] - 74.8[1]
Preopercular		
Anterior:	1st	7.4 - 26.3[3]
	2nd	absent in all sizes examined
	3rd	7.4 - 26.3[3]
Posterior:	1st	7.4 - 74.8
	2nd	7.4 - 74.8
	3rd	7.4 - 74.8
	4th	7.4[2] - 74.8
	5th	7.4[2] - 74.8
Opercular		
Superior		7.4[2] - 74.8
Inferior		8.5[2] - 74.8
Interopercular		7.9[2] - 74.8[3]
Subopercular		12.7[2] - 26.3[3], 31.2[3]
Preocular		14.8[2] - 74.8
Supraocular		absent in all sizes examined
Postocular		7.4 - 74.8[3]
Infraorbital		
Inferior:	1st	7.4[2] - 74.8[3]
	2nd	8.5[2] - 74.8
	3rd	absent in all sizes examined
Superior	1st	7.4 - 35.3[3]
	2nd	14.8 - 30.1[3]
	3rd	14.0[2] - 35.3[3]
	4th	8.5[2] - 35.3
Nasal		9.9[2] - 74.8
Coronal		absent in all sizes examined
Tympanic		16.8[2] - 74.8
Pterotic		7.4 - 35.3[3]
Posttemporal		
Superior		17.3[2] - 74.8
Inferior		7.4 - 74.8
Supracleithral		8.5 - 74.5
Cleithral		19.6[2] - 74.8

[1] Parietal and Nuchals fuse, only one tip visible at ≥ 65.0 mm.
[2] May first be visible as a bump in smaller larvae.
[3] May appear as a bump before being overgrown on larger larvae.

The development of scales begins around 19 mm and first appears above the pectoral fins, with completion of scaling by 30 mm.

Laroche and Richardson (1981) collected larval and transforming pelagic specimens at 46 to 148 km off the coast of Oregon at depths between 270-2800 m and suggested that zacentrus may have a more restricted offshore distribution than some other rockfish species (esp. entomelas, pinniger, flavidus, and melanops). The smallest larvae (< 10 mm) were collected in August only, with larger pelagic individuals present in August through December, and a demersal juvenile was collected in October.

Sebastolobus alascanus - Shortspine thornyhead

Range: Baja California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: semi-demersal

Spawning habitat: unknown

Spawning season: Table 42.2

Mode of reproduction: oviparous

Eggs: pelagic egg masses, adhesive

Larvae: pelagic

Shortspine thornyhead range from Baja California to the Bering Sea and Commander Islands and favor deeper waters (90-1460 m)(Hart 1973).

Unlike the Sebastes spp., Sebastololus is oviparous producing a large gelatinous, bilobed egg mass which floats at the surface. Each lobe may measure between 15 and 61 cm and consists of a hollow conical sheath containing a single layer of eggs embedded in a gelatinous matrix. No structures are discernible within the clear matrix between the eggs and the eggs appear to float freely within the egg mass. The eggs are 1.2-1.4 mm in diameter and each possesses a .2 mm diameter oil globule which causes the eggs to float with the globule up and the embryo underneath. Pigmentation appears on the embryos prior to hatching and consists of thin melanistic streaks on the posterior part of the body midway between the end of the tail and the anus. Several less distinct melanophores occur on the hindgut and posterior part of the yolk sac.

The larvae are 2.6 mm at hatching and have a large yolk sac that is about 40% of total length. Eyes are not completely pigmented at hatching, but within 10 days of hatching, the mouth is open and the eyes are fully pigmented (Pearcy 1962).

In the plankton, Sebastolobus spp. larvae (up to 6.0 mm) can be distinguished from Sebastes spp. on the basis of pigmentation. Sebastolobus are unique in having two large melanistic blotches about midway along the tail, one at the dorsal midline and one at the ventral midline. These melanophores often run together creating a single tail band (Fig. 42.26 A, B). However, these melanophores begin to disappear in 5.0-6.5 mm larvae. Soon after the disappearance of the tail melanophores, the larvae develop prominent crestlike parietal ridges that terminate in double spines with the nuchal spine larger than the parietal spine (Fig. 42.26 D-F). Pigmentation is also present on the gut of small larvae and increases throughout the larval period. Melanophores

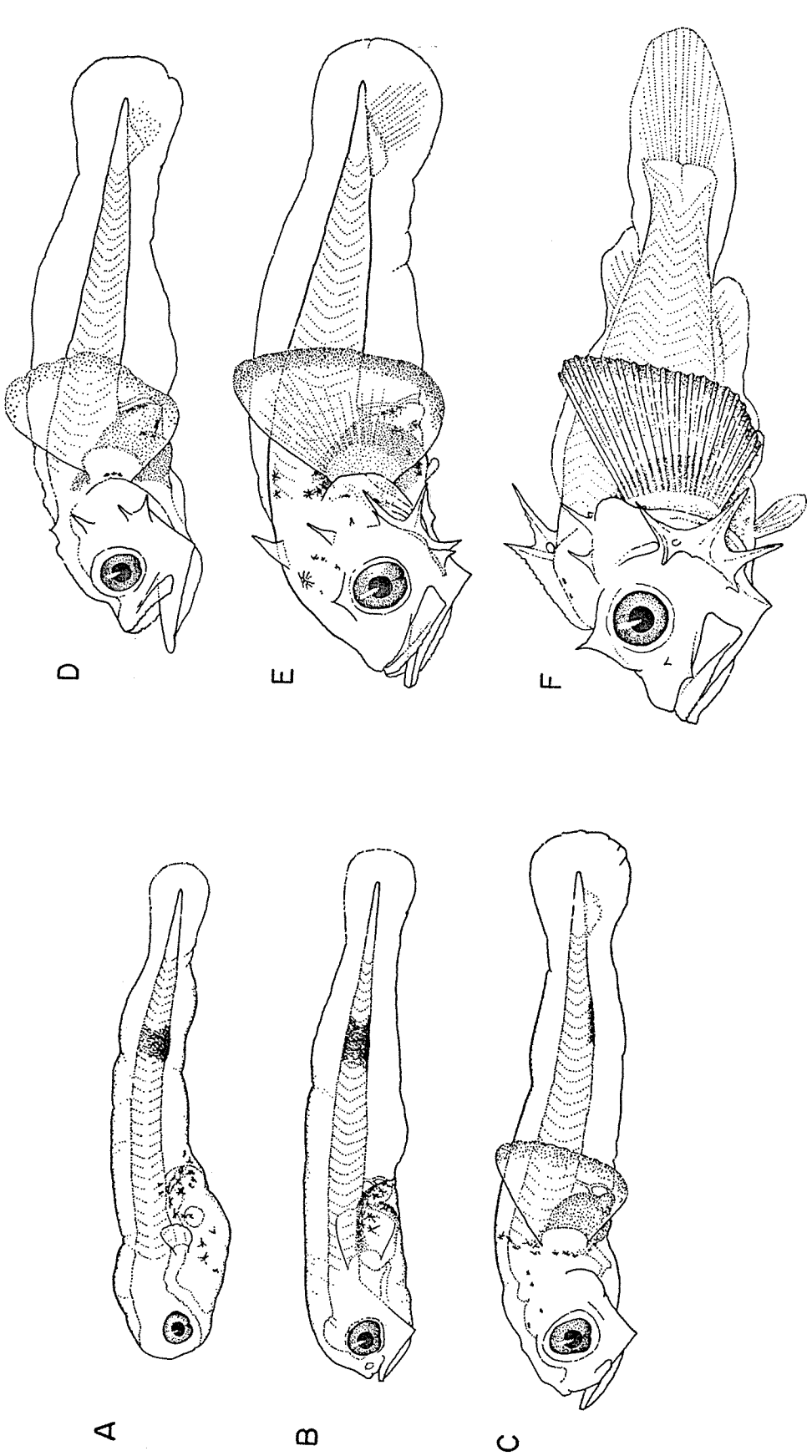


Fig. 42.26. Larvae of Sebastolobus spp.: A) 3.0 mm; B) 3.5 mm; C) 5.2 mm; D) 5.7 mm; E) 6.2 mm; F) 7.7 mm. (Source: Moser et al. 1977).

appear on the posterior margin of each pectoral fin in some larvae as small as 4.0 mm, but all larvae 5.0-11.0 mm possess these melanophores. After 11.0 mm, pigment on the pectoral fins disappears. The posterior lobe of the brain becomes pigmented in 5.2-7.0 mm larvae and these spots are present in all larvae larger than this. Melanophores also appear in the anterior lobe of the brain in larvae > 7.0 mm (Moser 1974).

At present, planktonic larvae of Sebastolobus alascanus less than 10 mm cannot be identified from S. altivelis, but larvae larger than this can be identified to species based on body depth and pectoral fin shape. Larval and transforming specimens of S. altivelis are more robust and deeper-bodied than S. alascanus and the pectorals are longer and have a deeper base in S. altivelis compared to S. alascanus. The two species can also be separated by a combination of meristics (Moser et al. 1977).

Transformation into juvenile characters occurs between 14 and 20 mm when juvenile pigmentation begins to appear. The first head pigment to appear is a melanistic blotch on the opercle (Fig. 42.27 B) which gradually spreads anteriorly onto the cheek and eventually speckles the whole head in pelagic juveniles. Lateral body pigment extends dorsally from the gut to the dorsal fin and develops posteriorly as an irregular mottled pattern (Fig. 42.27 C). In the largest pelagic juveniles, mottling expands posteriorly to the anus and covers the rest of the body in the benthic juveniles. Benthic residence is established after 22.5 mm (Moser 1974).

Off California, Sebastolobus spp. probably spawn from January-February through June (Moser 1974) and off Oregon, egg mass are found during spring (Pearcy 1962).

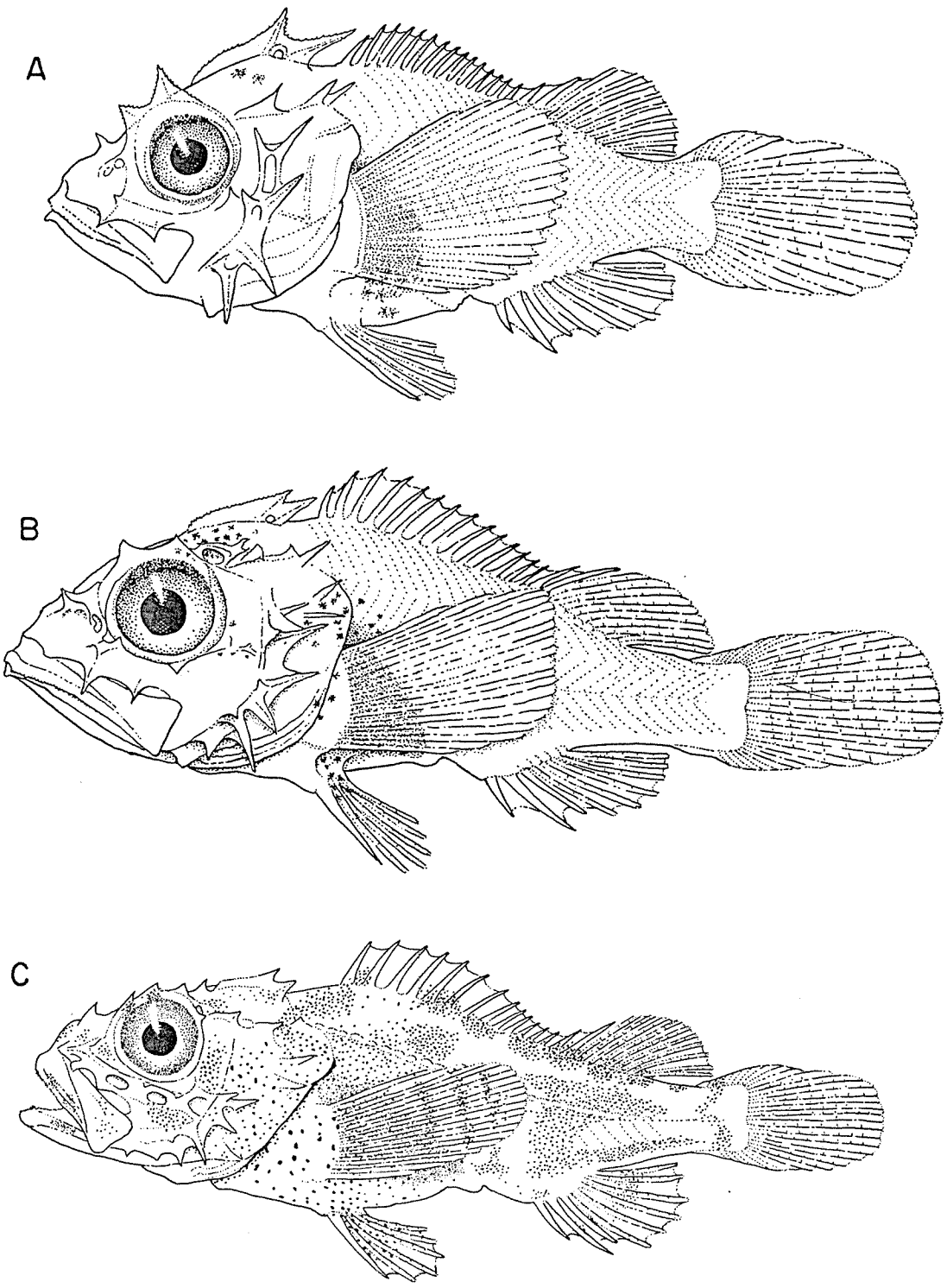


Fig. 42.27. Developmental series of Sebastolobus alascanus. A) 10.3 mm larva; B) 16.0 mm transforming specimen; C) 25.3 mm pelagic juvenile. (Source: Moser et al. 1977).

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43. ANOPLOPOMATIDAE

Anoplopoma fimbria - Sablefish

Range: Baja California to Bering Sea; Kamchatka and Japan

Occurrence in Puget Sound: common

Adult habitat: pelagic

Spawning habitat: pelagic, depths unknown

Spawning season: autumn-winter (California coast - Bering Sea)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: pelagic

Sablefish are distributed in the eastern Pacific Ocean from Baja California to the Bering Sea and are found off Kamchatka and Hokkaido, Japan in the western Pacific (Hart 1973). They are commonly found in Puget Sound (Miller and Borton 1980). Along the coast, adults prefer the deeper waters of the continental slope and shelf, often concentrating within or near submarine canyons or depressions.

Very little of the spawning biology of sablefish has been studied. Off California, the spawning season is reported to last from December to April with a peak in January and February (Phillips and Imamura 1954). Off the coast of Oregon to Vancouver Island, sablefish spawn from September to February, and in the Bering Sea, sablefish spawning reaches a peak in autumn and they are primarily spawned out by spring, although some spawning continues into summer (Kodolov 1968).

Off California, sablefish are believed to enter deeper water, sometimes down to 750 m, in the winter and early spring months when spawning is in progress. During summer months, adults move into shallower areas (Phillips and Imamura 1954).

In the California populations, 50% of male sablefish are mature at ~ 60 cm, and 50% of females are mature at ~ 70 cm. All males greater than 72 cm and all females over 81 cm are mature (Phillips and Imamura 1954).

It is thought that females mature only one batch of eggs per spawning season (Phillips and Imamura 1954) and that the eggs are pelagic (Thompson 1941). Spawning behavior and location are unknown.

Fecundity of sablefish has not been extensively studied but the following estimates are available:

	Length	Number of eggs per female
Kodolov (1968) (Bering Sea)	72.5 cm	438,000
	74.0 cm	468,000
	82.5 cm	503,000
Phillips and Imamura (1954) (California)	53 cm	100,000
	102 cm	up to 1×10^6

The mean diameter of sablefish eggs, based on water hardened eggs removed from a mature ovary, is reported to be 2.056 mm, S.D. = 0.0414 mm. The outer egg membrane is smooth and eggs contain a small vitelline space and no oil globules (Thompson 1941). Descriptions of fertilized eggs, development time, and embryological events are unreported.

Sablefish larvae are known to inhabit surface waters in summer along the U.S. and Canadian coasts and in well-heated bays in Alaska (Kodolov 1968) and young (21-35 mm) have been taken up to 185 miles off the coast of Oregon in surface waters (Brock 1940). Kodolov (1968) postulated that at lengths of ~ 12 cm and 5-7 months of age, young sablefish approach the shore and may descend to the bottom on the shelf or upper slope, with massive descent of young occurring in autumn when fish are about 30 cm in length.

In the Bering Sea, sablefish larvae 11.3 - 30.2 mm TL were collected during July and August and described by Kobayashi (1957). The larvae are characterized by being well covered by melanophores on their dorsal and lateral body surfaces and have the anus located at about midbody. At 11.3 mm TL, the fins are largely larval in appearance but by 18 mm TL, fin rays are present in the second dorsal, anal, pectoral, and caudal fins. At 22 mm TL, rays have appeared in the first dorsal, and the number of rays in the second dorsal, anal, and pectoral fins equals the adult complement. Pelvic fin buds do not appear until larvae are 18 mm, and pelvic rays appears by about 25 mm and reach full number in 30 mm TL larvae (Fig. 43.1). A striking feature of young sablefish is the development of an elongated pectoral fin which becomes darkly pigmented in its distal half. The pectoral fin reaches its relative maximum length in postlarval sablefish of 21-35 mm SL and extends as far back as the insertion of the second dorsal fin and is about 1/3 of the fish's standard length (Brock 1940). Brock also observed that the large pectorals were not used directly in swimming, and suggested they may serve to help keep the young fish at the surface.

A larval series of sablefish caught off northern Oregon was also reported on by Ahlstrom and Stevens (1976). The northern Oregon larvae (Fig. 43.2) were more heavily pigmented on the back and outer margins of the pectoral fins than those specimens described by Kobayashi (1957, Fig. 43.1).

Live postlarval sablefish are bluish to blue-green in color with a bright silvery abdomen. When preserved, it can be seen that young are densily covered by dark chromatophore, except for the abdomen which is unpigmented anterior to the pelvis and posterior to the anus (Brock 1940).

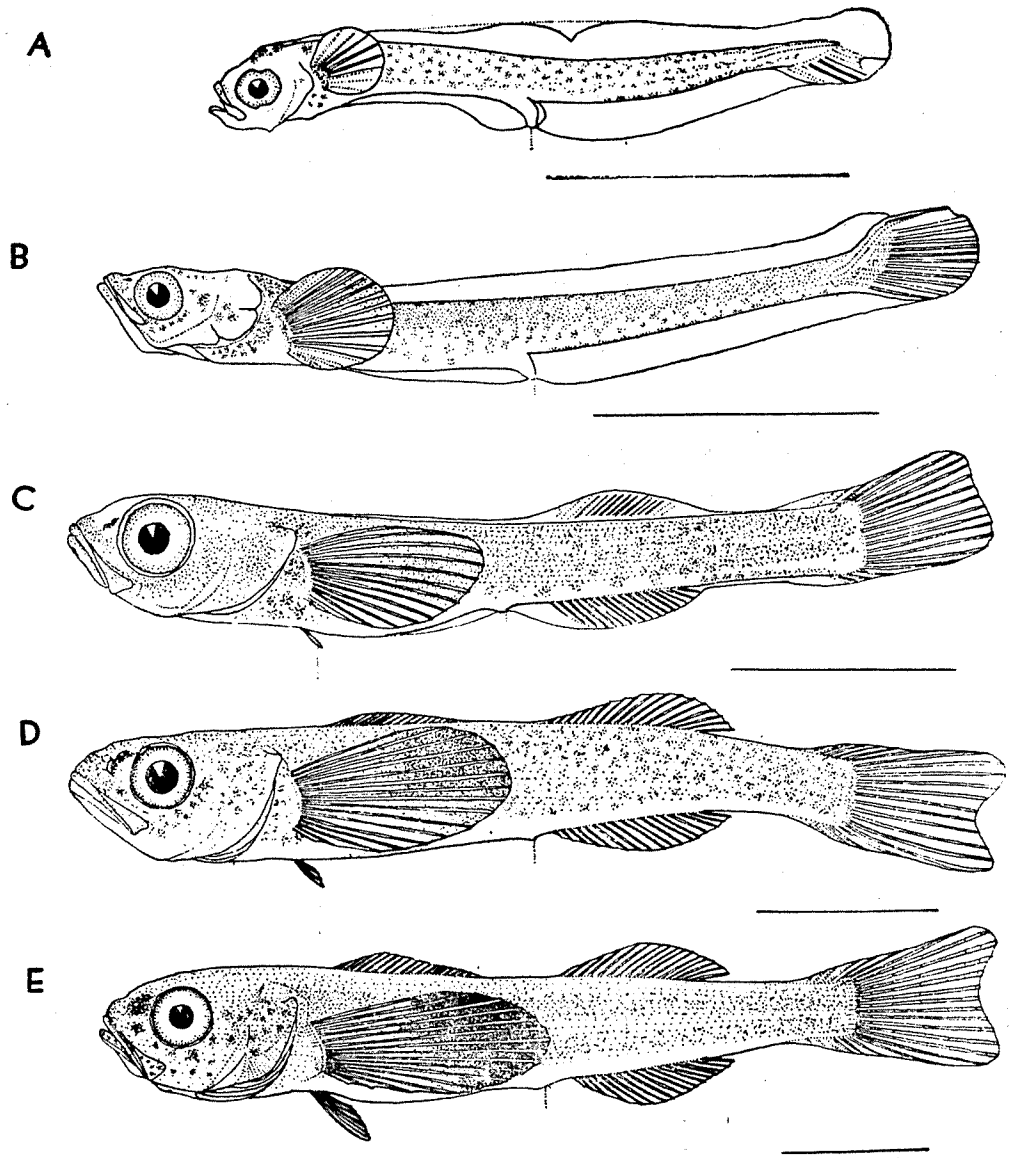

Fig. 43.1. Larvae and young of sablefish, Anoplopoma fimbria: A) 11.3 mm TL; B) 15.3 mm; C) 19.8 mm; D) 25.7 mm; E) 30.2 mm. (Source: Kobayashi 1957).

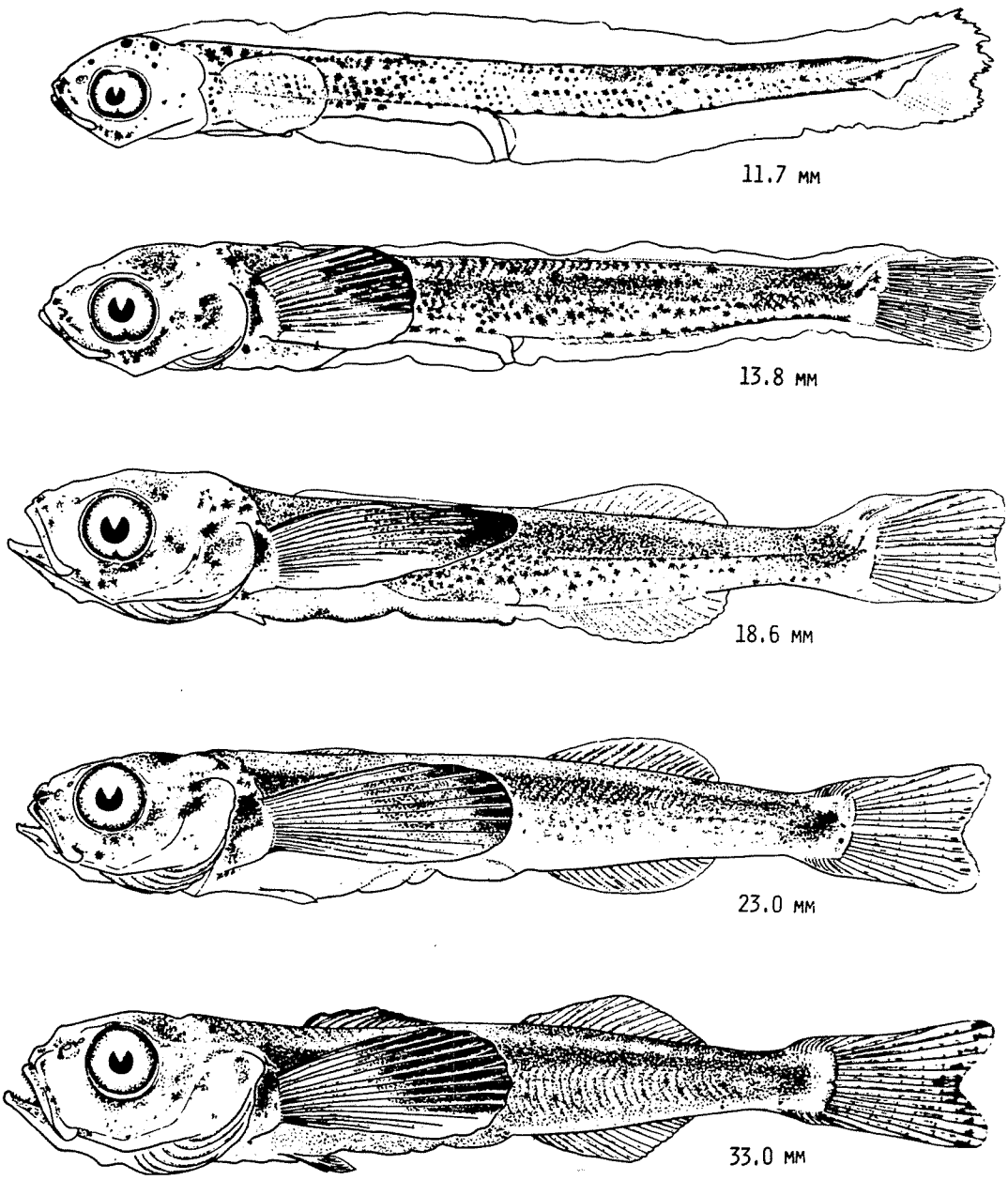

Fig. 43.2 Larvae of sablefish, Anoplopoma fimbria - length measurements indicated are standard length (SL). (Source: Ahlstrom and Stevens 1976).

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44. HEXAGRAMMIDAE

Hexagrammos decagrammus - Kelp greenling

Range: southern California to Alaska, Aleutian Islands

Occurrence in Puget Sound: common in some areas

Adult habitat: demersal, in rocky areas or kelp beds

Spawning habitat: demersal, on rocks

Spawning season: fall-winter

Mode of reproduction: oviparous

Eggs: demersal, undescribed

Larvae: pelagic

Kelp greenling are frequently encountered in shallow nearshore rocky areas or in kelp beds, or near jetties (Feder et al. 1974; Gorbunova 1962; Clemens and Wilby 1961; Moulton 1977). In the San Juan Islands, kelp greenling are observed at depths $\leq$ 13 m and primarily remain at these depths over the entire year. Males, on the average, appear to be located 3 m lower than females. Kelp greenling are usually solitary bottom dwellers which are often territorial. Most kelp greenling are active during the summer primarily during the day and inactive during the evening and night when they may hide under rocks or algae on the bottom (Moulton 1977).

Kelp greenling spawn large egg masses on rocks in the kelp zone during October-November in British Columbia (Marliave 1975; Clemens and Wilby 1961) and Puget Sound (Patten 1980) and slightly later in the southern part of its range (Feder et al. 1974; Gorbunova 1962). Marliave (1975) reported that egg masses are brown in color, and light blue eggs were reported by Clemens and Wilby (1961).

In Bamfield Inlet, B.C., larvae hatch in December at about 7-8 mm TL (Marliave 1975) and are neustonic (Rogers et al. 1979; Kendall et al. 1980). Larvae are moderately elongate with a short snout-to-anus distance (~ 33% TL), and are also characterized by large eyes. Fresh-caught planktonic larvae are striking in that they possess an irridescent green-blue color which is most intense along the dorsal body surface particularly where the dorsal fin develops. Unfortunately, this color fades with preservation, but characteristic melanophores remain. These melanophores consist of a continuous double row of spots along the dorsum from the occiput to the urostyle. There is a dense aggregate of melanophores on the occiput as well as melanophores on the snout, under the eyes, and on the dorsolateral surface of the gut. Lateral body pigment consists of two subsurface rows of cells along the midbody and a

surface row below the lateral midline. Other surface rows are added with development. Ventral postanal midline melanophores are lacking in small larvae, but later develop into a semi-complete row of melanophores. The pigment cells in the ventral row are stellate, but are sparse and haphazardly placed in the area of the anal fin, and do not form an even continuous row of pigment (Marliave 1975; Gorbunova 1962).

By 10-11 mm, the anlage of rays of the caudal and anal fins begin to appear and flexion is underway. At 12-13 mm, a supralateral row of surface pigment appears. By 13-14 mm, rays appear in the posterior portion of the dorsal fin, and in the pectorals. By 15-16 mm, the caudal fin rays are formed and become pigmented, flexion is completed, and rays appear in the anterior part of the dorsal fin, and in the anal fin as well. In addition, teeth appear in the jaws and pigment is intensified including on the urostyle, isthmus, and caudal fin rays. In larvae 18 mm in length, pectorals, anal, caudal, and posterior part of the dorsal fin are formed. At 21-22 mm, pigment consists of intense pigment covering the body, except for the lower part of the tail, and forms darker stripes along the back and sides. At 45 mm, scales appear (Fig. 44.1, 44.2)(Gorbunova 1962).

Larval kelp greenling go through a pelagic phase which lasts about one year in the open ocean and they may migrate out to sea sometimes up to 800-965 km (Gorbunova 1962; Clemens and Wilby 1961).

During the pelagic phase, young fish (~ 16-70 mm) feed primarily on copepods, but diets also include amphipods, brachyuran larvae, Oikopleura, cirripedia nauplii, cladocera, euphausiids, ostracods, and other larval fish particularly walleye pollock and eulachon (Barraclough 1967a, b, c; Robinson et al. 1968 a, b).

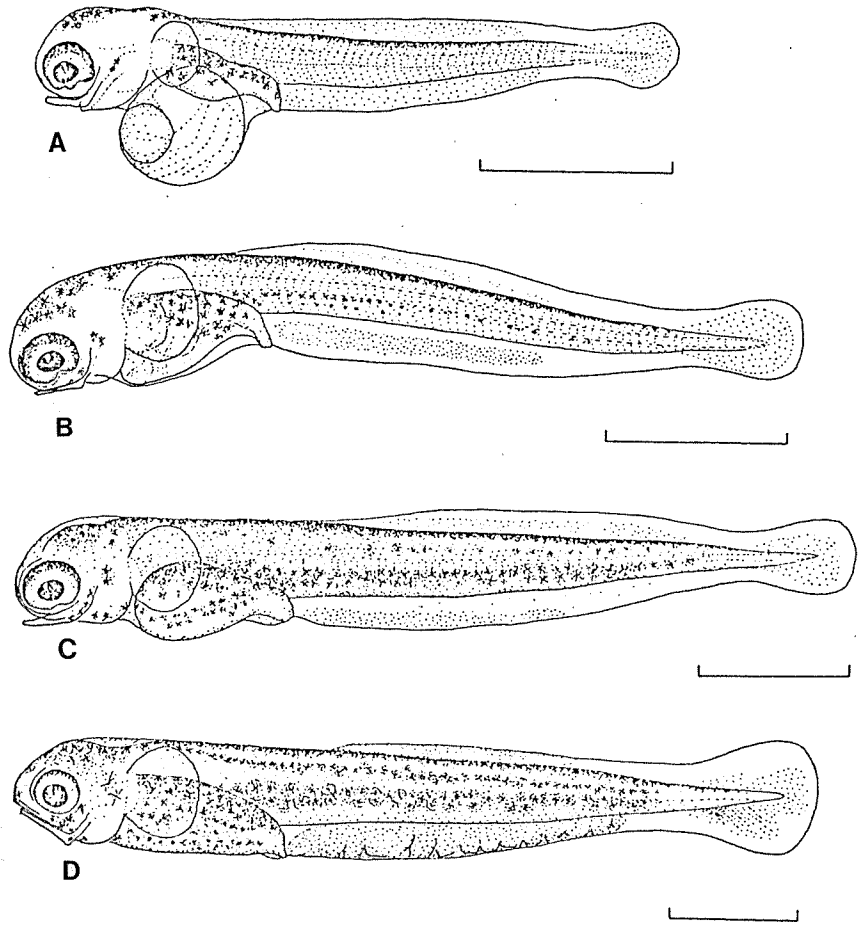

Fig. 44.1. Larvae of kelp greenling, Hexagrammos decagrammus, 2 mm scale: A) 0-day, 7 mm TL; B) 1-day, 9 mm TL; C) 5-day, 11.5 mm TL; D) 24-day, 13 mm TL. (Source: Marliave 1975).

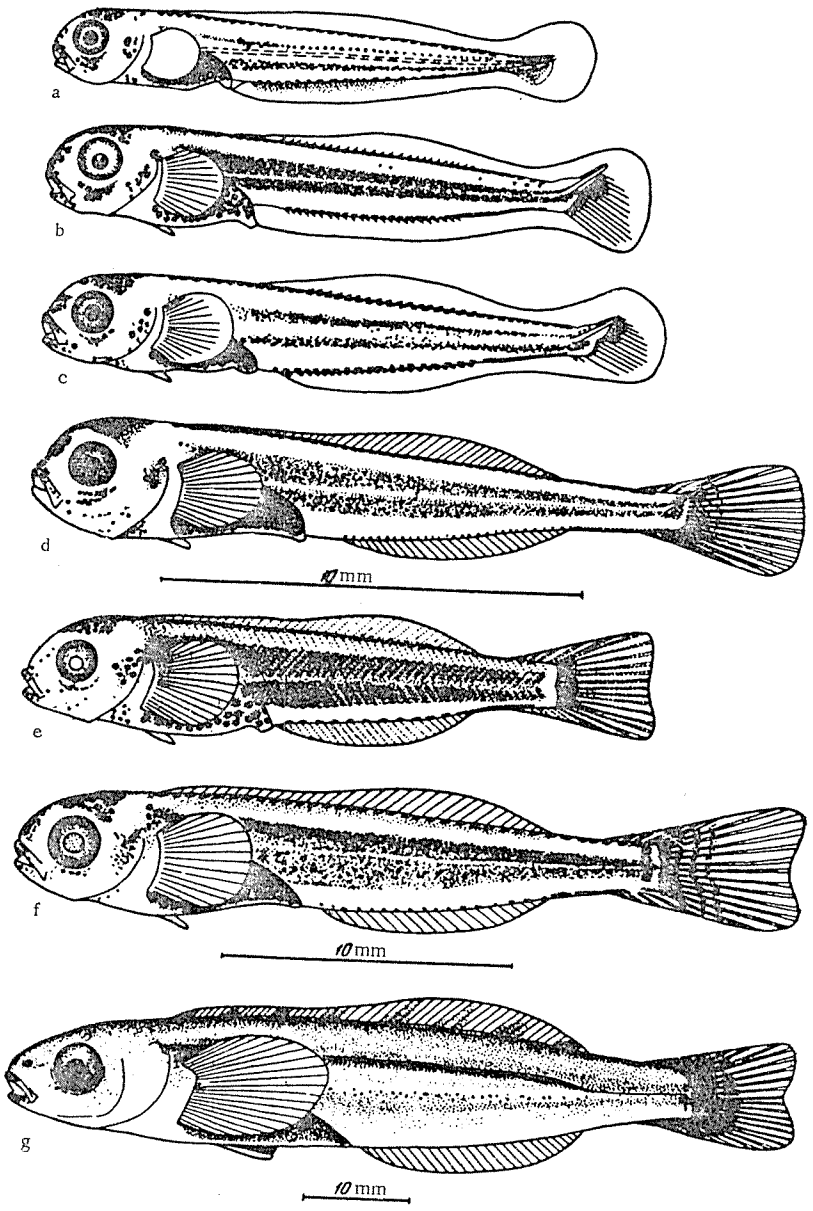

Fig. 44.2. Larvae and juveniles of kelp greenling, Hexagrammos decagrammus: a) 12.0 mm; b) 13.4 mm; c) 13.8 mm; d) 15.5 mm; e) 18.1 mm; f) 21.9 mm; g) 65.0 mm. (Source: Gorbunova 1962).

Hexagrammos lagocephalus - Rock greenling

Range: southern California to Bering Sea; Kurile Islands

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, near rocks or in kelp beds

Spawning habitat: same

Spawning season: summer-fall (Alaska)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached

Larvae: pelagic

Rock greenling occur from California to Alaska and the Bering Sea and the Kurile Islands (Hart 1973). They are not commonly reported in Puget Sound (Miller and Borton 1980). Adult rock greenling are found in the littoral to sublittoral region in areas characterized by strong currents, rocks, and/or dense algal growth (Rutenberg 1962; Gorbunova 1962; Simenstad 1971; Klyashtorin 1962). They are primarily a solitary, cryptic fish which may be observed moving through shallow water in loose feeding groups, but primarily are seen in the cover of algae or rocks (Simenstad 1971). Adults may move shoreward at night to feed (Klyashtorin 1962).

Rock greenling males can be separated from females by color differences which become apparent when fish are 2 years old and about 20 cm in length. Males range from bright cherry red (Gorbunova 1962) to dark red, sometimes brownish red, with bright orange abdomen and underside of the head (Klyashtorin 1962). Females are greenish brown (Gorbunova 1962) to golden-green or grayish yellow with a gray abdomen and yellow underside of the head, and sometimes have dark transverse bands (Klyashtorin 1962).

Rock greenling reach maturity at 3-4 years of age or at lengths of 29-35 cm. The majority of fish on the spawning grounds are older though, usually 5-7 years of age (Gorbunova 1962).

Spawning takes place from mid-June to early August in the Aleutian Islands (Simenstad 1971), and from June through September in the western Pacific (Gorbunova 1962; Klyashtorin 1962). Mature ovaries are compact, massive and the two gonads are fused in their lower part forming a bicornuate organ. The ovarian membrane is dense but eggs can be seen through it, and several size groups of eggs may exist in the ovaries during the spawning season. The smallest eggs are yolkless and probably will be spawned the following season. Larger eggs 1.0-2.5-2.8 mm are probably spawned during the present season and spawning is reported to be intermittent (Gorbunova 1962; Klyashtorin 1962). Fecundity is reported

at 17,000 eggs for a 465 g female to 26,330 eggs for a 1,330 g female (Klyashtorin 1962) or from 16,000 eggs at 35 cm to 100,000 eggs at 50 cm (Table 44.1).

Spawning takes place in areas of strong current and eggs are laid in small spawns on algal holdfasts in the subtidal fringe where they are constantly washed by surge (Simenstad 1971), or on rocks (Klyashtorin 1962). Deposited eggs are surrounded by mucus which binds the eggs into a round mass and adheres it securely to the holdfasts of algae such as Hedophyllum or Desmarestia (Gorbunova 1962; Simenstad 1971). Fertilized eggs are purple, light brown (Simenstad 1971; Gorbunova 1962), or dark gray with a bluish tinge (Klyashtorin 1962) and average 2.5-3.0 mm in diameter (Simenstad 1971; Gorbunova 1962; Klyashtorin 1962). Development requires about one month at temperatures of 6-10°C and proceeds as follows (Gorbunova 1962):

Day 1	Fertilization
1-4	Cleavages, end of blastula (Fig. 44.3-top left).
5	Beginning of epiboly.
6	Epiboly continues; anlage of neural tube and optic vesicles.
7	Closure of blastopore.
9	Embryo occupies 1/3 circumference of yolk; tail lifts from egg surface.
10	Embryo continues to lengthen.
14	Embryo surrounds yolk, dorsal row of pigment appears (Fig. 44.3-top right).

Unfortunately these eggs did not survive beyond day 14.

Under natural conditions, newly hatched larvae are about 9 mm in length. At 11-12 mm, the caudal fin begins to form. Pigmentation consists of a dorsal row of closely spaced melanophores from the occiput to the urostyle. The snout, isthmus, occiput, urostyle, and peritoneum are also pigmented. The operculum has a single, large spot. There are also melanophores on the ventral surface of the caudal peduncle and under the developing hypural plate. This ventral pigment is retained through development and extends from about the posterior end of the anal fin toward the tail. Rows of surface and subsurface pigment extend along the body midline above and below the spinal column. At 15-16 mm, flexion is underway and rudiments of dorsal and anal fin rays appear. Pigmentation generally is the same, but more intense. At 17-18 mm, paired fins continue to develop and the base of the pectoral and caudal fins are pigmented. Fin formation is almost complete in 21-23 mm larvae and teeth appear. Lateral pigment spreads to join the dorsal pigment. At 25 mm, transformation to the juvenile stage is complete. Scales appear during the first spring at about 45-50 mm (Fig. 44.3)(Gorbunova 1962).

Larval rock greenling are pelagic at hatching and are carried by the neuston many miles offshore (Gorbunova 1962; Simenstad 1971).

Table 44.1. Fecundity of rock greenling, Hexagrammos lagocephalus. (Source: Gorbunova 1962).

Length cm	Fecundity Total no. eggs	Length cm	Fecundity Total no. eggs
35	16,827	45	33,930
36	5,794	46	60,871
37	22,438	48	61,222-67,424
38	15,177-50,474	49	-
39	18,457	50	94,186 102,911
40	14,381-30,960	51	7,520-78,253*
41	40,936	52	-
42	20,755	53	9,537*
43	54,269		

*Low counts due to some females having spawned some eggs.

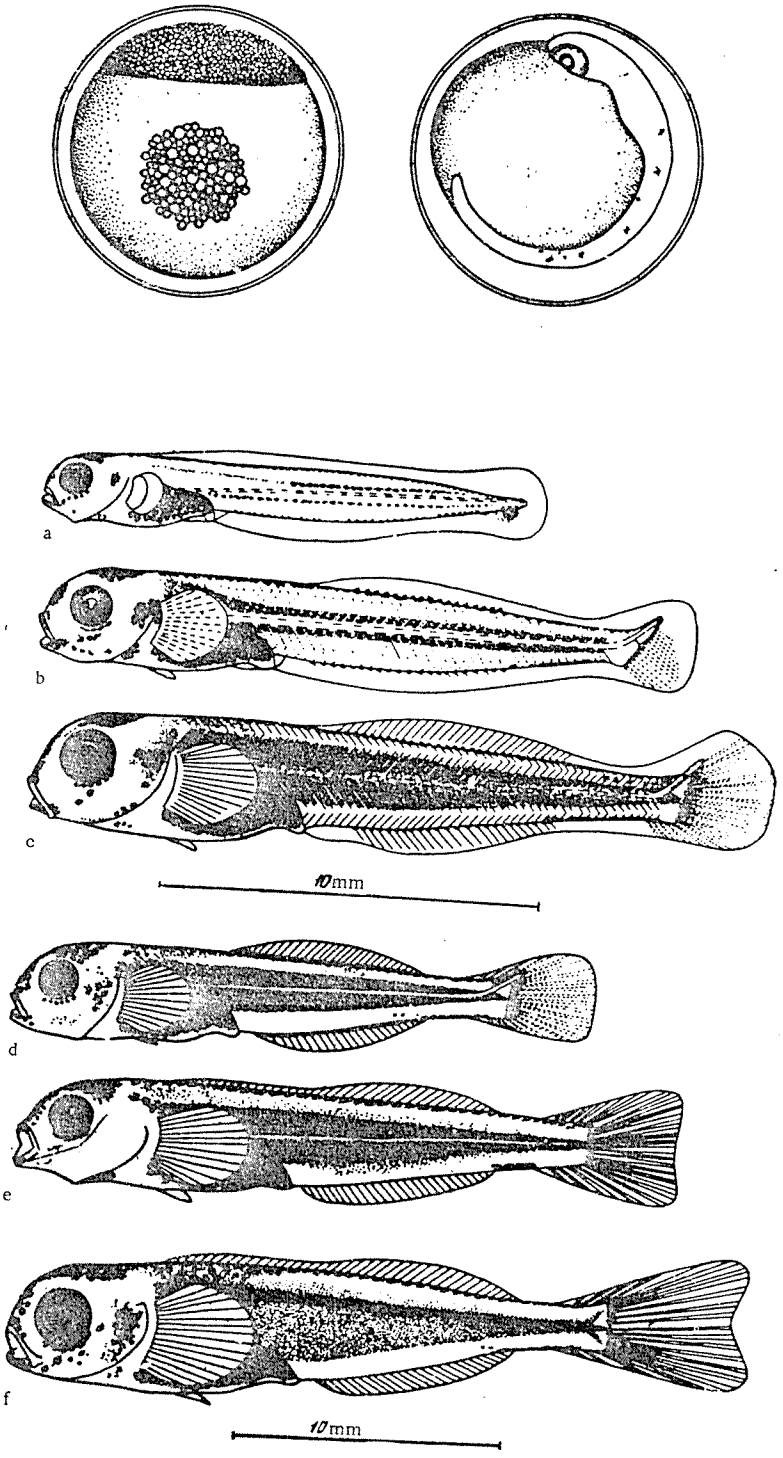

Fig. 44.3. Eggs, larvae, and juveniles of rock greenling, Hexagrammos lagocephalus: top left) end of blastula stage; top right) appearance of dorsal row of pigment; a) 12.6 mm; b) 16.1 mm; c) 17.0 mm; d) 18.6 mm; e) 21.5 mm; f) 23.0 mm. (Source: Gorbunova 1962).

Hexagrammos stelleri - Whitespotted greenling

Range: northern California to Bering Sea, Aleutian Islands; Kamchatka, Hokkaido, Peter the Great Bay, Tatar Strait

Occurrence in Puget Sound: common

Adult habitat: demersal, may be in kelpbeds or near rocks, but may be deeper

Spawning habitat: unknown

Spawning season: winter-spring (B.C.)

Mode of reproduction: oviparous

Eggs: demersal, undescribed

Larvae: pelagic

Whitespotted greenling are widely distributed on both the Asian and American sides of the North Pacific (Hart 1973) and are commonly found in Puget Sound (Miller and Borton 1980). The adults live among rocks and algae in the littoral zone, and are often encountered in shallow water over sandy beaches (Gorbunova 1962; Rutenberg 1962; Clemens and Wilby 1961), but can be found deeper.

Spawning has been reported to be summer in the northern part of its range and early fall in the southern part for the western Pacific (Gorbunova 1962; Rutenberg 1962), but is reported to be February (Clemens and Wilby 1961) or April (Hart 1973) in British Columbia. Whitespotted greenling eggs used for thermal experiments were collected from Puget Sound during October (Patten 1980). Eggs are blue (Hart 1973) and about 2 mm in diameter (Rutenberg 1962) and have been deposited on rocks in an aquarium (Clemens and Wilby 1961).

Embryonic development takes approximately 30 days (Gorbunova 1962) and larvae are pelagic and neustonic (Rogers et al. 1979; Kendall et al. 1980). Larvae are characterized by a large eye, short snout to anus length, and the characteristic blue-green tinge to the dorsal flesh. In 11 mm larvae, melanophores are concentrated on the head, dorsolateral surface of the gut, snout, operculum, laterally in 2 surface and 2 subsurface rows, and along the dorsal body surface from the occiput to the anterior portion of the urostyle. The isthmus lacks pigment or is weakly pigmented and no pigment exists along the ventral margin of the tail. In 12-13 mm larvae, rays are beginning to form on the posterior part of the dorsal fin, in the anal fin, and in the pectoral fins. By 15 mm, flexion is complete and the caudal fin is almost completed. Also, pelvic fins and teeth appear. Pigment is darker, but there is no pigment on the rays of the caudal fin. At 17-18 mm, a short row of melanophores appears posterior to the anal fin (row is shorter than in rock green-

ling), and indistinct melanophores appear along the base of the anal rays. These ventral melanophores do not form a distinct infracaudal row as in rock greenling or kelp greenling. Transformation occurs at about 25-30 mm and pigmentation intensifies on the back and sides and appears at the base of the caudal rays. Traces of scale appear at 40-45 mm and young whitespotted greenling reach a length of 60-80 mm in their second year of life (Fig. 44.4).

During the pelagic stage, larvae may travel far from land (Gorbunova 1962). Crustacean zooplankton forms the major part of the diet of pelagic larvae and includes copepods, ostracods, brachyuran zoea, amphipods, barnacle nauplii, harpacticoids, euphausiids and euphausiid eggs, Oikopleura, fish eggs, and even fish scales (Robinson et al. 1968 a, b).

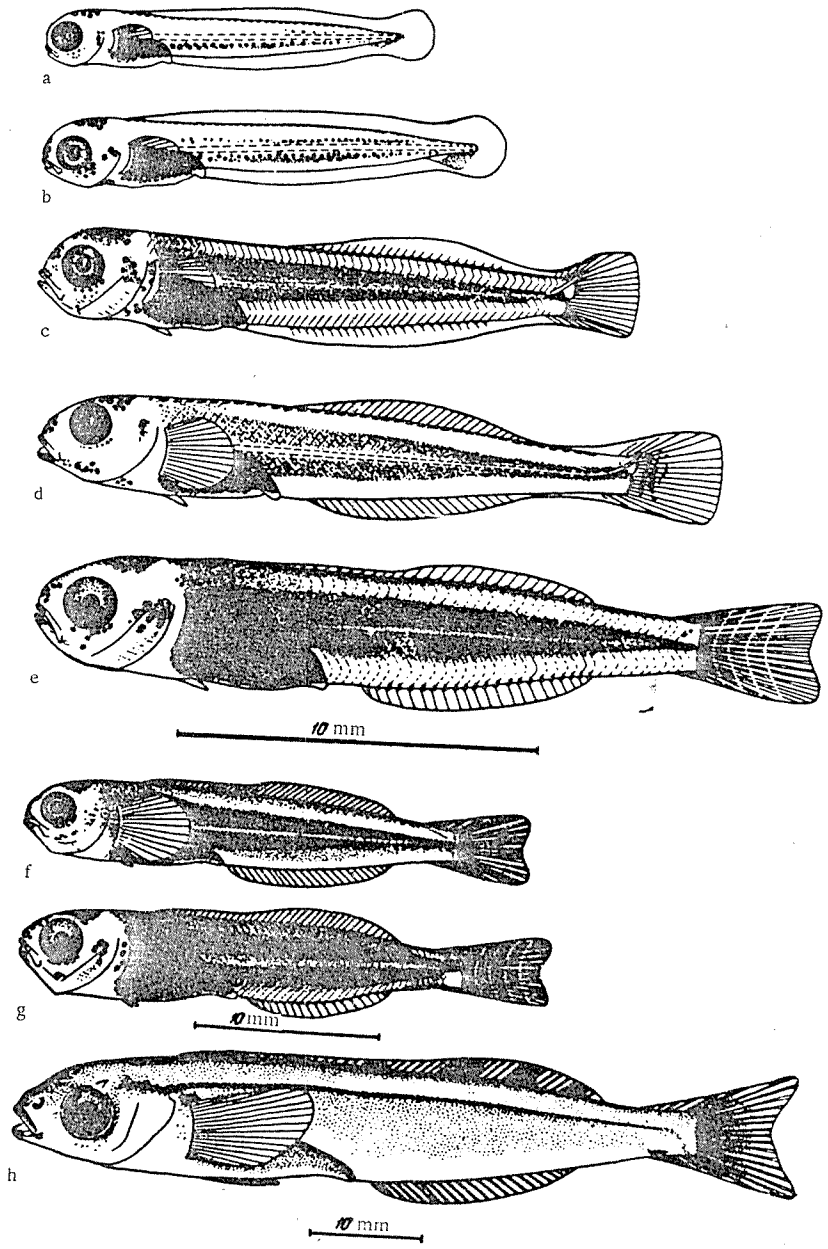

Fig. 44.4. Larvae and juveniles of whitespotted greenling, Hexagrammos stelleri: a) 10.1 mm; b) 12.2 mm; c) 15.0 mm; d) 16.6 mm; e) 18.6 mm; f) 23.5 mm; g) 24.0 mm; h) 61.5 mm. (Source: Gorbunova 1962).

Ophiodon elongatus - Lingcod

Range: Baja California to Kodiak and Shumigan Islands in the Gulf of Alaska

Occurrence in Puget Sound: common

Adult habitat: demersal, on or near reefs or kelp beds

Spawning habitat: demersal, on rocks or in rocky crevices

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached, guarded

Larvae: pelagic

Lingcod are common in Puget Sound and range along the Pacific coast from California to the Gulf of Alaska (Hart 1973). Adult lingcod are found from intertidal depths to ~ 425 m, but are most abundant at 18-60 m (Miller and Geibel 1973; Grinols 1965; Phillips 1959). In general, larger fish (primarily females) inhabit the deeper banks and reefs and males and juvenile fish are more frequent in relatively shallow water adjacent to the shoreline (Chatwin 1956; Wilby 1937; Phillips 1959).

Lingcod adults prefer areas where there is a definite water movement and an abundant supply of food in the form of small fish. They are generally absent from areas of muddy bottoms and stagnant water. Wilby (1937) described two favored environments of lingcod:

1) more or less precipitous slopes of submerged banks from 18-73 m below the surface where there is a rich growth of seaweeds, kelp, eelgrass, and hydroids forming a large feeding ground for many species of small fish, and

2) channels with strong currents which flow over and around reefs and carry large quantities of plankton and planktivorous fishes which concentrate in the tide-rips and whirlpools.

Adult lingcod are relatively sedentary (Chatwin 1956; Anon. 1954), but may undertake migrations of more than a nautical mile (Hart 1943). It is postulated that some adults migrate into shallow water to spawn while others remain year-round residents on rocky reefs (Miller and Geibel 1973; Forrester 1969).

In California, females may begin to mature at lengths of 510 mm TL (20 in) and males at 390 mm TL (15.3 in) and all females greater than 765 mm TL (30 in) and males greater than 590 mm TL (23.2 in) are mature (Miller and Geibel 1973).

Spawning takes place in Puget Sound from December to mid-March or April with most nests laid down during December-early February (Jewell 1968; LaRiviere et al. 1981). Larger fish appear to spawn earlier in the spawning season than younger fish (Miller and Geibel 1973).

Nests are located in crevices or beneath overhanging rocks, and may be located from the lower intertidal to at least 19 m below low tide (Miller and Geibel 1973; Moulton 1977; LaRiviere et al. 1981). It is also noted that lingcod nests are frequently in areas of high current velocities, indicating that water movement may be a stimulus for spawning site selection (Giorgi 1981; Low and Beamish 1978).

Lingcod are oviparous, spawning large masses of eggs which are tended by the males. Males may be monogamous or polygamous as they commonly guard more than one egg mass at a time, with different nests laid down at different times, probalby by different females. However, it may just be territorial instinct which causes them to guard other nearby nests (Jewell 1968). In San Juan Channel, LaRiviere et al. (1981) noted that nests of different males were found as close as 2 m apart, and in two cases, observed 1 male with 2 nests deposited at different times within 0.5 m of each other. In another case, after the disappearance of one egg mass, the male remained in the same territory and acquired a new nest in the same location.

Fertilization of lingcod eggs is external and spawning behavior has been observed (Wilby 1937): The female extrudes the eggs directly on the chosen spot together with a transparent, yellowish secretion, which upon contact with water, forms a strong adhesive for attachment of the eggs to the rocks and to each other. After a layer of several eggs in thickness is laid, the male swims slowly over the mass and fertilizes the eggs with short successive jets of milt. The female then returns and continues to add to the egg mass and the male periodically swims over them and covers them with milt. The egg laying process lasts about one-half hour, after which the female leaves the nest site. The male however, moves in to guard the egg mass and has been observed stirring the surrounding water with his pectoral fins, actually touching the eggs occasionally until the whole cluster has set into a tough, springy, opaque mass. Males may continue to fan the eggs during development to keep surfaces clear of growth and allow a continuous change of water (Wilby 1937); however, this fanning behavior is not always observed (Moulton 1977).

Males are aggressive defenders of their eggs and will repel some intruders such as starfish, dogfish or other fishes, by vigorously biting them or butting with their heads. Other predators of lingcod eggs include gastropods (Calliostoma ligatum and Amphissa columbiana), fish (Jordania zonope, Artedius lateralis, A. harringtoni, Sebastes emphaeus), crab (Phyllolithodes papillosus, Pagurus sp., Scyra acutifrons), and sea urchins (Strongylocentrotus franciscanus, S. drobachiensis, S. purpuratus) (Moulton 1977; LaRiviere et al. 1981; Wilby 1937). Dusky perch and possibly cabezon can also be added to the list of egg mass predators (Jewell 1968).

Fecundity of lingcod increases with size and age of the female, and ranges from 60,000 for a 77.5 cm fish to ~500,000 for 104-118 cm fish (Phillips 1959). An equation for fecundity vs. length was determined by Hart (1967) to be:

$Y = 3.001L\ Xi - 3.5491$ or

$$N = \frac{1}{3541} L^{3.001}$$

N = egg number, L = length

Y = log number, Xi = log length

Spawning nests are quite large; one clump found weighed 33 kg and was 80 cm across (Forrester 1969). The eggs are pinkish in color when first laid, and about 2.8 mm in diameter, but swell to almost 3.5 mm after deposition (Wilby 1937). They turn whitish in a few days and later become yellowish or greenish-brown due to accumulation of diatoms on the surface of the egg mass. The egg mass becomes dark grey near the end of incubation due to development of larval pigmentation (Miller and Geibel 1973).

The incubation of lingcod eggs takes about 6 weeks and hatching occurs over a 3 to 7 day period (Jewell 1968). Hatching is progressive with the outside eggs hatching first. The outer egg capsules then disintegrate, allowing the inner eggs to hatch (Wilby 1937). Larvae are ~ 10 mm when they hatch and contain a reduced yolk sac with a bright yellow oil globule, and have large blue eyes and an elongated body (Forrester 1969). Larval lingcod lack the irridescent blue-green color of larval Hexagrammos, and are light grayish-silver in color. However, melanophore patterns are similar. Lingcod larvae also develop a more prominent lower jaw than in larval Hexagrammos species (Marliave 1975). Descriptions of larvae are lacking, although Marliave (1975) illustrated several sizes (Fig. 44.5). Larvae possess the typical greenling pattern of intensive melanophores on the head, dorsal body surface, dorsal surface of the peritoneum, ventral postanal midline melanophores, and lateral body melanophres which increase with development. Larvae appear to be transformed by ~55 m and take up a demersal residence (Marliave 1975).

Young lingcod, 10-75 mm, are found in the Strait of Georgia during April-May and are reported to consume primarily copepods (including egg and larval stages) and feed to a lesser extent on amphipods, crabs and shrimp larvae, and euphausiids (Barraclough 1967b, c; Barraclough et al. 1968; Robinson et al. 1968a, b).

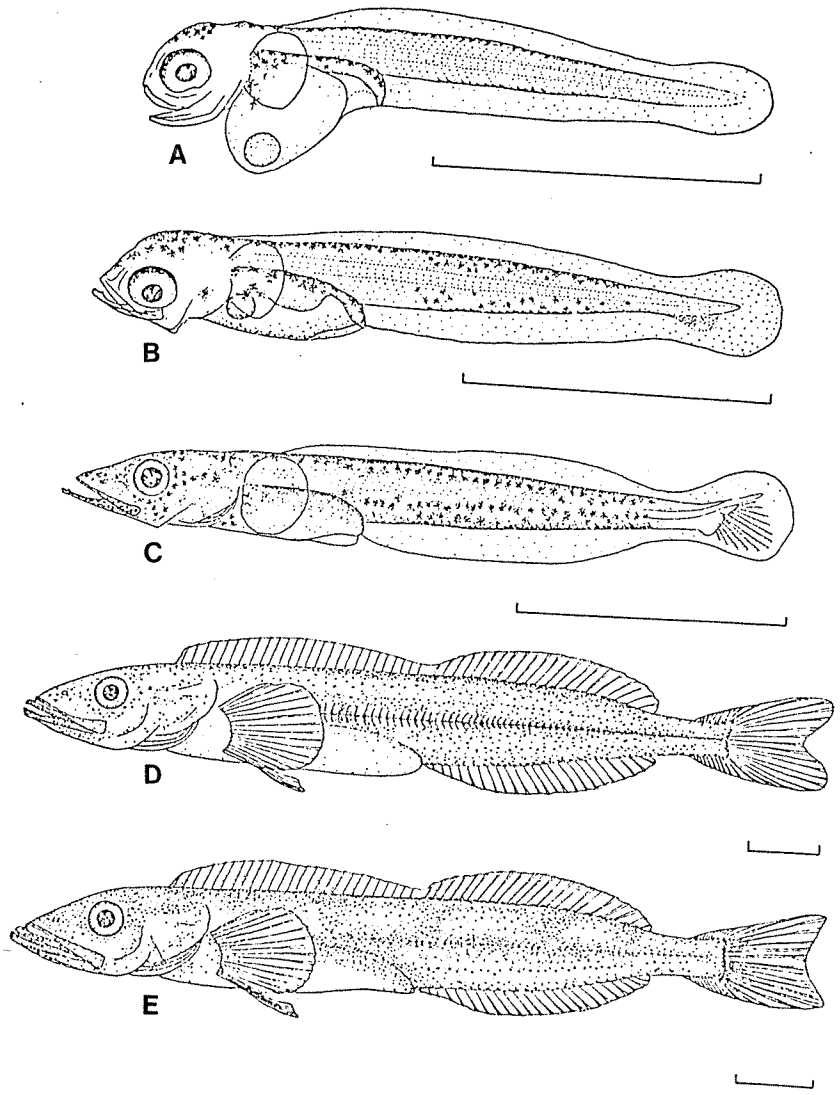

Fig. 44.5. Larvae of lingcod, Ophiodon elongatus, 5 mm scale: A) 0-day, 9.5 mm TL (premature); B) 0 day, 10.5 mm TL; C) 13.5 mm TL from plankton; D) 56 mm TL from plankton; E) 92-day, 55 mm TL, settled. (Source: Marliave 1975).

Oxylebius pictus - Painted greenling

Range: southern California to Queen Charlotte Islands, B.C.

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, on or near rocky reefs

Spawning habitat: demersal, on or near rocks

Spawning season: spring-summer

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: pelagic

Painted greenling range from southern California, through Puget Sound to Queen Charlotte Islands, British Columbia (Hart 1973). Depth distribution of this greenling species is from the surface to 50 m with the majority of them between 1 and 40 m (Feder et al. 1974).

Adults are demersal, and year-round residents on rocky reefs. Individuals are solitary and pugnaciously territorial, but may be concentrated in favorable areas with territories of males occupying ~10 m^2 each. Males are generally distributed in all-male areas which are often on high topography of reefs that are exposed to tidal currents or ocean surge. Females are also solitary, but inhabit the peripheral lower relief sand and rock areas along with juveniles. Males usually remain within a meter of their selected spawning site within their territory, but females have a greater range, and "visit" the males during the breeding season (DeMartini 1976).

Males and females of painted greenling are different in coloration. Females are usually much brighter than males with irregular vertical brown bars on their bodies that are much more distinct. The paired and caudal fins of the female bear burnt-orange and brown bars. The vertical body markings extend into the dorsal and ventral fins, and the ventral surface of the head and body are white and yellow flecked with orange or light brown. The males, in contrast, have dark brown fins, and a light gray-brown and dark-brown undersurface, and the jaws and opercule are flecked in white while the dusky lower surface has large, less dense, amorphous white markings. Edwards (1971) concluded the above color dimorphism was probably temporary during the spawning season and becomes less distinct during the non-breeding season.

In Puget Sound, spawning takes place in May-August (possibly September, Patten 1980), but is protracted in California and occurs from October to July (DeMartini 1976). Males reach sexual maturity at two years (based on otoliths) and ~ 135 mm; however, most males which tend eggs are

3-4 years or more in age. Females spawn for the first time at 3 years of age and at ~ 160 mm (DeMartini 1976). In Puget Sound, where painted greenling spawn primarily in summer, gonads are in the resting stage in fall; however, the fish remain active until December. From December to March, fish are inactive and in sheltered holes or crevices (DeMartini 1976).

During the breeding season, fish exhibit up to 3 complete spawning cycles. For males, one cycle lasts about 30 days, half of which is mating and the other half is parental care. During each cycle, the males have a female-receptive "mating phase" when the males acquire the eggs of usually several females, followed by an unreceptive "parental care" phase in which the male tends the eggs and chases away other fish including ripe courting females. Males may acquire up to 10 (average maximum 5-7, mode 2-3) clutches of female spawn and continue spawning with females in their territory until some eggs reach a mid-development stage and have pigmented eyes (DeMartini 1976).

Females ripen several clutches per season (based on ova diameter [Fig. 44.7] and tagging observations), but lay each entire clutch with one male. Some tagged females have been seen courting with different males when their subsequent clutches were ripe. Courtship is decribed below (DeMartini 1976):

> "Females elicit courtship display from the male with a characteristic 'approach' swim in which the female's anterior body is inclined upwards to expose her enlarged bright yellow venter and yellow branchiostegal membranes. Females accentuate their condition with a peculiar 'loping' motion produced by intermittent sculling with the pectoral fins. The female flank coloration meanwhile changes to a solid dark brown color. Male response to female approach is a rapid (less than one minute) complete darkening to an intense black. The contrast of silvery white quanine areas on the male's branchiostegals and ventral trunk is thus enhanced and displayed to the female in an immediate frantic bout of lateral 'head wagging' and 'circling.' While swimming rapidly around the female in circles, the male characteristically prods her tactilely by quickly swimming past her tail, apparently 'herding' her into the center of his territory. On each circle the male slows down as he passes the female's head, to give a series of lateral head wags which accentuate the brilliant white on black blotches of his flared branchiostegals. At irregular intervals the female is nipped and chased about the male's territory."

Individual male/female displays last about 15 minutes or more, but the actual disposition of eggs has not been observed. DeMartini (1976) suggested that spawning of eggs occurs around dawn.

Males remain in the vicinity of the egg clusters and although no fanning or brooding behavior is observed, they play an important role in chasing away intruding predators which include conspecific rivals.

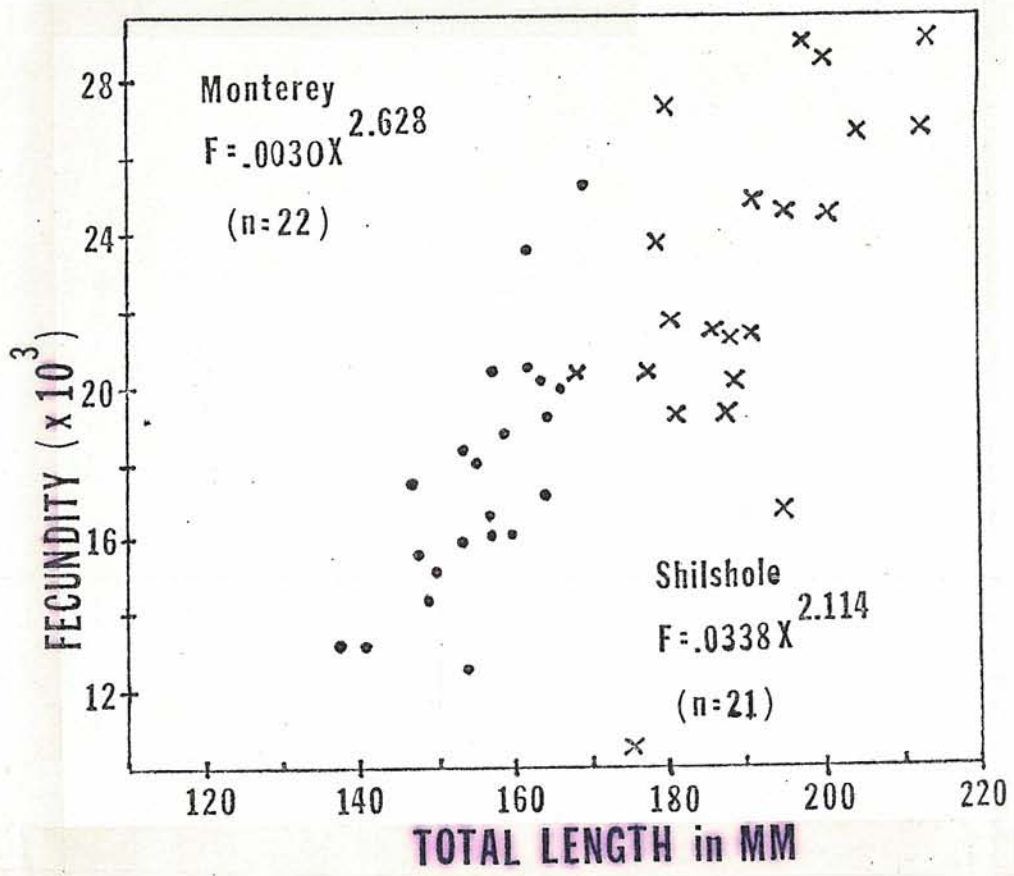

Fig. 44.6. Fecundity-length relationship of painted greenling, Oxylebius pictus, from Monterey, Calif., ( ) and from Shilshole breakwater, Wash., (x). Only ovarian eggs of the largest size mode from ripe fish were used. (Source: DeMartini 1976).

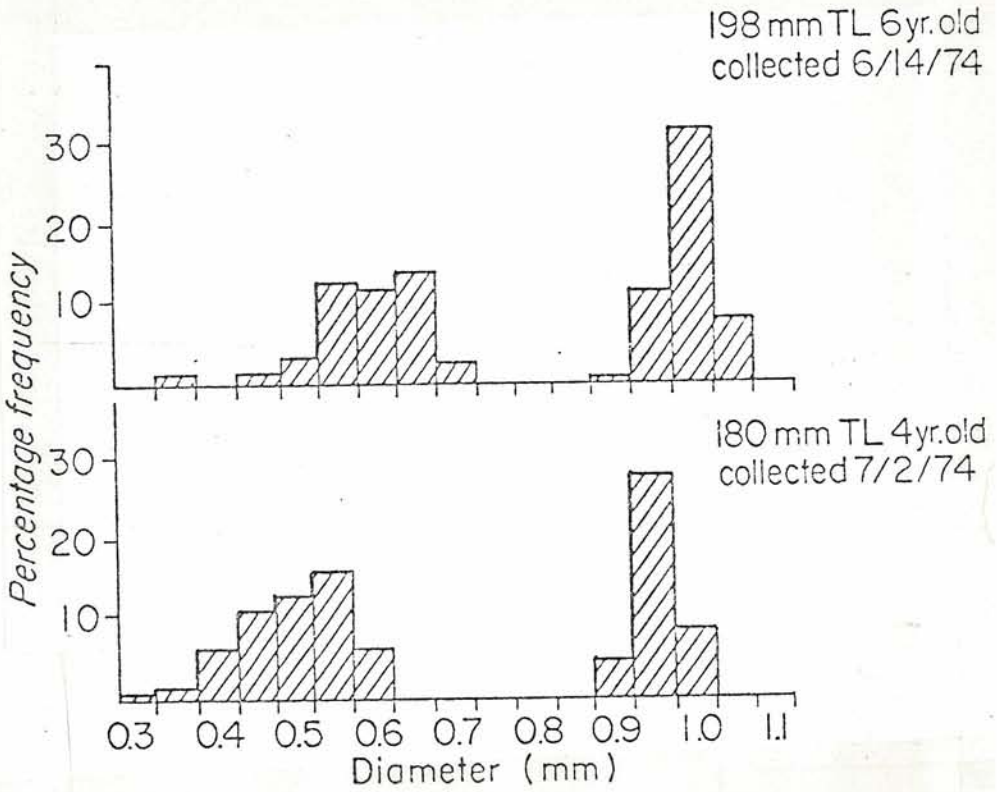

Fig. 44.7. Size distribution of ovarian eggs of two representative painted greenling, Oxylebius pictus, collected from Shilshole breakwater in summer, 1974. Minute oogenia less than 0.3 mm in diameter were omitted. (Source: DeMartini 1976).

Unguarded eggs are devoured within 15-30 minutes (DeMartini 1976). Egg cannibalism is common among painted greenling and contributes to ~ 25% of the diets of males who feed on eggs and ~ 5% of the diets of egg-consuming females. In some cases, males were found to have fed on their own eggs as well as eggs of other males. DeMartini (1976) estimates that in a Puget Sound spawning habitat, cannibalism by adult males and females accounts for 83% and 17%, respectively, of the egg loss between spawning and hatching. In other words, egg loss to other predators is minor.

The number of eggs produced per female increases with body size and ranges from about 12,000 eggs to over 28,000 (Fig. 44.6). The eggs are deposited as walnut-sized clusters of ~2000 pink-orange eggs which are 1.3-1.4 mm in diameter and adherent to each other, but not to the substrate. They are laid in rocky crevices or between sessile encrusting invertebrates such as barnacles and mussels (Edwards 1971; DeMartini 1976). As mentioned earlier, females ripen 3-4 batches of eggs per breeding season.

At ambient temperatures at 9-12^{o}C, eggs hatch in 24-17 days and hatching takes one to several days, with the outermost eggs hatching first. Based on aquarium experiments, hatching success is greater and development time is less in eggs reared in 4 cm/sec current compared to those which develop in a 1 cm/sec current. In nature, spawns are located in exposed locations and are oriented toward the surge as opposed to being in sheltered areas (DeMartini 1976).

The larvae are active swimmers and have a well-developed mouth at hatching. They are positively phototactic and probably neustonic. At 6.3 mm, larvae have the remains of a yolk sac. Snout-to-anus distance is greater than in Hexagrammos species and is about 51% of body length. Larvae are intensely pigmented, with melanophores covering the entire body from the operculum to the caudal peduncle. Melanophores are denser on the dorsum and along the ventral part of the tail where they form paired rows. Body sides are heavily pigmented with large stellate cells, the snout and peritoneum are also pigmented (Fig. 44.8). At 6.5 mm, caudal ray rudiments are visible and by 7.3 mm, yolk sac and oil globule are almost resorbed. Anlages of anal and dorsal fins are forming and pigment has intensified, particularly in the caudal region (Gorbunova 1962). Later larval stages of painted greenlings are undescribed.

Larvae remain pelagic for 1-3 months before settling into the appropriate habitat (DeMartini 1976).

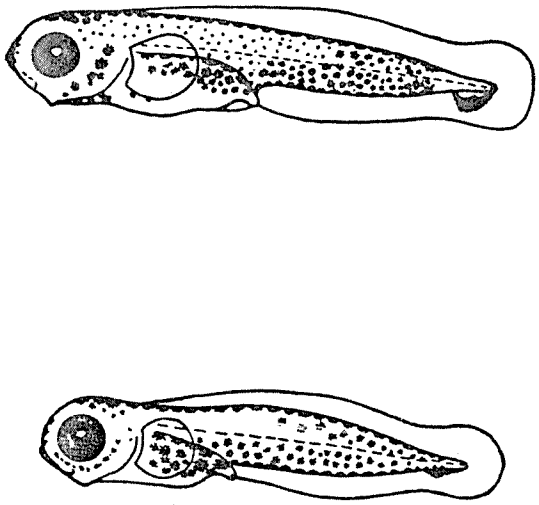

Fig. 44.8. Larvae of painted greenling, Oxylebius pictus, 7.6 mm (top) and longspine combfish, Zaniolepis latipinnis, 6.7 mm (bottom). (Source: Gorbunova 1962).

Zaniolepis latipinnis - Longspine combfish

Range: southern California to Vancouver Island

Occurrence in Puget Sound: common in some areas

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: fall-winter (California)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: pelagic

Longspine combfish range from southern California to Vancouver Island and are fairly common in central-south Puget Sound (Hart 1973; Miller and Borton 1980). Very little reproductive information is available on this greenling species.

In California, spawning occurs in late fall through winter (Goldberg 1980; Gorbunova 1962). Based on an examination of ovaries during winter, clutch sizes range from 350-1,154 ($\bar{X}$ = 639, n = 57) eggs and there is a positive correlation between standard length of the female and egg number (Fig. 44.9). Longspine combfish may produce as many as three egg clutches per reproductive season (Goldberg 1980).

According to Johnson and Adams (1970), longspine combfish from California reached sexual maturity at 110-115 mm. Fecundity was reported to range from 622 to 6,530 eggs for fish between 110 and 160 mm. Also, during April ova diameters ranged from .41 to 2.15 mm ($\bar{X}$ = 1.32 mm).

Larvae have tentatively been identified by Gorbunova (1962) and are similar to larval painted greenling (Fig. 44.8). At 5.2 mm, larvae have an unresorbed yolk sac and oil globule and snout-to-anus length is about 42% TL. Pigmentation consists of an accumulation of spots on the head, a few spots on the snout and operculum, a dorsal row of melanophores which extends from the occiput to the urostyle and covering the upper part of the caudal peduncle (a feature which distinguishes larval longspine combfish from painted greenling), a postanal row of midventral melanophores which runs from the anus to the urostyle, pigment on the lateral body surface which begins behind the anus and consists of large stellate melanophores, and a heavily pigmented peritoneum. At 6.5 mm, the anlage of about 20 rays in the anal fin is seen, and vertebrae number (counted in the larvae) is 40 (Gorbunova 1962).

No other information is presently available.

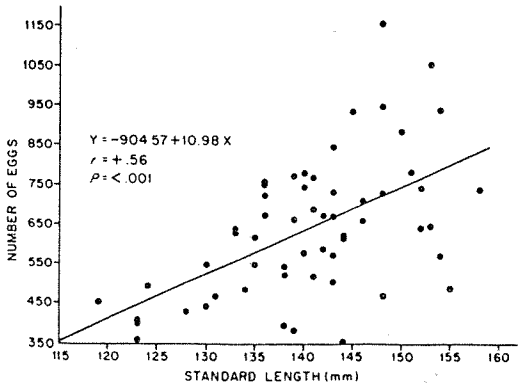

Fig. 44.9. Regression of clutch size on body size (SL) for 57 female of longspine combfish, Zaniolepis latipinnis. (Source: Goldberg 1980).

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45. COTTIDAE

General

Sculpins or cottids are the most speciose family of fishes occurring in Puget Sound with a total of 36 species (Miller and Borton 1980). They are also one of the dominant groups of fishes in the North Pacific fauna and appear to have originated in this region and spread southward along the continental shelves as well as across the Polar Basin to Atlantic waters (Sandercock and Wilimovsky 1968). Ranges of some of the Puget Sound sculpin species extend from Alaska to California, but for 8 species, Puget Sound or coastal Washington represents the southernmost range limit (Table 45.1).

Sculpins are primarily bottom dwellers and may be found from intertidal depths, where they occur in tidepools, to moderate subtidal depths. In Puget Sound (or relatively nearby areas) spawning by the majority of cottid species takes place during winter or spring months (Table 45.2). As far as is known for most species, spawning occurs once per season, and eggs are deposited demersally in adhesive, attached egg masses which are often brightly colored. Unfortunately, for the majority of Puget Sound sculpins, information on spawning behavior and descriptions of eggs are lacking (Table 45.3). For some species, internal fertilization is reported, and in some, parental care of the egg masses is exhibited.

Larval sculpin are generally planktonic for several months after hatching. Transformation from larval to juvenile appearance may precede or immediately follow settlement to the demersal habitat.

Sculpin larvae and rockfish larvae are the two major groups possessing head spines. Number and location of these spines may be species specific, and can aid in identification of larvae. In the following sections, terminology of head spination follows Richardson and Laroche (1979) for rockfish larvae (Fig. 42.1).

Table 45.1. Distribution in the Northeast Pacific of sculpin species found in Puget Sound, Washington. B = Baja California, N = Northern California, O = Oregon, W = Washington, P = Puget Sound, C = British Columbia, E = Southeast Alaska, G = Gulf of Alaska, A = Aleutian Islands. (Source: Howe and Richardson 1978).

Species	Southern range limit	B S N O W P C E G A	Northern range limit
Artedius fenestralis	Diablo Cove	———————	Unalaska Is.
Artedius harringtoni	San Miguel Is.	———————	Kodiak Is.
Artedius lateralis	San Quentin	——————— - -	Kodiak Is., Bering Sea(?)
Artedius meanyi	Pt. Arena	———————	Fillmore Is.
Artedius notospilotus	Pt. San Telmo	———————	Puget Sound
Ascelichthys rhodorus	Moss Beach, CA	———————	Sitka
Blepsias cirrhosus	San Simeon	———————	Bering Sea
Chitonotus pugetensis	San Maria Bay	———————	Work Canal
Clinocottus acuticeps	Big Sur River	———————	Bering Sea
Clinocottus embryum	Pt. Banda	———————	Bering Sea
Clinocottus globiceps	Gaviota	———————	Kodiak Is.
Dasycottus setiger	Puget Sound	———————	Bering Sea
Enophrys bison	Monterey	———————	Kodiak Is.
Gilbertidia sigalutes	Puget Sound	———————	Bering Sea
Hemilepidotus hemilepidotus	Monterey Bay	———————	Bering Sea
Hemilepidotus spinosus	Ventura	———————	Puffin Bay
Icelinus borealis	Puget Sound	———————	Bering Sea
Icelinus burchami	La Jolla	———————	Behm Canal
Icelinus filamentosus	Cortez Bank	———————	N. British Columbia
Icelinus tenuis	San Benito Isls.	———————	Queen Charlotte Isls.
Jordania zonope	Diablo Canyon	———————	Vancouver Is.
Leptocottus armatus	San Quintin Bay	———————	Chignik
Malacocottus kincaidi	Puget Sound	———————	Bering Sea (?)
Myoxocephalus polyacanthocephalus	WA Coast	———————	Bering Sea
Nautichthys oculofasciatus	San Miguel Is.	———————	Bering Sea
Oligocottus maculosus	White Pt.	———————	Sea of Okhotsk; Bering Sea(?)
Oligocottus rimensis	San Nicolas Is.	———————	Welcome Harbor
Oligocottus snyderi	Rio Socorro	———————	Sitka
Psychrolutes paradoxus	Puget Sound	———————	Bering Sea
Radulinus asprellus	Los Coronados Isls.	———————	Kodiak Is.
Radulinus boleoides	Santa Catalina Is.	———————	Langara Is.
Rhamphocottus richardsoni	Santa Monica Bay	———————	Bering Sea
Scorpaenichthys marmoratus	Pt. Abreojos	———————	Sitka
Synchirus gilli	San Miguel Is.	———————	Sitka
Triglops macellus	Puget Sound	———————	Bering Sea
Triglops pingeli	Puget Sound	———————	Arctic

Table 45.2. Months of reported spawning time of sculpins, by species and area, that are found in Puget Sound, Washington. (Blanks indicate spawning times are unknown).

Species	Month												Area	References
	J	F	M	A	M	J	J	A	S	O	N	D		
Artedius fenestralis		X	X	X	X								British Columbia	Marliave 1975
Artedius harringtoni					X								California	Burge and Schultz 1973 (based on one fish)
Artedius lateralis		X	X	X	X								British Columbia	Marliave 1975
Artedius meanyi														
Artedius notospilotus														
Ascelichthys rhodorus														
Blepsias cirrhosus		X											British Columbia	Marliave 1975
Chitonotus pugetensis			X										Puget Sound	Misitano 1980
Clinocottus acuticeps				X			X						Puget Sound	Hart 1973 (based on two fish)
Clinocottus embryum														
Clinocottus globiceps														
Dasycottus setiger														
Enophrys bison		X	X	X	X								Puget Sound	DeMartini - unpubl. data
Gilbertidia sigalutes								X					Barkley Sound, B.C.	Marliave 1975
Hemilepidotus hemilepidotus	X									X	X	X	Puget Sound	DeMartini and Patten - unpubl. data
Hemilepidotus spinosus														
Icelinus borealis														
Icelinus burchami														
Icelinus filamentosus														
Icelinus tenuis														
Jordania zonope										X			British Columbia	Hart 1973
Leptocottus armatus	X	X	X							X	X	X	California	Jones 1962
Malacocottus kincaidi														
Myoxocephalus polyacanthocephalus[1]			X										Skagit Bay, WA	Blackburn 1973
Nautichthys oculofasciatus[1]	X	X	X	X	X								British Columbia	Marliave 1975
Oligocottus maculosus				X	X	X	X						Puget Sound	Atkinson 1939
Oligocottus rimensis														
Oligocottus snyderi														
Psychrolutes paradoxus[1]		X	X		X								Barkley Sound, B.C.	Marliave 1975
Radulinus asprellus														
Radulinus boleoides														
Rhamphocottus richardsoni[1]		X	X	X	X								British Columbia	Marliave 1975
Scorpaenichthys marmoratus	X	X	X	X	X								British Columbia	Pillbury 1957
Synchirus gilli					X								British Columbia	Hart 1973
Triglops macellus														
Triglops pingeli														

[1]Collection of planktonic larvae.

Table 45.3. Summary of egg color and characteristics, by species of sculpin found in Puget Sound, Washington. (W = winter, SP = spring, S = summer, F = fall, U = unknown.

Species	Common name	Spawning season	Egg color(s)	Egg diameter mm	Oil globules Number	Oil globules Size, mm[1]	Other
Artedius fenestralis	Padded sculpin	W-SP	slate gray, light blue maroon, deep purple	U	U	U	
Artedius harringtoni	Scalyhead sculpin	SP?	U	U	U	U	
Artedius lateralis	Smoothhead sculpin	W-SP	yellow, orange, red	1.07	1	.22	Shell membrane .031mm, "pin-pricked" in appearance
Artedius meanyi	Puget Sound sculpin	U	U	U	U	U	
Artedius notospilotus	Bonehead sculpin	U	U	U	U	U	
Ascelichthys rhodorus	Rosylip sculpin	U	U	U	U	U	
Blepsias cirrhosus	Silverspotted sculpin	W	light brown	U	U	U	
Chitonotus pugetensis	Roughback sculpin	SP	light pink	1.02-1.05	1 lg&5-8 sm	.3	
Clinocottus acuticeps	Sharpnose sculpin	SP-S?	brown	∿1	U	U	
Clinocottus embryum	Calico sculpin	U	U	U	U	U	
Clinocottus globiceps	Mosshead sculpin	U	U	U	U	U	
Dasycottus setiger	Spinyhead sculpin	U	U	U	U	U	
Enophrys bison	Buffalo sculpin	W-SP	purple, pink, red, orange, yellow, tan	1.7-2.0	1	.36	
Gilbertidia sigalutes	Soft sculpin	S	U	2.3	U	U	
Hemilepidotus hemilepidotus	Red Irish lord	F	tan, pale green, pink, orange, red	U	U	U	
Hemilepidotus spinosus	Brown Irish lord	U	U	U	U	U	
Icelinus borealis	Northern sculpin	U	U	U	U	U	
Icelinus burchami	Dusky sculpin	U	U	U	U	U	
Icelinus filamentosus	Threadfin sculpin	U	U	U	U	U	
Icelinus tenuis	Spotfin sculpin	U	U	U	U	U	
Jordania zonope	Longfin sculpin	F	U	U	U	U	
Leptocottus armatus	Pacific staghorn sculpin	F-W-Sp	creamy white, pale yellow-orange, deep orange	1.36-1.50	1-7 total	U	Shell membrane "pebbly" in appearance, yolk contains brown floculent material
Malacocottus kincaidi	Blackfin sculpin	U	U	U	U	U	
Myoxocephalus polyacanthocephalus	Great sculpin	W-SP	U	U	U	U	
Nautichthys oculofasciatus	Sailfin sculpin	W-SP	red	∿2	U	U	
Oligocottus maculosus	Tidepool sculpin	SP-S	green, red	1.4-1.55	1-3 lg & several smlr	U	
Oligocottus rimensis	Saddleback sculpin	U	U	U	U	U	
Oligocottus snyderi	Fluffy sculpin	U	U	U	U	U	
Psychrolutes paradoxus	Tadpole sculpin	W-SP	U	1.4	U	U	
Radulinus asprellus	Slim sculpin	U	U	U	U	U	
Radulinus boleoides	Darter sculpin	U	U	U	U	U	
Rhamphocottus richardsoni	Grunt sculpin	W-SP	creamy white, yellow, orange	U	U	U	
Scorpaenichthys marmoratus	Cabezon	W-SP	maroon, crimson, white, pink, blue-green, olive,	1.4-1.7	1 lg&1-4 sm	.27	
Synchirus gilli	Manacle! sculpin	SP	pink	U	U	U	
Triglops macellus	Roughspine sculpin	U	U	U	U	U	
Triglops pingeli	Ribbed sculpin	U	U	U	U	U	

[1]Size of largest oil globule.

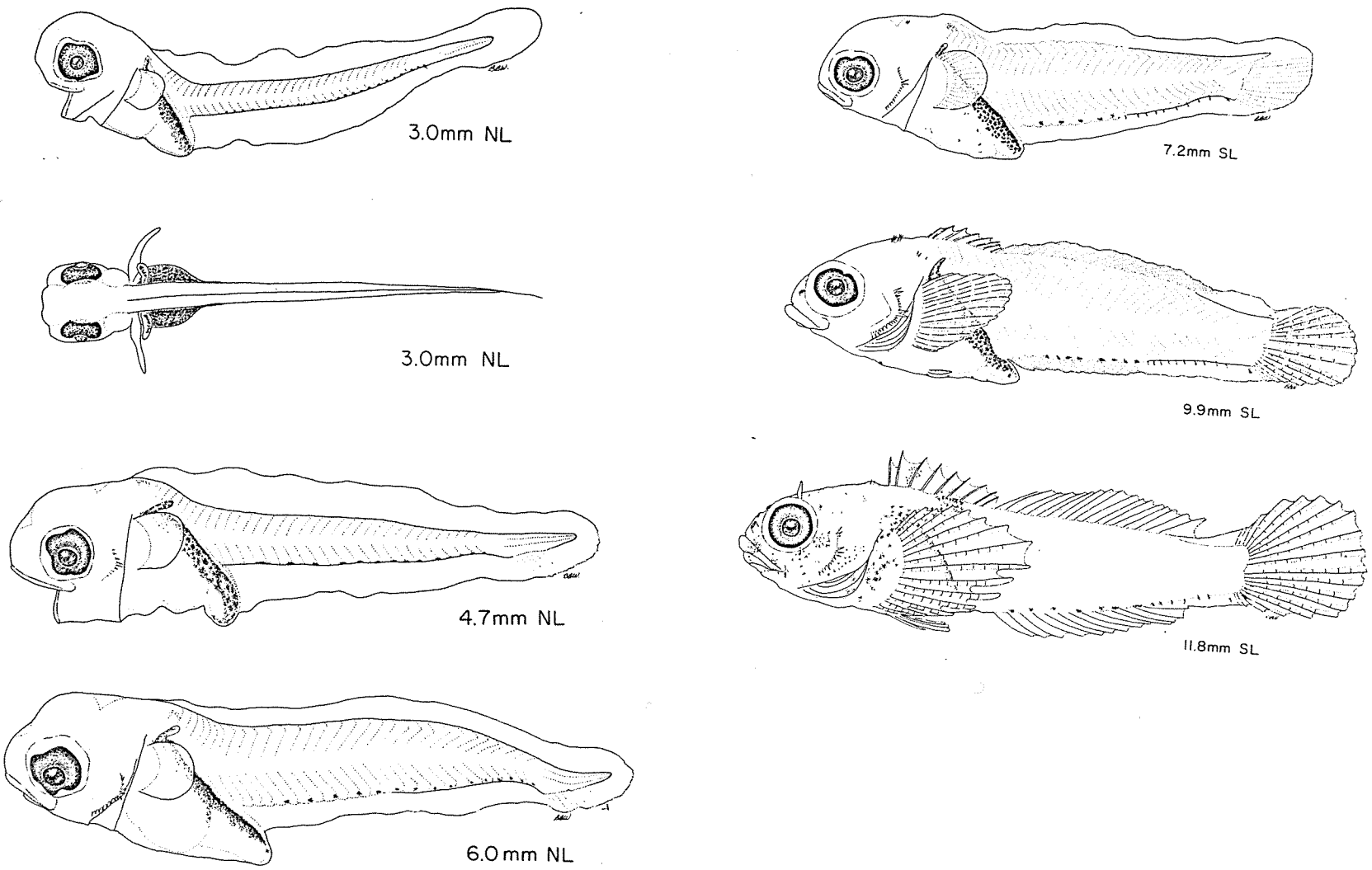

Fig. 45.1. Planktonic larvae of "padded sculpin-type" collected off Oregon. (Source: Richardson and Washington 1980).

Artedius fenestralis - Padded sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal to subtidal depths

Spawning habitat: demersal, on rocks

Spawning season: winter-spring (B.C.)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached

Larvae: pelagic

Padded sculpin inhabit nearshore waters from the intertidal zone where they may be found in tidepools to subtidal depths of 55 m (Green 1971c; Hart 1973).

In Barkley Sound, British Columbia, eggs are laid in clusters under boulders in the low intertidal area from February to May (Marliave 1975). Males may return to the nest with different females as egg masses consist of several smaller masses of eggs at various stages of development. Each smaller egg mass is uniformly colored, but different masses vary in color from slate gray to light blue, or to maroon and deep purple. The masses are globular, slightly compressed, and laid so that they overlap each other (Marliave 1975).

Larvae reared in the laboratory, hatch at about 3.7 mm and are characterized by a short gut and body, ventral melanophores on the tail and a red pigment patch with melanophores over the gut. No nape pigment is present at hatching, but develops later. Yolk sac larvae of padded sculpin are very similar to smoothhead sculpin, Artedius lateralis, at this stage, except they are smaller. Marliave (1975) reported that by the onset of fin ray formation, padded sculpin larvae have a patch of melanophores on the nape, but none on the head, in contrast to smoothhead sculpin which have no nape pigment, but develop spots on the head.

A planktonic series of Artedius put together from specimens collected off Oregon may be padded sculpin based on the meristics of the largest larvae; however, species identification remains somewhat tentative (Richardson and Washington 1980). These larvae possessed the following pigmentation patterning:

1) melanophores concentrated over the dorsolateral surface of the gut;
2) nape pigment present in larvae exept at smallest sizes but becomes embedded and obscured in larvae > 8 mm; and

3) a postanal midventral row of < 20 melanophores (often 15-20, but < 25 in larvae < 5 mm). Half of these melanophores extend as characteristic pigment dashes onto the ventral finfold in larvae > 7 mm. The number of ventral midline melanophores helps distinguish "padded sculpin-type" from scalyhead sculpin, A. harringtoni, which has usually > 20 postanal midventral melanophores.
4) Pigment is added to the head region, at the base of the pectoral fin, to the anterior part of the spinous dorsal fin as a bar extending from the dorsal surface of the abdominal cavity near the dorsal origin of the pectoral fin to the middle of the spinous dorsal fin, and as groups of melanophores along the lateral midline from the gut region to the caudal fin, in larvae 12-14 mm.

Larvae of "padded sculpin-type," as well as scalyhead sculpin larvae, possess a series of small spines along the margin of the preopercle, which begin to appear in 4.5-5.0 mm larvae (Fig. 45.1C). By 7-11 mm, about 20-25 spines are visible and the ones in the dorsal part of the series at the posterior-most angle of the preopercle are largest (Fig. 45.1E). Clusters of spines also develop in the parietal region appearing as 1 or 2 spines in 6-7 mm larvae and increasing to 3 or more in larvae > 7.5 mm. At about 9-9.5 mm, clusters of spines occur in both the parietal and posttemporal regions (Fig. 45.1F). These spine clusters are not obvious in larval scalyhead sculpin.

A final distinctive feature of larval "padded sculpin-type" is the presence of gut diverticula which protrude laterally from each side of the dorsal surface of the gut cavity just posterior to the top of the pectoral fin. This feature is most obvious in the small larvae and is probably lost during transformation to the juvenile stage (Fig. 45.1).

The adult complements of pelvic, pectoral, dorsal, and anal fin rays are formed by the time larvae reach 10 mm and postocular cirri are formed in larvae ~ 11.8 mm (Fig. 45.1G).

Artedius harringtoni - Scalyhead sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, subtidal

Spawning habitat: unknown

Spawning season: unknown (possibly spring - California)

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

According to Green (1971c), adult scalyhead sculpin are primarily found subtidally and may frequently reside on rocky reefs and pilings between 5 and 11 m (Hart 1973). Scalyhead sculpin are common in Puget Sound (Miller and Borton 1980).

Spawning season is unknown except that one female taken in California in May was reported to contain nearly ripe eggs (Burge and Schultz 1973). Males are morphologically different from females at maturity. They become robust, develop a large head, have enlarged anterior teeth and plumose cirri. Males also assume a series of colors and color patterns quite unlike the femles and immature males (Clemens and Wilby 1961).

Information on fecundity, spawning behavior, and egg descriptions is absent; however, a planktonic series of scalyhead larvae has been described from off Oregon (Richardson and Washington 1980). Larvae hatch at about 3-4 mm, are stubby in shape and often have a humped appearance in the nape region (Fig. 45.2B). Gut diverticula are not present like they are in "padded sculpin-type" (see A. fenestralis). Pigmentation of scalyhead larvae consists of the following:

1) a dense concentration of melanophores over the gut;

2) pigment on the nape, except in smallest larvae, which becomes embedded in larvae > 9 mm;

3) a postanal midventral row of > 20 melanophores (often 20-30, but > 25 in larvae less than 6 mm), which extends as dashes of pigment into the finfold of larvae > 7 mm (Fig. 45.2E). (Compared to < 20 in the "padded sculpin-type"), and

4) pigment which is added to the head and pectoral fin base in specimens > 12 mm.

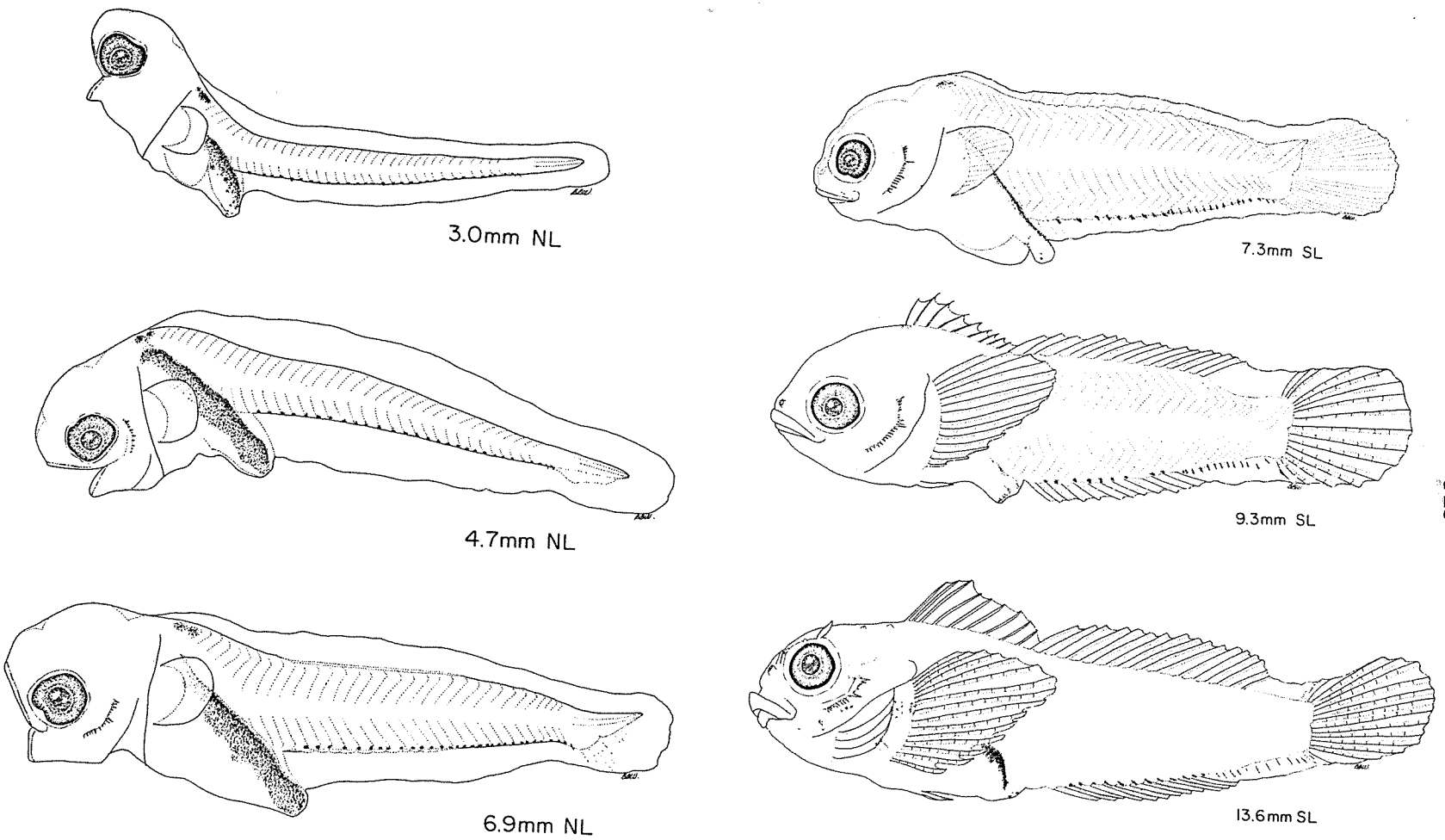

Fig. 45.2. Planktonic larvae of scalyhead sculpin, Artedius harringtoni, collected off Oregon. (Source: Richardson and Washington 1980).

Scalyhead sculpin develop preopercular spines similar to the "padded sculpin-type" and number 20-25 in postflexion larvae, but never develop pronounced multiple spines in the parietal and posttemporal region as the padded sculpin-type does. However, minute serrations are sometimes visible and a bump develops in the parietal region of larger larvae.

By 10 mm, adult complements of the dorsal, anal, and paired fin rays or ray elements are formed. Cirri pattern on the 13.6 mm larvae consists of preorbital and nasal cirri (Fig. 45.2F).

Artedius lateralis - Smoothhead sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal to subtidal

Spawning habitat: demersal, on rocks

Spawning season: winter-spring (Barkley Sound, B.C.)

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached

Larvae: pelagic

Smoothhead sculpin are common in intertidal and subtidal areas of Puget Sound. Adults seem to inhabit a variety of substrates including sandy beaches, rocky tidepools, boulder beaches, and shores with mixed sand, pebbles, and rocks (Marliave 1977; Cross 1982).

Spawning habits of smoothhead sculpin are similar to the padded sculpin in that egg masses are laid in clusters attached to rocks during winter and spring. They differ, however, in that the masses are more compressed than those of the padded sculpin and taper to a monolayer of eggs at the edges of the mass. Eggs of the smoothhead sculpin vary in color from yellow to orange to red, in contrast to the blue hues of padded sculpin eggs (Marliave 1977).

The eggs of smoothhead sculpin are almost spherical, but are slightly flattened at their points of contact. Egg diameters average 1.07 mm, but have a fairly wide range of sizes. Each egg consists of a heavy shell membrane up to 0.031 mm in thickness, which is clear, transparent, and pierced by many fine radiating canals which give it a "pin-pricked" appearance. They contain a single large oil globule which measures 0.22 mm in diameter and an irregularly shaped mass of granular material (Fig. 45.3A).

In eggs reared in the laboratory, development to the hatching stage requires about 16 days (at about 15°C). The embryo becomes established after 40 hours from fertilization and by 98 hours encircles half the circumference of the yolk sac. In addition, pupils and auditory capsules have appeared, the head is delineated by a constriction at the nape, the notochord is developed, and the heart makes a prominent bulge in the yolk below the nape. At approximately 200 hours, the heart is beating and the embryo may twitch. The head is broadened and otoliths are present, and the body narrows abruptly behind the head and tapers to the tail. The iris and pupil are dull gray, and the body of the embryo has become more opaque and appears slightly mottled. Blood vessels

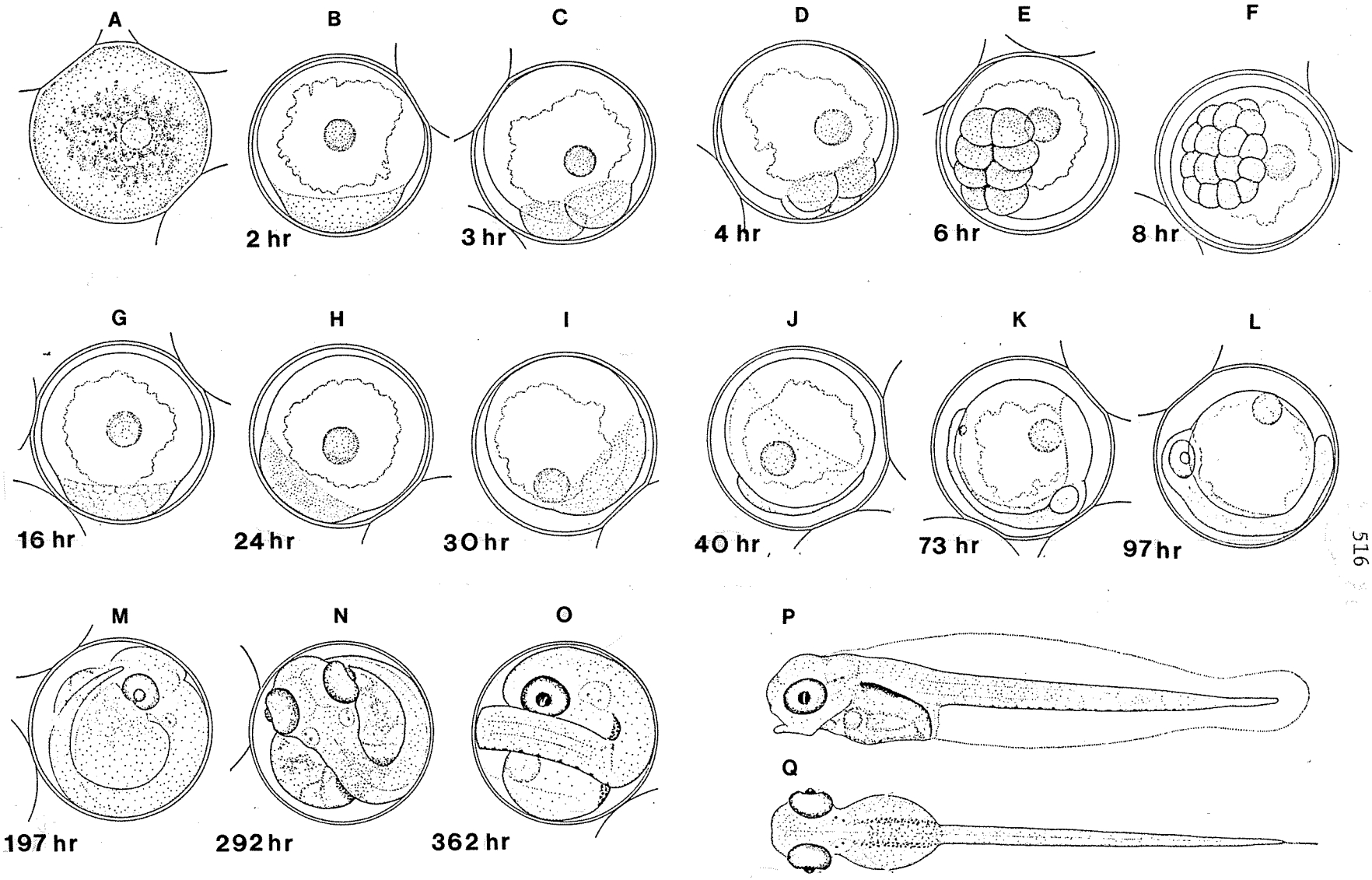

Fig. 45.3. Developmental sequence of eggs of smoothhead sculpin, Artedius lateralis: (A) Recently fertilized egg; (B) blastodisc; (C) two cells; (D) four cells; (E) eight cells; (F) sixteen cells; (G) early blastodermal cap; (H) late blastodermal cap; (I) segmentation cavity; (J) embryo; (K) blastopore closure; (L) tail free of yolk; (M) tail encircling yolk; (N) late embryo; (O) prior to hatch; (P) larva just hatched, lateral view; (Q) larva just hatched, dorsal view. (Source: Modified from Budd 1940).

appear in the yolk sac below the cephalic region and others extend below the notochord carrying blood to the tail and back to the heart. By 250 hours, the embryonic head has widened greatly and the body has increased in length, eyes have become almost black, and other yolk and body color has deepened. Numerous small and closely spaced scarlet pigment spots appear on the dorsal surface of the yolk sac on either side of the body. This scarlet area later expands slightly and becomes evenly spotted by many melanophores. Shortly before hatching (about 360 hours), the eyes are large, pigmented, and the tail encircles the yolk sac which is considerably reduced. The oil globule remains the same size throughout development and rests just below the head within the yolk sac. Melanophores cover the dorsal surface of the yolk sac and appear on the ventral surface of the tail. Several days before hatching, a patch of minute nodules appears on the crown of the embryo's head and may aid as a rasp in breaking through the shell allowing the embryo to escape head first (Budd 1940). Development events are summarized in Table 45.4 and Fig. 45.3.

Larvae hatch at about 4.0 mm (Marliave 1975; Budd 1940) and are active swimmers right after hatching. Aquarium reared larvae have a planktonic stage which lasts 41-60 days. During this period, settlement occurs abruptly and is immediately followed by the onset of juvenile coloration. Larvae are about 11.0 mm TL when they settle. In substrate preference experiments where larvae are offered trays of varying substrate types, they show no significant preference, but rather settle at random on the trays provided as well as on the tank bottom and walls (Marliave 1975).

The recently hatched larvae are characterized by the following pigmentation pattern: numerous densely spaced melanophores on the dorsal surface of the gut and a postanal midventral row of about 20 distinct melanophores (Fig. 45.3 P, Q). According to Marliave (1975), smoothhead sculpin larvae differ from padded sculpin larvae in that no nape pigment is present and pigmentation develops in the occipital region (Fig. 45.4). As in the "padded sculpin-type," dorsal gut diverticula are also present in larval stages of smoothhead sculpin (Marliave 1975).

Table 45.4. Summary of developmental events of eggs of smoothhead sculpin, Artedius lateralis, average rearing temperature about 15.5°C. (Source: Budd 1940).

Time (hours from fertilization)	Developmental event
2	Blastocap formation (Fig. 45.3., B).
3	First cleavage complete (Fig. 45.3, C).
16	Early blastodermal cap (Fig. 45.3, G).
24	Late blastodermal cap (Fig. 45.3, H).
30	Formation of segmentation cavity (Fig. 45.3, I).
40	Germ ring migration to almost equatorial position. Embryo established (Fig. 45.3, J).
50	Blastodermal pore closed.
73	Eyes well formed but without pupils; Kupffer's vesicle present; body color light amber (Fig. 45.3, K).
∿ 98	Pupils have appeared; head delineated; auditory capsule developed; heart forms a bulge in the yolk; embryo encircles about 1/2 circumference of yolk; Kupffer's vesicle disappears (Fig. 45.3, L).
∿ 197	Heart beating; embryo moves; head broadens; otoliths present; iris and pupil dull gray; blood vessels appear in the yolk sac (Fig. 45.3, M).
∿ 292	Eyes almost black; embryo enlarged and scarlet chromatophores appear on dorsal surface of the yolk sac (Fig. 45.3, N).
∿ 362	Embryo wraps completely around yolk; head and eyes large; yolk sac reduced; notochord and myomeres evident. Melanophores appear on ventral surface of tail and obscure scarlet yolk sac chromatophores; eyes are black (Fig. 45.3, O).
380	Hatch (Fig. 45.3, P, Q).

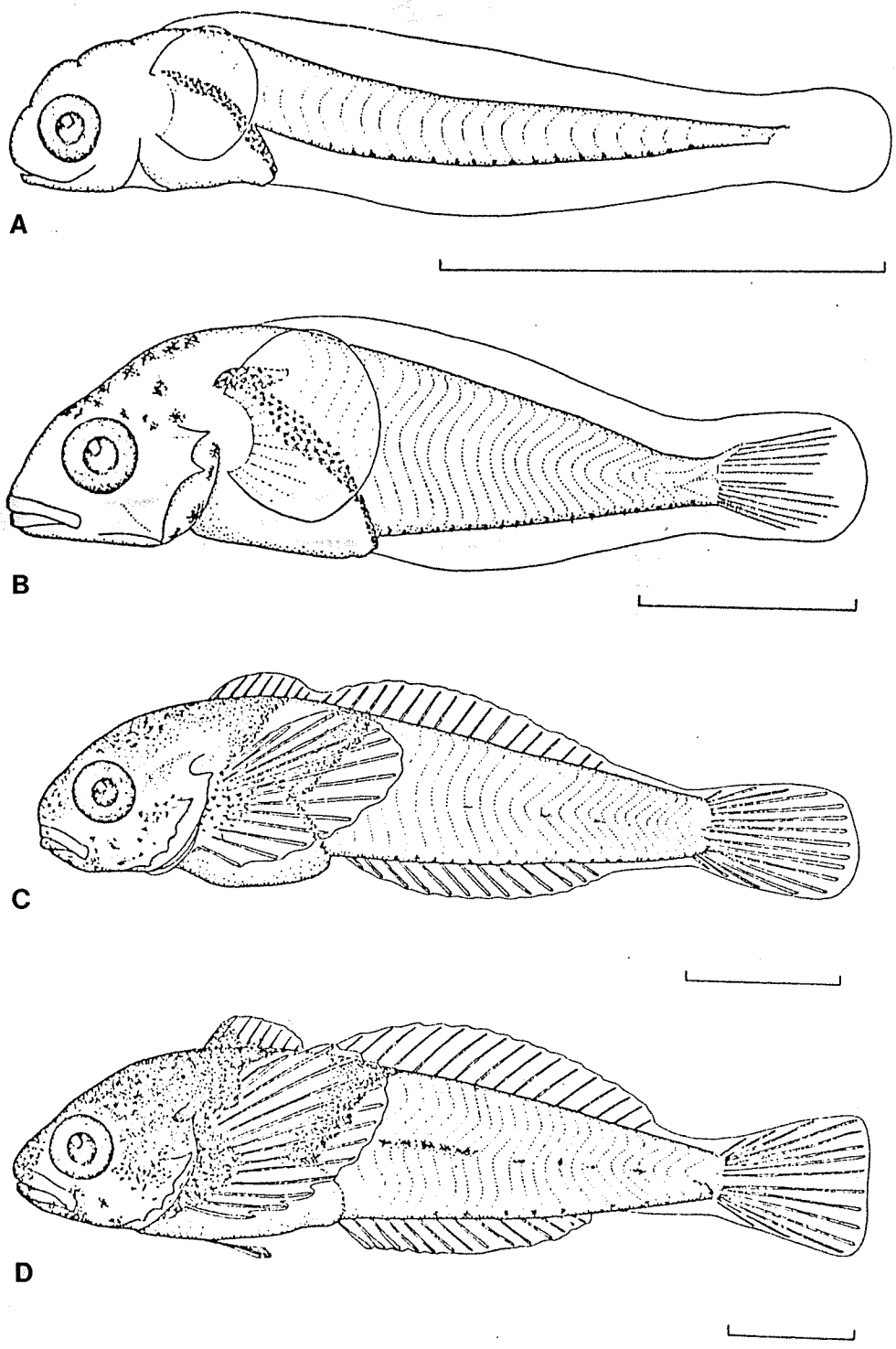

Fig. 45.4. Larvae of smoothhead sculpin, Artedius lateralis, reared in the laboratory, 2 mm scale: (A) 0-day, 4 mm TL; (B) 30-day, 8 mm TL; (C) 48-day, 11 mm TL; (D) 58-day, 14 mm TL, settled. (Source: Marliave 1975).

Artedius meanyi - Puget Sound sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, nearshore

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Attaining lengths of up to only 5 cm, Puget Sound sculpin are probably inaccessible to many types of sampling gear and may be more common than they appear (Hart 1973). Information on early life history of this species does not exist at present.

Artedius notospilotus - Bonehead sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, intertidal and deeper

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Bonehead sculpin are demersal, occurring from the intertidal zone to depths of 45 m (Miller and Lea 1972). They are uncommonly found in Puget Sound which is the northern limit (to date) of this species. Their uncommonality may in part be due to a habitat preference which is not readily accessible to most sampling gears. The early life history of this Artedius species has not been studied.

Ascelichthys rhodorus - Rosylip sculpin

Range: Table 45.1

Occurrence in Puget Sound: common in some areas

Adult habitat: demersal, intertidal to subtidal zones

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Rosylip sculpin adults are fairly common in the San Juans (Miller and Borton 1980) and are found in both tidepool and subtidal habitats (Green 1971c; Cross 1982). Cross (1982) observed that the larvae in northern Puget Sound settled subtidally and moved into the intertidal zones at sizes $\geq$ 30 mm TL. Most of the early life history of this species remains unstudied.

Blepsias cirrhosis - Silverspotted sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, in shallow water associated with algae or eelgrass

Spawning habitat: demersal, on rocks

Spawning season: late winter (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, undescribed

Larvae: pelagic

Silverspotted sculpin inhabit shallow water and are common in some areas in eelgrass beds, Macrocystic beds, or tidepools filled with Alaria (Marliave 1975; Clemens and Wilby 1961). Eggs have not been described but are reportedly spawned onto rocks and are clear light brown (Clemens and Wilby 1961). Based on collections of planktonic larvae, spawning occurs in late winter (Marliave 1975).

The planktonic larvae are well covered with brown pigmentation. Melanophores are large and evenly spaced along the body back to the caudal peduncle, which is clear of pigment until metamorphosis. The head is large and knobby in profile, and four blunt preopercular spines are formed by 20 mm. Pectorals are present in the smallest planktonic larvae and dorsal and anal fin rays appear by 14 mm. Metamorphosis is completed prior to settling and metamorphosed juveniles (25.5 mm) are collected from the plankton (Fig. 45.5). Larvae assume juvenile characters rapidly, within a two week period, after which they may settle onto floating algae (Marliave 1975).

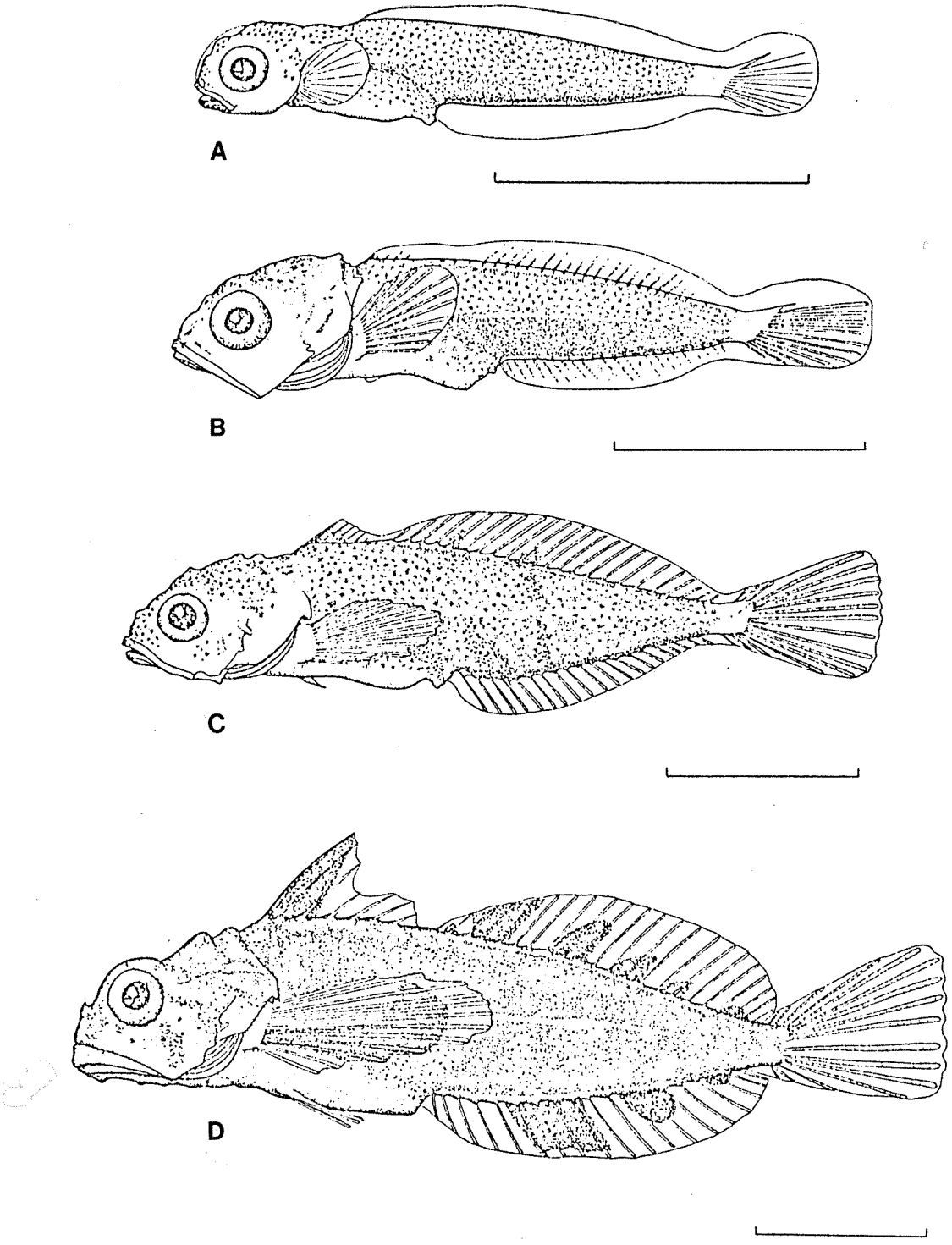

Fig. 45.5. Larvae of silverspotted sculpin, Blepsias cirrhosus, collected from the plankton, 5 mm scale: A) 10 mm TL; B) 14 mm TL; C) 19 mm TL; D) 25.5 mm TL. (Source: Marliave 1975).

Chitonotus pugetensis - Roughback sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal and deeper

Spawning habitat: unknown

Spawning season: spring

Mode of reproduction: oviparous, internal fertilization

Eggs: demersal, adhesive

Larvae: pelagic

Adult roughback sculpin are demersal at depths from the intertidal zone to 140 m (Miller and Lea 1972), but are most common at depths less than 75 m (Hart 1973).

In California, peak spawning occurs during late winter to early spring; however, some ripe females are found during the other seasons as well. From histological observations it is speculated that three egg clutches per female may be produced in a reproductive season in Californian waters. Each clutch may contain up to 1900 eggs (mean of 17 females was 1,043) (Goldberg 1980). The smallest reproductively active female reported by Goldberg (1980) was 66 mm SL and there was a positive correlation between egg number and body size (Fig. 45.6).

Males of this species are known to possess an intromittent organ (Bolin 1944), but internal fertilization had not been documented until recently. In March 1977, a gravid female was collected by trawl gear in 38 m of water in Puget Sound. The extruded eggs were found to be already fertilized demonstrating that fertilization occurs prior to spawning (Misitano 1980). The eggs adhere tightly to each other within a few minutes after contacting water, but do not adhere to the walls of a glass beaker. They are spherical, light pink in color, and range in diameter from 1.02 mm to 1.05 mm (mean 1.04 mm for 10 eggs). The perivitelline space is about 0.05 mm and the yolk contains a large oil droplet (0.3 mm in diameter) surrounded by five to eight smaller oil droplets. An irregularly shaped opaque whitish mass, slightly larger than the large oil droplet is suspended in the yolk. Twenty-two hours after extru- sion, a blastodermal cap is evident and after eight days the embryonic heart is beating and the embryo becomes vascularized (Misitano 1980).

Newly hatched larvae are 2.9-3.0 mm SL and at six days of age are about 4.8-4.9 mm. Early larvae are characterized by a short preanal distance (about 38% SL), 43-48 myomeres, and a diagnostic pigmentation

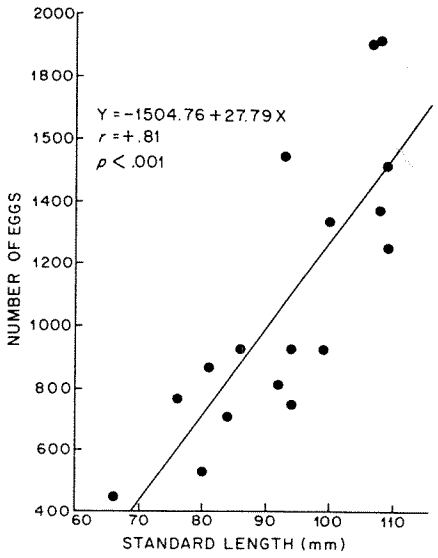

Fig. 45.6. Regression of clutch size on body size (SL) for 17 Chitonotus pugetensis females. (Source: Goldberg 1980).

pattern. At hatching, 32-37 small melanophores are present along the midventral surface beginning on the fourth postanal myomere and continuing posteriorly to the last myomere. Two to four dendritic melanophores are also present in the ventral finfold below the tip of the notochord and a vertical row of about seven melanophores is present along the base of each pectoral fin (Fig. 45.7A). In slightly older larvae, these melanophores increase in number and extend vertically to the isthmus (Fig. 45.7B). About 11-13 large stellate melanophores occur on the surface of the dorsal, lateral, and ventral posterior half of the abdomen (Fig. 45.7A). With development, these gut melanophores become rearranged resulting in a dense row of melanophores on the dorsal surface of the gut and a continuous row of seven or eight melanophores along the ventral midline of the gut (Fig. 45.7B). Newly hatched larvae lack head pigmentation, but by six days, 16-18 melanophores appear on the dorsal cephalic region and four melanophores develop in the interorbital region (Misitano 1980). In larger planktonic larvae, 15-16 mm, melanophores are added to the anterior portion of the spinous dorsal fin, in the nape region, along the lateral midline and on the pectoral fin (Fig. 45.7G-H) (Richardson and Washington 1980).

Spines are visible on the preopercle of larvae as small as 6 mm, and develop into four spines. During the postflexion period, small parietal and nuchal spines develop and fuse as one spine. Several small posttemporal and supracleithral spines also develop, but become inconspicuous by 16.6 mm. A nasal spine also forms and is visible by 15 mm (Fig. 45.7G).

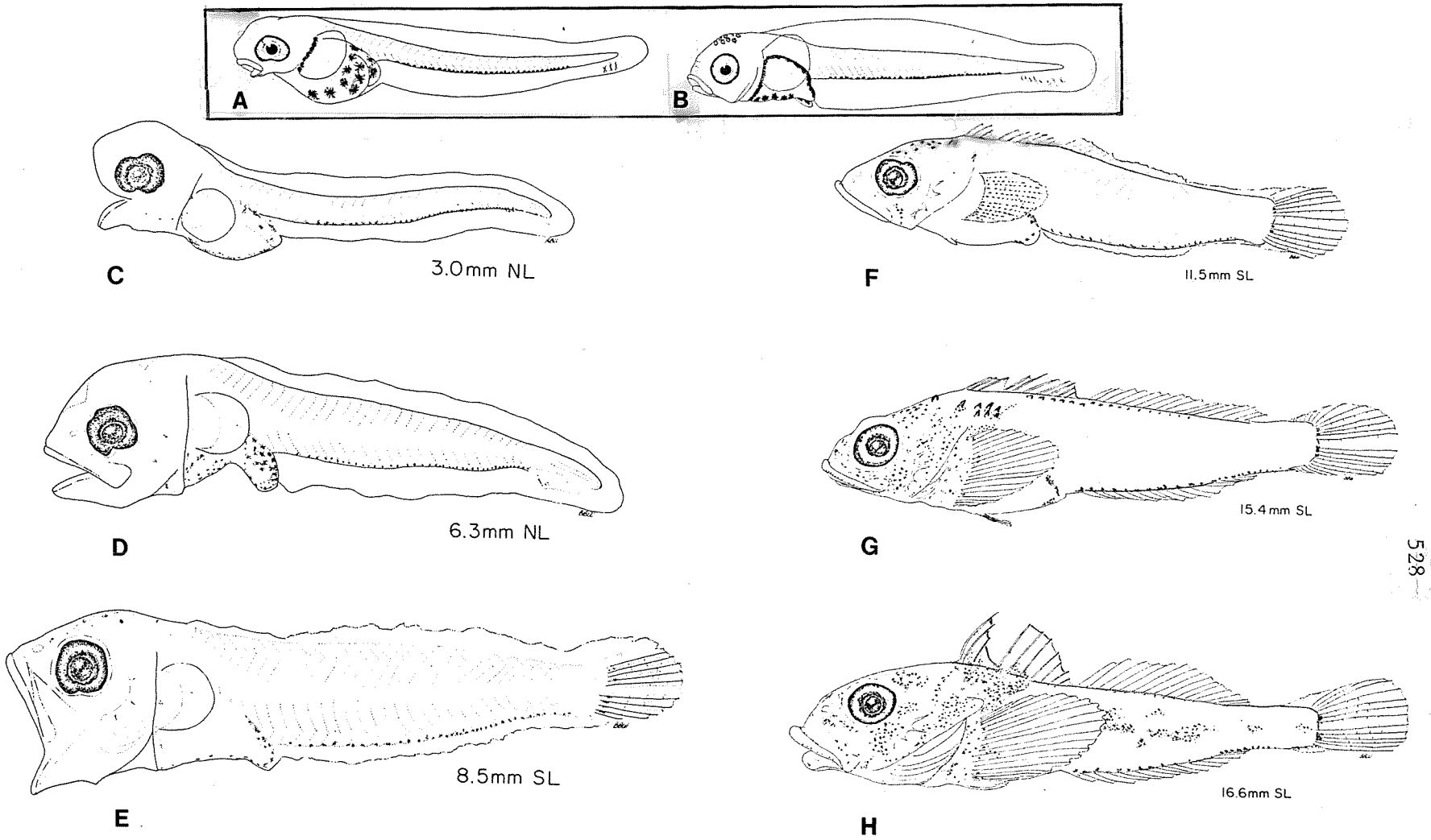

Fig. 45.7. Larval stages of roughback sculpin, Chitonotus pugetensis: A) Newly hatched larva, 3.0 mm; B) six-day-old larva, 4.8 mm; C-H) larva collected from the plankton off Oregon. (Sources: A-B, Misitano 1980; C-H, Richardson and Washington 1980).

Clinocottus acuticeps - Sharpnose sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal, shallow water

Spawning habitat: unknown

Spawning season: unknown (possibly spring-summer)

Mode of reproduction: oviparous

Eggs: demersal, undescribed

Larvae: pelagic

This small (to 5.1 cm) cottid is found in shallow nearshore water and often occurs in tidepools (Green 1971c; Cross 1982). Hart (1973) reported that breeding was observed in July in the San Juan Islands and the eggs were about 1 mm in diameter and brown in color. A female from a different area had mature eggs during April.

Sharpnose sculpin larvae are easily identified by their unusually shaped gut. The posterior portion trails well below the body and near the anus, two diverticula or protrusion are evident through the larval period (Fig. 45.8B). Snout-to-anus distance is long, relative to other cottids and ranges from 62% to 71% SL during the larval stage. Larvae are rather "flabby" in appearance and sometimes appear to be encased in a bubble of loose outer skin, particularly around the head (Fig. 45.8).

Larvae are also characterized by a series of 10-15 small spines which begin to develop on the preopercle margin at about 6-7 mm. The upper spines become the most prominent, but all spines decrease in size during transformation until only one dorsal spine is visible in 19 mm juveniles. Other head spines are absent in larval stages (Richardson and Washington 1980).

Larval pigmentation consists of a moderate scattering of melanophores on the dorsolateral surface of the gut, nape pigment which is present in small larvae and becomes embedded with growth, and pigment on the head which is present in most sizes of larvae and increases with development. Less than 15 ventral postanal midline melanophores occur from a vertical through the anus and extend posteriorly. Posterior melanophores in this series may occur on the anal finfold. A single pigment spot persists near the notochord tip, and eventually appears at the middle of the caudal fin base (Richardson and Washington 1980).

Larval sharpnose sculpin hatch at about 3-4 mm and by 7-8 mm the adult complements of fin rays (or elements) can be counted and larvae

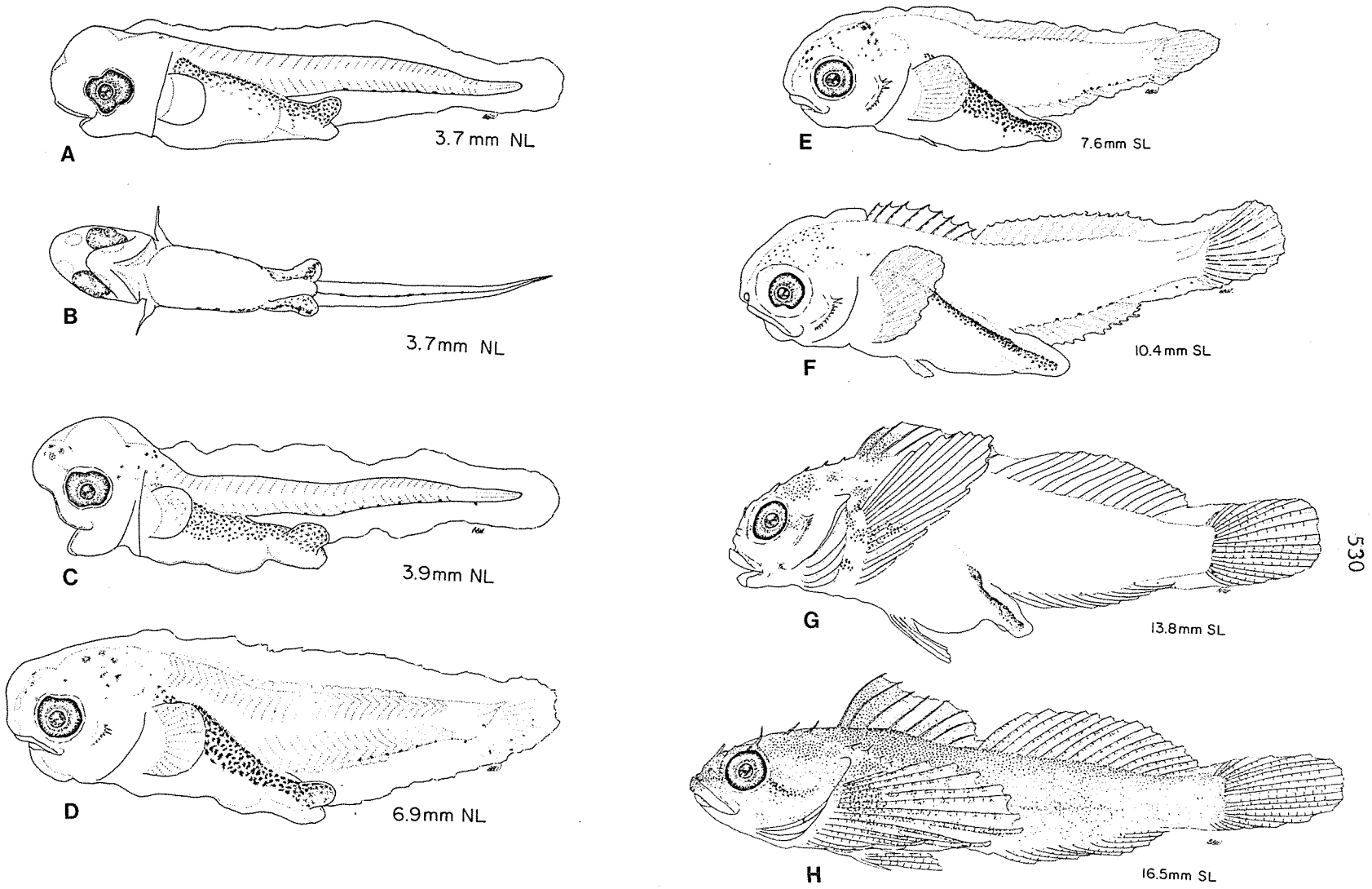

Fig. 45.8. Larvae and young of sharpnose sculpin, Clinocottus acuticeps, collected from the plankton A--G) and from tidepools (H) off Oregon. Specimen B is a ventral view showing the postero-ventral gut diverticula. (Source: Richardson and Washington 1980).

begin to transform to juveniles at 13-14 mm. During transformation, pigment is added to the head, pectoral fin base, and to the anterior end of the spinous dorsal fin. At 16.5 mm, a specimen is fully transformed and resides in tidepools (Richardson and Washington 1980).

Clinocottus embryum - Calico sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, intertidal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Calico sculpin is a small (up to 7 cm) nearshore demersal cottid species which ranges from Baja California to the Bering Sea (Hart 1973). It is found in tidepools in the mid to low intertidal zone in exposed and moderately exposed rocky areas (Cross 1982), but not in protected areas (Green 1971c). Features of the early life history of calico sculpin are unknown.

Clinocottus globiceps - Mosshead sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, intertidal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Mosshead sculpin adults are principally found in tidepools throughout the entire intertidal zone in exposed areas, but are restricted to the high intertidal zone in very sheltered areas (Green 1971c). Observations on 86 tagged specimens demonstrated that displaced fish returned to the tidepool where they were tagged (Green 1973).

No information is currently available on their early life history or reproductive biology.

Dasycottus setiger - Spinyhead sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Spinyhead sculpin are not uncommon in Puget Sound which is the southern limit of its range. In British Columbia it is common at moderate depths (18-110 m) and is often taken in shrimp trawls in the Strait of Georgia (Hart 1973).

Spinyhead larvae from Skagit Bay, Washington, were described by Blackburn (1973). At 7.4 mm, the larvae appear to be recently hatched. The head and gut are large, about 2-1/2 times as deep as the body immediately behind the anus. The lower jaw of the subterminal mouth reaches to the margin of the eye. Large distinct, stellate melanophores cover most of the gut, including the anterior surface except for a small, unpigmented area which remains on the ventral surface of the gut and is delineated by two rows of parallel melanophores. The dorsal surface of the brain is also covered with large stellate melanophores from the olfactory lobes on the snout to the nape, directly above the pectoral fins. Other head melanophores occur on the posterior floor of the otic capsule, on the upper jaw, behind the eye, and on the anteroventral half of the lower jaw. No pigmentation is present on any of the body myomeres which total 34 (8 preanal + 26 postanal). At 10.3 mm, the pigment is more intense, but relatively similar, and fin rays are forming. Melanophores appear on the pectoral fin rays and there is an indistinct pair of rows of ventral midline melanophores from the lower jaw to the anus. By 12 mm, fine rays are completely formed and pigment remains unchanged up through 19 mm larvae when lateral line pores and head spines appear.

Additional information on the spawning ecology of spinyhead sculpin is lacking.

Enophrys bison - Buffalo sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal to subtidal depths

Spawning habitat: demersal, on rocks or pilings

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached, guarded

Larvae: pelagic

Buffalo sculpin is primarily a shallow water species, occurring in tidepools or subtidally (Green 1971c). Spawning takes places primarily from February to April or May in Puget Sound and eggs are laid in multi-layered egg masses at the entrance to crevices, among encrusting invertebrates (such as barnacles and mussels), or on exposed rocks or wooden pilings. Spawning occurs within a relatively narrow depth range between -15 m and +1.6 m with the majority of egg masses within $\pm$ 1 m of mean low water. Individual egg masses are separated from their neighbors by 1.25-5.5 m, and are aggregated within a relatively small subarea within a larger area of suitable substrate and depth. Spawning aggregations are typically located near points, on reef crests, at channel entrances, on ferry landing pilings, and other areas of maximum current speeds (DeMartini 1978).

The egg masses are circular, about 7-14 cm in diameter and 1-4 cm thick, and exhibit a wide range of colors from purple, pink or red, to orange, yellow or tan; however, each female contains ova of a single color. Females appear to spawn two batches of eggs during the 1-2 month breeding season and may produce 18,800-31,900 eggs per spawning per female (DeMartini 1978).

After spawning, the fertilized eggs range from 1.7 to 2.0 mm (Misitano 1978; DeMartini 1978) with a mean perivitelline space of .09 mm, and a mean oil globule diameter of .36 mm (Misitano 1978). The male tends the egg mass which may be comprised of several different colored clusters of eggs which may be at various stages of development. It is likely that several females contribute to the nest (Misitano 1978; DeMartini 1978).

At each submerged spawning site a single male lies motionless on top of the developing eggs or very close to the mass for up to 39 days or more, the time it takes for eggs to hatch. Attending males have been observed to rise off the eggs and vigorously fan them with their pec-

toral fins and have also been observed to protect the eggs from predators such as Embiotoca lateralis. During low tide, eggs laid in the intertidal zone are unattended but little predation of the embryos by terrestrial predators occurs (DeMartini 1978).

Eggs in late blastodermal cap stage have been artificially reared at 11-13.5°C. Hatching occurred in about 22-24 days and produced larvae of about 5.0 (4.9-5.2) mm in length. In the aquarium, larvae emerged head first from the eggs and settled to the bottom, but became pelagic within three days (Misitano 1978).

At hatching, the head is round and the mouth is subterminal, but becomes terminal after 8 days. Recently hatched larvae also possess a single oil drop (.27 mm) located near the anterior margin of the bulbous yolk sac (Fig. 45.9A). Larvae are characterized by pigment in four areas, ventral midline, nape, dorsal surface of the gut, and ventrolateral surface of the gut, which becomes more intense as the larvae grow. The ventral midline pigment ranges from 4 to 16 (mostly 9-14) melanophores on larvae > 5.5 mm. These melanophores begin on the 9th or 10th postanal myomere and continue posteriorly, one per myomere. One to three dendritic melanophores appear on the caudal finfold below the developing hypural plate when larvae are ~ 5.4 mm and remain throughout the larval period (Fig. 45.9B).

Nape pigment is present at hatching and consists of a row of 3 to 6 distinct melanophores on each side of the dorsal finfold insertion. This pigment is present during the larval period, but becomes embedded and obscured during transformation. Buffalo sculpin are also characterized by intense dorsal gut pigmentation and 10-12 stellate melanophores which occur on the ventrolateral surface of the gut. A ring of about 7 melanophores surrounds the anus and remains visible from hatching to metamorphosis. Pigment is also present at the base of the pectoral fins and head pigment appears internally at the base of the optic capsule. By 5.8 mm, melanophores appear externally on the preopercule, on the lobes of the midbrain and hindbrain, and on the lower jaw. Cephalic pigment continues to increase through the late larval period and completely covers the head region by 7.6 mm. Prior to transformation, pigment appears on the body sides and is present in two bands in newly transformed juveniles (Figs. 45.9, 45.10).

Larval buffalo sculpin develop very prominent head spines. Four preopercular spines are present by 5.7 mm and by 6 mm a rather large parietal spine is formed. With development, a nuchal spine forms behind the parietal and fuses with it. Another spine develops on the parietal ridge anterior to the parietal spine. At 6.7 mm, a supraocular spine appears above each eye and at 7.1 mm a small supracleithral spine appears, followed by the appearance of a small nasal spine in 7.6 mm larvae. Two spiny tips (midopercular and interopercular-subopercular) appear on the margin of the operculum (Richardson and Washington 1980; Misitano 1978). At 7.4 mm, two rows of modified scales resembling small spinules appear on each side of the body, one row below the dorsum and the second row above the anal fin (Fig. 45.9 F).

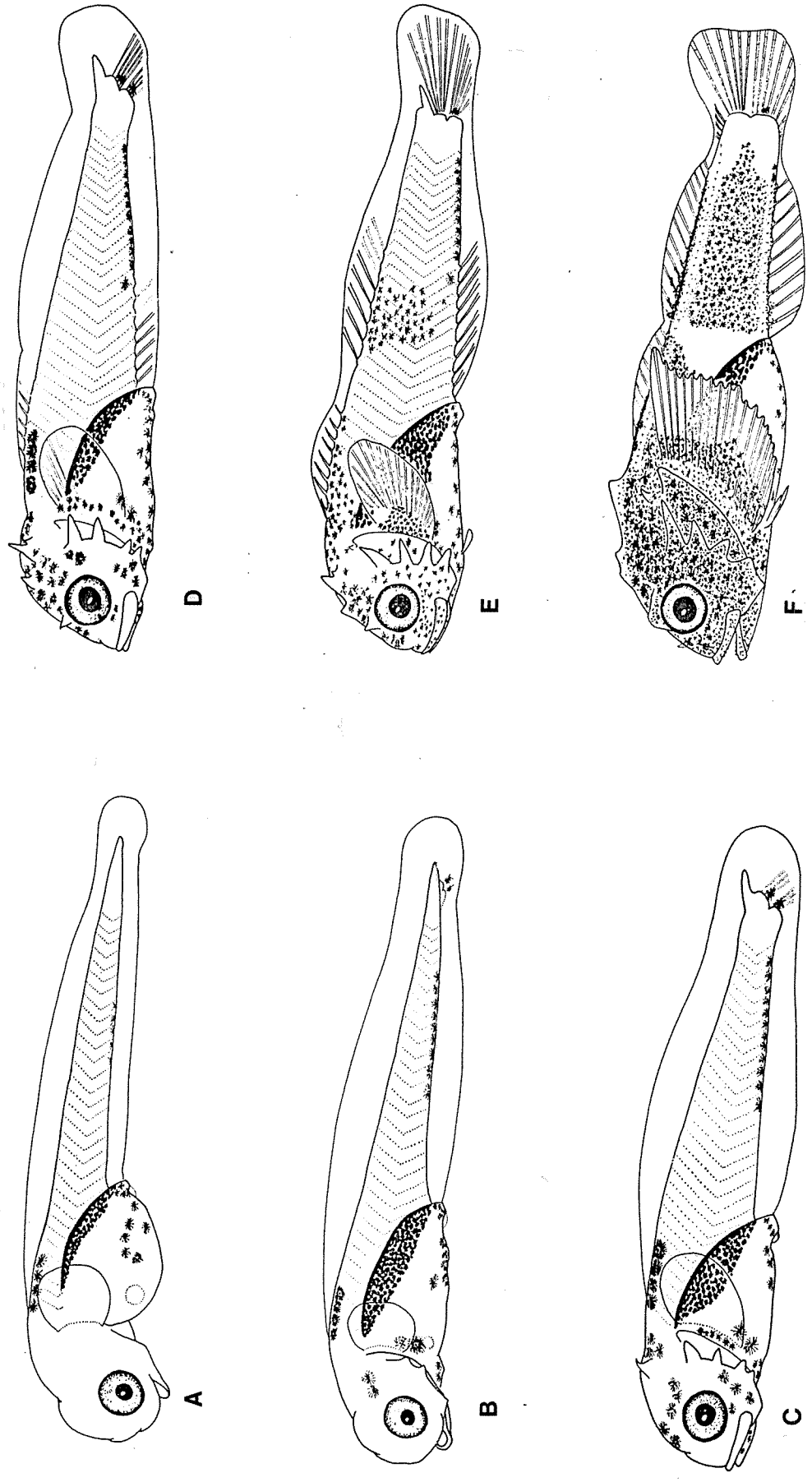

Fig. 45.9. Laboratory reared larvae of buffalo sculpin, Enophrys bison: A) newly hatched 5.0 mm; B) 5.4 mm; C) 5.8 mm; D) 6.7 mm; E) 7.1 mm; F) 7.6 mm. (Source: Misitano 1978).

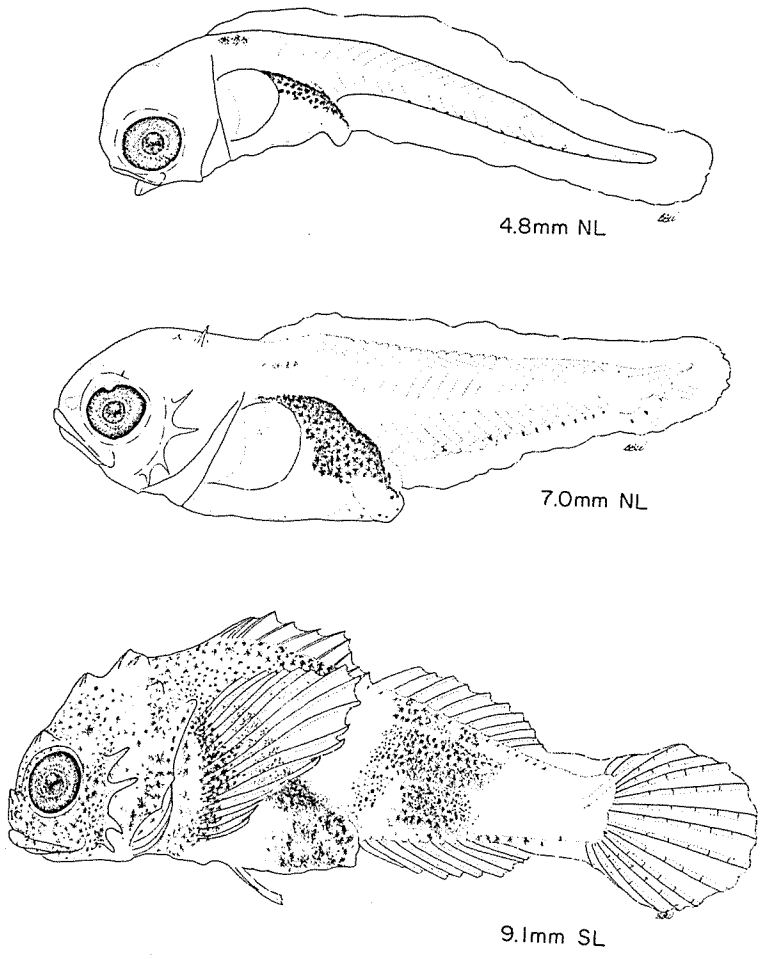

Fig. 45.10. Larval buffalo sculpin, Enophrys bison, collected from the plankton off Oregon. (Source: Richardson and Washington 1980).

Buffalo sculpin may be unique in that transformation from the larval to the juvenile stage occurs at a relatively small size. For larvae reared in the lab, transformation to juvenile coloration and habitat occurred at 7.6-7.8 mm (Misitano 1978) and Richardson and Washington (1980) and Marliave (1975) collected specimens from the plankton which were transforming at 9-10 mm lengths.

Gilbertidia sigalutes - Soft sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, subtidal

Spawning habitat: demersal, on solid substrates

Spawning season: late summer (Barkley Sound, B.C.)

Mode of reproduction: oviparous

Eggs: demersal, guarded

Larvae: pelagic

Soft sculpin are a small (to 8 cm) subtidal cottid species which lives in sheltered crevices along boulder slopes or rock cliffs (Marliave 1975) and in Puget Sound, they have been found in sponges (Hart 1973).

Spawning occurs during August in Barkley Sound. An individual male may court several females simultaneously within a small area, and the eggs are large (~ 2.3 mm in diameter), pink, and laid on a solid substrate in a monolayer. Only about 130 eggs per female are laid. The female parents tend their eggs until hatching in late October to early November and prevent fungal fouling by brushing their bodies over their eggs. They also fan the eggs during the last few weeks of development. The male remains in the vicinity of the females and their nests and prevents the approach of other soft sculpins (Marliave 1975).

At hatching, the females remove their larvae form the nest site and "spit" them toward the surface (Marliave 1975). Larval soft sculpin are easily recognized from other fish larvae by their rotund body shape, large head and gut resembling a tadpole, large pectoral fins, and coloration (Fig. 45.11). Planktonic stage larvae appear purple-black in color with bright orange pectoral fins (Marliave 1975). At 7.3 mm, preserved larvae have no pigment posterior to the anus, but have dense dark pigment over the peritoneum, pectoral fins, and brain region. All melanophores are dendritic and in the gut region are most dense on the sides of the gut. The ventral gut surface is unpigmented or lightly pigmented with melanophores primarily surrounding the anus. Head pigment is primarily internal and covers the dorsal surface of the brain and spinal cord from the snout to midway over the gut. The pectoral fins are completely covered with small melanophores. On the proximal half of the fin, melanophores are arranged in a series of lines suggesting fin rays, and the distal half is covered with random dendritic melanophores. At 9.5 mm, pigment remains similar, except melanophores in the gut region are no longer dendritic. Pectoral fin rays are formed, and dorsal and anal rays are partially formed (Blackburn 1973).

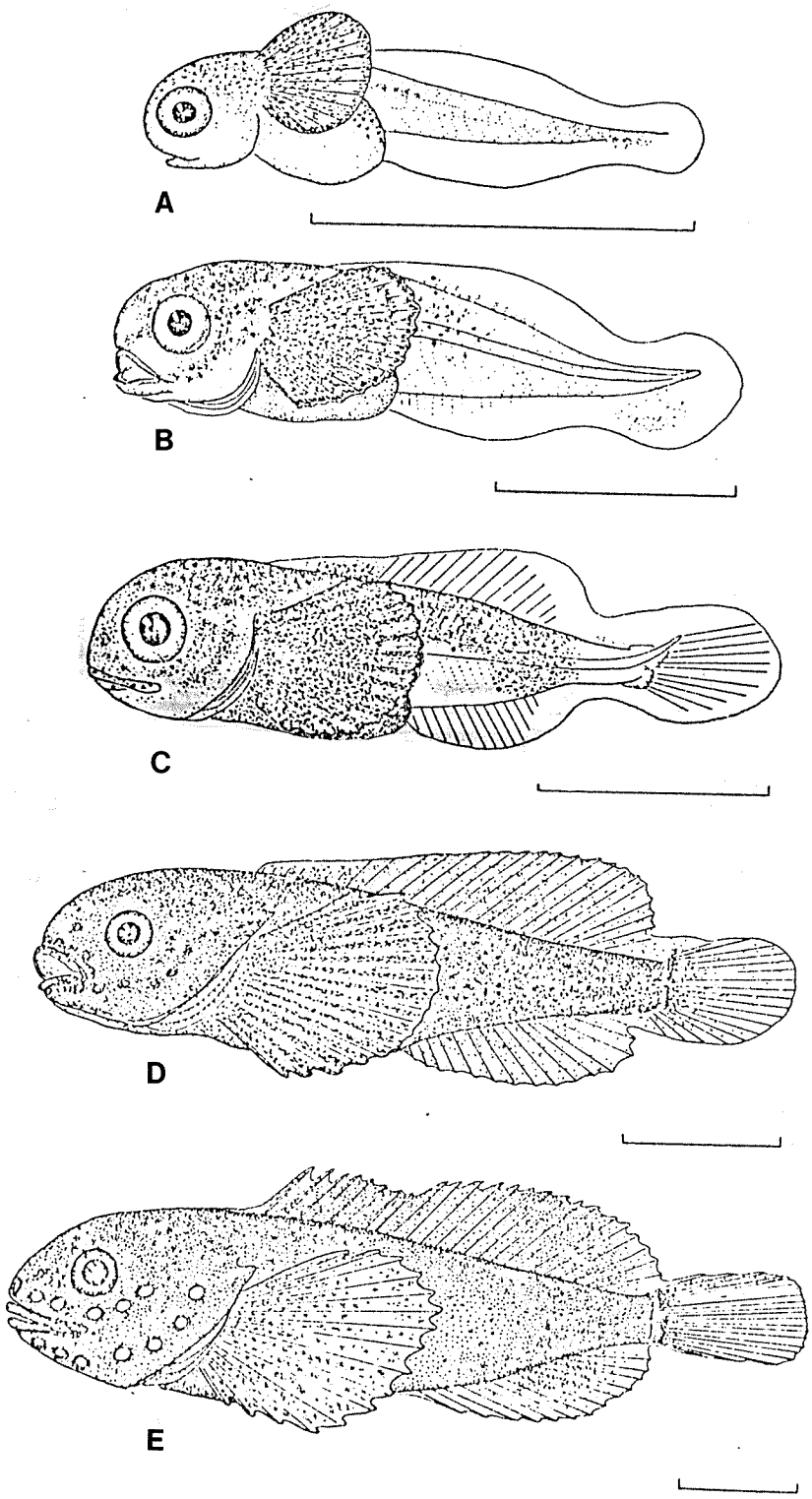

Fig. 45.11. Larvae of soft sculpin, Gilbertidia sigalutes, collected from the plankton, 5 mm scale: A) 7 mm TL, B) 13 mm TL, C) 15 mm TL, D) 25 mm TL, E) 34 mm TL. (Source: Marliave 1975).

During transformation to the demersal habitat, soft sculpin lose the orange color in the pectoral fins which recedes to the fin tips and is replaced by yellow. At this time, body color becomes mottled brown and black and head pores enlarge to a noticeable size (Fig. 45.11E).

Soft sculpin larvae are very similar in morphology and pigmentation to tadpole sculpin, Psychrolutes paradoxus, but can be separated based on size, melanophore type, and meristics (Table 45.5).

Newly hatched soft sculpin are pelagic and have a tendency to hover at the surface with their head up and in contact with the surface film. They spend about 40 days as strictly pelagic larvae, then begin alternating between the benthic adult and the pelagic larval behavior patterns for about 120 days. During this time, the larvae settles to the bottom for short periods before resuming swimming upward into the water column. This relatively long period of settlement and reentry into the plankton may be an adaptive strategy for locating a suitable adult habitat while allowing larvae to exploit the rich plankton food source (Marliave 1975).

Table 45.5. Characters used to distinguish between the larvae of soft sculpin and tadpole sculpin. (Source: Marliave 1975; Blackburn 1973).

Characters:	*Gilbertidia sigalutes* Soft sculpin	*Psychrolutes paradoxus* Tadpole sculpin
Size	Relatively larger	Relatively smaller
Pigmentation (unpreserved specimens)	Bright orange pigment on pectoral fins	Relatively more melanin which obscures orange color of pectoral fins
Melanophore type	dendritic-coalesced	discrete-separate
Pectoral fin rays	15-17	20-23
Dorsal notch in caudal finfold	Does not develop	Does develop

Hemilepidotus hemilipidotus - Red Irish lord

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal to subtidal depths

Spawning habitat: demersal, on rocks or pilings

Spawning season: fall

Mode of reproduction: oviparous

Eggs: demersal, adhesive, guarded

Larvae: pelagic

Red Irish lord live in relative shallow water and may be found in tidepools or subtidally (Green 1971c). Males may be recognized from females by their black and white pelvic fins.

In Puget Sound, spawning takes place during a 1-1/2 month period at any one location between the months of October and January. Common spawning areas are jetties, rock rip-rap, and dock pilings and most spawning occurs at midintertidal to shallow subtidal depths, usually within $\pm$ 1 m of mean low low water. The egg masses are approximately spherical and are 10-20 cm in diameter and 2-4 cm thick. The eggs may be tan, pale green, or less often pink, orange, or red in color and are adhesive to each other, but not to the substrate (DeMartini and Patten, unpubl. manusc.).

Several fish will spawn within a given spawning area and the egg masses are usually separated by several meters. The females deposit their eggs among sessile invertebrate growths such as barnacles or mussels, at the entrance to rock crevices, or in hollows or breaks in pilings. The habitats selected for spawning are also usually characterized by high currents. For example, most spawns on jetties are located on rocky points and channel entrances that receive maximum tidal flush. Also, a large number of spawn nests on pilings near ferry landings are oriented toward the propeller wash, rather than on the more protected side (DeMartini and Patten, unpubl. manusc.).

During the spawning season, males aggregate in the spawning area prior to the appearance of the females which seem to arrive (or become obvious to divers) only a few days before they spawn. Breeding females average 287-385 mm TL, and males are 220-313 mm TL and between 4 and 6 years of age. A ripe female may produce between 59,000 and 126,000 eggs (Fig. 45.12), and only one batch is produced per season (DeMartini and Patten, unpubl. manusc.).

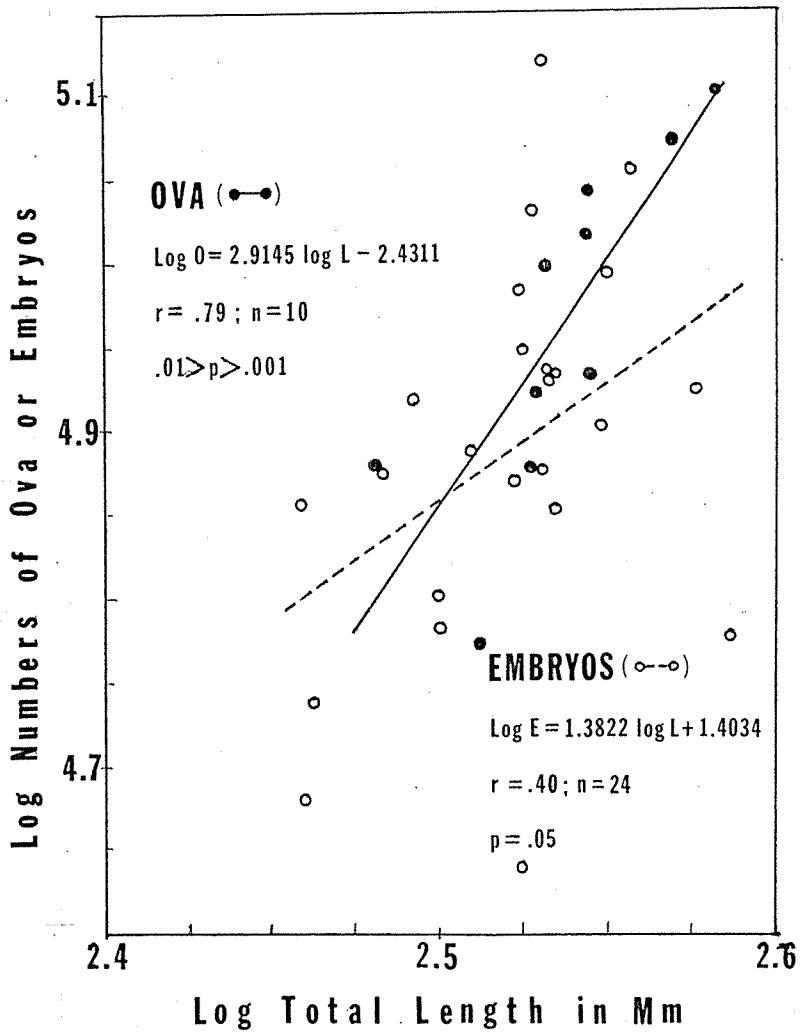

Fig. 45.12. Relationship between fish length and the number of ova in ripe fish and the number of embryos in a mass tended by spent females of different lengths for red Irish lord, Hemilepidotus hemilepidotus. (Source: DeMartini and Patten - unpubl. manuscr.).

Females are the most frequently seen parent guarding the developing eggs, but occasionally a cluster is guarded by a male or by a male and a female. If the female is removed from her eggs, a "secondary guardian," usually a male takes up the guarding position. Guarding fish are incapable of distinguishing their own egg mass, but rather exhibit a strong affinity for spawn on their nest site. Parental care is limited to guarding the eggs, adults have not been observed fanning or cleaning the eggs. The major predators of red Irish lord eggs are Embiotoca lateralis and Artedius spp. and if an egg mass is left unattended, these species move in immediately to devour the embryos. A guarding parent, however, will exhibit a threat response if approached by either of these predators. The guarding fish is usually on top of or very near the egg mass during the day and night, but do not attend intertidal spawns when the tide is out (DeMartini and Patten, unpubl. manus.).

The larvae hatch at about 5-6 mm (Richardson and Washington 1980) and take up a planktonic residence. Larvae have been illustrated and described by Gorbunova (1964, 7.25 mm, 10.5 mm) and by Richardson and Washington (1980)(Fig. 45.13). Small larvae (< 9 mm) are recognized by their large eye, relatively short snout-to-anus length, ~ 37 myomeres, and pigment along the dorsal body surface which extends from the head to the posterior-most 3rd or 4th myomere with an unpigmented area between the anterior 4th and 11th myomeres (Fig. 45.13A, B). Pigment also occurs on the dorsal gut surface and along the ventral midline at about the 9th or 10th postanal myomere to the last 3rd or 4th myomere. With development, pigment is added to the head, anterodorsal body surface and gut, and internal melanophores appear ventrolaterally between the notochord and the ventral midline and internally as a row above the notochord (Fig. 45.13C). External lateral melanophores are added when larvae are > 11 mm (Fig. 45.13 D, E). The internal lateral melanophores remain visible through the skin and help differentiate red Irish lord larvae from brown Irish lord larvae. By 19 mm, the larva resembles the juvenile form.

Red Irish lord larvae possess four prominent preopercular spines which may be visible at ~ 9 mm. A parietal and nuchal spine are also visible at this time, but fuse in later stages. Other spines are: postocular spines at sizes of 9-11 mm and three spines in the post-temporal-supracleithral region which reduce to bumps in larger specimens. At 19-20 mm, cleithral and nasal spines develop and three opercular spines are present (Fig. 45.13F). At ~ 14 mm, 4-5 dorsal scale rows can be counted in red Irish lord larvae, and is a useful character to separate them from brown Irish lord larvae which have 6-8 rows (Richardson and Washington 1980).

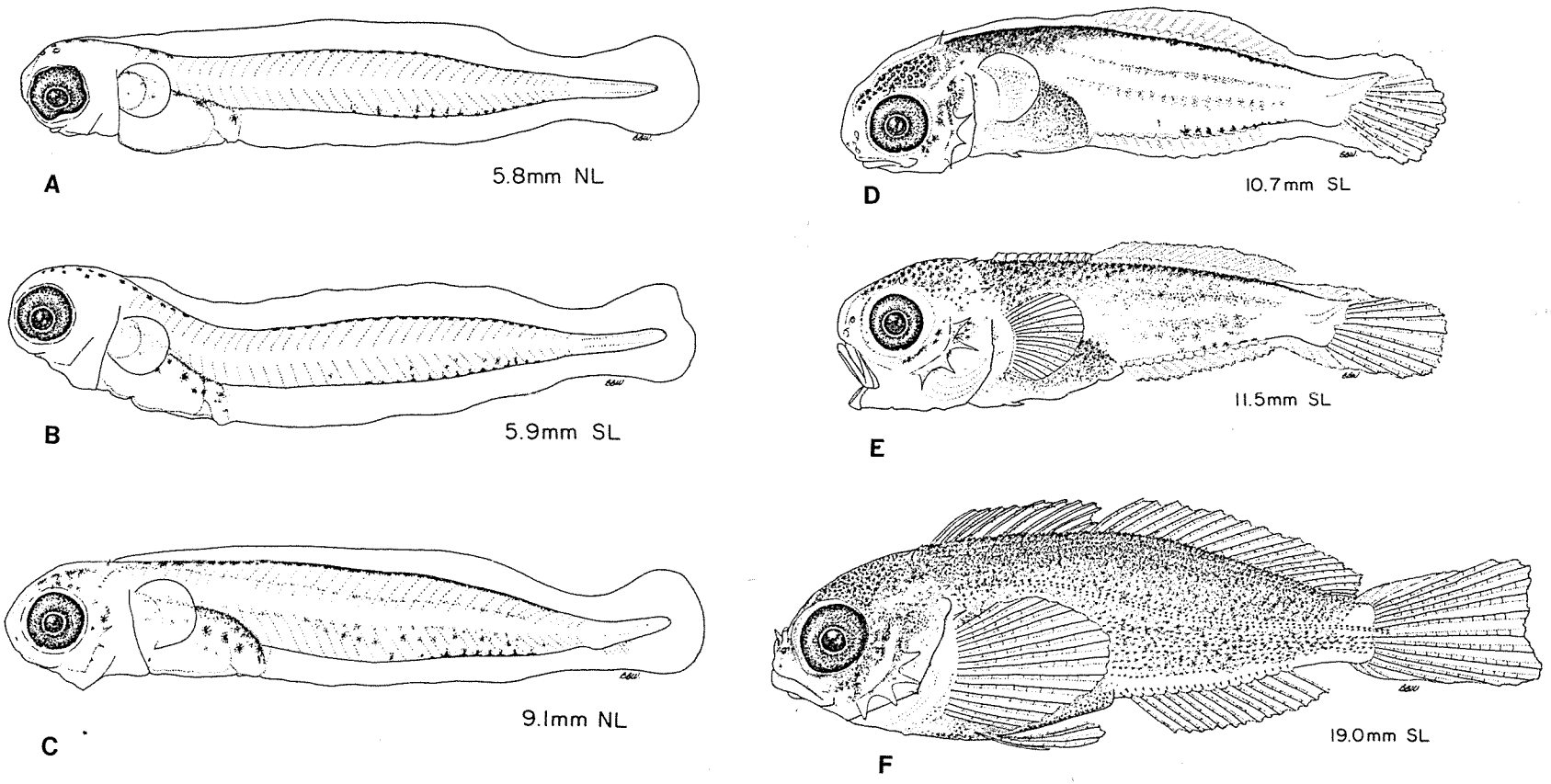

Fig. 45.13. Larvae of red Irish lord, Hemilepidotus hemilepidotus. (Source: Richardson and Washington 1980).

Hemilepidotus spinosus - Brown Irish lord

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: pelagic

Adult brown Irish lord have been collected from the Port Angeles Bay area in Puget Sound, but their occurrence is unreported in other areas of the Sound (Miller and Borton 1980). Larvae and juveniles have been described (Follett 1952; Peden 1964; Richardson and Washington 1980), but most aspects of their reproductive biology are unstudied.

Brown Irish lord larvae are similar in morphology to red Irish lord, possessing large eyes, a short preanal length, and pigment along the dorsal and ventral midlines, as well as on the head and gut. However, there are a few pigmentation differences between the two species which facilitates identification. Larvae of brown Irish lord have a continuous dorsal midline row of melanophores at small sizes as opposed to the dorsal gap in pigment in red Irish lord larvae of a similar size. Brown Irish lord also have a more or less continuous row of postanal midventral melanophores which extends from the anus to the posteriormost myomere (Fig. 45.13A vs. Fig. 45.14A). Another difference is the addition of external melanophores on the head, gut, and lateral surfaces in brown Irish lord larvae as small as 6 mm in contrast to red Irish lord (Fig. 45.13C vs. Fig. 45.14C), and brown Irish lord never develop internal pigment below the notochord as red Irish lord do. Development of head spination in brown Irish lord is similar to red Irish lord, except for the postocular spine which is minute in the former species and appears at 8-9.3 mm then disappears.

By 19 mm, full adult members of fin rays and dorsal scale rows are developed in brown Irish lord and the larvae are well pigmented, becoming juvenile in appearance (Richardson and Washington 1980).

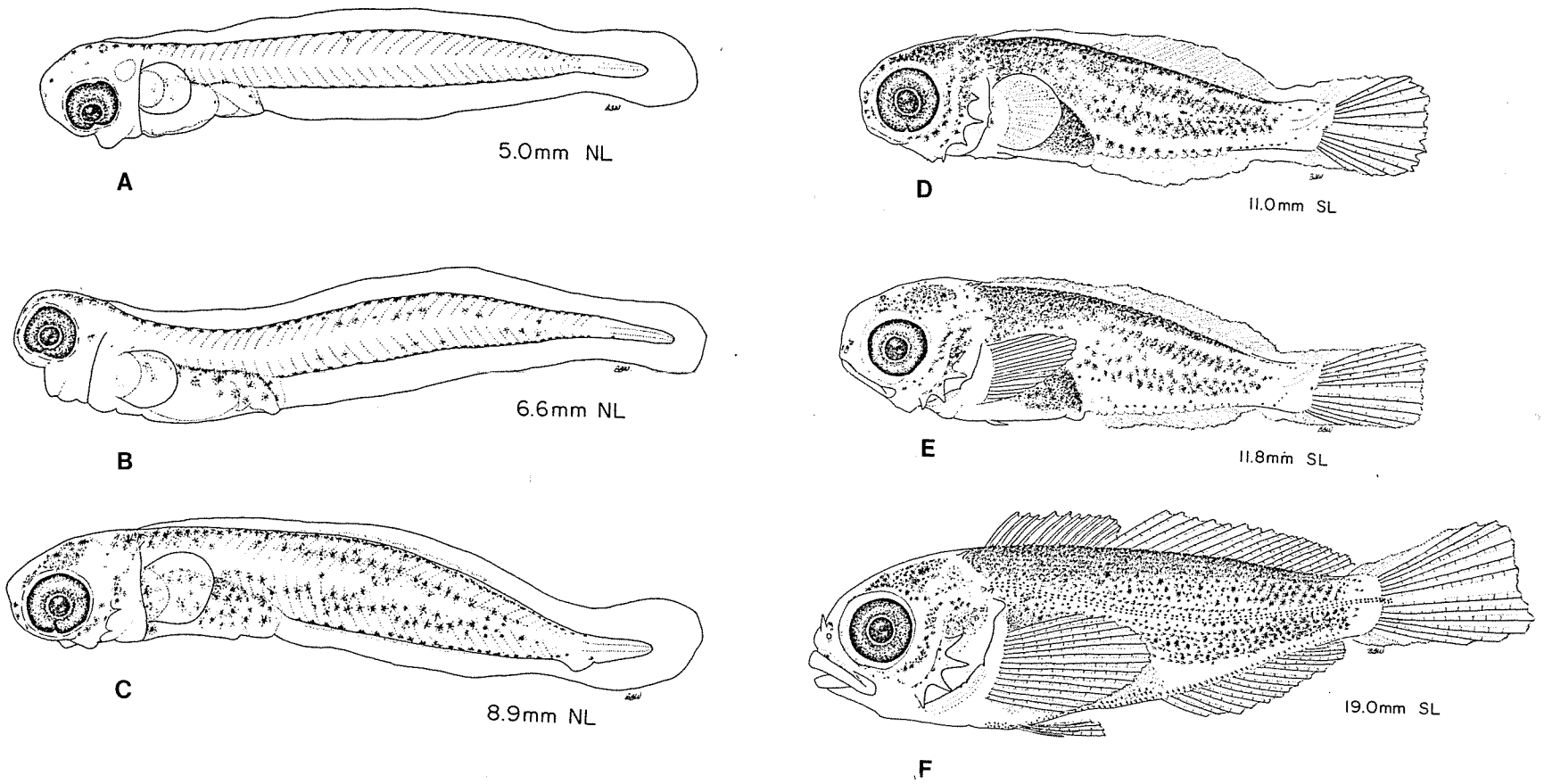

Fig. 45.14. Larvae of brown Irish lord, Hemilepidotus spinosus. (Source: Richardson and Washington 1980).

Icelinus borealis - Northern sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: unknown

Larvae: unknown

Northern sculpin occur from Puget Sound to Bering Sea at depths from 9-221 m (Hart 1973). No early life history information is available.

Icelinus burchami - Dusky sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon, reported in Hood Canal (Miller and Borton 1980)

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

No early life history information exists for this uncommon species in Puget Sound.

Icelinus filamentosus - Threadfin sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

The early life history of threadfin sculpin is unknown. Adults are not commonly reported in Puget Sound (Miller and Borton 1980) and are taken at depths up to 110 m in British Columbia (Hart 1973).

Icelinus tenuis - Spotfin sculpin

Range: Table 45.1

Occurrence in Puget Sound: common in some areas

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Frequently encountered off Alki and Meadow points in Puget Sound, but uncommon in other areas of the Sound (Miller and Borton 1980), spotfin sculpin are also taken at 37-128 m depths in British Columbia (Hart 1973).

Reproductive ecology of spotfin sculpin is unstudied.

Jordania zonope - Longfin sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, subtidal in rocky areas

Spawning habitat: unknown

Spawning season: fall

Mode of reproduction: oviparous

Eggs: demersal, guarded, undescribed

Larvae: undescribed

In Puget Sound, adult longfin sculpin have been most commonly found in the San Juan Islands area (Miller and Borton 1980). Their relative infrequency is probably due to their habitat preference. They appear locally abundant (based on SCUBA observations) in the Strait of Juan de Fuca and Strait of Georgia where they inhabit rocky areas between 1.5 and 18 m in depth. Their red-banded color pattern blends well with crustose and thallose red algae, making them hard to see (Wilkie 1963).

Breeding has been observed in October when several clusters of 20 to 30 eggs were released (Hart 1973) and females have been observed guarding the eggs (DeMartini and Patten, unpubl. manusc.). Females and especially males, darken in color during the breeding season and are active and highly territorial (Hart 1973).

Leptocottus armatus - Pacific staghorn sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal to subtidal depths

Spawning habitat: unknown

Spawning season: mid-fall to early spring (California)

Mode of reproduction: oviparous

Eggs: demersal

Larvae: pelagic

Pacific staghorn sculpin are abundant in protected bays and estuaries where they can tolerate relatively low salinities (Jones 1962), and are frequently found on mudflats from high intertidal and subtidal depths (Morris 1961). When disturbed, it will rush to a new spot and bury itself in the sand, leaving only its eyes exposed (MacGinitie 1935). If further threatened, it will flatten its head and expand the operculum, extending the opercular spines laterally and the sharp recurved hooks upward (Tasto 1975).

In California, spawning occurs from October to March and peaks in January-February (Jones 1962), and in British Columbia, planktonic larvae are taken during this same time period (Marliave 1975). Sexual dimorphism is not evident in Pacific staghorn sculpin, although some ripening females may develop a red tinge to their caudal fins and a light red on the tips of the outer margin of the anal fin (Tasto 1975).

The adults, which appear to be less tolerant to lower salinity than younger stages, are limited to marine waters during the breeding season for successful reproduction (i.e., for egg survival). Larvae and juveniles, however, are more tolerant to reduced salinities and may use estuarine habitats as nurseries, although it is not essential as some probably spend their complete life cycle in marine bays or in the ocean (Jones 1962).

Males and females reach sexual maturity at the end of their first year (Jones 1962; Tasto 1975). Gonads first become apparent when the fish is ~ 50 mm and sexes can be identified at ~ 70 mm (Tasto 1975). The ovaries are short, cone-shaped structures which join broadly at the anterior end (Tasto 1975):

> "During the maturing phase, individual eggs are visible only microscopically and are homogeneously interspersed with the connective tissue. In the ripening phase, the egs are arranged in

leaves of nonuniform thickness. There are from 20 to 25 of these leaves per ovary. Two distinct sizes of eggs are evident in this stage. Large, maturing eggs, uniform in size and shape are encompassed by many smaller, immature eggs of varying sizes. In the third and final stage of development the eggs are ready for release. The mature eggs, all of uniform size occupy the ventral portion of the ovary, while the nonmaturing eggs comprise 28.2% of the weight of the entire ovary of 11 ripe fish measured. An average of 3,200 mature eggs was found in these 11 ripe females."

The relationship of length to fecundity is shown in Fig. 45.15 (Jones 1962). Individuals probably only spawn once per year.

The egg masses have not been observed in nature, but laboratory spawned eggs and egg development have been described. Pacific staghorn sculpin eggs are demersal, adhesive, and vary in color from creamy white to pale yellow-orange to deep orange, but the eggs in a single mass are all the same color. Egg diameters range from 1.36-1.50 mm and average 1.43 mm. The outer membrane of each egg has a "pebbly" appearance caused by the arrangement of fine radial canals (similar to eggs of A. lateralis)(Fig. 45.16A)(Jones 1962).

As the ripe eggs contact the water, they adhere to each other and anything else they contact. After 1 hour, the membrane is no longer sticky, but the eggs remain firmly attached together. The eggs are spherical but slightly flattened at their points of contact with each other. About 1 minute after the eggs come in contact with the water, the outer membrane splits from the vitelline membrane leaving a prominent perivitelline space. About 1 to 7 oil globules and a mass of brown flocculent material is contained within each egg (Jones 1962).

The eggs at the edges of the egg mass develop more rapidly than those at the center, probably due to better oxygen conditions. Egg development requires 9-14 days at 15 $\pm$ .5°C (Fig. 45.16, Table 45.6). When hatching, the embryo moves vigorously rupturing the shell coat, and emerges head first. The larvae swim actively toward the surface and are positively phototrophic. The newly hatched larvae are 3.9-4.8 mm TL with a large globular yolk sac containing oil globules. Pectoral fins are lobe-shaped, somites are well-devloped, and the body is surrounded by a continuous finfold (Fig. 45.16P). Larvae have a distinctive pigment pattern which includes 6-8 bars of pigment over the dorsolateral surface of the gut. No other known cottid larvae has this distinct configuration (Fig. 45.17A). Larvae also have characteristic internal pigment on the snout and from the eye to the pectoral fin, which becomes obscured with tissue growth. The ventral surface of the gut contains several melanophores, and a row of prominent postanal midventral melanophores (usually < 15) begins on the fifth postanal myomere. During larval development, melanophores appear on the head and at the base of the caudal fin. Four prominent preopercular spines, appearing at ~ 7 mm, are the only head spines formed (Richardson and Washington 1980).

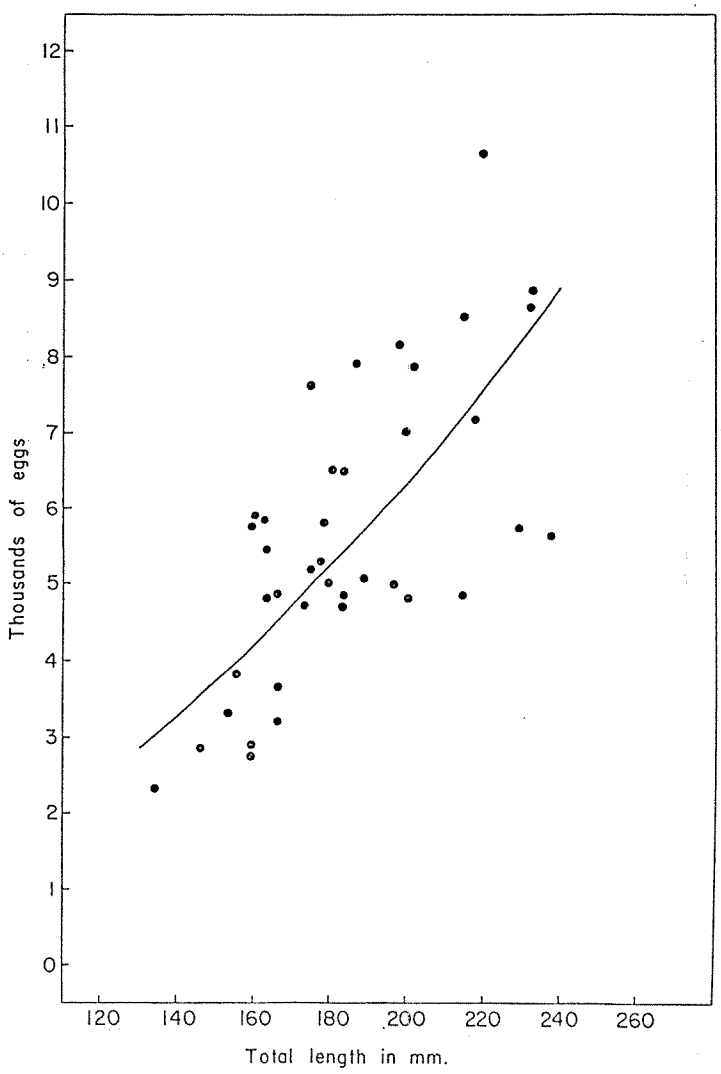

Fig. 45.15. Fecundity-length relationship of Pacific staghorn sculpin, Leptocottus armatus. The relationship was determined by fitting a linear regression line to the logarithms of the egg count and length data. The values obtained were $N = 0.355\ L^{1.840}$, where N equals the number of maturing eggs, and L equals the total length of the fish in mm. (Source: Jones 1962).

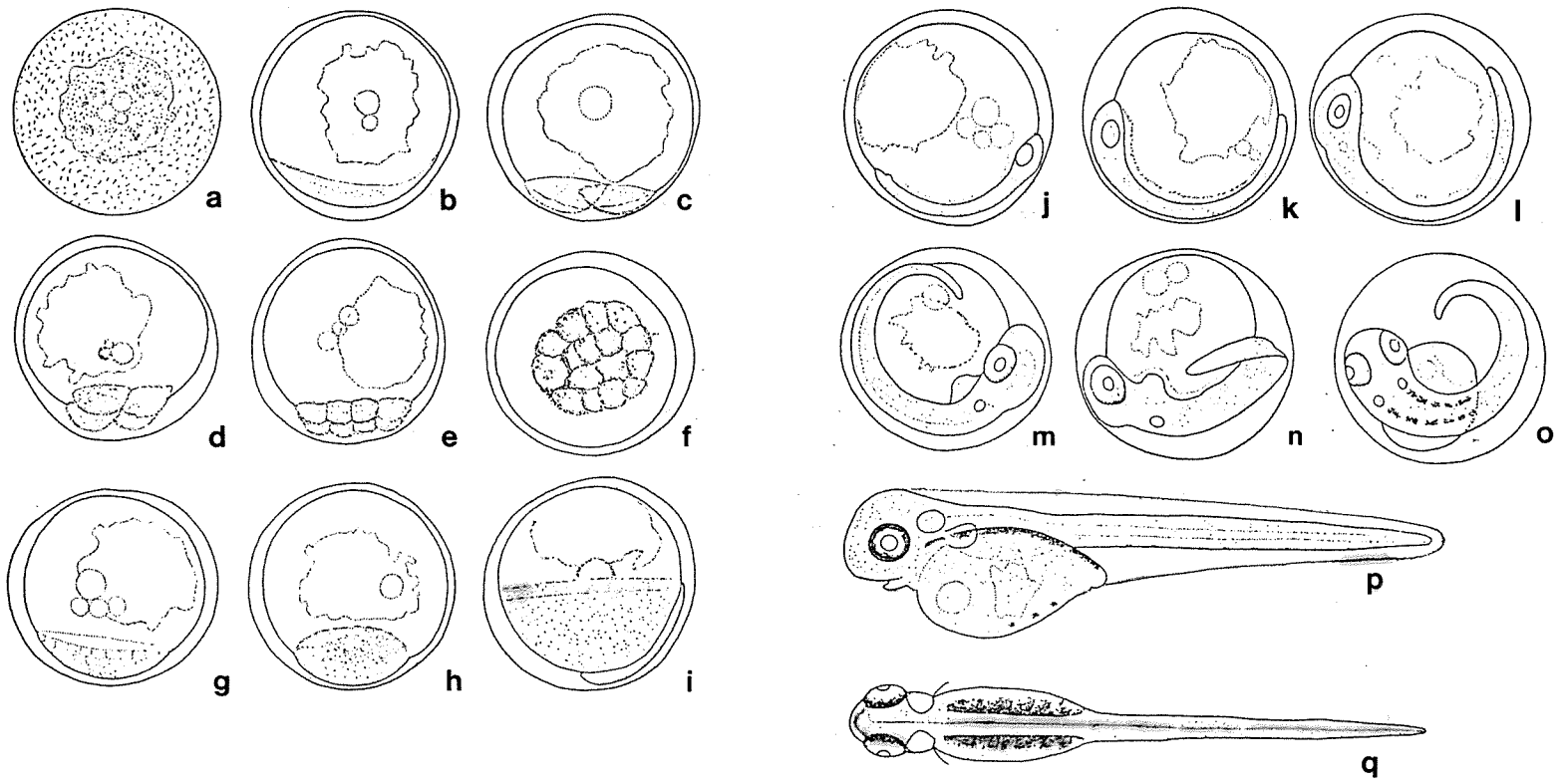

Fig. 45.16. Development of eggs of Pacific staghorn sculpin, Leptocottus armatus, at 15 ± .5°C: a) unfertilized egg, b) blastodisc, c) 2-cell stage, d) 4-cell stage, e) 8-cell stage, f) 16-cell stage, g) early blastodermal cap, h) late blastodermal cap, i) germ ring, j) 65-hr embryo, k) 75-hr embryo, l) 4-day embryo, m) 5-day embryo, n) 6-day embryo, o) 8-day embryo, p) newly hatched larva, q) newly hatched larva, dorsal view. (Source: Jones 1962).

Table 45.6. Development of eggs of Pacific staghorn sculpin, Leptocottus armatus, reared at 15 ± .5°C. (Source: Jones 1962).

Incubation time (time since fertilization)	Developmental event
2 hr	Blastodisc formation.
3 hr	Cleavage begins; subsequent cleavages occur at 2 1/2 hr intervals.
25 hr	Late blastodermal cap.
41-43 hr	Germ ring is in equatorial position.
50 hr	Blastopore closure.
65 hr	Embryo with four somites; Kupffer's vesicle, and outline of eyes, are visible.
71 hr	Embryo with 10 somites.
75 hr	Embryo with 15 somites; lens can be distinguished.
92 hr	Eyes and lens increase in size, yolk noticably reduced, constriction in neck marking posterior limit of the brain.
4 days	Auditory capsule visible, embryo twitches within shell, 27 somites, pectoral fin buds present.
5 days	Heart beat, eyes pigmented, yolk decreased.
6 days	Blood circulation, end of tail free from yolk.
8 days	Pigment on trunk region, paired melanophores on dorsal gut cavity.
9-14 days	Hatching.

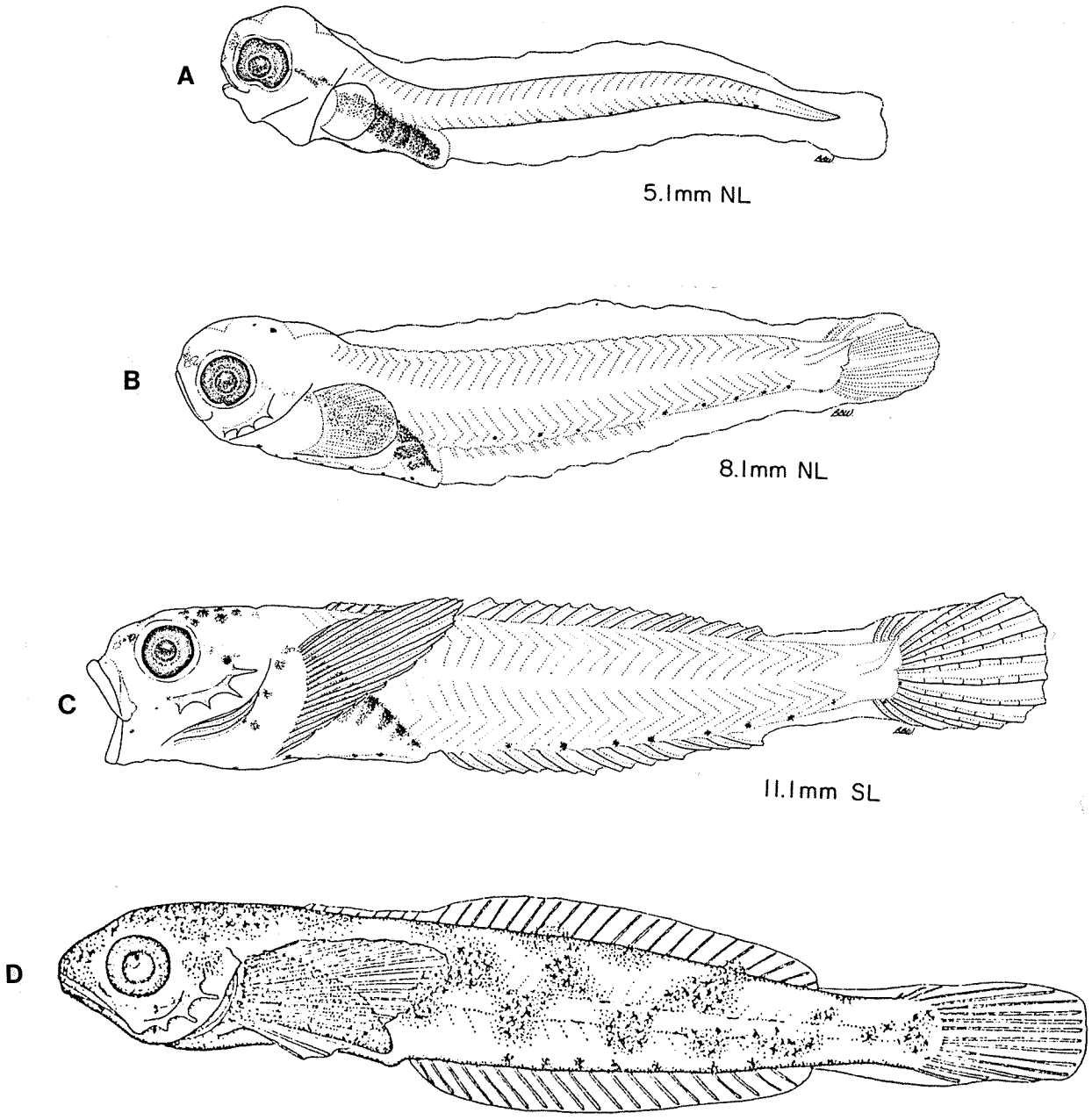

Fig. 45.17. Larvae of Pacific staghorn sculpin, Leptocottus armatus: A-C) larvae collected from the plankton off Oregon (Richardson and Washington 1980), D) 13 mm TL settled juvenile (Marliave 1975).

Marliave (1975) reported that Pacific staghorn sculpin larvae transform at about 13 mm to become benthic juveniles. In larval substrate preference experiments, most larvae settled on sand instead of pebbles and showed a "marginally significant" preference for white or mixed black and white sand over black sand (Marliave 1977).

Malacocottus kincaidi - Blackfin sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Life history and spawning characteristics of blackfin sculpin are unknown. In the Strait of Georgia adults are reported from depths of 27 to 120 m (Hart 1973) and have been reported in Hood Canal, Carr Inlet, Saratoga Passage, Admiralty Inlet, and the San Juan Islands in Puget Sound (Miller and Borton 1980).

Eggs and larvae of M. kincaidi are undescribed. Richardson and Bond (1978) described and illustrated a series of larvae they call Malacocottus zonurus - Type 1 (Fig. 45.18); however, identification is not positive and similarities to Malacocottus kincaidi larvae are unknown at this time.

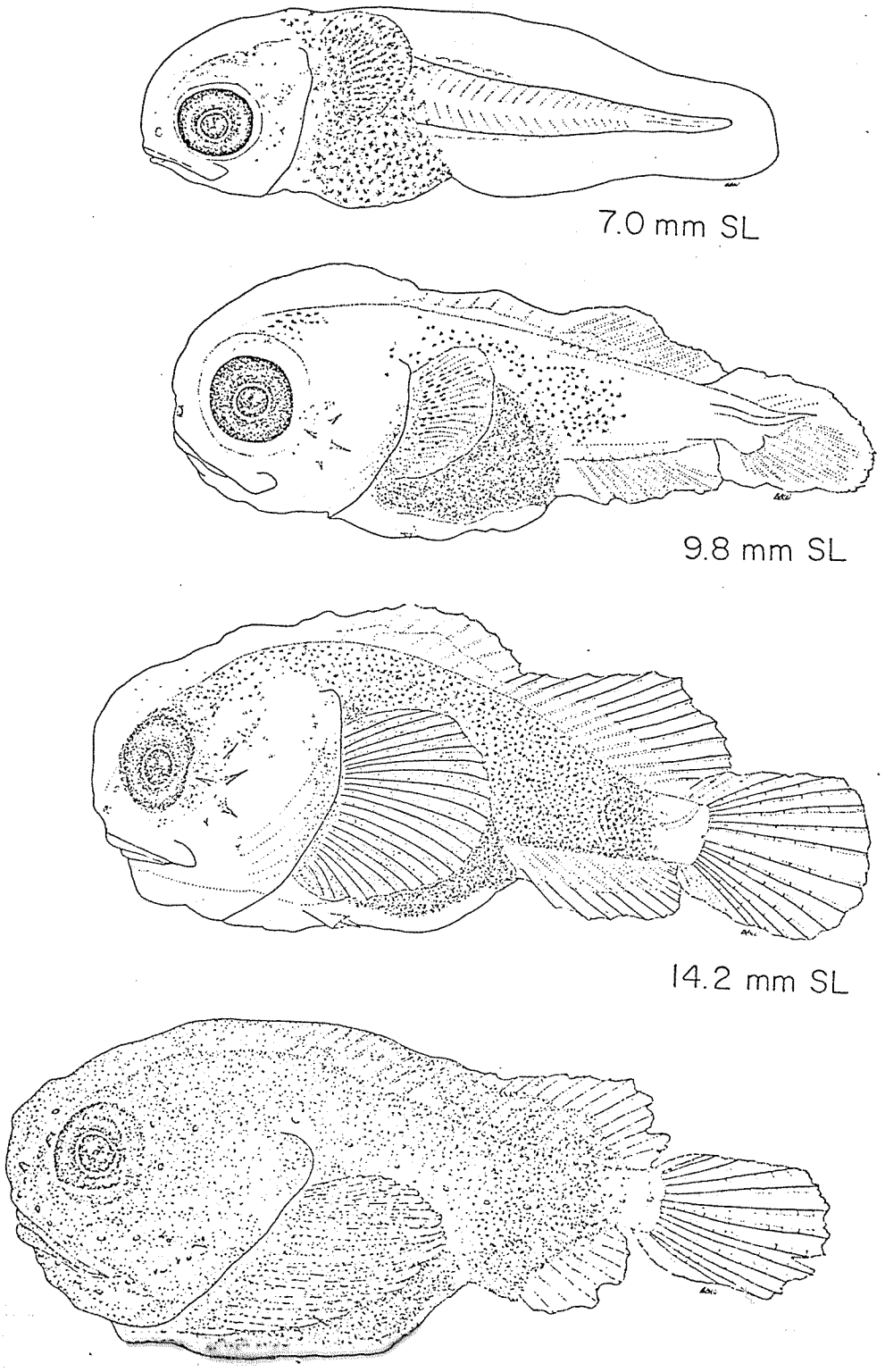

Fig. 45.18. Larval series identified as Malacocottus zonurus - Type 1 by Richardson and Bond (1978). Bottom larva is 24.0 mm SL.

Myoxocephalus polyacanthocephalus - Great sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: late winter - early spring

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Most features of the early life history of great sculpin have not been studied. Larvae collected from the plankton during March in Skagit Bay, Washington have been briefly described (Blackburn 1973). At 7.4 mm, larvae contain an oil globule and are probably recently hatched. At 7.7 mm, larvae are characterized by numerous melanophores which cover the body of the larvae from the head to midway between the anus and the end of the notochord, and one spine projects dorsally from the top of the otic capsules. Pigmentation remains unchanged through 10.7 mm larvae, but fin rays have developed. In addition, two spines project from the region of each otic capsule and five preopercular spines, the lowest of which is on the ventral articulation of the lower jaw, have appeared.

Larvae resembling these were also collected near Kodiak Island during March-June implying a winter-spring spawning period along the northern coast as well (Rogers et al. 1979).

Nautichthys oculofasciatus - Sailfin sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal and deeper

Spawning habitat: demersal, on rocks

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached

Larvae: pelagic

Adult sailfin sculpin are commonly found in rocky tidepools and on rock and sand bottoms with laminarians (Marliave 1975). They are also taken in shrimp trawls down to 110 m (Hart 1973). Adults are nocturnal, only active after dark, and may be pressed tightly into crevasses during the day (Moulton 1977).

In California, ripe females 119, 138 and 142 mm SL were observed (Burge and Schultz 1973). In British Columbia, larvae of sailfin sculpin are taken from the plankton from January to early March, implying a winter-spring season of reproduction. The eggs are about 2 mm in diameter, red in color, and are laid on the underside of rocks in the intertidal zone (Marliave 1975).

Larvae have been described (Blackburn 1973; Marliave 1975; Richardson and Washington 1980) and hatch at a relatively large size, ~ 7 mm SL. Larvae are easily recognized by their long pectoral fins and orange-brown color, patches of which extend into the dorsal and anal finfolds (Fig. 45.19A-C). The pectoral fins are also tipped with this color. Along the body, melanophores cover the head and extend over the lateral surface with the exception of the caudal peduncle which remains unpigmented until after transformation.

The pectoral fin rays develop prior to hatching and the large fan-like pectoral fins are used to hover and maneuver. In the early stages, the pectorals represent 42-59% of SL. With growth, the relative length decreases and an elongated first dorsal fin develops (Fig. 45.19D-F). Pronounced sharp spines do not appear to develop on the head, but bumps (4) appear on the preopercle, in the parietal region, along the parietal ridge, in the postocular region, nasal region, and in the posttemporal-supracleithral region (Richardson and Washington 1980). After formation of dorsal and anal fin rays, lateral rows of body spines develop and are most prominent along the lateral line (Marliave 1975).

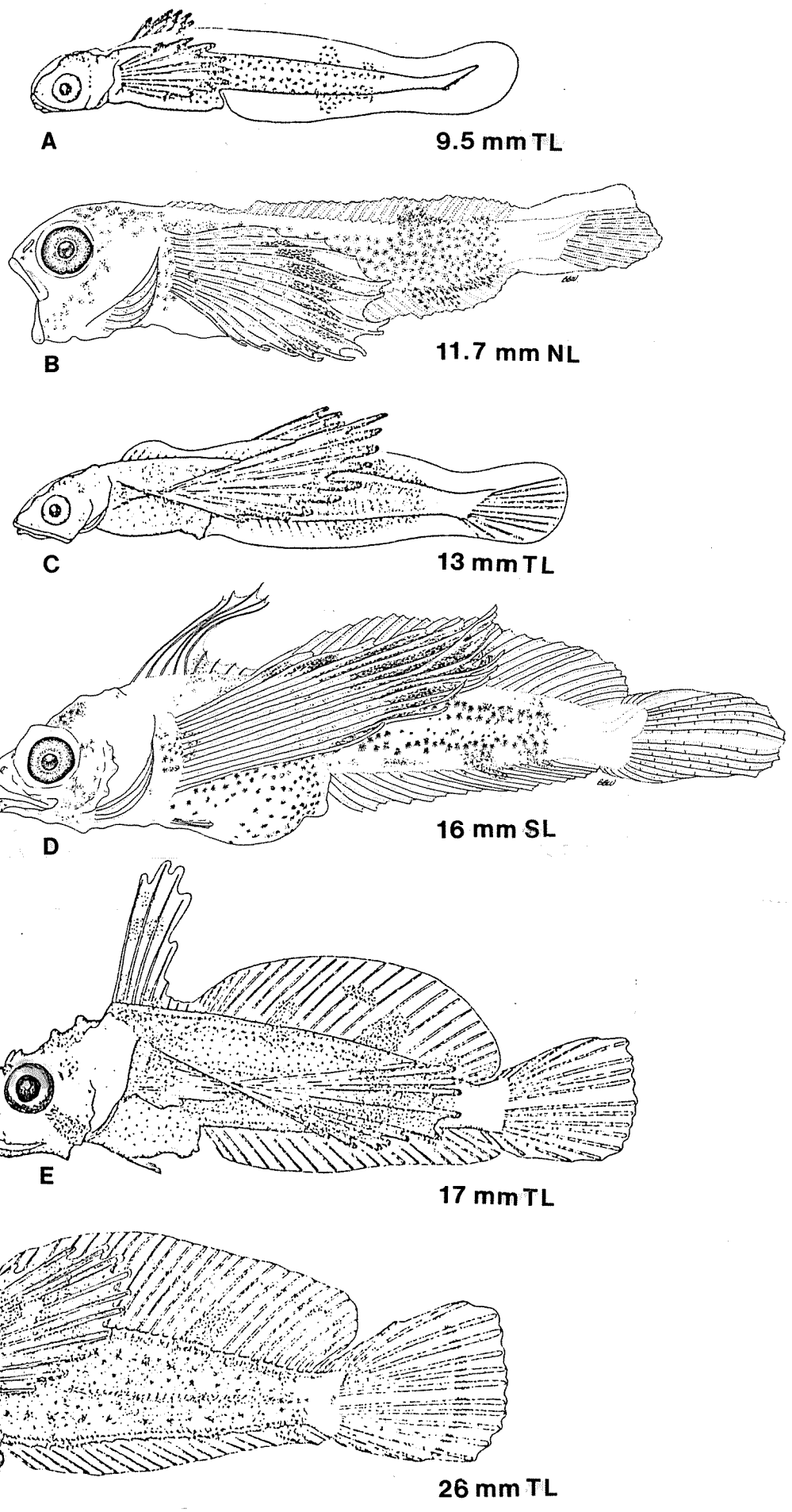

Fig. 45.19. Larvae and early juvenile (26 mm) of sailfin sculpin, Nautichthys oculofasciatus. (Sources: A, C, E, F — Marliave 1975; B, D — Richardson and Washington 1980).

Larvae begin metamorphosing at about 16 mm TL and are usually transformed to juveniles by 40 mm TL, requiring about one month (Fig. 45.19F)(Marliave 1975).

Oligocottus maculosus - Tidepool sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal depths

Spawning habitat: same

Spawning season: spring-summer

Mode of reproduction: oviparous, internal fertilization

Eggs: demersal, adhesive

Larvae: pelagic

Tidepool sculpin is a common nearshore cottid species which, as its name implies, occurs primarily in tidepools. It has a wide distribution in tidepools throughout the intertidal area due to its lack of preference for a particular substrate or a particular biota, and its physical tolerance to a wide range of temperatures and salinities (Nakamura 1976; Green 1971a, b, c; Cross 1981).

Tidepool sculpin show an affinity for a specific tidepool (Gersbacher and Denison 1930; Green 1971b) which can probably be expanded to cover a restricted "home range" of pools (Khoo 1971). Fish that are < 1 year old ($\sim$<55 m) are often found in pools as shallow as 10 cm or less and are not distributed as low in the intertidal zone as adults (Green 1971a). Tidepool sculpin as small as 15 mm may occur in depressions no more than several cm deep. The population in tidepools in British Columbia was found to decrease in winter and spring and increase over summer and fall primarily due to the recruitment of 0-1 year old fish as opposed to reinvasion by adults (Green 1971a).

Tidepool sculpin exhibit a remarkable ability to return to a "home pool" or "home range," after being displaced. Some individuals were able to return to their pool even after being blinded, rendered anosmic, being removed for distances up to 300 m, being held in aquarium for up to 6 months before being released or despite having their home pool burned of all life (Khoo 1971; Green 1971b).

Adult male tidepool sculpin can be distinguished from females by the enlarged first 2 or 3 anal fin rays which develop in males $\geq$ 30 mm. Males also have an elongated anal papilla.

In Puget Sound, spawning takes place from April through July and mature females are usually $\geq$ 1 year and between 24-45 mm (Atkinson 1939). Internal fertilization is reported (Stein 1973) and mating takes place with the male placing one pectoral fin in the notch between the two dorsal fins of the female (Atkinson 1939; Hart 1973).

The eggs are laid in multilayered clusters and in one case, a cluster was 20 mm long by 7-17 mm wide and contained 240-400 tightly adhesive eggs (Stein 1973). They may be deposited between rocks and are not particularly strongly attached to the substrate (Stein 1973; Atkinson 1939). Diameter of deposited eggs ranges from 1.4-1.55 mm with a perivitelline space of ~.05 mm (Stein 1973). The yolks may appear greenish (Stein 1973; Hart 1973) or deep red (Atkinson 1939) and contain 1-3 large oil globules plus several smaller ones which coalesce with development (Stein 1973; Atkinson 1939). At 11-12°C, egg development requires 24 days (Stein 1973). Three modes (based on ova diameter) of eggs from a mature female suggest multiple spawning (Atkinson 1939).

Larvae hatch at 4.6-5.2 mm and are active and well oriented upon hatching. The yolk sac larva (Fig. 45.20A) has 7-8 preanal and 26-27 postanal myomeres. Pigmentation consists of numerous (150 or more) pigment spots on the dorsal surface of the gut, several spots on the nape and anterior portion of the yolk sac and 11-20 ventral postanal midline melanophores. After 15 days or by ~ 6.0 mm, a preopercle is forming which has a series of 7-9 tiny spines along the margin. With development, melanophores are added to the head, nape, and gut and dendritic melanophores appear in the developing caudal fin (Fig. 45.20 B, C). By 9.0 mm, flexion is completed, and fin spines and rays are developed. Pigment spots appear along the spinal cord and increase in other areas (Fig. 45.20D). After 51 days or by 12.2 mm, transformation from larval to juvenile characters is almost complete. The young fish become bottom-oriented and take up a benthic habitat. Pigmentation has increased to include 4 pigment saddles which extend from the dorsal midline anterolaterally to the lateral midline. These bands begin forming sequentially from anterior to posterior in about 40 day old specimens. Melanophores are present on the dorsal surface of the gut, and the pectoral fin base is heavily pigmented. Melanophores are also present on the anterior elements of both dorsal fins and on the basal portion of the pectoral fins (Fig. 45.20)(Stein 1973).

In Puget Sound, young-of-the-year appear in tidepools in June (Atkinson 1939). Fish of < 1 year in age living in moderately sheltered or sheltered areas move shoreward with the incoming tide and retreat on the ebb (Green 1971).

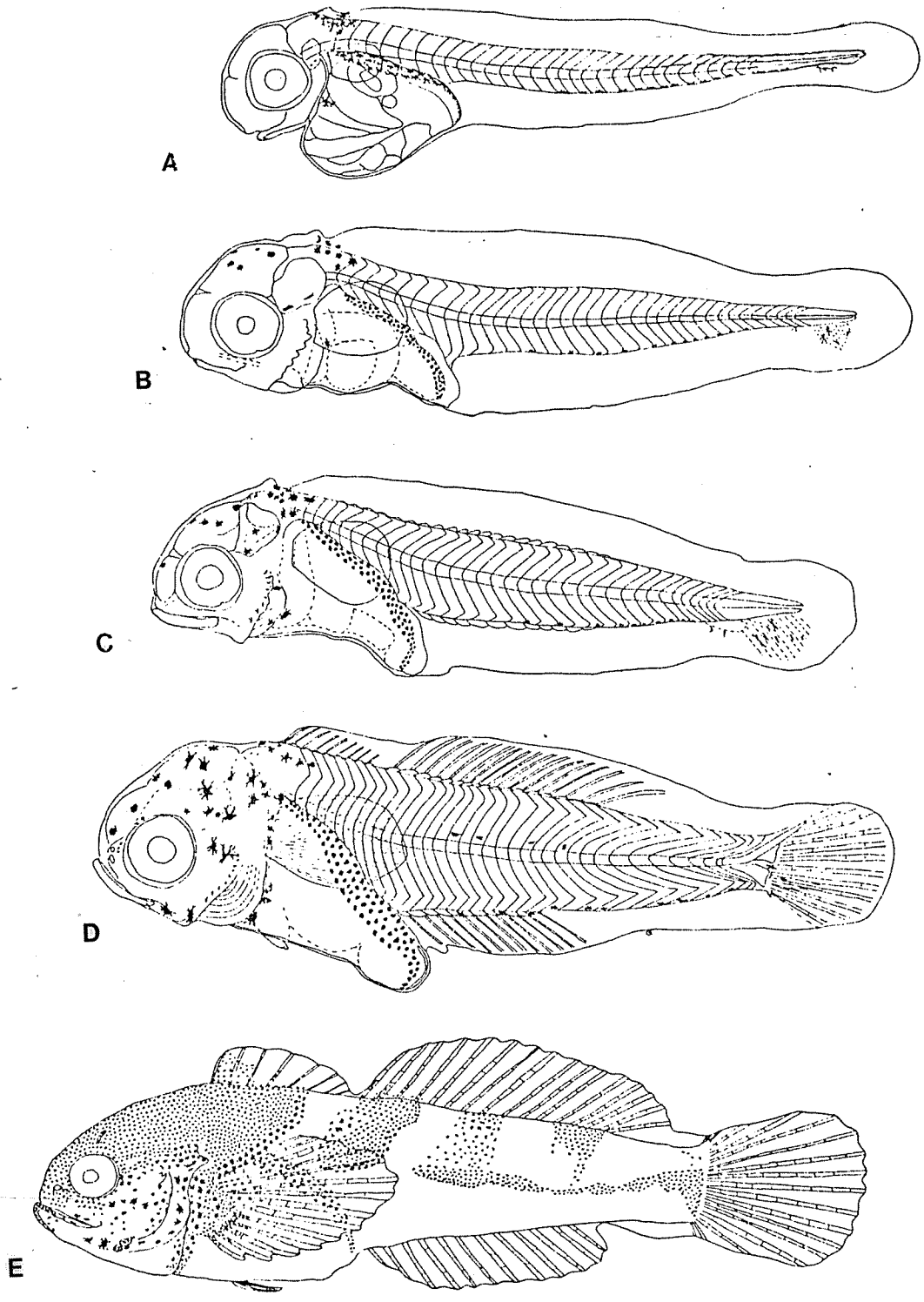

Fig. 45.20. Larval stages of tidepool sculpin, Oligocottus maculosus: A) 5.0 mm TL; B) 6.0 mm TL; C) 6.6 mm TL; D) 9.2 mm TL; E) 12.2 mm TL. (Source: Stein 1973).

Oligocottus rimensis - Saddleback sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Saddleback sculpin adults appear to use the intertidal area on a seasonal basis, moving into tidepools to reproduce. The larvae are believed to settle subtidally and remain there during early juvenile life (Cross 1982).

Saddleback sculpin males can be distinguished from females by their elongated first two anal rays.

Additional information on early life history is not available.

Oligocottus snyderi - Fluffy sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, intertidal to subtidal depths

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: oviparous, internal fertilization

Eggs: undescribed

Larvae: undescribed

Fluffy sculpin are found in the low intertidal to subtidal zones. They seem to prefer tidepools with macrophyte cover such as eelgrass. They are rarely found in rocky pools which are devoid of algae and never found in open sandy pools. They are also absent in upper intertidal pools which have macrophytic algae, which may be due to their intolerance to the warmer water in these areas (Nakamura 1976b; Green 1971c; Cross 1982).

Male fluffy sculpin differ from females in that they possess an enlarged and prehensile first ray of the anal fin (Fig. 45.21) and a well developed papilla. Spawning season is unreported, but mating has been observed in the aquarium. No definite pattern of display or courtship is apparent. When mating, the two fish align themselves side by side, and the male uses his large first anal ray to hold the female during copulation (Fig. 45.21C).

Copulation may occur at least 3 months before spawning. Eggs contain light yellow yolk and average about 1.25 mm. Development is estimated at 22-23 days at 10.9-12^{o}C (Stein 1973).

Stein (1973) described and illustrated yolk sac larvae 4.5-4.75 mm TL, and 5.5 mm TL larvae. Laboratory reared larvae of O. snyderi differ from O. maculosus primarily by being less pigmented (Table 45.7). At hatching, fluffy sculpin larvae are 4.5-4.75 mm TL and are active and well-oriented immediately after they hatch. The head is large, bluntly rounded anteriorly, and unpigmented except for a small amount of diffuse melanin on the crown. The mouth is subterminal and the lower jaw becomes functional within a few hours after hatching. There are ~ 39 myomeres. Pigmentation includes about 50 stellate melanophores on the dorsal surface of the gut which are arranged in 3-4 ill-defined rows. A small pigment patch also occurs on the nape. In newly hatched larvae, no pigment exists posterior to the anus, but within two days, 5-7 small stellate melanophores appear on the posterior half of the postanal

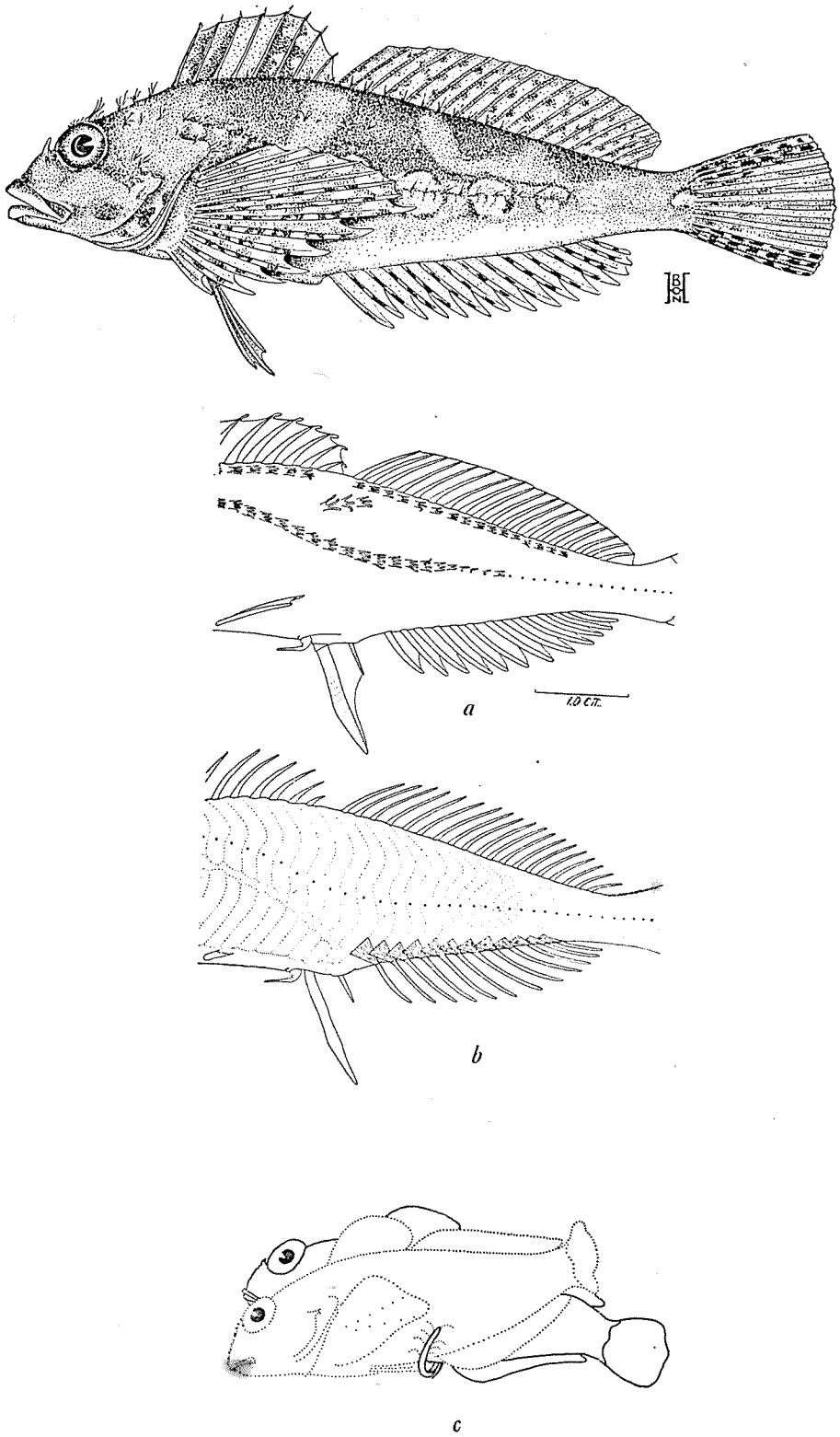

Fig. 45.21. Adult fluffy sculpin, Oligocottus snyderi: a) Lateral view of a male showing the penis, enlarged first anal ray, second anal ray, and 12 unmodified anal rays; b) same view, after removal of skin. Inclinator muscles of unmodified anal rays are shaded; c) position of male (solid line) and female (dotted line) during mating. Note position of modified first anal ray. (Sources: a-c, Morris 1956; top, Hart 1973).

Table 45.7. Comparison of early larvae of fluffy sculpin, Oligocottus snyderi, and tidepool sculpin, O. maculosus, reared in the laboratory. (Source: Stein 1973).

Characters	Tidepool sculpin, Oligocottus maculosus	Fluffy sculpin, Oligocottus snyderi
Size at hatching	4.6-5.2 mm	4.5-4.75 mm
Preanal myomeres	7-8	9
Postanal myomeres	26-27	30
Xanthin over body cavity	pale	bright
No. melanophores over body cavity	>150	50-75
No. melanophores on nape	8-10	2-3
Ventral postanal midline melanophores	11-20	5-7

ventral midline and within 10 days, one or two more appear closer to the anus and on the ventral finfold near the tip of the notochord (Fig. 45.22). The pectoral fin rays begin to form at 10 days and flexion begins by about 12 days from hatching. At 17 days the anlage of the caudal fin rays appear. At 21 days, larvae are about 5.5 mm and the mouth is becoming more terminal in position. Pigmentation along the postanal ventral surface remains unchanged. The melanophores overlying the gut cavity have enlarged, but have not increased in number. Six large, stellate melanophores, which appeared on the 14th day, lie on the dorsal surface of the head in roughly a circular pattern (Fig. 45.22). Later stage larve are undescribed.

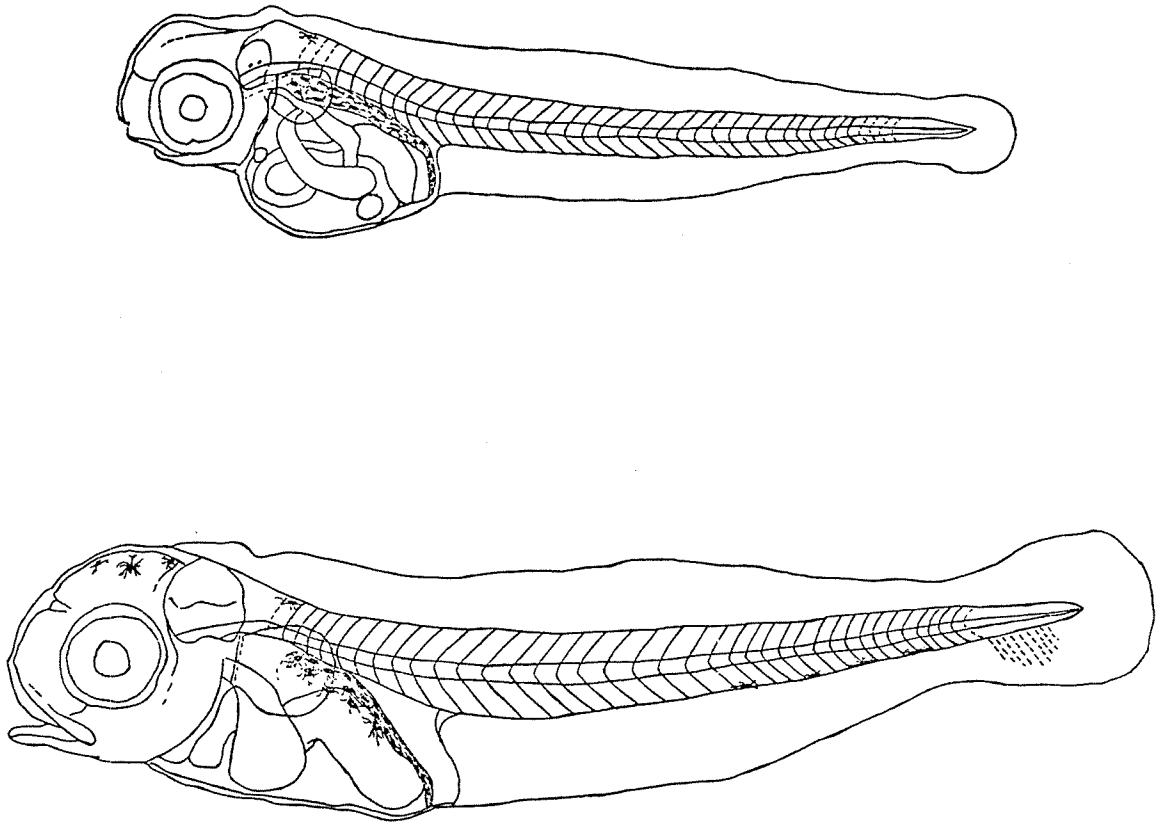

Fig. 45.22. Larvae of fluffy sculpin, Oligocottus snyderi: yolk sac larva, 4.5-4.75 mm TL; 5.5 mm TL larva. (Source: Stein 1973).

Psychrolutes paradoxus - Tadpole sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: winter-spring (Barkley Sound, B.C.)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: pelagic

Tadpole sculpin are small (length to 5.8 cm) nearshore sculpins taken in some areas in trawls out to 40 m and by beach seining (Hart 1973). There is no information on spawning behavior or habitat, but larvae are collected from the plankton in Barkley Sound, British Columbia, during February, March, and May (Marliave 1975) implying a winter-spring spawning period. Eggs are reported to be 1.4 mm in diameter (Hart 1973).

Larval tadpole sculpin are similar in appearance to soft sculpin, as mentioned earlier (Fig. 45.23). They are both characterized by large pectoral fins, and a "tadpole" resemblance due to the large head and gut. With practice, however, larvae of the two species can be separated based on several characters (Table 45.5).

Tadpole sculpin settle at a relatively small size ~ 13-14 mm Tl, with a head length of ~ 25% TL. After settlement, the head length increases to about 30% TL in 18 mm TL specimens (Marliave 1975).

Tadpole sculpin 12-22 mm also occur in the plankton in low salinity water near the Fraser River (B.C.) outlet during April and May. They consume barnacle larvae, crab larvae, ostracods, copepods, algae, and amphipods (Barraclough 1967 a, b; Robinson et al. 1968).

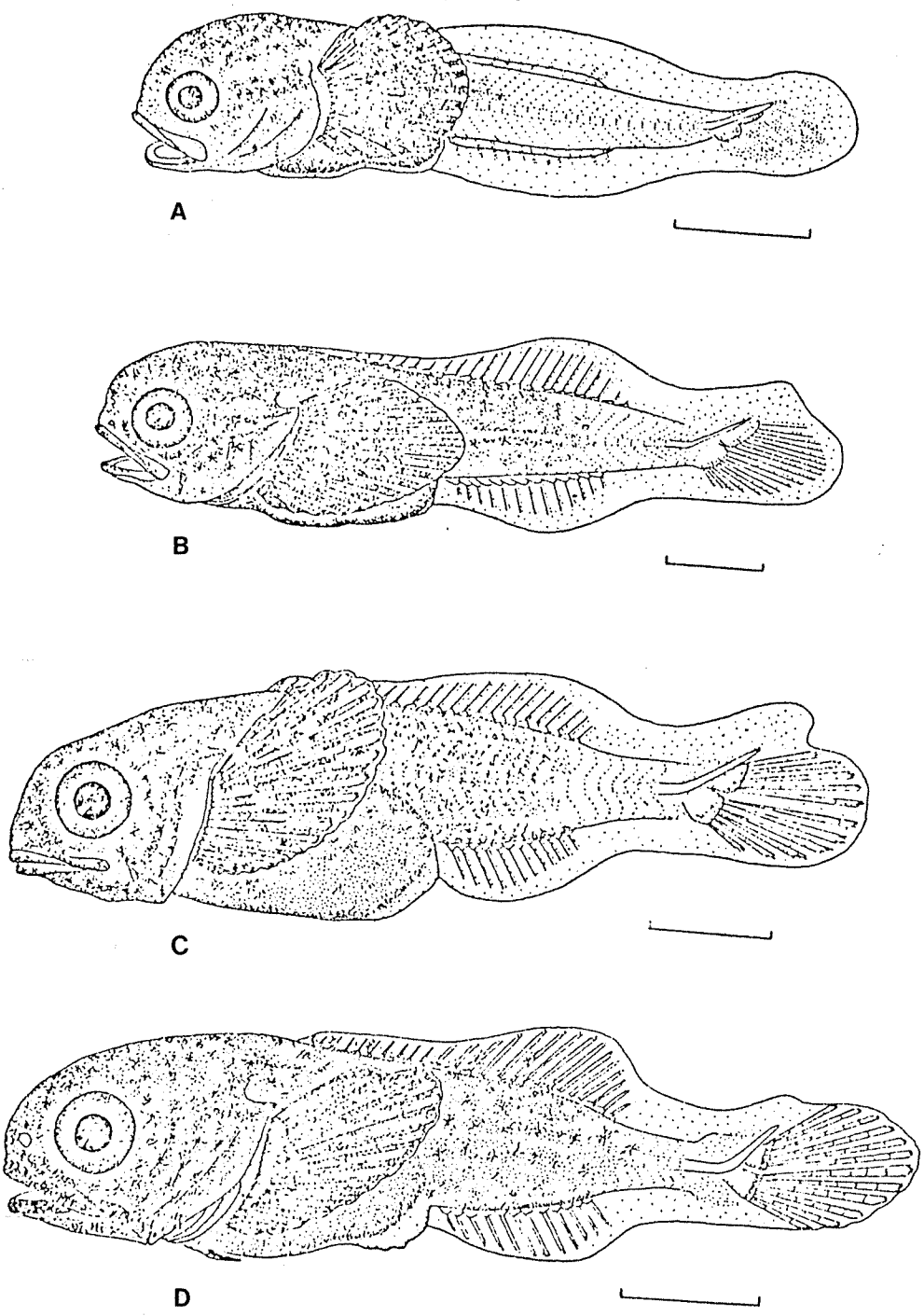

Fig. 45.23. Larvae of tadpole sculpin, Psychrolutes paradoxus collected from the plankton, 2 mm scale: A) 10.5 mm TL, B) 13 mm TL, C) 14 mm TL, D) 13 mm TL - settled (Source: Marliave 1975).

Radulinus asprellus - Slim sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Although common at moderate depths (18-128 m) in British Columbia and Puget Sound, slim sculpin early life history has been little studied.

Larvae were first described and illustrated by Richardson and Washington (1980) based on collections from the plankton off Oregon. They are characterized by a distinctly coiled gut, snout-to-anus length of 44-54% SL, an increasingly pointed snout, and are well covered with pigment. Melanophores occur over most of the body including the head, gut, dorsal and ventral midlines, and laterally at midbody (Fig. 45.24). Body pigment does not extend into the caudal peduncle, although small larvae may have ventral pigment spots extending to the tip of the tail (Fig. 45.24A). A distinctive series of elongate melanophores is present along the lateral midline and almost forms a solid line of pigment. This feature helps separate larval slim sculpin from cabezon, Scorpaenichthys marmoratus, larvae which are similar at small sizes. With development, pigmentation increases over the body, except for the caudal peduncle which remains unpigmented (Fig. 45.24D-E).

Four preopercular spines appear at ~ 10-11 mm, but never become prominent. Parietal and nuchal spines also develop, but appear only as minute spines which soon become bumps. Adult fin ray complements are formed by 11-12 mm and transforming specimens are about 14-15 mm and may have a nasal spine and lateral line scales (Richardson and Washington 1980).

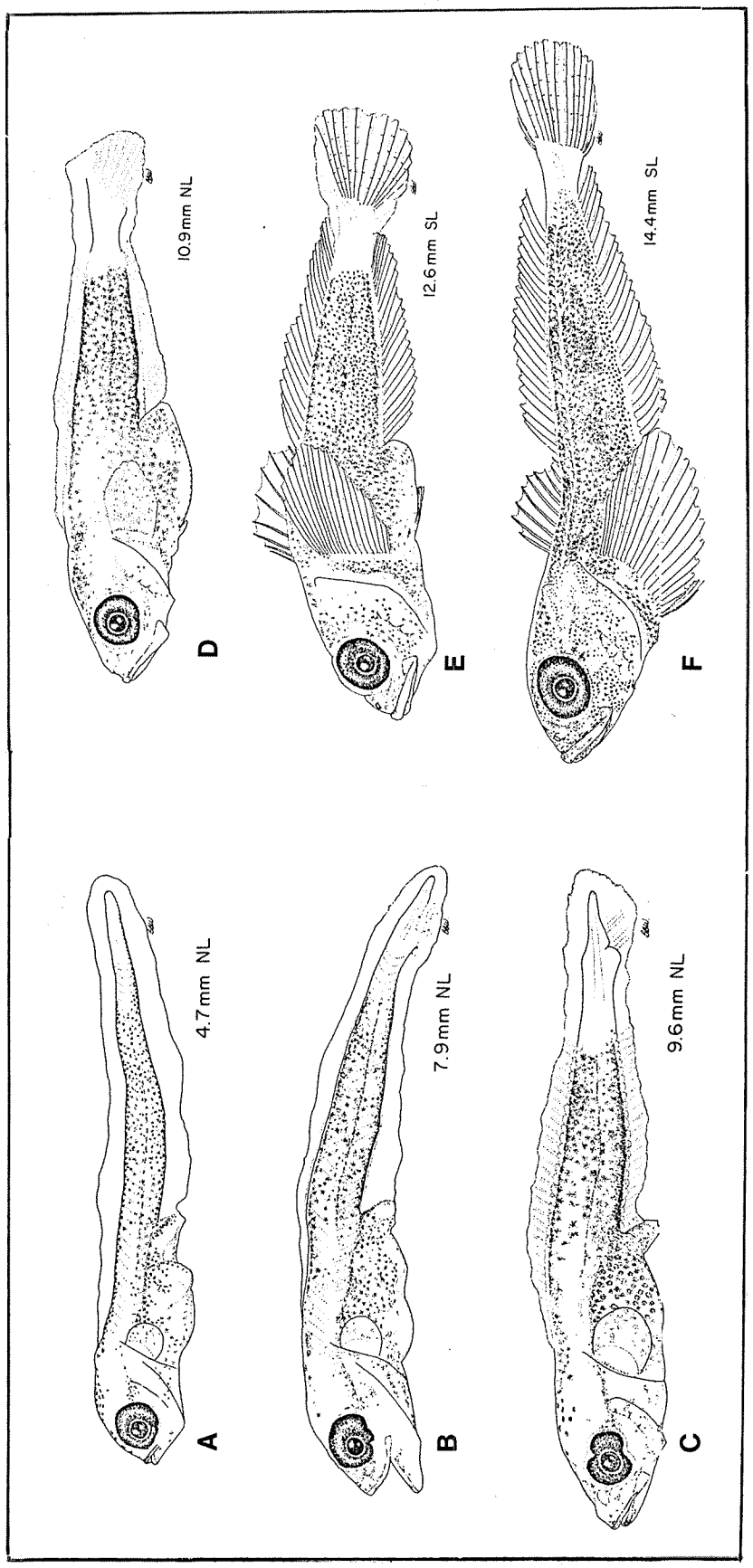

Fig. 45.24. Larvae of slim sculpin, Radulinus asprellus (Source: Richardson and Washington 1980).

Radulinus boleoides - Darter sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Darter sculpin are infrequently found in Puget Sound and their early life history is unstudied. Richardson and Washington (1980) tentatively identified larvae of this species based on two specimens collected off Oregon. Larval darter sculpin are similar in pigmentation to slim sculpin, Radulinus asprellus, with melanophores covering most of the body laterally except the tail tip. A greater portion of the tail tip appears to be unpigmented in darter sculpin than in slim sculpin. Also, darter sculpin are more advanced in development than slim sculpin at comparable sizes. Other differences are a possibly longer snout-to-anus length (~ 58% SL) in darter sculpin than in slim sculpin (44-47% SL) at similar sizes, and a greater body depth at the pectoral fin base is also found in darter sculpin (22-23% SL) than in slim sculpin (16-18% SL). More larvae are needed to verify the identification of darter sculpin, and to adequately describe their characteristics.

Rhamphocottus richardsoni - Grunt sculpin

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, intertidal to subtidal depths

Spawning habitat: demersal

Spawning season: winter-spring (B.C.)

Mode of reproduction: oviparous

Eggs: demersal, guarded

Larvae: pelagic

Grunt sculpin are common in some areas of Puget Sound being found in tidepools and shallow water usually along rocky shores. They are also taken in beach seines from sandy areas and in trawls down to 165 m. They generally crawl over rocks and seaweeds using their long pectoral fin rays. The common name was derived from the hissing-grunting noise they make when removed from water (Hart 1973).

Spawning behavior has been infrequently observed, but on one occasion, it was reported that eggs were laid inside a can in about 60 ft of water. The eggs were creamy white and were being guarded by an adult grunt sculpin (D. Somerton, pers. comm.). DeMartini and Patten (unpubl. manusc.) reported that females guarded the eggs masses. According to Hart (1973), eggs are yellow to orange and laid in winter. Grunt sculpin larvae are planktonic and are present from February to early May in Barkley Sound, B.C. (Marliave 1975) and March to May in Skagit Bay, Washington (Blackburn 1973).

Hatching occurs at 6-7 mm with transformation occurring at 14-15 mm. Larvae are unusual and distinctive. They are deep-bodied (29-40% SL between 8-12 mm) and have a snout to anus distance which is > 60% SL. They are also well covered with pigment except for the tail tip which remains unpigmented through the pelagic period. Melanophores cover the head, cheeks, ventral surface of the gut and bases of the pectoral fins. Some melanophores appear in the dorsal and anal finfolds. Larvae have a distinct preanal finfold which is also pigmented, and remains evident anterior to the anus until ~ 12 mm. As transformation approaches, melanophores are added to the spinous dorsal fin and pectoral fin base, and pigment bands begin to develop on the body. For head spines, a single preopercular spine develops by ~ 8 mm and becomes pronounced in larger specimens, a parietal and nuchal spine develop and fuse as one, two spines become visible in the posttemporal-supracleithral region, and a cleithral and nasal spine appear on ~ 12 mm larvae. During transformation, the body becomes covered with distinct spine-like scales (Fig. 45.25)(Richardson and Washington 1980).

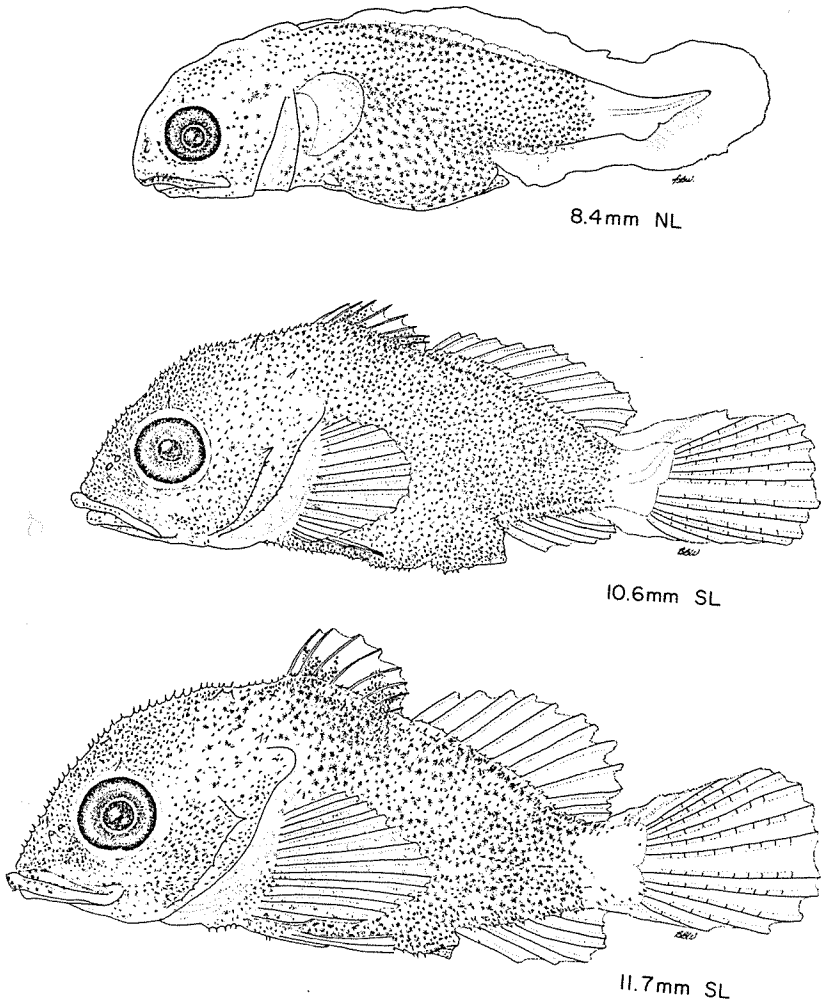

Fig. 45.25. Larval grunt sculpin, Rhamphocottus richardsoni, collected from the plankton off Oregon. (Source: Richardson and Washington 1980).

While residing in the plankton, larval grunt sculpin consume copepods, amphipods, euphausiids, crab larvae, and other fish larvae (including walleye pollock larvae)(Barraclough 1967 a, b; Robinson et al. 1968).

Scorpaenichthys marmoratus - Cabezon

Range: Table 45.1

Occurrence in Puget Sound: common

Adult habitat: demersal, in rocky areas or kelp beds

Spawning habitat: demersal, on rocks or algae

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: demersal, adhesive, attached

Larvae: pelagic

Cabezon are one of the few Northeast Pacific cottid fishes utilized by a commercial fishery (taken incidental to rockfish catches). They are fairly common in some areas and range from Baja California to Sitka, Alaska. Adults are found in shallow (usually < 12 m) protected areas and are associated with dense algal cover and deep rocky crevices (Burge and Schultz 1973).

In California, spawning season of cabezon is about 5 months long from November to March (O'Connell 1953) and in British Columbia, fish spawn from January to May (Pillsbury 1957). Eggs are laid in large masses, up to 1/2 m across and 4 cm thick, on rocks, in deep crevices (Feder et al. 1974) or on algae (Burge and Schultz 1973). Nesting sites appear to be restricted to specific areas from intertidal depth (in tidepools) to 17 m, which are reused each year. Several spawning sites occupy each area and nests may be within 2.4-3.0 m of each other. Males tend the eggs, driving intruders away and fertilizing further spawnings (Feder et al. 1974).

Males are sexually mature after their second or third year and females at slightly older ages, 3 or 4. Males lack a copulatory organ, which suggests that fertilization is external. In the females, ovaries are blunt anteriorly, round in cross-section, and broadly joined in the posterior. The united ovaries open directly through the genital pore without the invervention of any tubular oviduct. During late spring and summer, the ovaries are small, firm, smooth-walled, and are grayish-white in color. During the fall, the ovaries begin to mature and enlarge and are grayish-pink in color. As maturity is reached, the ovary lumen is filled with clear, amber-colored eggs. It is unclear if more than one spawning occurs per season, although two modes of egg sizes are present in the ovaries. The number of larger sized eggs matured by a 433 mm, 1.4 kg female is about 48,700 and increases by about 1,500 eggs per each 100 g of total weight. A 4.6 kg female may produce 97,600 eggs (O'Connell 1953).

Mature unfertilized eggs are about 1.4-1.7 mm in diameter with a shell thickness of 0.045 mm. The egg surface appears smooth and translucent to the naked eye. The yolk is clear and amber in color and contains a large oil globule ~ .27 mm in diameter and several (1-4) smaller ones. After contact with water, the eggs form a hard compact mass and the shells become flattened at their points of contact (O'Connell 1953). After deposition and fertilization, eggs are bright maroon to crimson in B.C. (Pillsbury 1957), and in southern California, exhibit a variety of colors and are reported to be white, pink, or blue-green becoming olive as they mature (Feder et al. 1974).

Intertidally spawned eggs do not seem to be preyed upon despite the presence of fish-eating and scavenging birds and mammals (Pillsbury 1957) and roe may be toxic (Hubbs 1951). It is unclear how long the incubation time is. Artificially reared eggs are reported to hatch in about 17 days (O'Connell 1953).

At hatching, larvae are ~ 4-6 mm and pelagic. They are most common in inshore waters, but have been collected up to 200 miles off the coast of California (O'Connell 1953). Preflexion larvae are relatively slender with an oval-shaped gut and a snout-to-anus length of about 50% SL. Larvae becomes more deeper bodied with development and the snout is rounded, never pointed as in slim sculpin larvae. An unpigmented preanal finfold is present and remains visible up to 13-14 mm (Richardson and Washington 1980).

Like slim sculpin and grunt sculpin, cabezon larvae are well pigmented but are usually darker in appearance than the other two species. Melanophores cover the head, gut (except the ventral margin), dorsal and ventral body margins, and the lateral body surface except for the tail tip, and extend more posteriorly than in slim sculpin larvae. The fins and finfolds are unpigmented. As the larvae develop, melanophores increase in number on the head and lateral body surface, but not along the ventral margin of the gut until 8-9 mm, and not at the caudal peduncle until ~ 14-15 mm (Fig. 45.26 A-F). At ~ 13-14 mm, a distinct melanophore appears at the base of most dorsal fin soft rays (Fig. 45.26F). Cabezon larvae are different from slim sculpin larvae in that they generally do not develop a lateral midline concentration of pigment (Richardson and Washington 1980).

At about 8 mm, preopercular spines begin to develop (Fig. 45.26C) and are striking in postflexion larvae and larger larvae (Fig. 45.26E). Four spines develop, but only the upper three are pronounced (Fig. 45.26F).

By 13-14 mm, larvae resemble juveniles in appearance and have fully formed fins. Pelagic specimens, up to 35 mm have been collected off Oregon (Richardson and Washington 1980). While they are pelagic, cabezon larvae start out eating copepod larvae and barnacle naulplii (Barraclough et al. 1968; Barraclough and Fulton 1968), switching to adult copepods and other larval fish with devlepment (Barraclough 1967b;

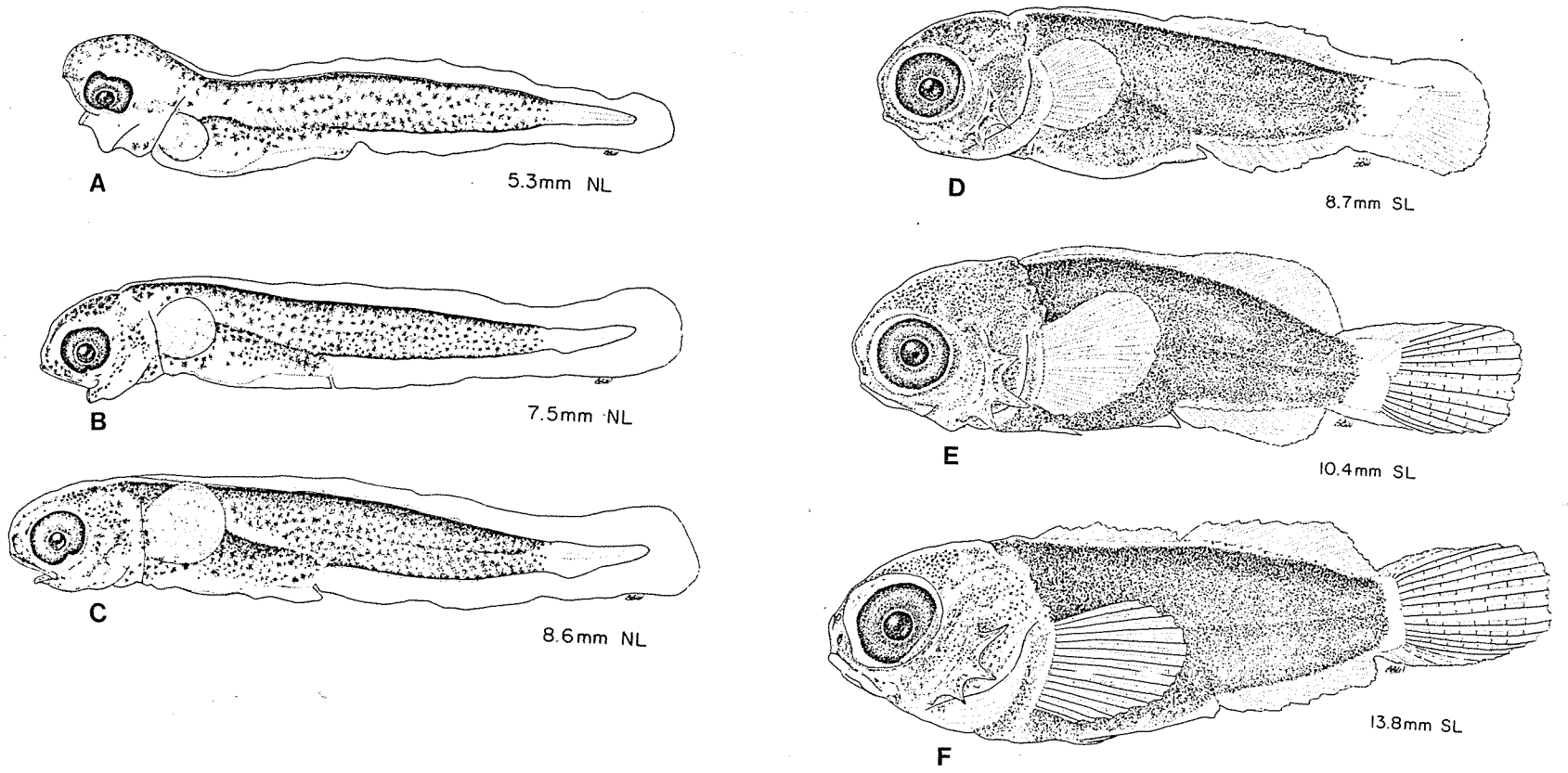

Fig. 45.26. Larvae of cabezon, Scorpaenichthys marmoratus, collected from the plankton off Oregon. (Source: Richardson and Washington 1980).

O'Connell 1953). By 40 mm, cabezon leave the plankton to take up a demersal residence in tidepools and in other shallow areas. At this time they are silvery-red with darker color forming five irregular vertical bars. Food consists of crustaceans, including shrimp and amphipods. By 150 mm, they are consuming crab and small (1-3") tidepool fishes (O'Connell 1953).

Synchirus gilli - Manacled sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, clinging to algae, pilings

Spawning habitat: unknown

Spawning season: spring (B.C.)

Mode of reproduction: oviparous, internal fertilization

Eggs: demersal, adhesive, undescribed

Larvae: undescribed

Adult manacled sculpin are readily identified by their small size (to 5 cm) and their anterioventrally united pectoral fins. The pelvic fins have recurved tips and together with the pectoral fins allow the fish to cling to a variety of substrates. Adults live in broad leafed algae on floats (Hart 1973) or clinging to macroalgae (Miller and Erdman 1948; Burge and Schultz 1973), sea anemones, barnacles, pilings, and rocks (Miller and Erdman 1948).

Both sexes are olive green to brown, and the male has a prominent silvery lateral stripe (Krejsa 1964). Males also have a large cylindrical papilla which is more slender at the tip and retracts into a deep pit between the anus and the anal fin. The lower jaw in males also has a symphysial pad and can open to a greater extent in males than in females (Fig. 45.27C). Fertilization is internal and involves a unique copulatory position. The male approaches the female from the side and curls around her body, embracing her with his lower jaw on top of her and his forwardly curved pelvic fins underneath (Fig. 45.27A, B).

Eggs are laid in May and are pink and adherent (Hart 1973). Larvae of manacled sculpin have not been described.

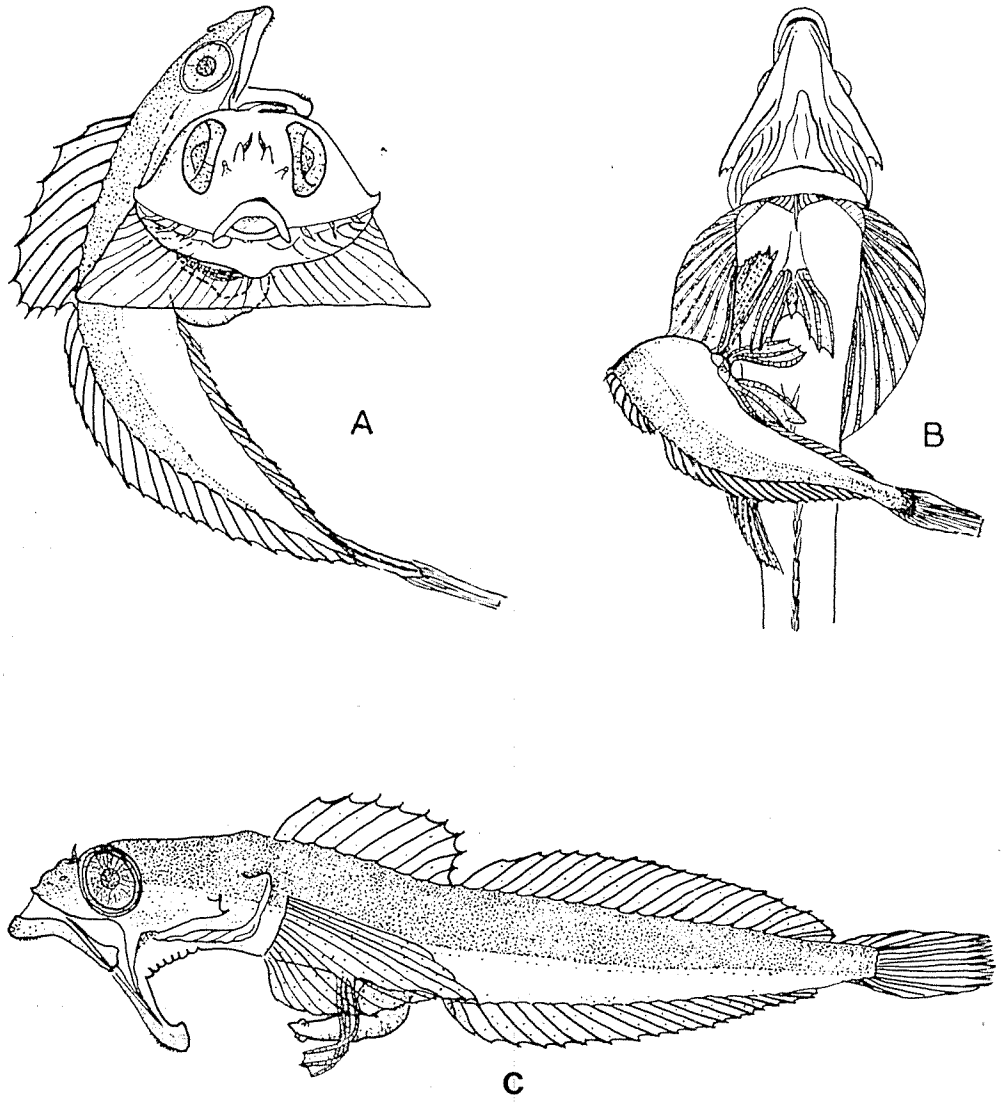

Fig. 45.27. Manacled sculpin, Synchirus gilli, male (34.5 mm) and female (45.5 mm) in mating position: A) frontal aspect; B) ventral view; C) 41.2 mm male, note the fully opened mouth, symphysial pad, wrinkled hyoid skin, and forward-curved pelvin fins. (Source: Krejsa 1964).

Triglops macellus - Roughspine sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawing season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Little information is available on the early life history and reproductive characteristics of roughspine sculpin. Adults range from Puget Sound, Washington to the Bering Sea and are taken from 18-91 m (Hart 1973).

Larvae (8.3, 12.0 mm SL) taken in Skagit Bay, Washington (Blackburn 1973) resembled larvae (6.9, 7.4, 15.4) collected off Oregon identified as Triglops sp. (Richardson and Washington 1980). These larvae are relatively slender, have a snout to anus length of 38-44% SL, and a higher number of myomeres ~ 45-46, which distinguishes them from most other cottids. Identification to species has not been verified, and larvae may be T. macellus or T. pingelli, ribbed sculpin. They have a distinctive heavily pigmented gut, and pigment on the head and nape region, and on the pectoral fin base. The rest of the body remains unpigmented and no postanal midventral melanophores are present. Head spines of a 15.4 mm SL larva consist of a double row (anterior and posterior series) of four preopercualr spines, a nuchal spine, two spines in the posttemporal-supracleithral region, and two spines in the postocular region. Transformation is not complete at this size, and full fin complements of rays are unformed (Fig. 45.28)(Richardson and Washington 1980).

Positive identification to roughspine sculpin requires examination of additional specimens. Spawning behavior and egg stages also remain undescribed.

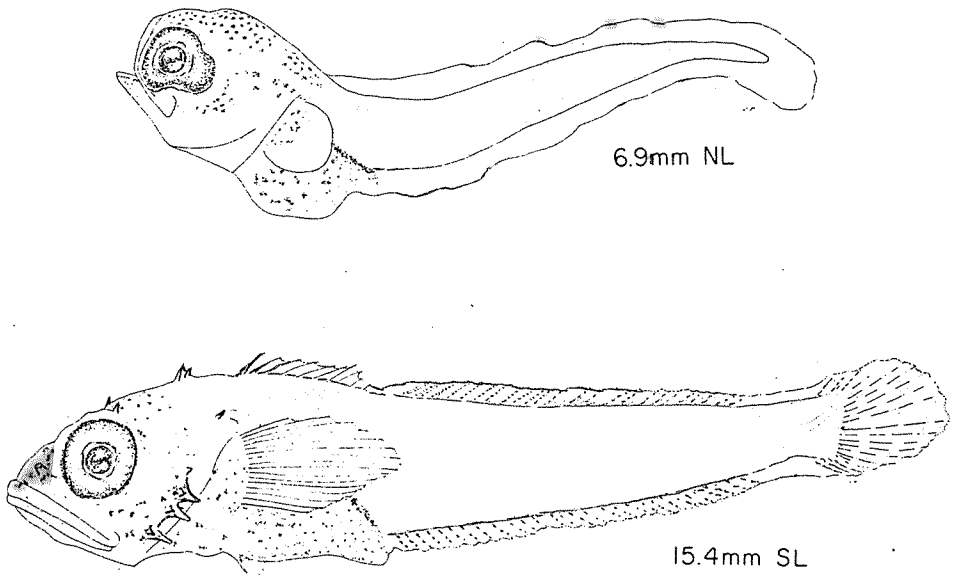

Fig. 45.28. Larvae identified as "Triglops sp." from off Oregon. (Source: Richardson and Washington 1980).

Triglops pingeli - Ribbed sculpin

Range: Table 45.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Ribbed sculpin range from Puget Sound (southern limit) to Arctic waters, Japan, and are also found in the North Atlantic (Hart 1973). Their early life history in the Northeast Pacific has not been studied. In the Atlantic Ocean and Barents Sea, some larval stages have been described (Ehrenbaum 1905-1909; Koefed 1907, cited in Khan 1972; Ross 1949; all cited by Richardson and Washington 1980).

Larvae of ribbed sculpin from the Atlantic and Barents Sea are similar in appearance to the unidentified Triglops species described by Richardson and Washington (1980) from the Northeast Pacific (see Triglops macellus). However, they differ in that they possess a row of postanal ventral midline melanophores along the base of the second dorsal fin by 10 mm and a mediolateral row by 11 mm. Head and trunk pigment and shape resemble the Triglops sp. (Richardson and Washington 1980). Other aspects of the reproductive biology remain unstudied and data on egg development are nonexistent.

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46. AGONIDAE

General

Members of the poacher family (Agonidae) are represented by 14 species in Puget Sound (Table 46.1). Adults are small bottom-dwelling fish which usually inhabit moderate depths. In the Sound, the most frequently encountered forms are apt to be Agonopsis emmelane (northern spearnose poacher), Agonus acipenserinus (sturgeon poacher), Odontopyxis trispinosa (pygmy poacher), and Xeneretmus latifrons (blacktip poacher).

Very little attention has been given to studying the early life history and reproductive ecology of poachers. Of the 14 Puget Sound species, only three species have been studied to any extent. Marliave (1975) identified larvae of tubenose poacher (Pallasina barbata) and blacktip poacher from spring plankton collections made in Barkley Sound, B.C., and reared and described rockhead (Bothragonus swani) larvae from eggs found on kelp. Whether all species of agonids have demersal attached eggs and pelagic larvae remains to be seen. No information is available on fecundity, spawning behavior, age and length of maturity, spawning season, descriptions of eggs and larvae, and any other aspects of reproductive biology for most of the Puget Sound poachers.

Table 46.1. Distribution of Puget Sound species of poachers (Family Agonidae) along the west coast of North America. (Source: Hart 1973). B = Baja California; C = California; O = Oregon; W = Washington; BC = British Columbia; S = Southeast Alaska; G = Gulf of Alaska; B = Bering Sea.

Species	Geographic location B	C	O	W	BC	S	G	B
Agonopsis emmelane - Northern spearnose poacher								
Agonus acipenserinus - Sturgeon poacher								
Anoplagonus inermis - Smooth alligatorfish								
Asterotheca alaseana - Gray starsnout								
Asterotheca infraspinata - Spinycheck starsnout								
Asterotheca pentacanthus - Bigeye poacher								
Bathyagonus nigripinnis - Blackfin poacher								
Bothragonus swani - Rockhead								
Hypsagonus quadricornis - Fourhorn poacher								
Ocella verrucusa - Warty poacher								
Odontopyxis trispinosa - Pygmy poacher								
Pallasina barbata - Tubenose poacher								
Xeneretmus latifrons - Blacktip poacher								
Xeneretmus triacanthus - Bluespotted poacher								

*Southern range extension by Lea 1973.

Bothragonus swani - Rockhead

Range: Table 46.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, near rocks or kelp

Spawning habitat: demersal, on kelp

Spawning season: unknown

Mode of reproduction: oviparous

Eggs: demersal, attached

Larvae: pelagic

Adult rockhead range from California to the Bering Sea (Hart 1973) and are known from the San Juans and near Port Townsend in Puget Sound (Miller and Borton 1980). They are taken in moderately exposed areas on boulder or gravel beaches, in kelp beds, or in tidepools (Marliave 1977; Schultz 1930).

Rockhead spawn demersally, and the egg masses consist of 2 mm brown eggs which may be deposted in the holdfast of lammarians such as Macrocystis integrefolia (Marliave 1975). Marliave (1975) was able to rear larval rockhead which hatched at about 7.5 mm TL with fully developed pectoral fins. They are also characterized by large, thin teeth at hatching and prefer to eat fish larvae over invertebrate prey. The body plates characteristic of poaches, first appear during the larval period as spines. From the illustrations by Marliave (1975), larval pigmentation consisted of pigmented pectoral fin tips and numerous large melanophore on the head, jaws, ventral gut surface and on the dorsal lateral body regions anterior to about mid-body. Lateral spines and the onset of dorsal, anal, and caudal fin development appeared at about 12 mm (Fig. 46.1).

In the aquarium, larvae began hovering at the tank walls at 48 days of age and began to settle periodically on the substrate at age 54 days. They showed a significant preference to settle on gravel over pebbles or rocks and also preferred to settle near the inlet to the tank (higher current area). Young rockhead showed a phase of repeated settlement for brief periods which lasted two weeks (Marliave 1975, 1977).

Other aspects of the early life history of rockhead are unstudied.

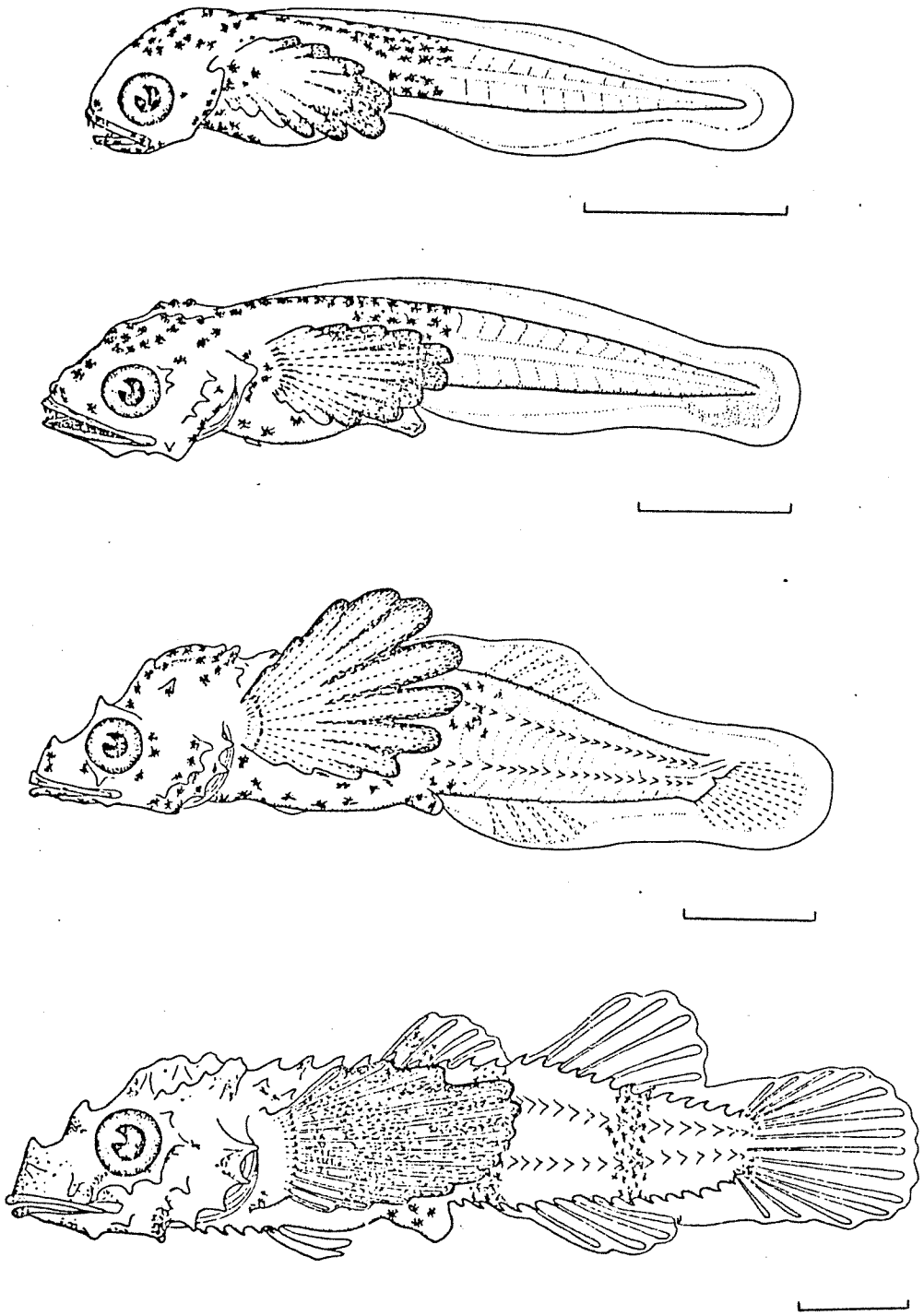

Fig. 46.1. Larvae of rockhead, Bothragonus swani, reared from eggs, (2 mm scale); 1-day, 7.5 mm TL; 11-day, 10 mm TL; 26-day, 12 mm TL; 48-day, 16.5 mm TL. (Source: Marliave 1975).

Pallasina barbata - Tubenose poacher

Range: Table 46.1

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: spring (British Columbia)

Mode of reproduction: unknown

Eggs: unknown

Larvae: pelagic

Information on spawning of tubenose poacher is scarce. Larvae are caught in the plankton in Barkley Sound, B.C., in April. At 10 mm, larvae are entirely covered by melanistic pigment and bony spines and ossification of all but the first dorsal and pelvic fins are underway (Fig. 46.2). Fin position, fin ray counts, spines, and head morphology can be used to recognize larvae and juveniles (Marliave 1975).

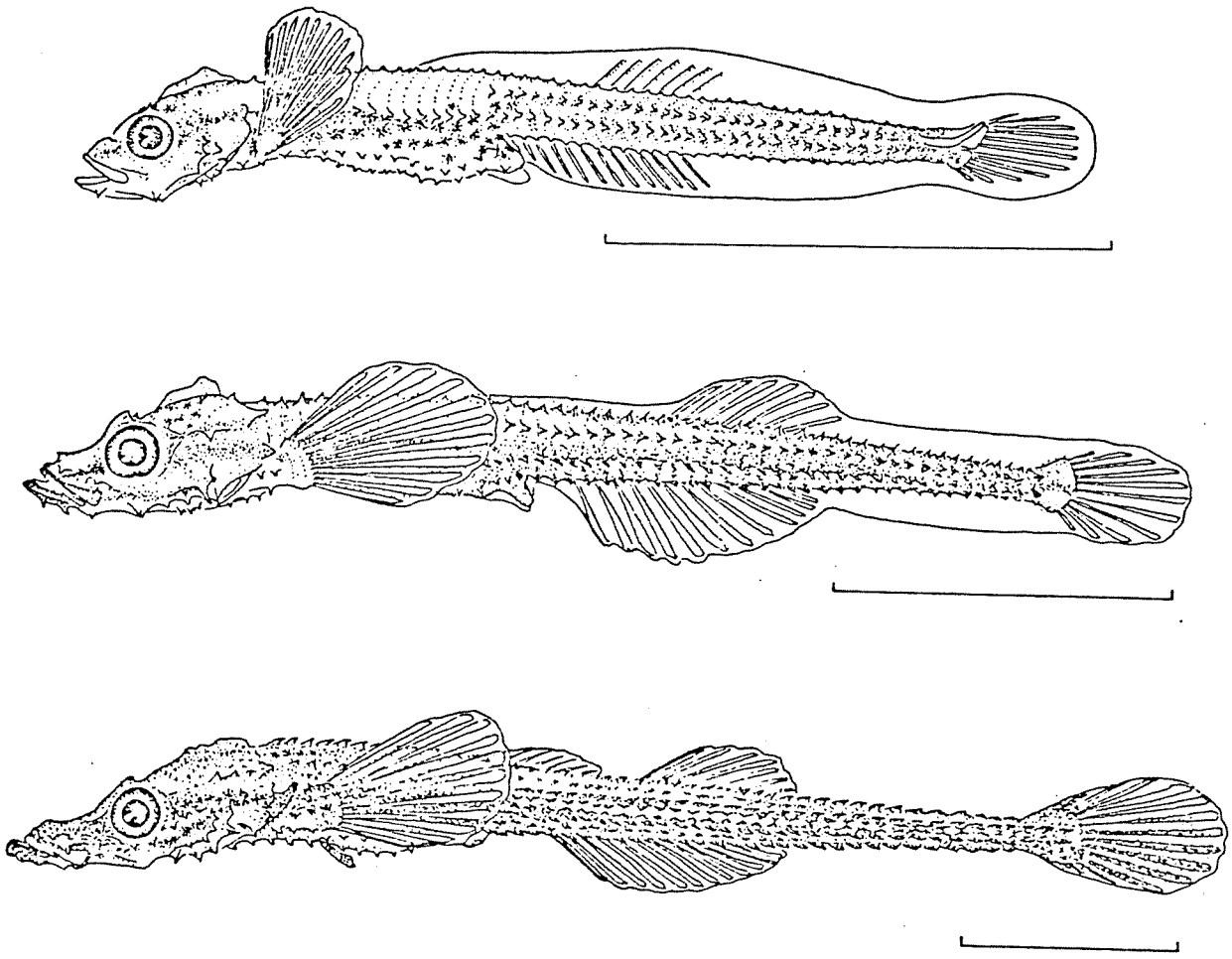

Fig. 46.2. Tubenose poacher, Pallasina barbata, collected from plankton, (5 mm scale); 10 mm TL, 17 mm TL, 28 mm TL. (Source: Marliave 1975).

Xeneretmus latifrons - Blacktip poacher

Range: Table 46.1

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: spring (British Columbia)

Mode of reproduction: unknown

Eggs: undescribed

Larvae: pelagic

Blacktip poacher are known from Baja California to British Columbia (Hart 1973) and have been frequently reported in Puget Sound south of Camano Island (Miller and Borton 1980). Adults live demersally at depths of 18 to 365 m, but generally occur in more shallow water in the northern part of their range (Fitch and Lavenberg 1968).

Spawning is reported to take place in spring in both British Columbia (Marliave 1975) and California (Fitch and Lavenberg 1968).

Larvae are pelagic and were briefly described and illustrated by Marliave (1975). They are elongate in body form and characterized by four prominent white patches on the dorsal finfold margin (not evident in illustrations). There is also a white patch over the anus. These white areas accent the dark body and finfold concentrations of melanin. The jaws are also well pigmented. Marliave (1975) described the body pigment as a "hexagonal lattice pattern of melanin" (Fig. 46.3).

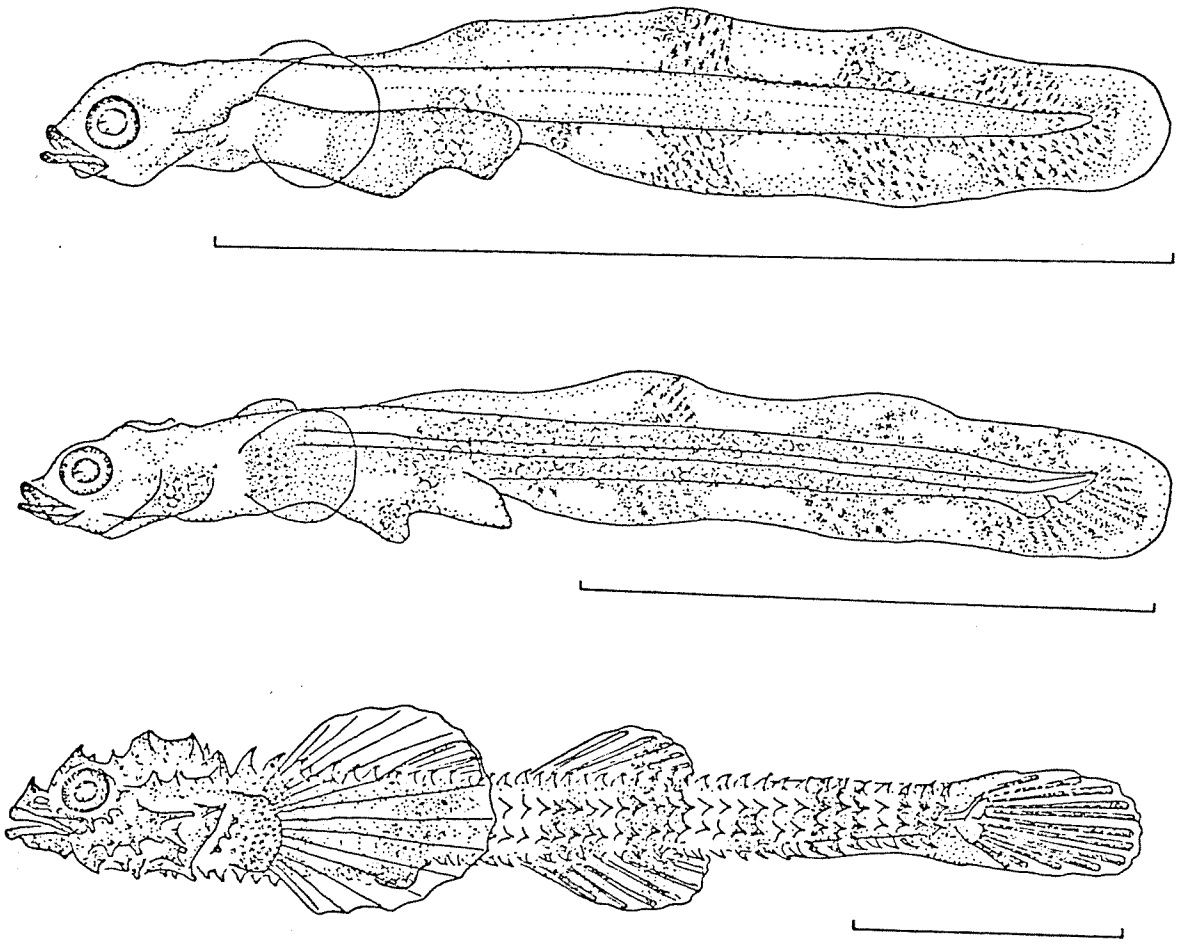

Fig. 46.3. Larvae of blacktip poacher, Xeneretmus latifrons, from plankton, (5 mm scale); 7 mm TL, 10 mm TL, 21 mm TL. (Source: Marliave 1975).

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47. CYCLOPTERIDAE

Careproctus melanurus - Blacktail snailfish

Range: southern California to British Columbia

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: possibly within carapace of crabs

Spawning season: spring-summer (Oregon)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: undescribed

Blacktail snailfish are known on one occasion from Bellingham Bay in Puget Sound (Miller and Borton 1980), and range along the Pacific coast from southern California to British Columbia. Adults are benthic and have been collected over their range at depths between 90 and 1,370 m (Hart 1973) and recently were collected as deep as 1,600 m off Oregon (Stein 1980).

Blacktail snailfish reach sexual maturity at lengths somewhere between 200 and 220 mm and mature males can be distinguished from females by possessing a genital papilla up to 7 mm in length (Stein 1980).

Off Oregon, spawning of blacktail snailfish may be seasonal as females with large eggs are collected only during April and June (Stein 1980).

According to Stein (1980), ripe eggs > 3.84 mm filled the anterior half of the ovary and distinctly smaller unripe eggs filled the posterior half. Free eggs within the lumen had a maximum diameter of 4.63 mm and the maximum fecundity of a mature female was 534 eggs. In a mature ovary, ripe eggs formed a group of eggs widely separated from smaller eggs.

On at least two occasions, eggs and larvae of Careproctus spp. (possibly melanurus) have been found within the gill chamber of box crab, Lopholithodes foraminatus. In one instance, a box crab was collected at 205 m off British Columbia during June and contained at least 424 eggs (diameter of 3.75 - 4.20 mm, $\bar{X}$ = 3.99) in its right gill chamber (Peden and Corbett 1973). On another occasion, larvae (9-12 mm) were observed emerging from box crab collected at 95-100 m and 140-150 m depths during October off Monterey, California. Later examination

revealed that eggs were associated with the gill filaments of the crab (Parrish 1972).

Eggs (~ 5 mm) of probably a different species of Careproctus have also been found in the pericardial cavity of king crab (Paralithodes camtschatica) in the Bering Sea (Hunter 1969).

Eumicrotremus orbis - Pacific spiny lumpsucker

Range: Washington to St. Lawrence Island; Kamchatka, Kuril Islands, Okhotsk Sea, Sakhalin

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: fall-winter (British Columbia)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: (description in press)

Pacific spiny lumpsucker are distributed from Washington through British Columbia, Alaska, and to St. Lawrence Island in the Bering Sea. They also occur along the Asian Pacific coast from Kamchatka to Sakhalin, including the Okhotsk Sea and Kuril Islands (Hart 1973). In British Columbia, adults have been taken in shrimp trawls over rocky bottoms and have been obtained at low tide in some areas where they are attached to rocks in fast moving tidal water. They are reported to occur to depths of 146 m (Clemens and Wilby 1961).

Sexually mature adults have been collected in B.C. from October to March, with peak abundance in November. Mature, stripped (unfertilized) eggs are orange, about 2.0 mm, and average 202 (range 169-229) per female (34-39 mm SL). Several size classes of eggs are contained within an ovary (Arita 1969).

Pacific spiny lumpsucker exhibit sexual dimorphism in color, disc size, and size and number of body tubercles. Females are characterized by a pale green color and large and numerous tubercles which form an almost complete covering of armor. Males are dull orange to reddish-brown in color and possess fewer and smaller tubercles (Arita 1969). Males also tend to have a larger adhesive disc than females (Arita 1967).

(Larvae and reproductive ecology are presently being described by A. Matarese and S. Borton.)

Liparis callyodon - Spotted snailfish

Range: Washington to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: demersal, nearshore

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Spotted snailfish have been recorded primarily in the San Juan area of Puget Sound and range fom Washington to the Bering Sea (Miller and Borton 1980; Hart 1973). It is largely a shore species, encountered in tidepools (Clemens and Wilby 1961).

Its reproductive biology and early life history remain unstudied.

Liparis cyclopus - Ribbon snailfish

Range: Washington to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Ribbon snailfish range from Washington to the Aleutian Islands and Bering Sea. They are not common in Puget Sound, but have been recorded from near Olympia, at various locations throughout the Sound, and northward to the San Juan Islands (Miller and Borton 1980). According to Hart (1973), adults have been taken at 183 m in the Strait of Juan de Fuca.

Reproductive biology and eggs and larvae are unstudied.

Liparis dennyi - Marbled snailfish

Range: Washington to Gulf of Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: winter (British Columbia)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: undescribed

Adults of this species range from Washington to the Gulf of Alaska and are reported at depths of 70-225 m in British Columbia (Hart 1973). They have been reported at various locations from southern Puget Sound to the San Juan Islands where numerous collections are recorded (Miller and Borton 1980).

Information on spawning biology consists of a collection of two mature 15 cm specimens which were obtained in January, 1934 in Active Pass, British Columbia. These females contained ripe eggs which were faintly pink in color and flowed freely from the vent (Clemens and Wilby 1961).

Liparis florae - Tidepool snailfish

Range: southern California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Lavae: undescribed

Tidepool snailfish are distributed from southern California to the Bering Sea (Hart 1973). In Puget Sound, they are not common and have primarily been recorded from the San Juan Islands (Miller and Borton 1980). According to Clemens and Wilby (1961), this species is found near shore and its coloration varies with the environment.

Liparis pulchellus - Showy snailfish

Range: California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: winter-spring (summer) (California)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: undescribed

Showy snailfish are found along the coast of North America from California to the Bering Sea. They are common along the whole coast of British Columbia and are abundant in the southern Strait of Georgia. Adults are taken in shrimp trawls down to 92 m as well as in beach seines (Hart 1973). In Puget Sound, showy snailfish are widely distributed and appear to be more frequently encountered than the other species of snailfish (Miller and Borton 1980).

Near Humboldt Bay, California, gravid females are abundant in late December to May, and a few are found as late as July. Sexual maturity is attained at lengths of 70-90 mm. The number of maturing ova increases with increasing weight of the fish and with increasing length of the fish and ranges from 941 for 70-80 mm fish (average ovum diameter 0.15 mm) to 9,196 for 160-170 mm fish (average ovum diameter 0.95)(Johnson 1969).

Larval showy snailfish of about 12 mm FL have been collected in the Strait of Georgia during May and were observed to have eaten copepods (Robinson et al. 1968).

Nectoliparis pelagicus - Tadpole snailfish

Range: southern California to Bering Sea; Okhotsk Sea, Hokkaido

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Tadpole snailfish have been taken at a wide range of depths, 55-1,160 m, from southern California to the Bering Sea. Adults are also taken in the Asian Pacific in the Okhotsk Sea and near Hokkaido (Hart 1973).

No information on spawning biology is presently available.

Polypera beringiana - Bering snailfish

Range: unknown

Occurrence in Puget Sound: uncommon

Adult habitat: unknown

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

Bering snailfish have only been recorded from Puget Sound on one occasion (Miller and Borton 1980). Information on the life history and spawning in this snailfish is lacking.

Polypera greeni - Lobefin snailfish

Range: Washington to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: unknown

Spawning habitat: unknown

Spawning season: unknown

Mode of reproduction: unknown

Eggs: undescribed

Larvae: undescribed

No early life history or reproductive biology data are available. Adults range from Washington to the Bering Sea, and are only known on a few occasions from Puget Sound (Miller and Borton 1980; Hart 1973).

Liparis fucensis - Slipskin snailfish

Range: northern California to southeast Alaska

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: demersal

Spawning season: spring (British Columbia)

Mode of reproduction: oviparous

Eggs: demersal, guarded

Larvae: pelagic

Adult slipskin snailfish are known from shallow water to ~ 400 m in British Columbia, and range along the northeastern Pacific coastline from northern California to southeast Alaska (Hart 1973).

Ripening females have been taken in Burrard Inlet in February (Hart 1973) and Marliave (1975) found an egg mass in late May in B.C. waters. These eggs were placed among the tubes of the worm Eudistylia polymorpha and were attended by a ripe male. The eggs were about 1 mm in diameter and light orange.

On another occasion, a 55 mm SL male slipskin snailfish and several egg masses were found inside a 136 mm long pair of empty Mytilus valves near Tatoosh Island in the western Strait of Juan de Fuca. The spawn consisted of four contiguous, but nonoverlapping, multilayered masses of eggs which were attached to the inside of the right valve. The masses ranged in size between 20-25 by 20-25 by 5-6 mm and the unattached surface of each mass was hollowed out (doughnut-shaped). Each mass was a different color (tan, pink, or orange) and the stage of development within a mass was similar, but varied between masses. Individual eggs had a total average diameter of 0.980 $\pm$ 0.004 (SE) mm and yolk diameters averaged 0.712 $\pm$ 0.015 mm. The numbers of developing embryos per mass were 1,550, 1,660, 1,860, and 2,870 (DeMartini 1978). Additional data on fecundity and season of gonad maturation, based on examination of museum specimens by DeMartini, are included in Table 47.1.

According to Marliave (1975), eggs of slipskin snailfish reach the eyed staged in about ten days at 11°C, and hatch in 15-16 days. In late stages of development, eggs become silver-gray in color. At hatching, larvae are 3 mm TL with a subterminal mouth and large larval pectoral fins. Early stage larvae are laterally compressed and the cranial region is enclosed in a finfold-like sac. Pigmentation consists of a honeycomb (hexagonal) pattern of melanin on the pectorals, a postanal midventral row of numerous melanophores, a second row of melanophores

Table 47.1. Fecundity and size of ovarian eggs of slipskin snailfish, Liparis fucensis, from museum specimens collected in Washington and Oregon. Data based on counts and measurements of the larger of two size modes of ova present. (Source: DeMartini 1978).

Location, date, sample No.	SL, mm	Fecundity	Average diameter of ova, mm
Washington			
San Juan Channel, 23 July, UWCF 1237	62	1700	0.45
Saratoga Passage, 19 April, UWCF 2666	86	2300	0.60
California			
Mendocino Co., 17 August, CAS 28851	61	2100	0.60
Humboldt Co., 31 July, LACM 31936-12	62	2400	0.60
Humboldt Co., 21 June, SIO H52-79	76	--	--
Del Norte Co., 11 November CAS-SU 16684	92	4800	0.45

which develops on the ventral finfold margin, and melanophores which develop on the lower jaw (Fig. 47.1). According to Marliave, late larval stages resemble the adults.

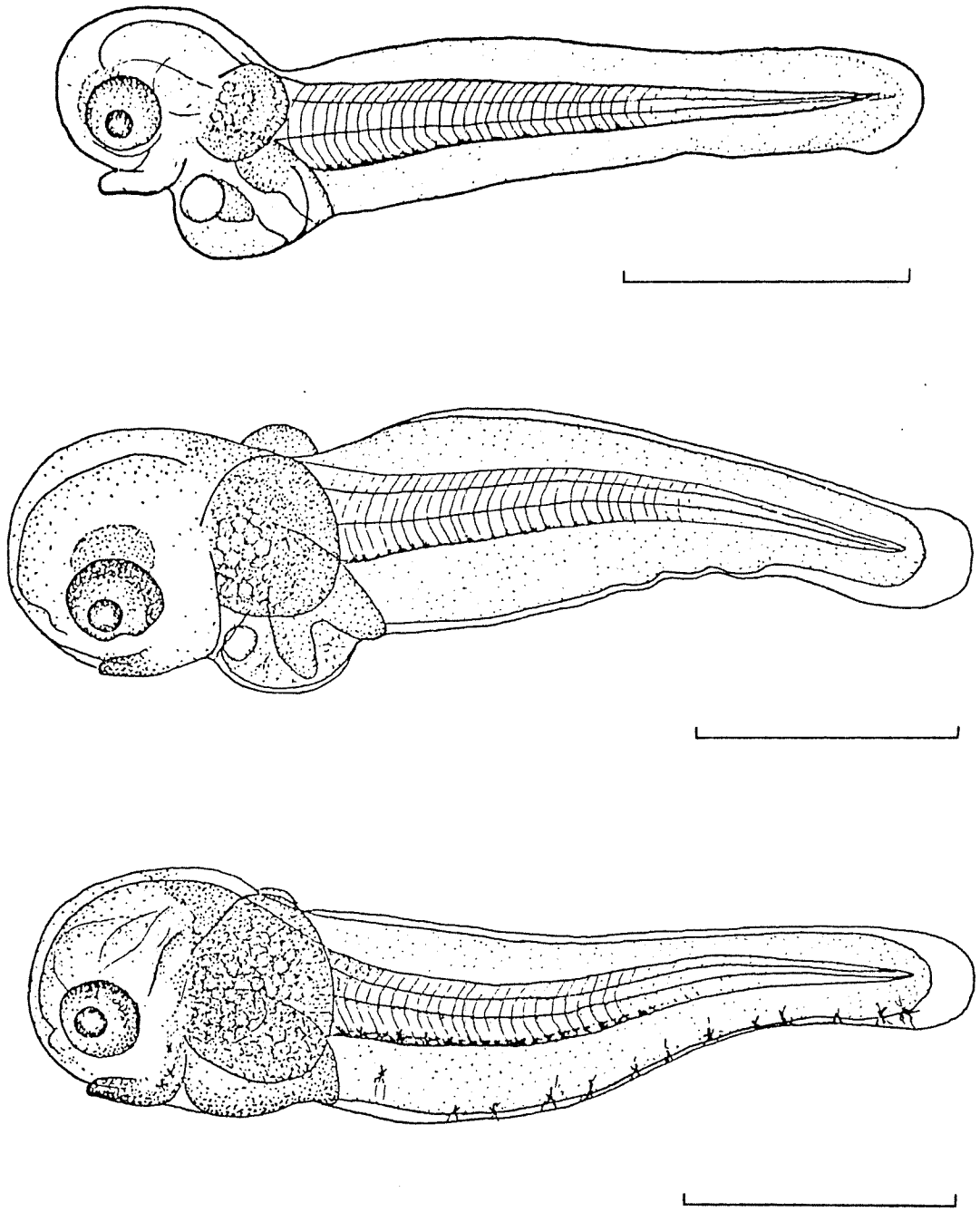

Fig. 47.1. Larvae of slipskin snailfish, Liparis fucensis: 1 mm scale; 0-day, 3 mm TL; 2-day, 3.5 mm TL; 7-day, 3.5 mm TL. (Source: Marliave 1975).

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48. BOTHIDAE

Citharichthys sordidus - Pacific sanddab

Range: Baja California to Bering Sea

Occurrence in Puget Sound: common

Adult habitat: demersal, shallow water

Spawning habitat: unknown

Spawning season: spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

The Pacific sanddab is a left-eyed flatfish which occurs commonly in Puget Sound and ranges from Baja California to the Bering Sea (Hart 1973; Miller and Borton 1980). It frequently inhabits shallow depths less than 20 m, but may occur as deep as 150 m (Demory 1971).

Only limited information is available on the spawning biology of this sanddab. In Puget Sound, males and females may reach sexual maturity at age II, although the majority mature at age III (Smith 1936). Off California, female sanddabs mature at 165 mm, with 23% mature at 185 mm, 50% mature at 191 mm, 90% mature at 205 mm, and almost all females over 225 mm are mature (Arora 1951).

Spawning season in Puget Sound is reported to be March through May with most spawning activity taking place in March and April (Smith 1936). In California, spawning occurs later in the year from July to September with a peak in August (Arora 1951).

Mature eggs of Pacific sanddab are spherical, translucent, contain a single oil globule and measure 0.55-0.77 mm in diameter. Females may mature more than one batch per season off California, although evidence is inconclusive (Arora 1951).

Larvae occur in the plankton, and off California the largest numbers are found during summer and are usually distributed inshore (Ahlstrom and Moser 1975).

Pacific sanddab larvae have not been described in any detail in the literature, but were illustrated by Ahlstrom (1965) and the figure was reproduced by Ahlstrom and Moser (1975)(Fig. 48.1). Larval Pacific sanddab less than 5 mm in length cannot be separated from larval speckled sanddab, C. stigmaeus, when they co-occur. However, when

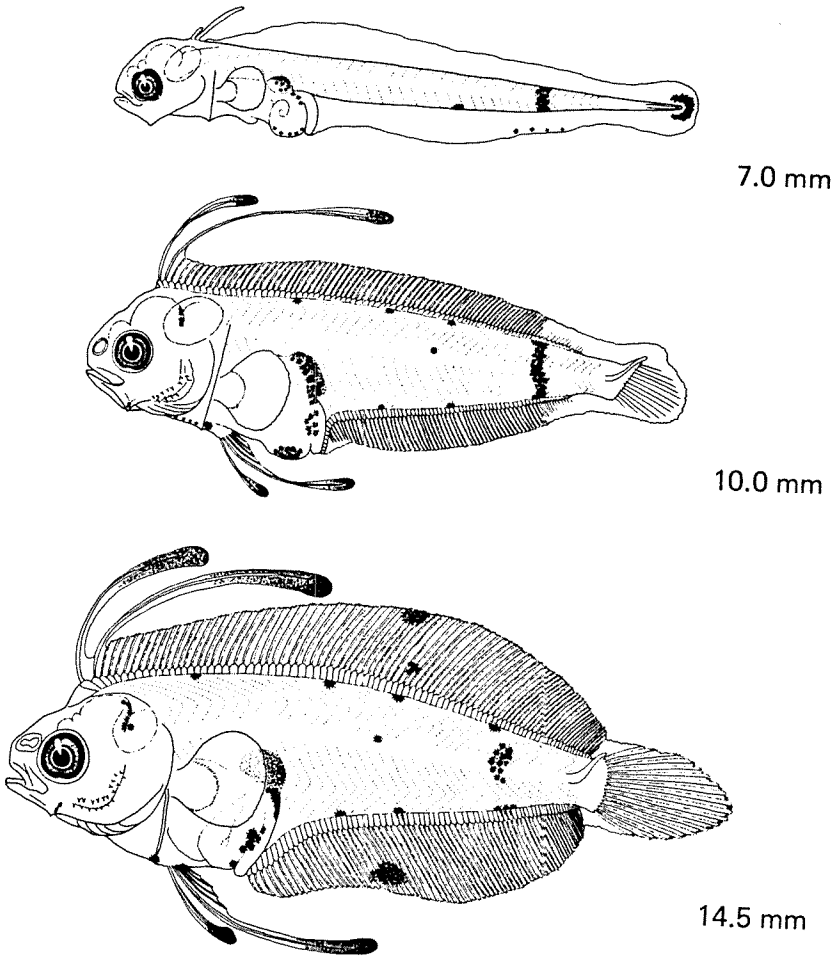


Fig. 48.1. Larvae of Pacific sanddab, Citharichthys sordidus. (Source: Ahlstrom and Moser 1975).

Pacific sanddab are over 5 mm, they develop characteristic fin ray modifications which make them easy to identify. These modifications consist of two elongated ornamented rays which develop at the beginning of the dorsal fin and two corresponding long, ornamented rays on the pelvic fin (Ahlstrom and Moser 1975).

Citharichthys stigmaeus - Speckled sanddab

Range: Baja California to southeast Alaska

Occurrence in Puget Sound: common

Adult habitat: demersal, shallow water

Spawning habitat: unknown

Spawning season: spring-summer (California)

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: pelagic

Speckled sanddab, a small, bothid flatfish, ranges from Baja California to southeast Alaska and is common in shallow nearshore sandy bottom areas (Hart 1973).

Very little is known about the reproductive biology of this species. Larvae are pelagic in the inshore region off California during June-August, but specimens up to 37 mm have been taken on occasion in the plankton offshore (Ahlstrom and Moser 1975). Speckled sanddab larvae 6.5, 10.0, and 14.75 mm were illustrated by Ahlstrom (1965) and the figure was reproduced by Ahlstrom and Moser (1975). They are characterized by eyes which become located on the left side of the head and the lack of elongated dorsal and pelvic rays like those found in Pacific sanddab larvae (Fig. 48.2).

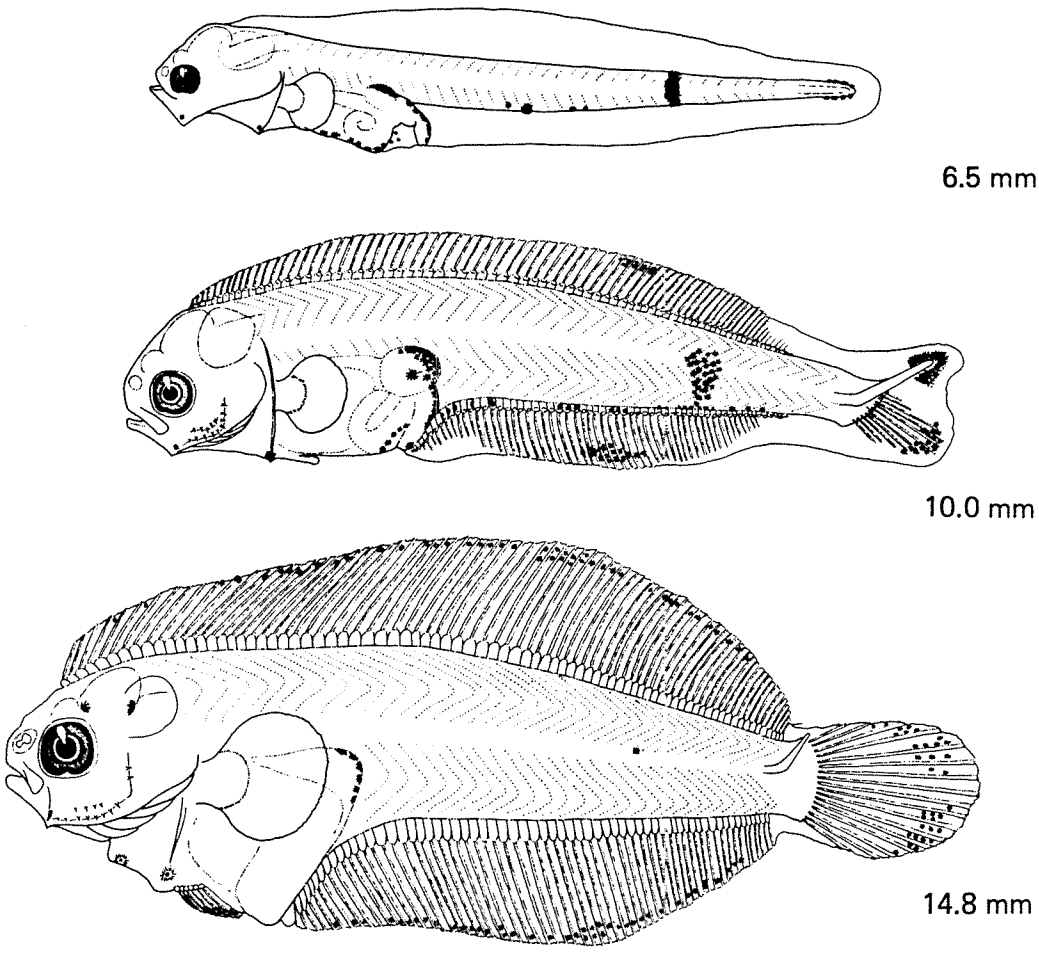


Fig. 48.2. Larvae of speckled sanddab, Citharichthys stigmaeus. (Source: Ahlstrom and Moser 1975).

49. PLEURONECTIDAE

Atheresthes stomias - Arrowtooth flounder

Range: central California to eastern Bering Sea

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: winter

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: pelagic

The early life history and reproductive biology of arrowtooth flounder is not well known. The adults, which inhabit deep water down to 900 m, are distributed from central California to the eastern Bering Sea where they overlap with the closely related Asian-dwelling species, A. evermanni (Hart 1973).

In the Bering Sea, arrowtooth flounder are reported to spawn from December to March with most fish spawning in January and February. It is thought that spawning takes place at depths greater than 150 m in water temperatures of 2-3^{o}C (Pertseva-Ostroumova 1960).

There is no information on size and age at spawning or fecundity of American arrowtooth flounder; however, the Asian species, A. evermanni is reported to mature at 9-10 years of age for females, and 6-7 years for males. Fecundity of A. evermanni is reported to be 130,000 to 500,000 eggs (Pertseva-Ostroumova 1961).

In March, eggs which were removed from a ripe female arrowtooth flounder near the Pribilof Islands measured 1.7 to 2.0 mm, although the eggs did not appear to be fully expanded. If fully expanded, diameters were estimated to be 2.5-3.5 mm. Spawned eggs may be bathypelagic (Pertseva-Ostroumova 1960, 1961).

Only a few larval stages of arrowtooth flounder have been described. Larval body form is reported to be low and "perch-like" and the yolk sac becomes absorbed in larvae by the time they are 9.8 mm in length. Pigmentation of small larvae is characterized by three concentrations of large stellate melanophores-- one located dorsal to the posterior half of the gut and the other two concentrations of pigment located on the tail. In older larvae, melanophores appear on the head and concentrations of pigment on the tail appear as bands (Fig. 49.1).

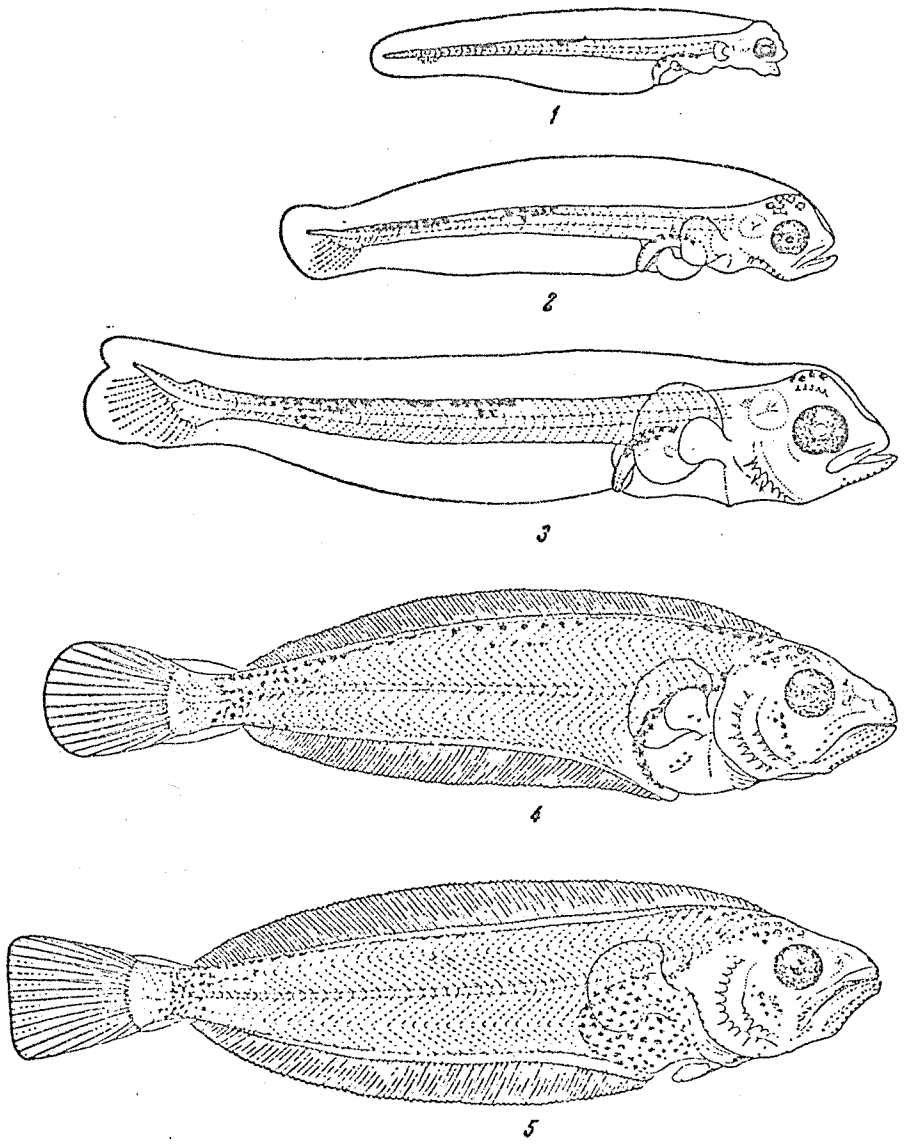


Fig. 49.1. Larvae of American arrowtooth flounder, Atheresthes stomias, (4-5), and Asian arrowtooth flounder A. evermanni (1-3). (Source: Pertseva-Ostroumova 1961).

At 26.8 mm TL, arrowtooth founder are still symmetrical. The body remains perch-shaped with a maximum body depth of 20-23% of its length. The mouth is large and the snout is rather long. By 38.5 mm TL, the left eye has migrated to a position slightly higher than the right eye. Fin rays have formed on the dorsal, anal, and caudal fins, but the pectorals remain fan-shaped and without rays. A unique feature of larval Atheresthes is the presence of preopercular and opercular spines, and spines on the upper portion of the head. These spines are present during the larval period and become embedded during development. Pigmentation of larvae 26.8 mm TL and 38.5 mm TL consists of a concentration of melanophores above the rear half of the gut and two concentrations on the dorsal body surface which divides the tail into three almost equal portions. Melanophores are also present on the trunk, head, and lobe of the pectoral fin (Fig. 49.1) (Pertseva-Ostroumova 1961).

Eopsetta jordani - Petrale sole

Range: Baja California to Bering Sea

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: demersal

Spawning season: winter

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Petrale sole are a commercially important flatfish species which ranges from Baja California to the Bering Sea (Hart 1973). They may be found on the bottom from nearshore (surfline) to the upper continental slope (460 m). Commercial quantities are found at a depth range of 70 to 128 m during spring through fall and to 460 m in winter (Forrester 1969a).

Off the west coasts of British Columbia, Washington, and Oregon, spawning takes place in winter primarily from December to April with some variability among areas (Alderdice and Forrester 1971; Harry 1959).

Along the coasts of California, Washington, and British Columbia, petrale sole are known to undertake spawning migrations to the deep waters of the continental shelf. Tagging studies have shown that most petrale sole spawn in the same deep water area each winter and migrate shoreward during summer to inshore feeding areas (Alverson and Chatwin 1957; Best 1963; Pederson 1975; DeDonato and Pasquale 1970). In summer, adults from several spawning groups may intermingle, but the extent of mixing is not well-known.

In the spawning population off Vancouver Island, known as Esteban Deep (Fig. 49.2), almost no small immature individuals are present, suggesting that immature fish do not participate in the annual offshore migration (Alverson and Chatwin 1957). From the Hecate Strait population, 50% of petrale sole males are mature at 38 cm and age VII and 50% of females are mature at 44 cm and age VIII. The smallest mature males are 32 cm (age IV) and smallest mature females are 35 cm (age V). Some males of 43 cm and females of 47 cm may remain immature (Ketchen and Forrest 1966). Off of the Columbia River, 50% of females are mature at 40 cm (smallest mature female is 31 cm) and 50% of males at 36 cm (smallest mature male is 29 cm)(Harry 1959).

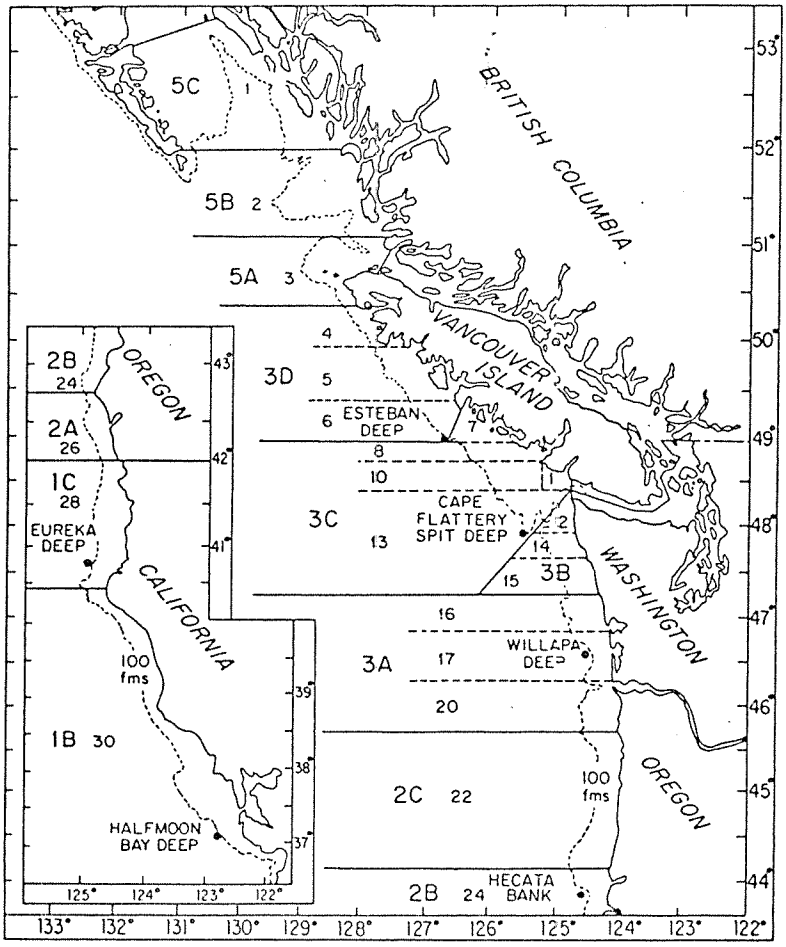


Fig. 49.2. Location of spawning areas (.) of petrale sole, Eopsetta jordani, off the coasts of California to British Columbia. (Source: Pederson 1975).

The fecundity of petrale sole ranges from 400,000 eggs for a female of 42 cm to 1,200,000 eggs for a 57 cm female (Forrester 1969a).

The unfertilized ovarian egg is plastic, nonadhesive, almost transparent, but not always spherical as it may be flattened at points of contact with other eggs. The mean diameter of fertilized eggs is 1.26 mm (1.13-1.52 mm)(Forrester and Alderdice 1967). Several studies were undertaken to study the effect of varying salinity and temperature on the development of petrale sole eggs (Forrester and Alderdice 1967; Alderdice and Forrester 1971). At 8.5°C and 27.5 °/oo, development from fertilization to hatching requires about 6 days. Development at 4.0°C and 27.5°/oo takes 13.5 days.

Larval petrale sole are about 3 mm at hatching and grow to about 5.5-5.7 mm at the point of yolk exhaustion, in 10-16 days (Alderdice and Forrester 1971).

Descriptions of petrale sole larvae from the literature are lacking, except for newly hatched larvae reared by Alderdice and Forrester (1971). These larvae are very undeveloped at hatching, appearing as if hatching was premature. They are unpigmented and even the eyes lack pigment, although the lens and optic cups are present. Larvae show the first sign of pigmentation at 63 hrs after hatching which consists of two rows of melanophores near the end of the tail on the dorsal and ventral body surfaces. At 104 hrs after hatching, additional pigment appears midway between the end of the tail and the anus, on the midline above the posterior margin of the yolk sac, on the hindgut, and in the region of the heart between the body midline and the yolk sac (Fig. 49.3 C, D). With development, golden yellow-brown pigment appears and underlies the primary areas of melanophores (shown as heavy stippling in Fig. 49.3). With further development, these areas of pigment and melanophores become prominent, especially on the hindgut and anus. The eyes show signs of pigmentation after 187-206 hrs and are well pigmented after 246 hrs (Alderdice and Forrester 1971).

Artificially reared larvae remain passive for most of their posthatch period and do not begin spontaneous swimming movements until they are 10 days old (Alderdice and Forrester 1971).

Pearcy et al. (1977) collected larval petrale sole 10-22 mm off the coast of Oregon during March-June and estimated their pelagic life to be about six months. He reported that age group 0 juveniles occurred only on the inner continental shelf during fall. Petrale sole of ages 1-2 yrs are known from bottom waters of 18-71 m (Forrester 1969).

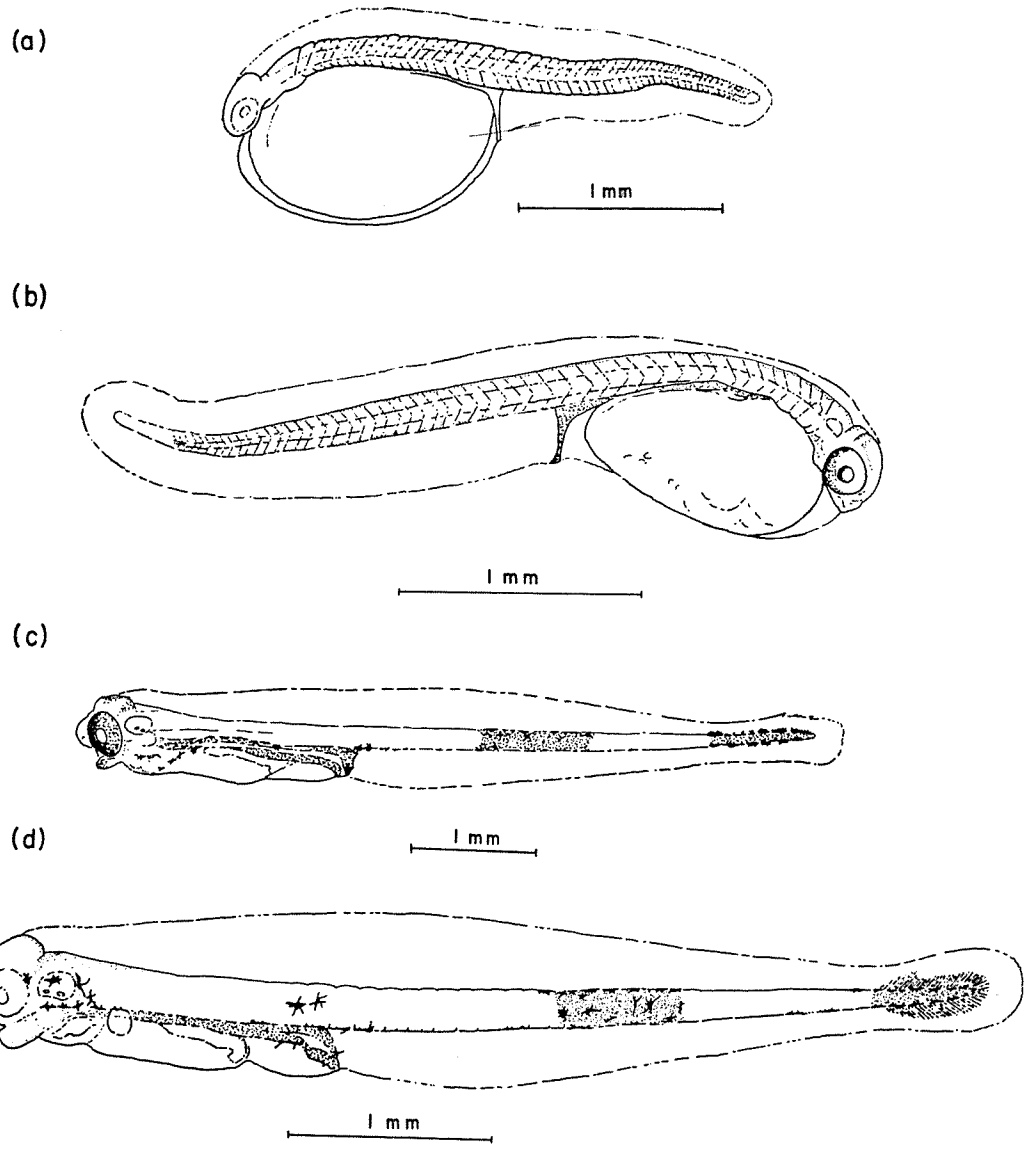


Fig. 49.3. Larvae of petrale sole, Eopsetta jordani: a) newly hatched; b) 2-day old larva, 3.33 mm; c) and d) 16.5-day old larvae, 6.20 mm. (Source: Alderdice and Forrester 1971).

Glyptocephalus zachirus - Rex sole

Range: southern California to Bering Sea

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: undescribed

Larvae: pelagic

Rex sole range from southern California to the Bering Sea (Hart 1973). Adults are most abundant in water deeper than 366 m and are found to depths of 730 m (Alverson et al. 1964).

There is little published information on the reproduction and early life history of rex sole. Off Oregon, spawning fish are found from January to June, although the peak of the spawning is in March-April (Hosie and Horton 1977). Smith (1936) found ripe female rex sole in Bellingham Bay and Strait of Georgia during February and March, respectively, and reported that rex sole spawn off the Washington coast during May and June.

Some rex sole males off the Oregon coast are mature at 13 cm, with 50% mature at 16 cm and age 3, and all males over 21 cm and 5 years of age are mature. Female rex sole in the same area do not reach maturity until 19 cm, with 50% mature at age 5 and 24 cm in length. All females of age 9 and greater and 30 cm or more are mature (Hosie and Horton 1977). Villadolid (1929, cited in Hosie and Horton 1977) found both males and females off San Francisco, California, were fully mature at age 4 and 21.8 cm for males and 22.8 cm for females.

Oregon rex sole females produce 3,900 eggs at 24 cm TL and 238,100 eggs at 59 cm TL (Fig. 49.4). In eleven out of thirteen fish examined, the right ovary contained between 100 to 12,700 more eggs than the left ovary. Fecundity was positively correlated with length (0.9620) and the formula for the linear regression was $F=5.3797 \times 10^{-7} L^{4.22667}$, F=number of ova, L=total length of fish (Hosie and Horton 1977).

Rex sole eggs have not been described in the literature, although they are reported to be 1.98-2.34 mm in diameter (Pearcy et al. 1977). Larvae are also undescribed, although Ahlstrom and Moser (1975) briefly described and illustrated several sizes (Fig. 49.5). According to Ahlstrom and Moser (1975), rex sole larvae are similar in appearance to

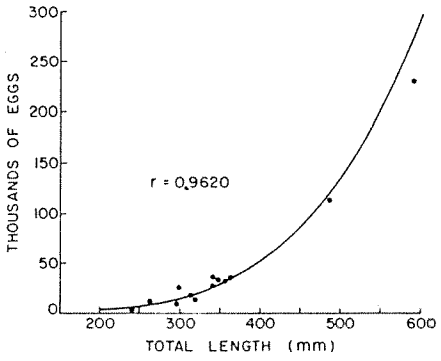


Fig. 49.4. Fecundity-length relationship for 13 rex sole, Glyptacephalus zachirus, collected off Oregon in February, 1970. (Source: Hosie and Horton 1977).

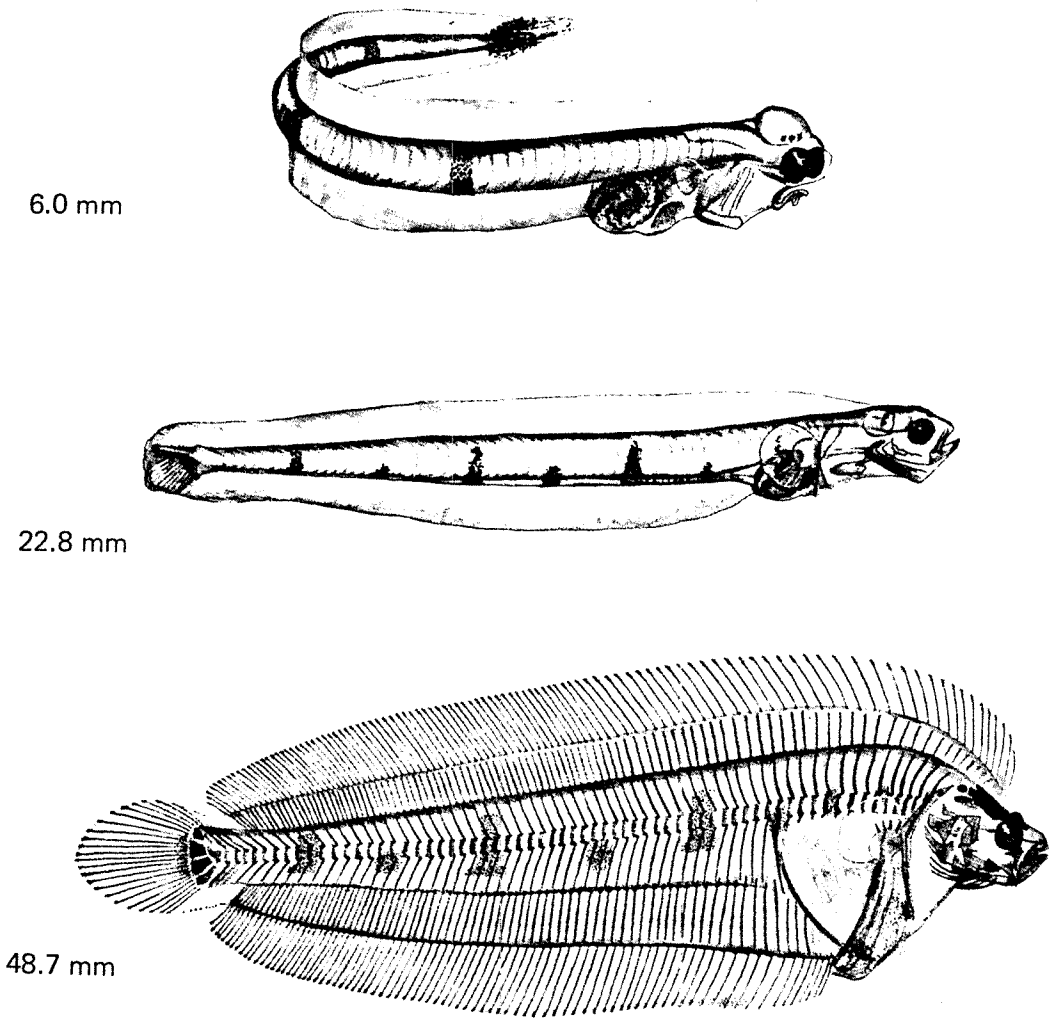


Fig. 49.5. Larvae of rex sole, Glyptocephalus zachirus. (Source: Ahlstrom and Moser 1975).

G. stelleri described by Deknik (1963), Pertseva-Ostroumova (1961) and Okiyama (1963). Rex sole are distinguished from other flatfish larvae by pigmentation (particularly the arrangement of pigment into several bands on the tail), a slender elongate body form, and a high myomere count, 62-65. Rex sole are also characterized by being able to attain a large size before transformation, up to 50-70 mm SL (Ahlstrom and Moser 1975). Off Oregon, rex sole larvae up to 89 mm which had not transformed were taken from the plankton (Table 49.1), and Pearcy et al. (1977) estimated some rex sole larvae may be pelagic for more than one year.

Off Oregon, rex sole larvae > 11 mm are most common in waters beyond the continental shelf and settle during winter at about 1 year of age on the outer continental shelf (Pearcy et al. 1977).

Table 49.1. Summary of captures of larvae of Dover sole, Microstomus pacificus, rex sole, Glyptocephalus zachirus, and petrale sole, Eopsetta jordani from mid-water trawls and plankton tows in the northeast Pacific. (Source: Pearcy et al. 1977).

Study	Location	Time	No. hauls	No hauls with Pleuronectids	*Microstomus*	*Glyptocephalus*	*Eopsetta*	No larvae taken	No. Pleuronectid larvae	No. *Microstomus* larvae	No. *Glyptocephalus* larvae	No. *Eopsetta* larvae
Aron[1]	Calif. to Alaska	July-Sept. 1957 June-Oct. 1958	564	67	24	10	0	7,400	232	66 (14-64 mm)	12 (15-77mm)	0
Porter (1964)	Northern Calif.	Jan. 1959-Jan. 1964	59	21	0	4	2	[2]192	154	0	10 (25-62 mm TL)	2 (21-22 mm TL)
LeBrasseur[3]	NE Pacific	1956-59	>3,000	70	30	9	0	1,287	98	35	13	0
Waldron (1972)	Oreg. to B.C.	Apr.-May 1967	88	19	4	4	0	4,577	626	4	10	0
Naplin et al.[4]	Wash. to B.C.	Oct.-Nov. 1971	30	3	1	1	0	343	14	1	1	0
Richardson (1973)	Oreg.	May-Oct. 1969	354	52	9	18	4	55,049	123	10 (12-61 mm SL)	31 (22-89 mm SL)	4 (13-21 mm SL)
This study												
Bongo transect	Oreg.	Jan. 1971-Aug. 1972	287		32	41	1	23,578		75 (5-26 mm SL)	107 (4-67 mm SL)	1 (20 mm SL)
Bongo grid	Oreg.	Mar.-Apr. 1972, 1973 Mar. 1974, 1975	306		36	75	1	34,029		51 (4-21 mm SL)	181 (5-24 mm SL)	1 (18 mm SL)
Mid-water trawls	Oreg.	1961-74	≈2,200		313	199	25			568 (9-65 mm SL)	360 (11-89 mm SL)	44 (10-22 mm SL)

[1]Aron, W. 1960. The distribution of animals in the eastern North Pacific and its relationship to physical and chemical conditions. Dep. Oceanogr. Univ. Wash. Tech. Rep. 63, 65 p.
[2]Flatfishes only.
[3]LeBrasseur, R. 1970. Larval fish species collected in zooplankton samples from the northeastern Pacific Ocean 1956-1959. Fish. Res. Board Can. Tech. Rep. 175, 47 p.
[4]Naplin, N. A., J. R. Dunn, and K. Niggol. 1973. Fish eggs, larvae, and juveniles collected from the northeast Pacific Ocean, October-November 1971. NOAA-NMFS, Northwest Fish. Cent. MARMAP Surv. I Rep. 10, 39 p. + 121 tables.

Hippoglossoides elassodon - Flathead sole

Range: northern California to Bering Sea; Asian coast

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Flathead sole range from northern California to the Bering Sea and across the Pacific to the Asian continent. However, its distribution in the Bering Sea and along the Asian coast is uncertain because of an overlap of meristic characters between H. elassodon, H. robustus, and H. dubius (Wilimovsky et al. 1967). There is no uniform agreement on the taxonomic distinction of these species, and some authors consider them to be subspecies of H. elassodon. However, only H. elassodon has been recorded in North American waters south of the Alaskan peninsula, including in Puget Sound.

Flathead sole are found at depths down to 550 m and on the continental shelf off British Columbia and Alaska, are mainly found at depths between 275-365 m (Hart 1973).

In Puget Sound, flathead sole are widely distributed, and found on mud bottoms in 20-46 m, seeming to prefer bays over open water (Smith 1936).

The reproductive biology of flathead sole in the western Pacific was studied by Pertseva-Ostroumova (1961) and some spawning information and fecundity data for flathead sole (H. elassodon elassodon) in the Bering Sea are given by Fadeev (1965).

In Puget Sound, Miller (1969) found all males and females in age group II (2 years + 10-11 months) or older to be in a spawning condition. Most males (75%), but only some females can spawn at age I (1 year + 10-11 months), and both sexes are immature at age group 0 (10-11 months).

Spawning in East Sound, Orcas Island is from March to May, with a peak in spawning activity occuring in April to early May (Miller 1969). Smith (1936) reported finding mature flathead sole in Puget Sound from February to April.

Fecundity of flathead sole was studied in relation to wet weight of ovary, eviscerated body weight, total length, and age (Fig. 49.6). A female of 207 mm (age 1 yr) produced about 70,000 eggs and a female of 377 mm (age 5 yrs) produced about 600,00 eggs (Table 49.2)(Miller 1969).

In the East Sound population, the ratio of males to females was close to unity during the peak spawning months, but females predominated in May. By age group, males dominated females by 3-4:1 in age group II, but in age group III, females outnumbered males of the same age 2-6:1 (Miller 1969).

Eggs of flathead sole are well-known and have been described from a number of areas. Fertilized eggs range in diameter from 1.97 mm to 3.67 mm (Table 49.3). Alderdice and Forrester (1974) found that eggs of flathead sole can vary in size depending on time from fertilization, incubation conditions (i.e., temperature and salinity), and parentage, and these factors may contribute to the ranges of egg sizes reported for flathead sole in Table 49.3.

The unfertilized eggs are spherical, non-adhesive, range from 1.3-1.5 mm, and increase in diameter due to a swelling of the perivitilline space following fertilization (Fig. 49.7). Maximum size was attained after 7.5 hrs in eggs incubated by Miller (1969)(~ 30°/oo, ~ 10°C) and in 18-25 hrs in experiments by Alderdice and Forrester (1974) (27.5°/oo and 4.5°C; 25°/oo and 6°C). Yolk diameter remains more constant, averaging 1.52 mm (1.47-1.55 mm) (Alderdice and Forrester 1974).

Laboratory incubation of flathead sole eggs at various temperature-salinity combinations determined that eggs could develop normally under a wide range of salinities (10.42-39.5°/oo), but are more restricted by temperature. Total hatching success and viable hatch are both maximized at temperatures at or near 7.3-7.5°C and egg development is limited at temperatures less than or equal to 3.5-4.0°C. After hatching, larvae are more susceptible to salinity extremes with the lower limit of normal development of larvae at ~ 20°/oo. Optimal salinity range for development is 28-32°/oo.

Egg development time is significantly affected by temperature (Fig. 49.8). At 2.4-4.0°C, development requires ~ 21 days and takes only 7.2 days at 10.65°C. The length of the larvae at hatching also varies depending on the salinity and temperature that the eggs are incubated at. Larvae range from 3.2 mm at 15°/oo, 3.0°C to 6.3 mm at 25°/oo, 6°C (Alderdice and Forrester 1974).

Developmental events of flathead sole eggs incubated at ~ 9.8°C and ~ 30°/oo are summarized in Table 49.4. Formation of the blastodisc is complete after 2-3 hours and the eggs reach maximum diameter at about the 16-cell stage. The embryo becomes differentiated after about 50 hours and pigment cells appear at about 60 hours. Hatching begins

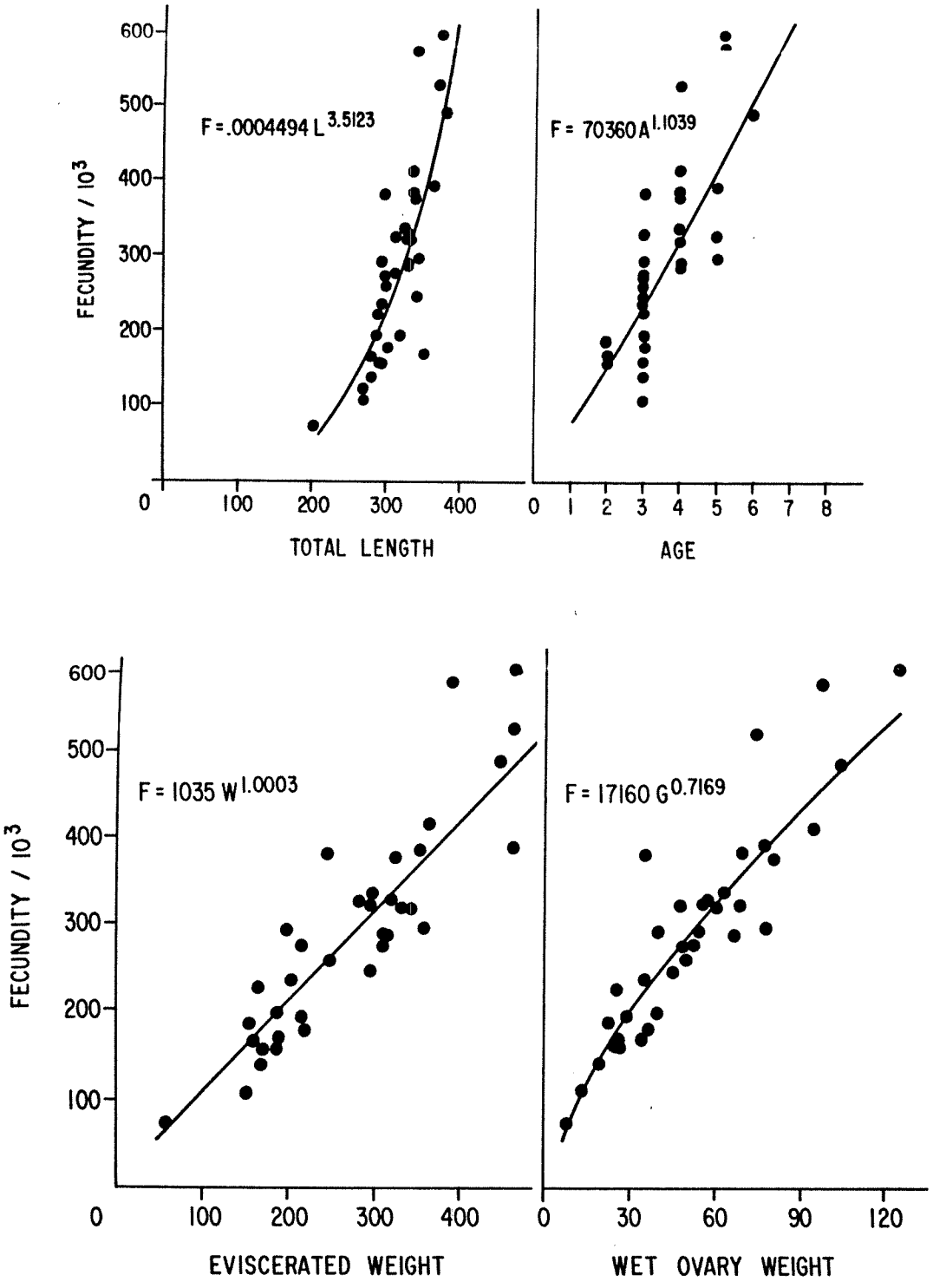


Fig. 49.6. Fecundity relationships by total length, age, eviscerated weight, and wet ovary weight for female flathead sole, Hippoglossoides elassodon. (Source: Miller 1969).

Table 49.2 Fecundity-length and fecundity-age data for flathead sole, Hippoglossoides elassodon, from East Sound, Orcas Island, Washington. (Source: Miller 1969).

Length, mm	Age, yr	Number of eggs
207	1	71,684
272	2	182,859
274	3	106,875
276	2	167,364
283	2	167,470
203	3	137,876
287	2	154,003
290	3	191,360
290	3	222,780
292	3	155,439
295	3	290,849
295	3	234,447
298	3	177,705
298	3	379,854
301	3	271,608
303	3	258,919
314	5	322,221
316	3	273,053
321	3	191,329
326	4	333,053
329	4	373,921
330	4	318,920
331	4	287,256
332	4	285,526
332	4	320,106
332	3	326,024
335	4	318,552
337	4	410,723
338	4	381,290
342	3	243,196
343	5	578,168
345	5	293,146
367	5	388,504
371	4	523,804
377	5	594,417
380	6	487,054

Table 49.3. Summary of size measurements for fertilized, unfertilized, live, and preserved[g] eggs of North Pacific Ocean Hippoglossoides. (Source: Alderdice and Forrester 1974).

Species and location	Total diameter (TD) mean (*mm*)	Total diameter (TD) range (*mm*)	Yolk diameter (YD) mean (*mm*)	Yolk diameter (YD) range (*mm*)	Perivitelline space (PVS) (*mm*)	PVS/TD (%)
H. elassodon — unfertilized, live						
Puget Sound, Wash., USA[a]	–	1.3–1.5	–	–	–	–
Strait of Georgia, B.C.[b] — unfertilized, preserved	1.31	–	–	–	–	–
Puget Sound, Wash.[a,g] — fertilized, live	1.4	1.3–1.5	–	–	–	–
Puget Sound, Wash.[a]	–	2.3–2.4	–	–	0.9–1.1	39–46
Puget Sound, Wash.[a]	2.4	2.1–2.7	–	–	0.8–1.3	42
Strait of Georgia, B.C.[b] — fertilized, preserved	2.48	1.97–2.96	1.52	1.47–1.55	–	25–48
Puget Sound, Wash.[a]	2.5	2.1–3.2	–	–	1.0–(1.4)[i]–2.2	57
Gulf of Alaska[c,g]	3.27	2.75–3.75	–	–	–	–
"Soviet waters"[d]	3.02–3.26	2.45–3.67	1.22–1.33	1.10–1.53	–	29–(31)–33
SW coast, Kamchatka Peninsula[e]	–	2.21–3.28	–	–	–	–
Central and SE Bering Sea[f,h]	–	2.4–3.55	–	–	–	–
H. robustus — fertilized, preserved						
SW Bering Sea[d]	2.27–2.54	2.04–2.69	0.98–1.10	0.86–1.14	–	26–(29.5)–32
Chukchi Sea[d]	–	2.17–2.46	–	0.90–1.02	–	25
H. dubius — unfertilized, live						
Ussuri Bay, USSR[d]	1.23	1.17–1.28	–	–	–	–
H. dubius — fertilized, live						
Ussuri Bay[d]	2.31	2.02–2.42	–	–	–	20–(23.7)–25.2
Ussuri Bay[d] — fertilized, preserved	2.27	2.02–2.34	1.03	0.97–1.1	–	–
Ussuri Bay[d]	–	–	–	–	–	32
Peter the Great Bay, USSR[g,h]	2.37–2.62	2.02–2.94	0.90–0.92	0.82–1.02	–	20–(27–30)–33

[a]Miller (1969); 48°40′N, 123°54′W. [b]This paper. [c]Thompson and Van Cleve (1936). [d]Pertseva-Ostroumova (1961). [e]Rass and Zheltenkova (1948); 53°00′N, 156°00′E. [f]Musienko (1963). [g]Preservatives: Miller — Stockard's solution (5% formalin-4% glacial acetic acid, 6% glycerin, 85% sea water); Thompson and Van Cleve — 3–4% formaldehyde; Pertseva, Ostroumova — 2% formalin. [h]Interpreted as preserved material. [i]Means in parentheses.

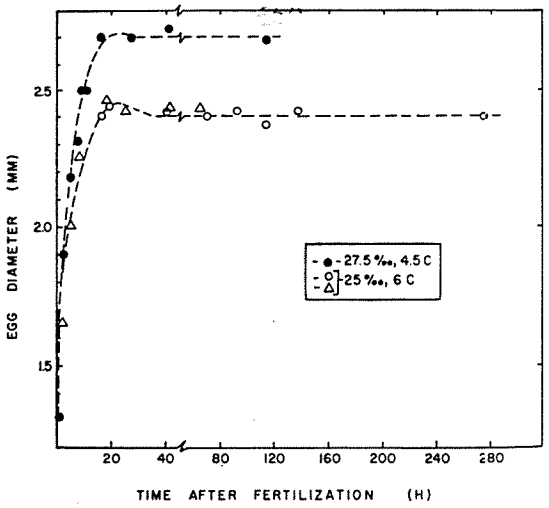


Fig. 49.7. Increase in egg diameter following fertilization of flathead sole, Hippoglossoides elassodon, eggs. (Source: Alderdice and Forrester 1974).

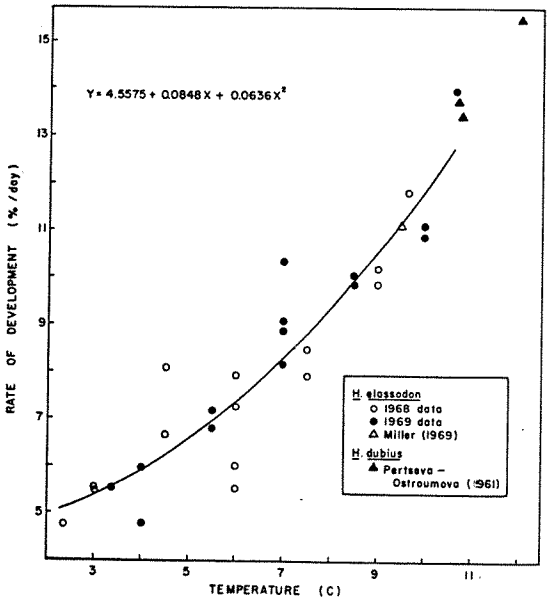


Fig. 49.8. Rate of development of flathead sole eggs in relation to incubation temperature. Multiple points at a given temperature represent trials at different salinities. (Source: Alderdice and Forrester 1974).

Table 49.4. Development of eggs of flathead sole, Hippoglossoides elassodon, from East Sound, Orcas Island, incubated at a mean temperature of 9.8°C and salinity of 30°/oo. (Source: Miller 1969).

Time (hours from fertilization)	Developmental event
.0	Unfertilized egg ∿1.3 mm.
.5	Yolk measures 1.4 mm, MPVS* is 0.1 mm.
3	Egg measures 1.8 mm with MPVS of 0.4 mm.
2-3	Formation of blastodisc.
3.5-4.5	2-cell stage; eggs measure 1.8-2.0 mm in diameter and MPVS is 0.4-0.6 mm.
5.5	4-cell stage; egg measures 2.1-2.2 with MPVS of 0.7-0.8 mm.
6.5	8-cell stage; egg measures 2.2-2.3 with MPVS of 0.8-0.9.
7.5	8-16-cell stage; egg reaches maximum size of 2.3-2.4 mm with MPVS of 0.9-1.1 mm.
8.5	16-cell stage.
10	32-cell stage.
15	Morula.
27	Blastodermal cap.
30	Germ ring visible.
47	Germ ring at equatorial position; embryo extends ∿1/4 of the way around the yolk.
52-58	Blastopore begins to close; notochord distinct; optic vesicles seen as lateral swellings, no lenses; Kupffer's vesicle appears.
60-62	Blastopore closed; brain apparent as slight swelling; pigment first appears.
90-115	Kupffer's vesicle disappears.
90-100	24 somites visible; tail begins to grow over the yolk; heart pulses; lenses present; auditory vesicles and olfactory sacs present; finfold and pectoral fins noticeable.
120-140	Otoliths appear in auditory capsules; embryo extends 1/2 circumference of shell; divisions of brain evident; embryos move.
190	Embryo extends 3/4 of the circumference of the shell.
216	Embryo extends almost one full circle and begins to hatch.

*Maximum perivitelline space

after 216 hours. Miller (1969) found that eggs began sinking to the bottom of the incubation containers about 24 hours before hatching began and were actually on the bottom for about 12 hr before the first hatching began.

Newly hatched larvae of flathead sole have been described by Miller (1969), Alderdice and Forrester (1974) and Pertseva-Ostroumova (1961). A comparison of their findings are summarized in Table 49.5 (Alderdice and Forrester 1974).

Pigment appears during the embryonic period as numerous small specks which are concentrated on the dorsal body surface between the head and tail regions with no order to the location of spots. These spots become larger and increase in number during development and cover the embryo from the tip of the head to the tip of the tail, except for a clear, lateral area on the posterior half of the body. Both xanthophores and melanophores are present during the embyronic stage. The yolk remains unpigmented until 140 hr after fertilization and melanophores appear on the edges of the finfold in the tail region at this time. Just prior to hatching, stellate melanophoresa appear on the yolk sac, body, and finfold. In pre-hatch embryos described by Pertseva-Ostroumova (1961), melanophores on the tail region are formed into 4 bands. However, Miller (1969) and Alderdice and Forrester (1974) report that banding does not become evident until after hatching (Table 49.5).

The newly hatching larvae are relatively undeveloped. The mouth is unformed and the eyes are colorless, except for a dark fringe around the lenses. Pigment is fairly widespread over the larva with several black stellate melanophores on the yolk and black melanophores in the posterior 2/3 of the finfolds, primarily along the dorsal and ventral edges. Black melanophore dominate, but xanthophores are also present. As the larva develops, the postanal body pigment begins to show banding which characterizes larval flathead sole. These consist of four bands of melanophores on the trunk musculature, each with a coincident band of yellowish xanthophores. The posterior three bands form first and a band of xanthophores precedes the formation of melanophores in the fourth, anterior-most band (Miller 1969; Alderdice and Forrester 1974). Pigment along the ventral surface extends from the dorsal gut area to the notochord tip. Dorsally, pigment is restricted to the bands and pigment is present in varying amount between individuals on the lateral body surface in the band areas. With development, the banding becomes distinct and melanophores appear on the lower jaw. Finfold pigment increases in number and intensity and melanophores sometimes merge with the postanal bands (Miller 1969).

The yolk sac is absorbed by the seventh day after hatching (Miller 1969) at sizes of 5.4-7.0 mm (Pertseva-Ostroumova 1961).

Larvae at 9.15-10.59 mm TL are still long and thin with a body height of only about 5% of body length. Snout to anus length is short,

Table 49.5. Comparison of larval characteristics of Hippoglossoides. The bulk of the table was extracted from Pertseva-Ostroumova (1961) and comparisons are made to North American larvae. (Source: Alderdice and Forrester 1974).

Characteristic		North American	Asian		
		H. elassodon		*H. robustus*	*H. dubius*
No. of times larvae encircle yolk prior to hatching		3/4[a]	1–1/2	–	3/4
Size of larvae (*mm*)					
at hatching	(live)	3.23–6.27[c,f]	–	–	3.0–(3.3)–3.4
	(fixed)	4.5–(4.6)–4.7[b]	5.3–(6.4)–6.94[g]	–	2.60–(3.0)–3.13
at yolk absorption	(live)	6.29–7.20[e] 6.60–(6.9)–7.20[b]	5.0–6.64[h]	–	5.28–5.75
	(fixed)	5.2–(5.6)–6.0[b]	5.39–(6.15)–6.97[g]	–	5.10–(5.40)–5.60
after yolk absorption	(fixed)	4.8–(5.2)–5.8[b]	6.10–(6.58)–7.12[i]	–	4.97–(5.20)–5.40
Yolk-sac length at hatching	(live)	1.16–1.91[d]	–	–	–
	(fixed)	–	0.79–1.01[g]	–	1.15–(1.26)–1.38
Pigmentation of embryo begins		prior to completion of tail-bud formation	prior to completion of tail-bud formation	prior to completion of tail-bud formation	prior to completion of tail-bud formation
Melanophore bands					
number		4	4	4	4
first occurrence		posthatching (2–13 days at 3.4–9.65 C)	prehatching	–	posthatching (3+ days at 13 C)
location		accumulation of melanophores above hindgut; origin of first band variable, starting on 2nd–5th myotome posterior to hindgut[a]	accumulation of melanophores above hindgut; origin of first band posterior to hindgut on tail myotomes 7–9[j]	–	accumulation of melanophores above hindgut, origin of first band posterior to hindgut on tail myotomes 5–10
Melanophores on finfold surrounding					
tip of tail		present	present	absent	absent
on dorsal margin of tail finfold		usually present	usually present	usually absent	usually absent

[a]This paper. [b]Miller (1969). [c]At mean hatching time, various temperatures (this paper). [d]From Fig. 4. [e]Calculated maximum lengths attained (this paper) [f]Miller (1969) obtained larvae at 9.5 C: 5.5–(6.0)–6.3 mm. [g]Field collection; material may have been somewhat older than stated. [h]"Recently hatched." [i]Range also shown as 6.10–7.42 in original text. [j]Estimated from sketches in original reference.

less than 1/3 of body length. The intestine forms a loop and the anus is at right angles to the body. Flexion of the notochord is underway and rudiments of the hypurals are forming. Pigment is present along the midline of the abdomen and the four tail bands remain (Fig. 49.9) (Pertseva-Ostroumova 1961).

At 11.0 mm, larvae show an increase in body depth and the lower jaw is long and straight creating a "pug-nose" appearance (Fig. 49.10). The larva is symmetrical and basal structures of the dorsal and anal fins appear. The pectorals are large and fan-like, the notochord is flexed, and caudal fin rays are appearing. The four band pigmentation arrangement is still clearly seen, although the fourth band is located along the posterior dorsally flexed notochord. Melanophores are also located along the edges of the dorsal and anal finfolds, on the caudal fin, in the anal area, and along the ventral margin of the cardiac region and at the angle of the lower jaw (Miller 1969).

At 22.0 mm, eye migration is underway and the dorsal, anal, and caudal fins bear the adult complements of rays. Pectorals are without rays and pelvic fins have appeared. Pigment consists of three bands on the dorsal and anal fins and partially transversing the body, and pigment occurs in the following areas: ventral edge in anal and cardiac region, lower jaw, anterior edge of dorsal fin, opercular area, snout, and caudal area. Pigment is the same on both sides of the body. Eye migration is further advanced in 28.6 mm TL specimen and is complete by about 31.5 mm (Miller 1969). At this size, the three bands are still visible but increasing pigment on the right side of the body is obscuring it. At 31.5 mm, the pectorals are pointed and fin ray development appears complete. At 47-58 mm, transformation is complete and flathead sole take on the adult form and coloration; the blindside is now completely colorless (Miller 1969).

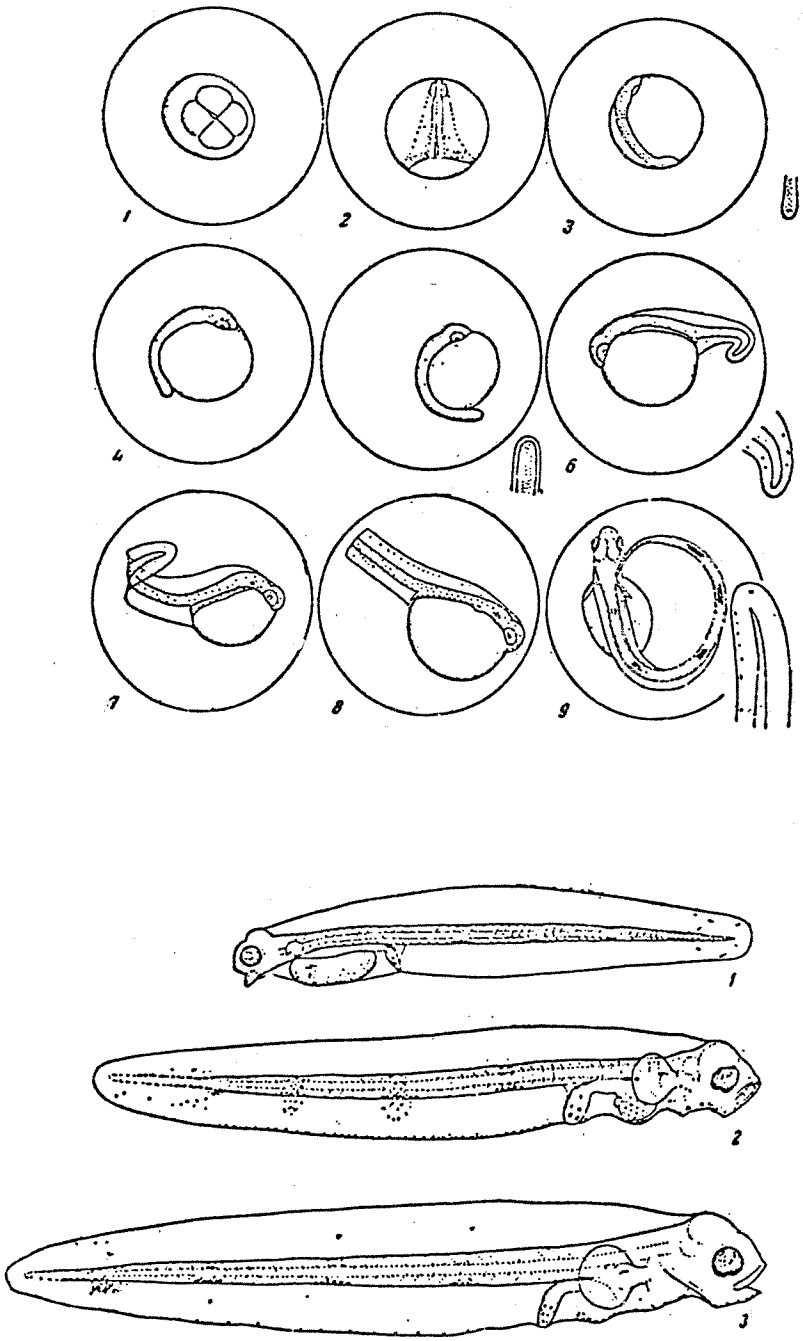


Fig. 49.9. Development of flathead sole, Hippoglossoides elassodon, eggs and larvae. Larval sizes are 5.6 mm, 9.15 mm, and 10.59 mm. (Source: Pertseva-Ostroumova 1961).

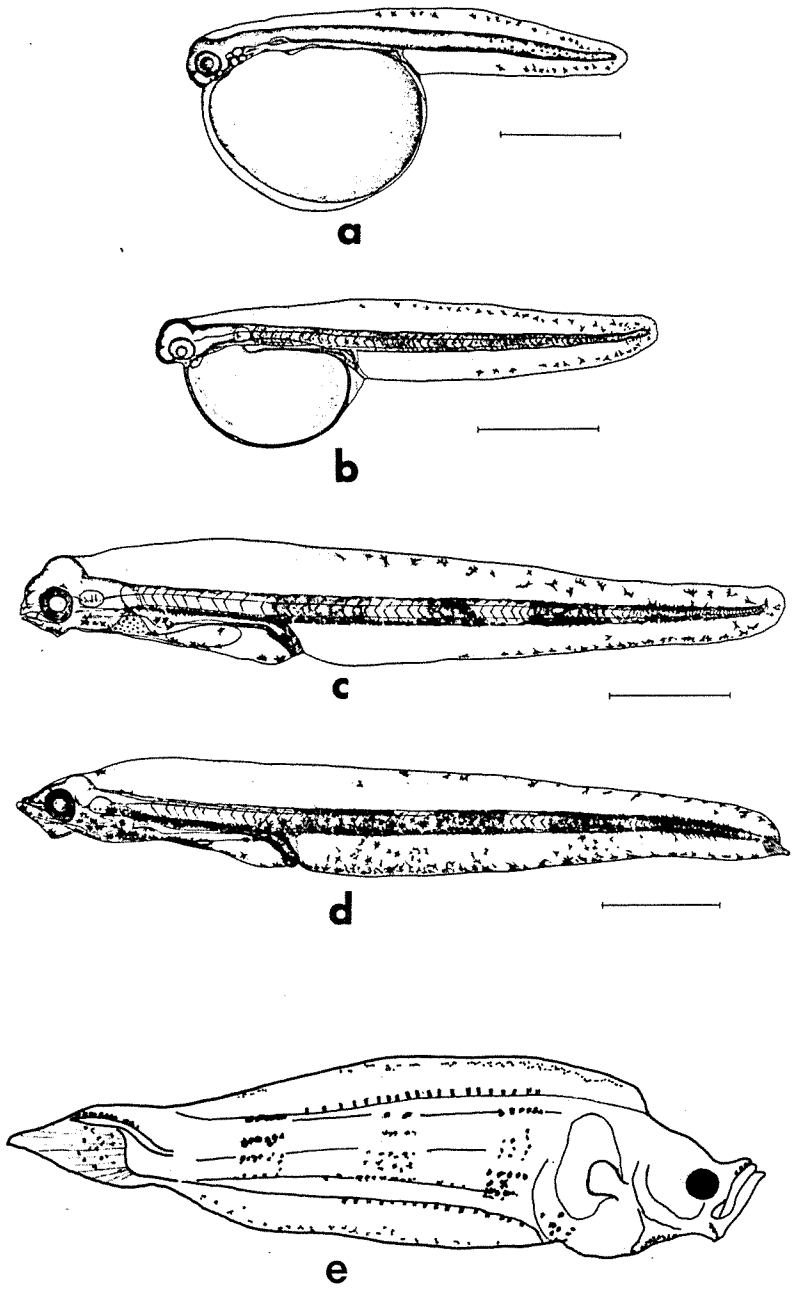


Fig. 49.10. Larval stages of flathead sole, Hippoglossoides elassodon: a,b) newly hatched larvae; c) 2-day-old larvae; d) 10-day-old larva; a-d, 1 mm scale, (Source: Alderdice and Forrester 1974); e) 11.0 mm TL larval, (Source: Miller 1969).

Hippoglossus stenolepis - Pacific halibut

Range: southern California to Norton Sound; Anadyr to Hokkaido

Occurrence in Puget Sound: uncommon

Adult habitat: demersal

Spawning habitat: demersal

Spawning season: winter

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Pacific halibut are a commercially important Northeast Pacific flatfish which ranges from southern California to the Bering Sea, Norton Sound and parts of the western Pacific from Anadyr to Hokkaido (Hart 1973). Adults are benthic to depths of 1100 m (Hart 1973) and associate with water temperatures of 3-8^{o}C (Thompson and Van Cleve 1936).

Halibut spawn during the winter months (Thompson 1915, 1917) at depths of 275-410 m. In the Gulf of Alaska, tagging studies indicate that adults generally migrate from summer feeding grounds to winter spawning areas and return after spawning. However, not all adults return to the same grounds each year and some have been found to make extensive migrations (Skud 1977).

Age of 50% maturity of female halibut is at 12 years (Thompson 1915, 1917; Schmitt and Skud 1978). Schmitt and Skud (1978) found that the age of 50% maturity decreased to 8.8-10.7 years on the winter spawning grounds, indicating that immature fish may not migrate with mature fish. Length of 50% maturity is at about 120 cm (Schmitt and Skud 1978).

Fecundity of the Pacific halibut is quite high, ranging from several hundreds of thousands to almost 4 million eggs per female. Fecundity data have been presented by Thompson (1917), Kolloen (1934), and Schmitt and Skud (1978) who compared estimates from all three studies. They found that the number of eggs produced by a female of a particular age had significantly increased since the 1920's (Fig. 49.11). However, the relationships between fecundity and length and weight have changed only slightly (Fig. 49.11). They also found that fecundity was best estimated by size, and the addition of age data did not significantly increase the precision of the fecundity estimate.

Pacific halibut eggs can be distinguished by their large size, small perivitelline space, lack of oil globules, and outer surface which

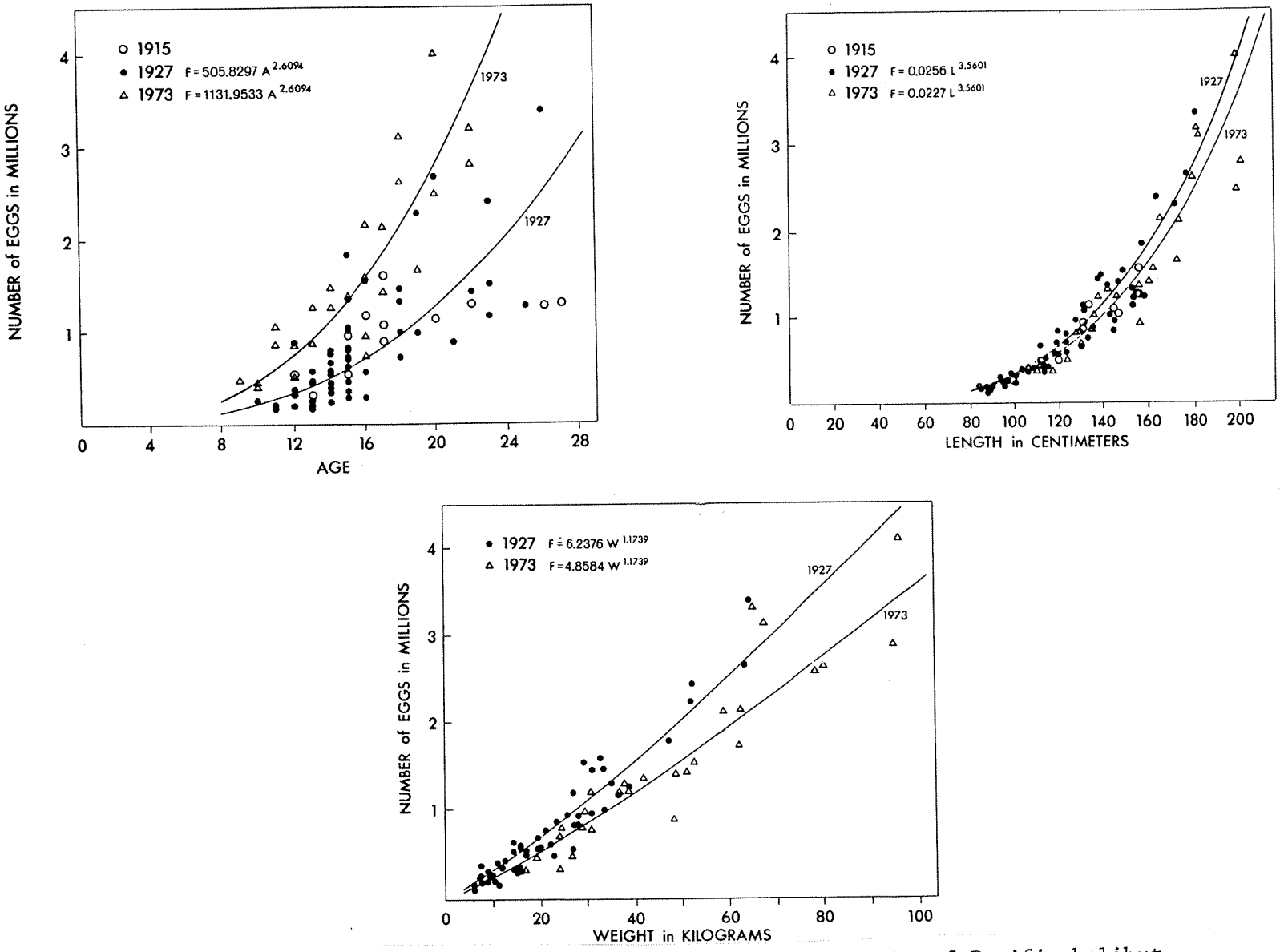


Fig. 49.11. Relationship of fecundity to age, length, and weight of Pacific halibut, Hippoglossus stenolepis. (Figures and 1973 data from Schmitt and Skud 1978; 1915 data from Thompson 1917; 1927 data from Kolloen 1934).

is covered by numerous small holes (Thompson and Van Cleve 1936). The unfertilized egg is plastic, nonadhesive, and transparent with a network of discontinuous striations on the surface. Their average size is 3.14 mm (range: 2.87-3.36 mm)(Forrester and Alderdice 1973), but after fertilization reach an average size of about 3.3 mm (Forrester and Alderdice 1973, range 2.95-3.52 mm; Thompson and Van Cleve 1936, range 2.05-3.85 for live material and 2.90-3.8 mm for preserved).

In incubation exeperiments, eggs were neutrally buoyant in water of salinity greater than 31.5°/oo, and although hatching success was generally poor in all experiments, the highest hatching percentage occurred at temperature of 7°C, and was lowest at 5°C. Development of embryos did not continue at 2, 4, 10 and 12°C. Incubation times ranged from 12.5 days at 8°C to 20 days at 5°C (Fig. 49.12, 49.13). Photos of egg development are provided by Forrester and Alderdice (1973). An interesting feature noted during development was the presence of 1-35 Kupffer's vesicles which occurred in eggs near the end of blastopore closure.

Halibut in the Gulf of Alaska congregate on spawning banks during the winter mostly from November to January, and eggs are found between 40 and 900 m, but are concentrated at 100-200 m. The newly hatched larvae are found lower than the eggs and in the Gulf of Alaska occur beyond the edge of the continental shelf and below depths of 200 m. With development, larvae rise into upper water layers and by the time they are 3-5 months old, they are at depths of 100 m or less. As they rise, larvae are carried inshore by surface currents and are found on the bottom near shore in May and June. Hence, the pelagic life of the Pacific halibut may be 6 months or so (Thompson and Van Cleve 1936). In the Gulf of Alaska, eggs and larvae tend to drift in a counterclockwise direction, and Skud (1977) has postulated that migration of juveniles and some adults is clockwise to offset the displacement of halibut populations due to larval drift.

Newly hatched halibut larvae are large (7.8-15.0, $\bar{x}$ = 11.2 mm), symmetrical, contain a large oval yolk sac and are unpigmented (Fig. 49.14). Compared to other flatfishes found in Puget Sound, halibut appear more undeveloped at a larger size than most. Larval pigmentation first appears along the margin of the anal and dorsal finfold and as scattered melanophores on the ventrolateral surface of the body. The yolk is absorbed and flexion begins at an average size of 15 mm. After flexion is underway, the body depth begins to deepen noticeably. Eye migration begins in larvae at sizes of 14 to 16 mm. Dorsal, anal, and caudal fin ray development is complete by ~ 18 mm, but pelvic fin ray development is not complete until ~ 19.6 mm, and pectoral fin rays do not form until larvae are 19-25 mm. Larval pigmentation begins to show definite grouping of chromatophores at sizes of 17.9-21.4 mm (Fig. 49.14H), which persists until transformation to juvenile coloration takes place (~ 26 mm) (Table 49.6; Fig. 49.14).

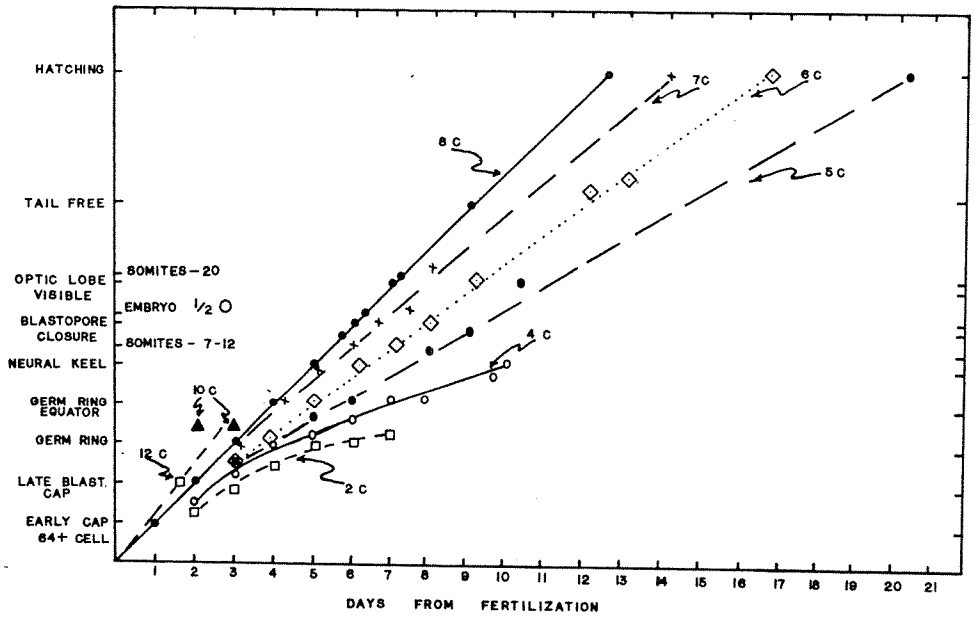


Fig. 49.12. Time required to reach various stages of development for Pacific halibut, Hippoglossus stenolepis, eggs incubated at 2° to 12°C and 33°/₀₀. (Source: Forrester and Alderdice 1973).

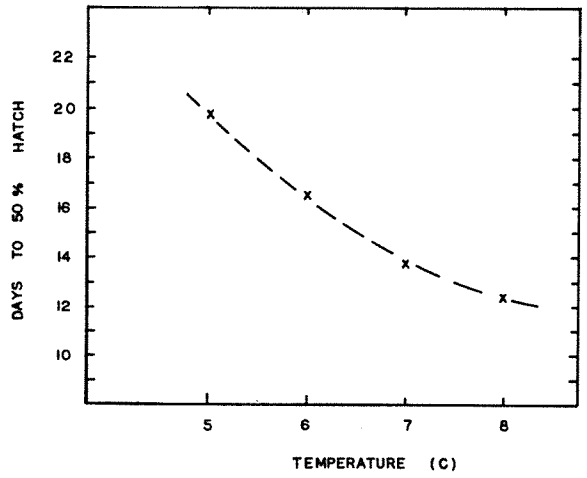


Fig. 49.13. Estimated time of 50% hatch of Pacific halibut eggs at various temperatures and 33°/₀₀. (Source: Forrester and Alderdice 1973).

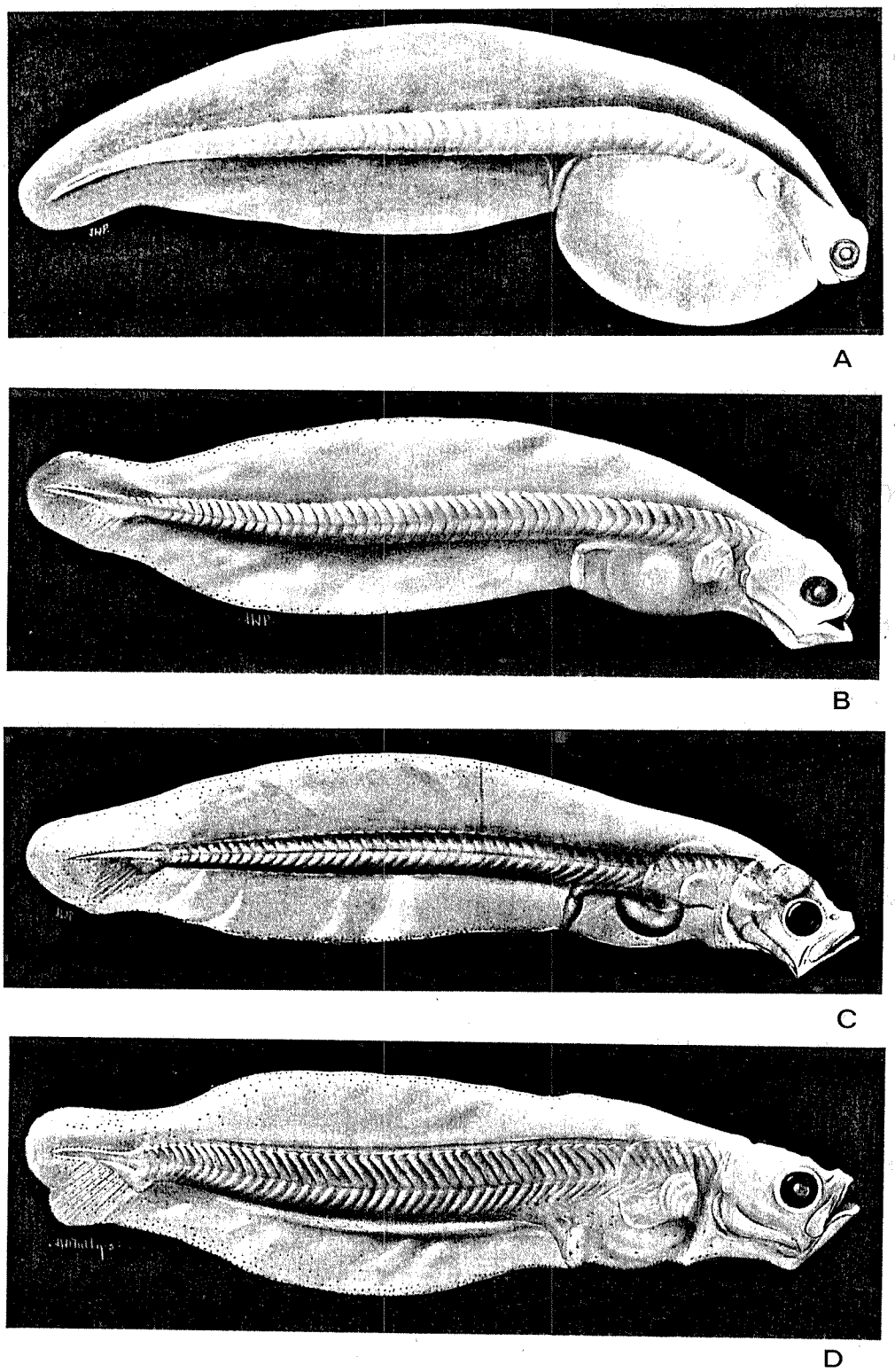


Fig. 49.14. Development of larval Pacific halibut, Hippoglossus stenolepis: A) stage 1, newly hatched; B) stage 2, 14 x natural size; C) stage 3, yolk absorbed, 12 x natural size; D) stage 4, 11 x natural size. (Source: Thompson and Van Cleve 1936).

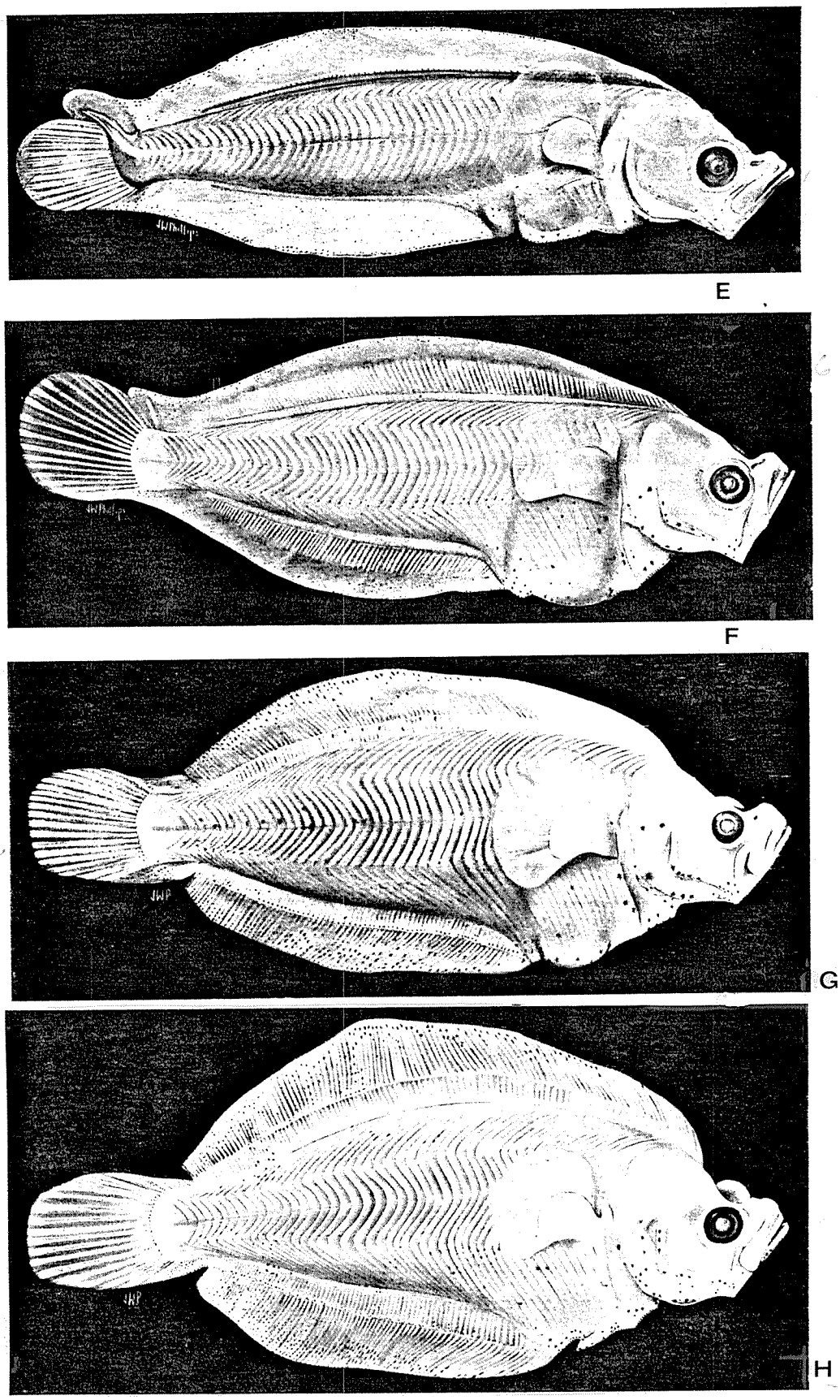


Fig. 49.14. (cont.'d) Development of larval Pacific halibut, Hippoglossus stenolepis: E) stage 5, appearance of basal structures in dorsal and anal fins, 12 x natural size; F) stage 6, development of fin rays, 11 x natural size; G) stage 7, 9 x natural size; H) stage 8, melanophores begin to form characteristic pattern. (Source: Thompson and Van Cleve 1936).

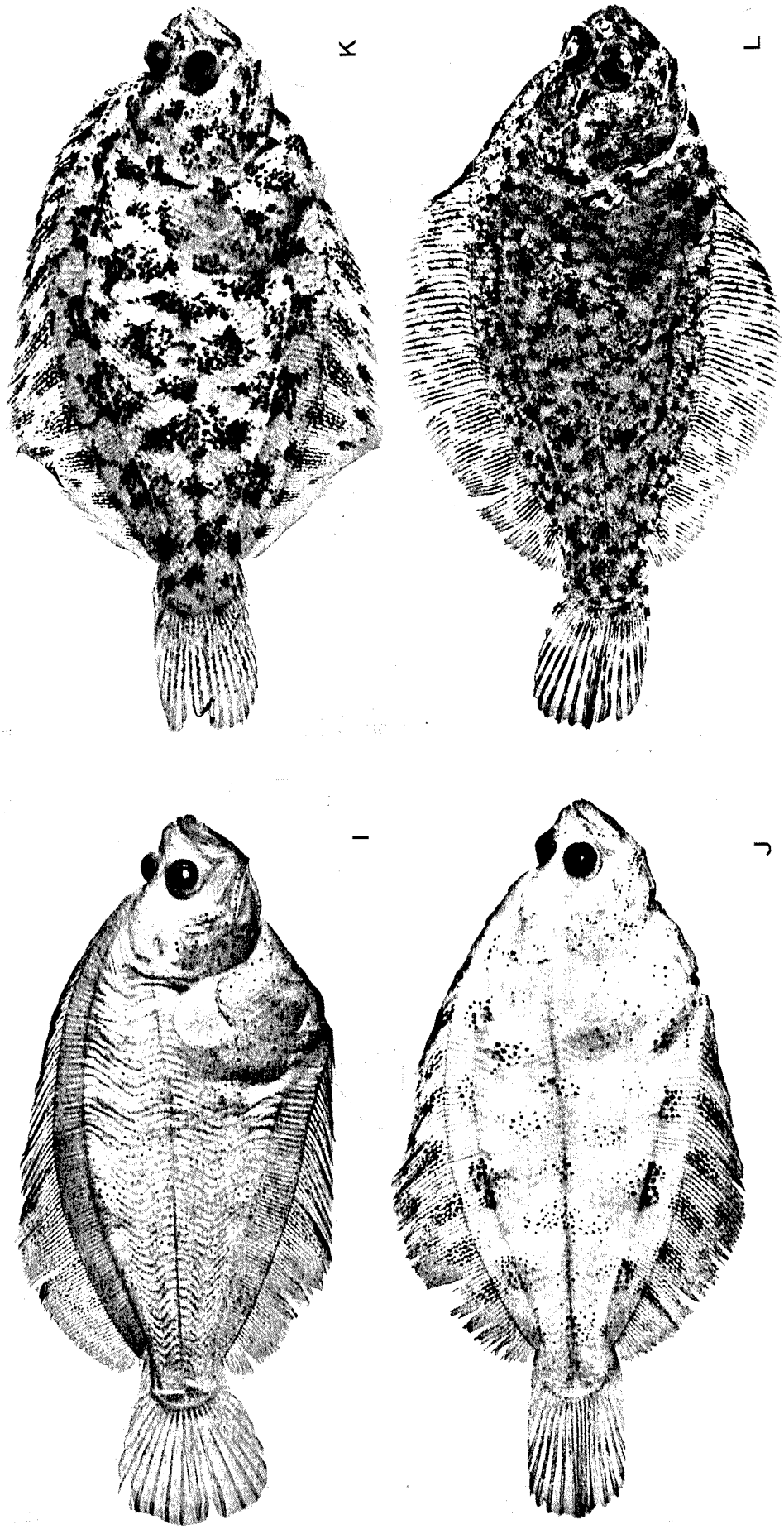


Fig. 49.14. Development of larval Pacific halibut, Hippoglossus stenolepis: stage 9, (cont.'d) 7 x natural size; J) stage 10, 7 x natural size; K) stage 11, 7 x natural size; L) stage 12, 7 x natural size. (Source: Thompson and Van Cleve 1936).

Table 49.6 Developmental stages of larval halibut, Hippoglossus stenolepis. (Source: Thompson and VanCleve 1936).

Stage	Length, mm	Larval features
1	7.8-15.0 ($\bar{x}$ = 11.2)	Newly hatched larvae. Distinguished by large size and undeveloped appearance; large yolk sac; lack of pigment except in eyes (Fig. 49.14, A).
2	9.8-17.8 ($\bar{x}$ = 13.4)	Development of hypurals begins; yolk present; lower jaw is well developed; actinotrichia appear in dorsal, anal finfolds and caudal area; notochord straight; melanophores appear in distal margin of anal and dorsal finfolds; some melanophores on ventrolateral surface of trunk (Fig. 49.14, B).
3	11.2-18.5 ($\bar{x}$ = 15.0)	Yolk is absorbed; lower jaw forms characteristic 45° angle; snout "pugged," notochord slightly flexed; 7-8 caudal fin rays; number of melanophores increased and present on abdominal region and side of head (Fig. 49.14, C).
4	13.6-17.8 ($\bar{x}$ = 15.2)	Flexion underway; body depth deepening; no anal or dorsal fin rays; increase in pigmentation, addition of chromatophores on dorsolateral surface of trunk (Fig. 49.14, D).
5	15.0-17.7 ($\bar{x}$ = 16.2)	Body depth increases to ~ 3 mm; pterygiophore cartilages are well developed on dorsal and anal fins; notochord tip at angle of 45°; 18 caudal rays visible; pelvic fin bud appears; melanophores appear along base of anal fin and on jaw angle; also melanophores appear along dorsolateral surface of vertebral column (Fig. 49.14, E).
6	14.1-17.3 ($\bar{x}$ = 15.9)	Body depth at anus averages 33% of length; eye migration begins; lepidotricha of dorsal and anal fins formed; flexion complete; 19th caudal fin ray developing (Fig. 49.14, F).
7	14.7-19.9 ($\bar{x}$ = 17.8)	Marked increase in body length and depth which averages 41% of length; left eye visible above dorsal profile of head; dorsal and anal fin rays present, 3 pelvic fin rays formed (Fig. 49.14,G).
8	17.9-21.4 ($\bar{x}$ = 19.6)	Shape approaches adult form; right eye begins to migrate ventrally; 5 pelvic fins present; definite grouping of chromatophores begins; both left and right sides remain pigmented (Fig. 49.14, H).
9	18.4-23.7 ($\bar{x}$ = 20.8)	Left eye almost at dorsal margin of head; characteristic grouping of pigment; less pigment present on left side (Fig. 49.14, I).
10	18.9-23.7 ($\bar{x}$ = 21.3)	Depth at anus is 44.0% of body length; eye lies on dorsal margin of head (Fig. 49.14, J).
11	18.7-24.6 ($\bar{x}$ = 22.1)	Transition toward adult pigmentation; left eye passed the dorsal margin of the head; pectoral fin rays begin to appear as fin looses its fan-like shape (Fig. 49.14, K).
12	22.3-28.8 ($\bar{x}$ = 25.7)	Body form is adult-like; pectoral fins fully developed; juvenile coloration complete, left side is colorless (Fig. 49.14, L).

Spawning of Pacific halibut in the Bering Sea has been reported by Novikov (1964) and was studied in the western Pacific by Pertseva-Ostroumova (1961).

Isopetta isolepis - Butter sole

Range: southern California to Bering Sea

Occurrence in Puget Sound: common

Adult habitat: demersal, shallow depths

Spawning habitat: demersal

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Butter sole are distributed from southern California to the Bering Sea (Miller and Lea 1972) and are usually found in shallow water (< 90 m), but are also known from the 275-365 m zone in western Alaska (Demory 1971; Hart 1973). In Puget Sound, Smith (1936) found butter sole to be abundant in Bellingham Bay in 20-35 m of water on a flat, silty, mud bottom.

Spawning takes place in Puget Sound from February to April with maximum activity in March (Smith 1936). A large spawning school of butter sole is known to concentrate in winter in Skidegate Inlet, B.C., at depths of 25-64 m (Manzer 1949; Levings 1968). Ripening fish are reported to accumulate in this area one month prior to spawning in February and March and the population does not include any immature fish (Hart 1944).

For Puget Sound butter sole, Smith (1936) found all age group II males and all age group III females to be mature. Similar ages of maturity occur in Skidegate Inlet butter sole and correpsonding lengths are 10 cm and greater for males and 25 cm and greater for females (Forrester 1969a).

A female of 32 cm may produce 350,000 to 650,000 eggs and up to a million eggs may be produced by a female of 38 cm (Forrester 1969a).

Fertilized butter sole eggs are spherical, transparent, have a narrow perivitelline space, a homogeneous yolk, and no oil globule. Diameters reported by Levings (1968) were 0.933-1.100 mm ($\bar{x}$ = 1.013 mm) and by Richardson et al. (1980) were 0.90-0.99 mm ($\bar{x}$ = 0.93 mm). Yolk diameters average 0.76 mm (0.60-0.95 mm)(Richardson et al. 1980).

Early and middle stage eggs of butter sole which occur in the plankton cannot be distinguished from eggs of sand sole (Psettichthys melanostictus), English sole (Parophys vetulus), or starry flounder

(Platichthys stellatus). All are about 1 mm in diameter with smooth, unsculptured chorions. However, late stage eggs of butter sole are recognized by containing embryos which lack scattered yolk sac melanophores (compared to sand sole embryos) and have unpigmented finfolds (compared to starry flounder)(Fig. 49.15). Late stage butter sole eggs cannot always be distinguished from those of English sole although butter sole embryos tend to have less ventral tail pigmentation and the melanophores on the head and trunk are less numerous and more dendritic. Description of development of pigmentation of butter sole embryos is described by Richardson et al. (1980).

Physical development of butter sole eggs is similar to other teleost fishes and eggs hatch when the embryo encircles seven-eighths of the yolk (Richardson et al. 1980).

Newly hatched butter sole larvae are 2.68-2.92 mm ($\bar{x}$ = 2.78) with a yolk sac that extends along the anterior third of the body. Larvae are relatively undeveloped, with an unformed mouth (Fig. 49.15A). The mouth forms two days (at 3.4-3.5 mm) after hatching and the yolk sac is absorbed in 7 days (at 3.9-4.1 mm). Coiling of the gut begins at 11 days (at 3.3-4.1 mm) and notochord flexion begins at 9-10 mm and is complete by 14 mm. The left eye begins to migrate when larvae are 12-13 mm to a position where it is directed upward.

In reared eggs, embryos hatch with unpigmented eyes although a planktonic caught larva of 2.9 mm had pigmented eyes. In the earliest larvae, pigment is scattered on the head, snout, and dorsal, lateral, and ventral body surface above the abdominal cavity and in the tail region (Fig. 49.15). With development, larval pigmentation is characterized by three tail bands located at 50, 67, and 90% of standard length. The middle band becomes the most pronounced and remains visible on the right side in some transformed benthic juveniles, or as long as 35 mm (Fig. 49.16). The posterolateral and ventral surfaces of the gut become covered with melanophores by 6.0 mm and are arranged in a crescent shape, and melanophores develop on the lower jaw and throat. In larvae > 10 mm, a series of discontinuous internal melanophores develops along the dorsal surface of the notochord and remains visible until the end of the transformation period. Additional details of pigment development are given by Richardson et al. (1980).

Transformation to the benthic juvenile occurs at 18-24 mm and is signified not only by the change in habitat, but by the completion of eye migration and development of juvenile pigmentation. Morphometric measurements, sequence of ossification (Fig. 49.17) and a detailed account of caudal fin development (Fig. 49.18) are described by Richardson et al. (1980).

Larval butter sole occur in the nearshore coastal zone off Oregon in winter and spring and off Washington and in Puget Sound during spring. Along the outer coasts, smaller juveniles may remain in offshore coastal areas instead of moving into bays, estuaries or other nearshore nursery habitats (Richardson et al. 1980).

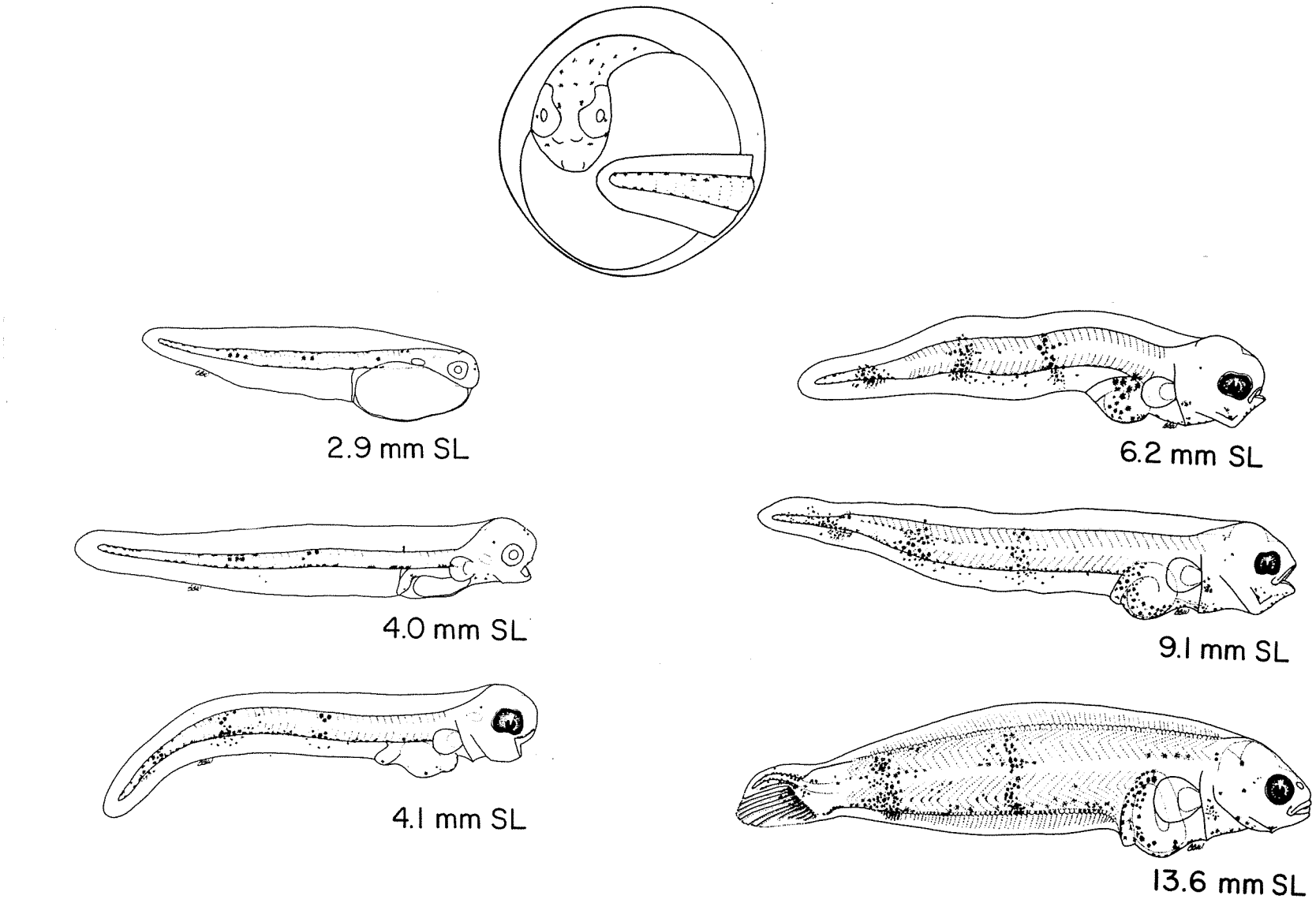


Fig. 49.15. Planktonic late stage egg and larvae of butter sole, Isopsetta isolepis; 2.9 and 4.0 mm larvae were reared. (Source: Richardson et al. 1980).

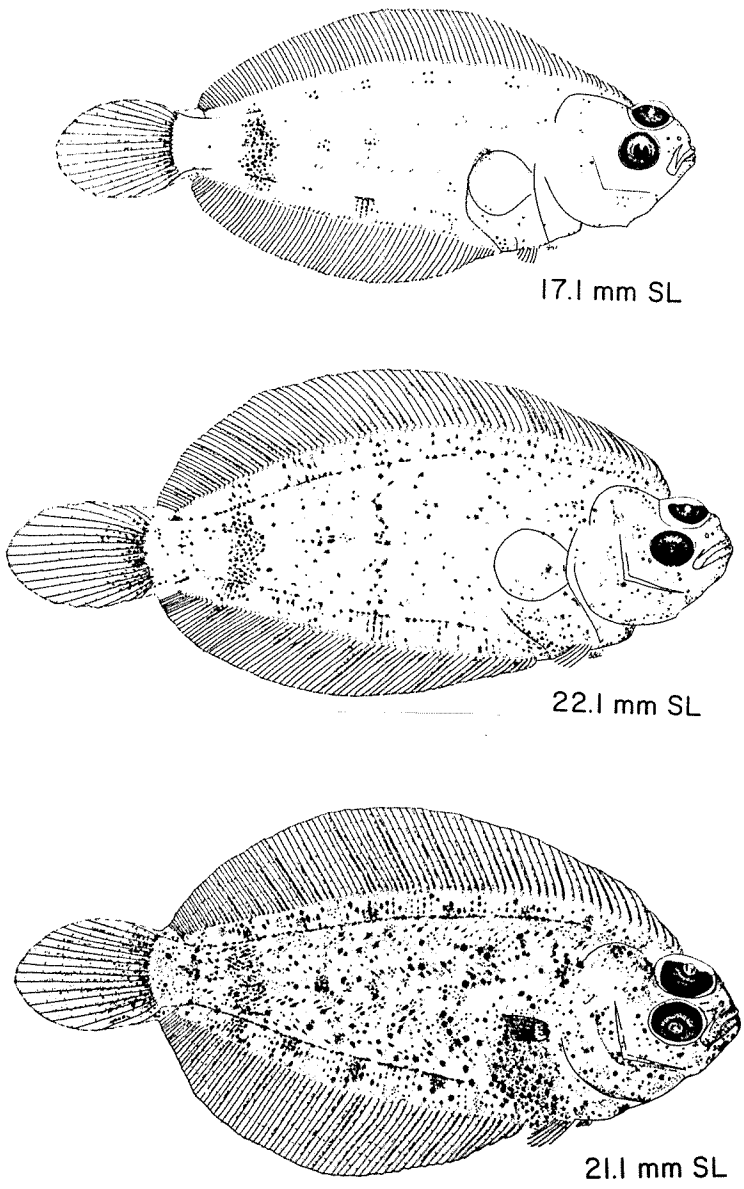


Fig. 49.16. Late stage larvae (17.1 and 22.1 mm SL) and recently transformed benthic juvenile (21.1 mm) of butter sole, Isopsetta isolepis. (Source: Richardson et al. 1980).

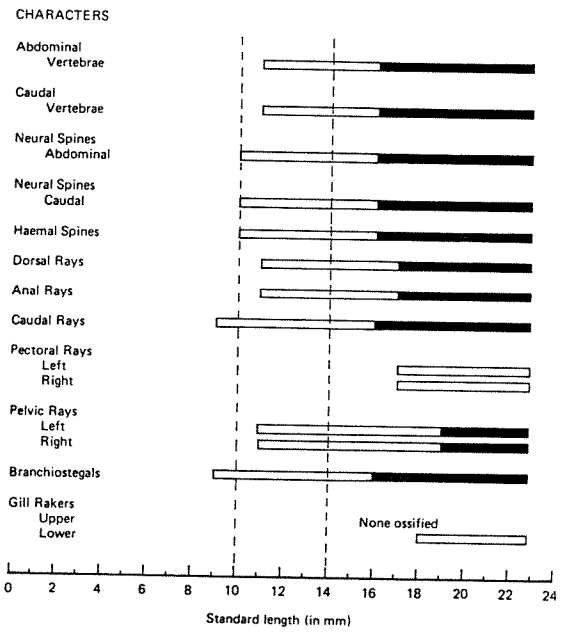


Fig. 49.17. Sequence of ossification of principal meristic structures in butter sole, Isopsetta isolepis. Dashed vertical lines indicate size range when notochord flexion occurs; open bars indicate ossification is underway; solid bars indicate ossification is complete. (Source: Richardson et al. 1980).

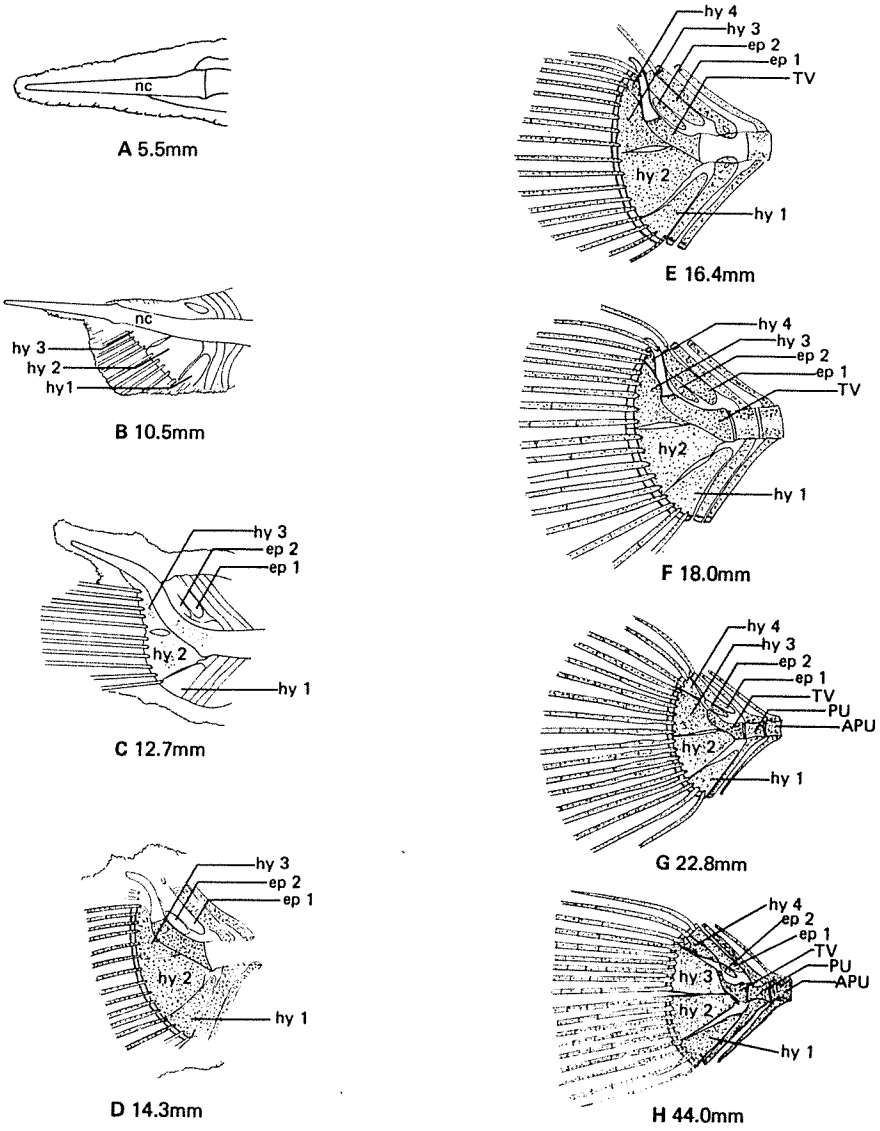


Fig. 49.18. Development of the caudal fin of butter sole, Isopsetta isolepis. Ossified elements are stippled. hy = hypurals; ep = epurals; nc = notochord; APU = antepenultimate vertebrae; PU = penultimate vertebrae; TV = terminal vertebrae. (Source: Richardson et al. 1980).

Lepidopsetta bilineata - Rock sole

Range: California to Bering Sea; Gulf of Anadyr to Korea

Occurrence in Puget Sound: common

Adult habitat: demersal, shallow to moderate depths

Spawning habitat: demersal

Spawning season: late winter-early spring

Mode of reproduction: oviparous

Eggs: demersal

Larvae: pelagic

According to Wilimovsky et al. (1967), rock sole form a complex of three subspecies. Lepidopsetta bilineata bilineata ranges from Monterey, California to the Queen Charlotte Islands, British Columbia, where it intergrades with L. bilineata perarcuatus. This subspecies is predominantly found from southeast Alaska to the Bering Sea, Gulf of Anadyr to northern Kurile Islands and northern Sea of Okhotsk where it is replaced by L. bilineata mochigarei in the southern Sea of Okhotsk and south to Korea. This summary includes references which reported on Lepidopsetta bilineata (primarily United States and Canada) or L. bilineata bilineata (primarily Soviet).

In Puget Sound, rock sole are widely distributed and are found between 10 and 40 m on a rocky or firm bottom, especially near rapidly sloping surfaces such as near points (Smith 1936). In British Columbia, rock sole are reported from the surfline to 365 m, but are scarce at depths over 180 m and are commercially abundant at 18 and 70 m. They may migrate between shallower water in summer and deeper water in winter, but migrations are not extensive (Forrester 1969a).

Rock sole appear to spawn during the late winter to spring throughout most of their range (Table 49.7). Puget Sound rock sole may mature at age group II for males and at III-IV for females (Smith 1936) and 50% of males mature by 4 years of age and 50% of females at 4-5 years. These ages of 50% maturity correspond to 30 cm for males and 32-33 cm for females (Forrester and Thomson 1969).

In some areas, ripe fish have been collected between 70 and 220 m at bottom temperatures near 0.0^{o}C. Spawning may take place over hard sand or soft substrates (Table 49.7), but eggs have not yet been obtained in the natural environment.

Ripe eggs are orange with a thick, elastic, and sticky shell membrane and newly spawned eggs have a specific gravity which is greater

Table 49.7. Summary of reproductive characteristics of rock sole from the western and eastern Pacific Ocean.

Reference	Species	Area	Age of Maturity Males	Age of Maturity Females	Length of Maturity Males	Length of Maturity Females	Spawning: Season	Spawning: Temperature[1]	Spawning: Depth[1]	Spawning: Substrate
Smith 1936	L. bilineata	Puget Sound	II	III-IV	--	--	Feb - Apr	--	--	soft bottom[2]
Forrester and Thomson 1969	L. bilineata	Hecate Strait, B.C.	50% at < 4	50% at 4-5 yr	50% at < 30cm	50% at 32-33 cm	--	--	--	--
Forrester 1969a	L. bilineata	British Columbia	--	--	--	--	late winter-early spring	--	--	--
Shubnikov and Lisovenko 1964	L. bilineata bilineata	SE Bering Sea	5-7 yr		--	--	Mar - Jun	0.7 - 3.5°C	70-140 m	--
Pertseva - Ostroumova 1961	L. bilineata bilineata	W. coast of Kamchatka	--	--	--	--	Mar - Apr	∿ 0°C	90-220 m	hard sand, sand-gravel[3]
Shvetsov 1979	L. bilineata bilineata	N. Kurile Islands	4-7 yr	5-8 yr	21 cm	25 cm	Feb - May	0.0 - 0.4°C	∿ 150 m	--

[1]Based on collection of ripe fish.

[2]Based on collection of spawning fish.

[3]Based on collection of early larvae.

than seawater. Hence, the eggs of rock sole are probably demersal and possibly attached (Pertseva-Ostroumova 1961; Forrester 1964a). Fertilized eggs range in size from 0.87-1.00 mm ($\bar{x}$ = 0.92) and contain a small perivitelline space (Forrester 1964b). Rate of development of rock sole eggs is dependent on incubation temperature: 25-27 days at 2.9°C, 21.6 days at 3.5°C, (Pertseva-Ostroumova 1961), 15.3 days at 5°C, 10.9 days at 7°C, 8.3 days at 9°C, and 6.4 days at 11°C (Forrester 1964b).

Fecundity has been studied in relation to length and weight of female rock sole in the western Pacific (Fig. 49.19), and can be expressed by the following equations (Shvetsov 1979):

$$F = 4.891 \times 10^{-4} L^{3.720} \quad (L = \text{length of fish in cm})$$

and

$$F = -178.7 + 0.695\ W \quad (W = \text{weight of fish, g})$$

In the Bering Sea, rock sole produce between 150,000 and 400,000 eggs per female, and in the western Pacific between 80,000 and 920,000 eggs per female (Table 49.8). Shvetsov (1979) reported that spawning is non-intermittent.

The development of rock sole eggs and larvae (L. bilineata bilineata) was described in detail by Pertseva-Ostroumova (1961) and embryonic events are summarized in Table 49.9. At 3.5°C, formation of the first two blastomeres is complete by 7 h after fertilization, gastrulation begins on the 4th day and the embryo is well-established by the 5-6th day. Both yellow and black chromatophores are present during development and appear about the 7th day at the formation of the tail bud. With development, the melanophores become oriented in longitudinal rows along the length of the embryo (Fig. 49.20). Hatching occurs when larvae are 3.6-4.0 mm ($\bar{x}$ = 3.86 mm) and the degree of development depends upon their size; the mouth may not be formed in the smallest larvae. Late stage embryos and larvae are characterized by two bands of melanophores and yellow chromatophores on the tail. The anterior band is located at the 6th to 10th postanal myomeres and the other band is at the 19th to 26th postanal myomere. These bands remain visible until transformation and are characteristic of rock sole larvae. Other melanophores are located on the dorsal and posterior surfaces of the gut, and single, sparsely scattered melanophores are visible near the end of the tail, on the ventral surface of the yolk sac, and in the finfolds near the tail bands (Fig. 49.21).

When rock sole larvae reach 6 mm, the yolk sac has been absorbed, flexion is beginning, and caudal fin rudiments are appearing. By 10 mm, rudiments of the dorsal and anal fins appear and by 15.5 mm SL, rays are formed in all fins except the pectorals. Eye migration begins by 15 mm SL and is complete and the larva has transformed by 24 mm. Additional details of larval development are provided by Pertseva-Ostroumova (1961).

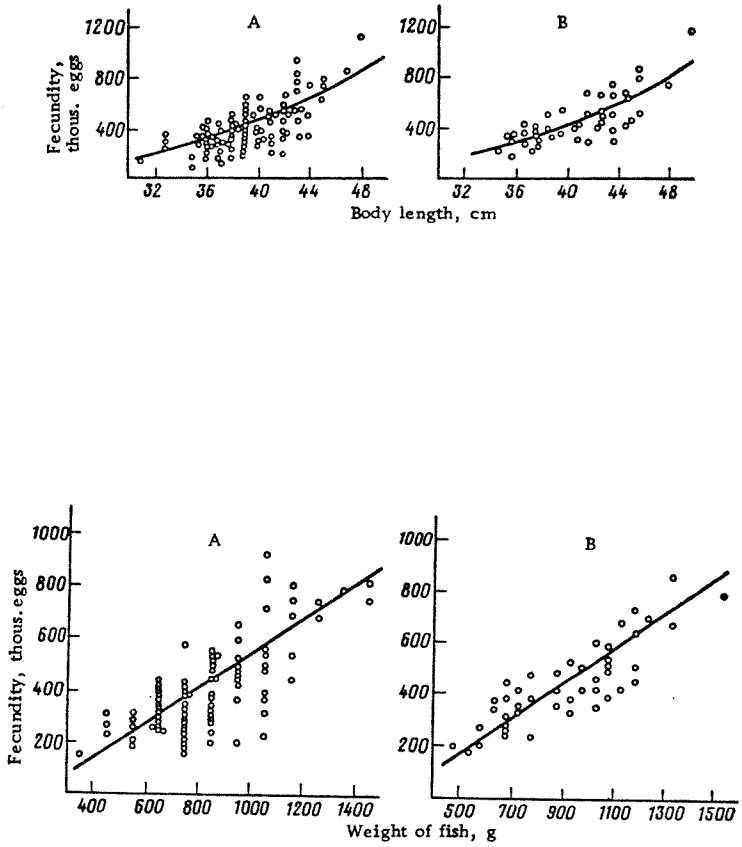


Fig. 49.19. Fecundity-length (top) and fecundity-weight (bottom) relationships for rock sole, Lepidopsetta bilineata bilineata from the northern Kurile Islands. Data from 1968(A) was not statistically different from 1971 data(B). (Source: Shvetsov 1979).

Table 49.8. Fecundity of rock sole, Lepidosetta bilineata bilineata, from the Bering Sea and western Pacific Ocean.

Bering Sea: Fadeev (1965)

Length, cm	Fecundity, x 10^3 eggs
22.1-24.0	151.7
30.1-32.0	180.6
32.1-34.0	179.1
34.1-36.0	226.9
36.1-38.0	287.1
38.1-40.0	297.5
40.1-42.0	404.2

North Kurile Islands: Shvetsov (1979)

Length, cm	Fecundity, x 10^3 eggs	
	Range	Mean
35-36	80-430	255
37-38	130-480	305
39-40	190-640	415
41-42	200-670	435
43-44	310-920	615

Table 49.9. Development of eggs of rock sole, Lepidopsetta bilineata bilineata, at an average temperature of 3.5°C. (Source: Pertseva-Ostroumova 1961).

Time (from fertilization)	Developmental event
2h	Rudiments of blastodisc.
7h	Two blastomeres.
1d, 1h	Sixteen blastomeres.
2d, 18h	Embryonic spinal column.
4d, 6h	Glastrulation begins.
4d, 23h	Embryonic nodule. Edges of blastodisc situated along equator of yolk. Embryonic stripe outlined.
5d, 23h	Blastopore closed. Optic vesicle outlined. Embryo envelopes 1/2 of yolk.
6d, 18h	Optic vesicles have appeared.
7d	Beginning both of segmentation and formation of tail bud. Fourteen myotomes in body. Kupffer's vesicle. Optic vesicles. Rudiments of crystalline lenses in some specimens. Yellow chromatophores along the orbit of the eyes and lower edge and sides of body.
8d, 18h	Sixteen myotomes. Tail bud fully formed. Beginning of tail separation. Punctuate melanophores and chromatophores scattered on head at level of rear edge of eyes, melanophores on sides of rear half of body oriented in longitudinal rows.
12d	Embryo fully envelopes yolk. Heart visible, but not beating. Pigmentary cells appear on the head in the region of the eyes.
14d	Embryo makes more than one turn; the end of its tail reaches the level of the forward edge of the eyes; 18 to 19 myotomes on the tail and 16-19 myotomes on the trunk. Body movement and weak pulsation of heart have begun. Rudiments of pectoral fins.
16d	End of embryo tail goes beyond eyes. Accumulation of pigment cells begins on the middle of the tail in certain embryos. Bright group of yellow chromatophores at the anus.
18d	End of embryo tail goes beyond auditory capsule.
19d	End of embryo tail reaches level of pectoral fins. Heart contracting 65 times a minute. Chromatophores and melanophores form two belts on the tail. Pigmentation of eyes begins.
20d	Embryo makes almost a turn and a half around the yolk, the end of its tail going beyond the pectoral fins and in some speciment, stopping slightly short of the anus.
21d, 15h	Beginning of hatching.
22d, 15h	Mass hatching
24d, 7h	End of hatching

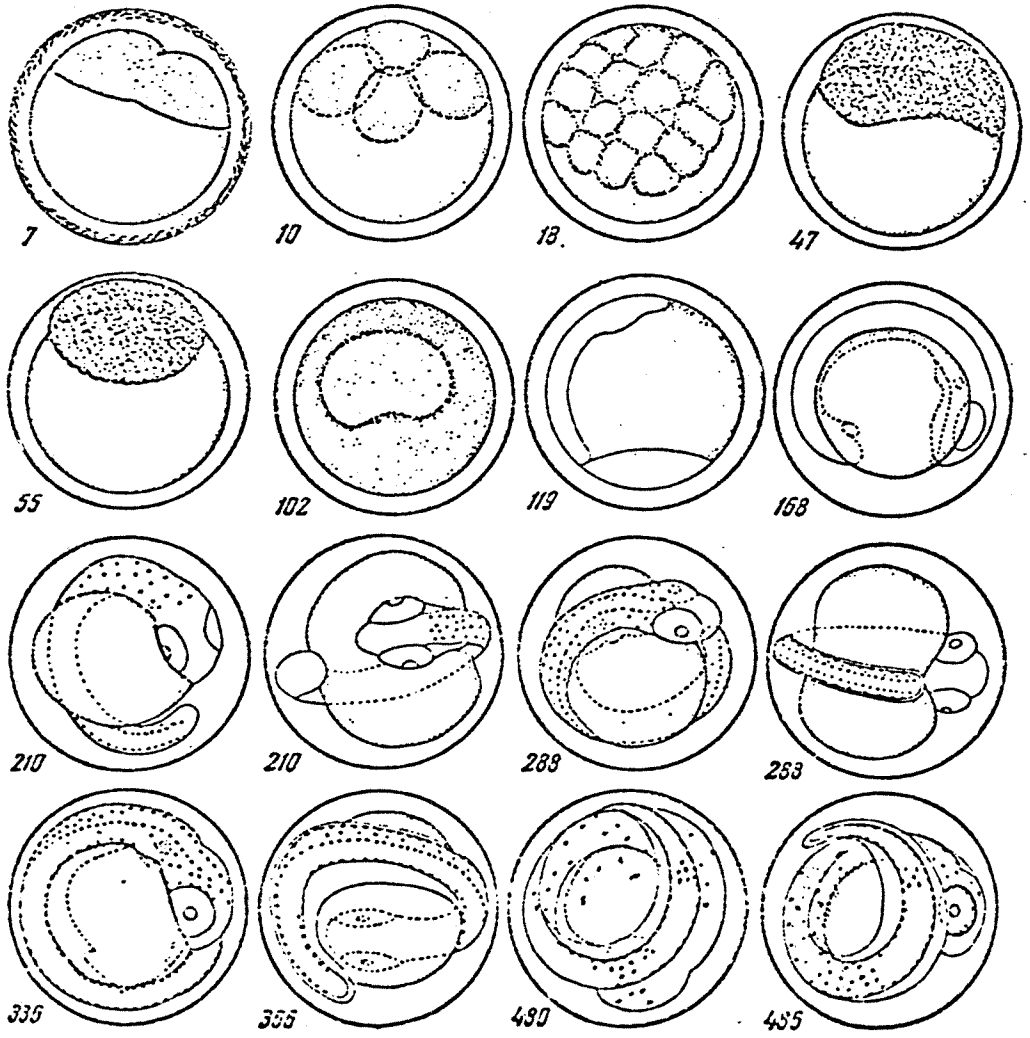


Fig. 49.20. Development of eggs of rock sole, Lepidopsetta bilineata bilineata, reared at ∿ 3.5°C. Numbers are hours from fertilization. The structure of the shell membrane is shown in the 7 h-old egg only. (Source: Pertseva-Ostroumova 1961).

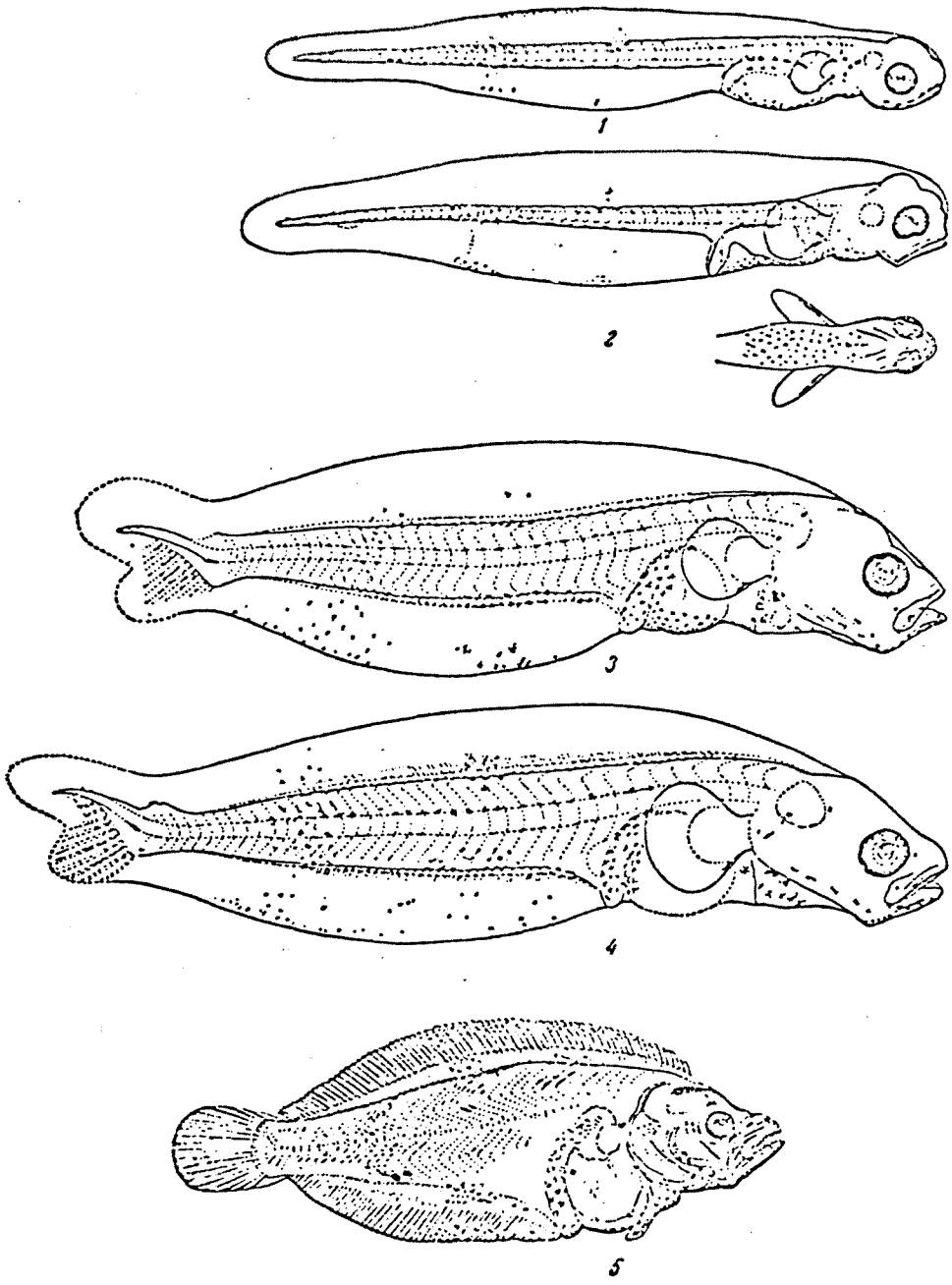


Fig. 49.21. Larvae of rock sole, Lepidopsetta bilineata bilineata, from the western Pacific: 1) 4.7 mm; 2) 5.6 mm; 3) 8.4 mm; 4) 9.9 mm; 5) 17.7 mm. (Source: Pertseva-Ostroumova 1961).

Blackburn (1973) described and sketched 4.4 and 11.0 mm larvae of Lepidopsetta bilineata from Puget Sound which are similar to larvae described by Pertseva-Ostroumova (1961).

Lyopsetta exilis - Slender sole

Range: Baja California to southeast Alaska

Occurrence in Puget Sound: common

Adult habitat: demersal, shallow to moderate depths

Spawning habitat: unknown

Spawning season: spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Slender sole are found at shallow to moderate depths from Baja California to southeast Alaska (Hart 1973) and are common and widespread throughout Puget Sound (Miller and Borton 1980).

The reproductive history of slender sole has been little studied. A spawning stock has been observed in April in Puget Sound (Smith 1936) and ripe females have been found in the Strait of Georgia in late February (Hart 1973).

Some males become mature after their second year and all are probably mature after their third. Females may be mature by their third year and all are mature by their fifth (Smith 1936). According to Hart (1973), 50% of males are mature at about 14 cm TL and females at 16 cm TL.

Eggs of the slender sole are pelagic, lack ornamentation of the outer shell, have a homogeneous yolk, lack oil globules, and are relatively large, 1.6-1.7 mm (Ahlstrom and Moser 1975). Blackburn (1973) found preserved, spawned eggs of slender sole in Puget Sound measured from 1.40 to 1.74 mm with a mode at 1.62 mm and reported that eggs from the plankton ranged from 1.42 mm to 1.64 mm with a mean of 1.54 mm.

A 5.1 mm larva of the slender sole was briefly described and sketched by Blackburn (1973) and is similar in appearance to the smallest larvae described by Ahlstrom and Moser (1975). Blackburn's larval series labeled "Lyopsetta exilis," should be labeled "Isopsetta isolepis" (Richardson et al. 1980).

Larvae hatch at about 5 mm and have pigment located along the dorsal and ventral body surfaces, some lateral pigment, and numerous melanophores in the posterior portion of the finfold (Fig. 49.22-top). With devleopment, pigment begins to outline the ventrolateral and dorsolateral myomeres. Pigment also develops on the lateral surface of the

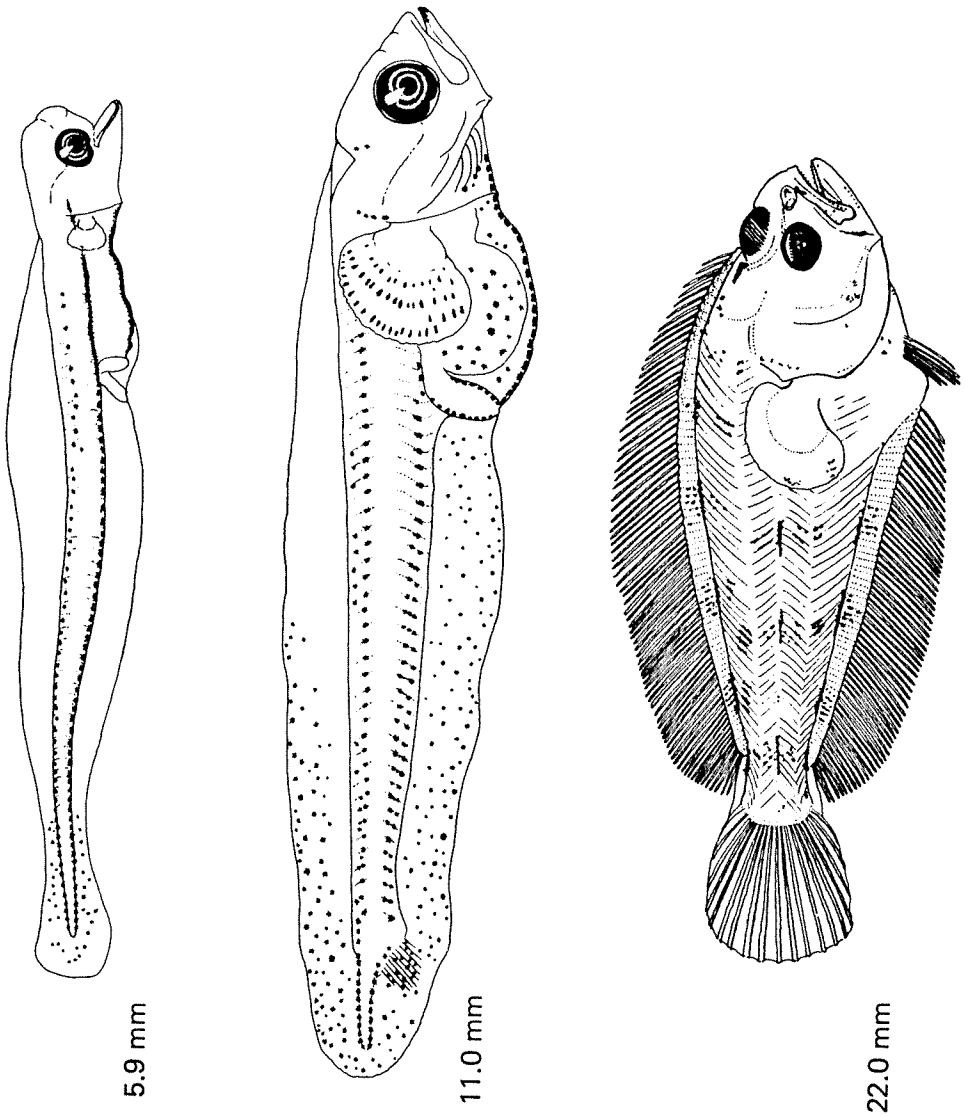


Fig. 49.22. Slender sole, Lyopsetta exilis, larvae. (Source: Ahlstrom and Moser 1975).

gut and outlines the anal pipe (Fig. 49.22-middle). In later stages, pigment becomes concentrated into a series of patches along the dorsal and ventral margins of the body and along the lateral midline (Fig. 49.22-bottom). Metamorphosis takes place between 18 and 22 mm (Ahlstrom and Moser 1975).

Off California, larvae are most abundant in the plankton during April and May (Ahlstrom and Moser 1975).

Microstomus pacificus - Dover sole

Range: northern Baja California to Bering Sea

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: deep water

Spawning season: winter

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Dover sole are found from northern Baja California to the Bering Sea and may be taken to depths of 1,100 m (Hart 1973). Adults are common and widespread in Puget Sound (Miller and Borton 1980). Off the Oregon coast, Dover sole undertake a limited seasonal migration between inshore areas (55-110 m) during June to Septebmer and offshore spawning areas (330-550 m) from November to April (Westrheim and Morgan 1963). A similar migration is noted for Dover sole off California which migrate to deeper water during winter for spawning followed by a return to shallower depths in summer for feeding (Hagerman 1952).

In Puget Sound, some spawning by Dover sole may take place during winter months (Table 49.10). Off Oregon, females may mature at 33 cm and 50% are mature at 38 cm, with all females mature at 42 cm (Harry 1959). Off California, first-mature females are 33 cm with 50% mature at 35 cm and all mature at 45 cm. Males mature at smaller sizes than females; males first mature at 30 cm, with 50% of males mature at 32 cm, and all mature at 39 cm (Hagerman 1952).

Fecundity of Dover sole was reported for California fish (Hagerman 1952)(Table 49.11) and Oregon fish (Harry 1959)(Fig. 49.23). Estimates range from 37,188 ova for a female of 36.2 cm to over 250,000 ova for a 64.0 cm female.

The unfertilized, mature eggs stripped from a ripe female were spherical, transparent, and contained a homogeneous yolk and no oil globules. The chorion was tough, thick and had a raised vermiculate pattern which produced a wrinkled appearance under magnification. Striped eggs ranged from 2.05-2.57 mm ($\bar{x}$ = 2.33)(Hagerman 1952).

Fertilized eggs are pelagic. The embryos are well-pigmented, including the eyes and form larval pectorals and a well-developed mouth before hatching. Newly hatched larvae are about 6.5 mm (Ahlstrom and Moser 1975).

Table 49.10. Spawning season of Dover sole, Microstomus pacificus, by area.

Reference	Area	Spawning season	peak
Smith 1936	Puget Sound	January-February[1]	-
Harry 1959	Oregon coast	November-March	-
Hagerman 1952	California Coast	November-April	December-February

[1]Spawning males encountered.

Table 49.11. Fecundity-length data for Dover sole, Microstomus pacificus, collected off California. (Source: Hagerman 1952).

Length of fish (cm)	Number of ova[1]
36.2	37,188
38.8	51,650
40.6	117,443
43.3	116,033
44.7	124,347
45.4	125,272
47.1	158,475
50.4	229,615

[1]Based on fish with "developing" eggs.

Dover Sole	
Length of Fish (cm.)	*Number of Ova*
42.5	51,900
43.0	77,700
44.0	68,400
44.5	75,700
45.5	58,500
45.5	80,200
45.5	100,600
46.5	142,900
48.0	99,100
48.5	119,900
49.5	122,900
51.0	137,700
51.5	183,900
52.0	134,100
52.0	191,600
52.5	192,200
54.0	132,100
54.0	142,100
54.5	148,300
57.0	162,400
57.5	265,800
64.0	256,700

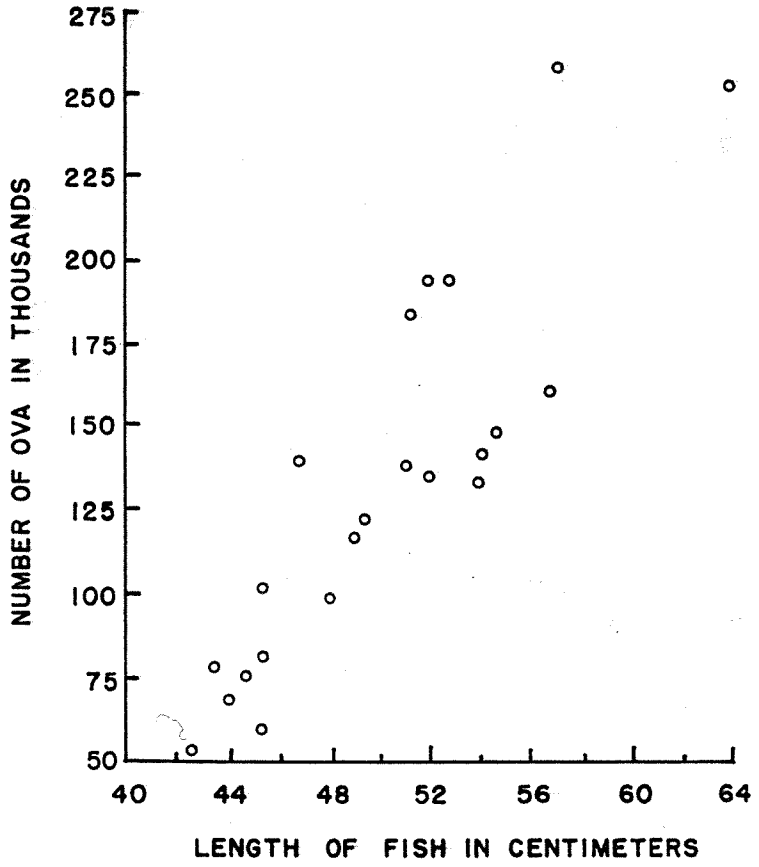


Fig. 49.23. Fecundity-length relationship for Dover sole, Microstomus pacificus, collected off Oregon. (Source: Harry 1959).

Larvae, 11.5 and 26.0 mm, were described and illustrated by Hagerman (1952), and Ahlstrom and Moser (1975) illustrated 7.0, 11.5, and 43.4 mm larvae (Fig. 49.24). Newly hatched larvae are long, thin, and transparent, but by 11.5 mm, the body has radically increased in height, and late-stage larvae are wide and "leaf-like." At about 11.5 mm larvae are characterized by the appearance of two pairs of spines which appear near the occipital region on each side of the chondrocranium. These spines disappear before metamorphosis and are not found in juveniles.

Pigmentation usually consists of five equally spaced goups of melanophores along the outer edge of the anal finfold and about six groups along the dorsal finfold edge. These concentrations are connected by a continuous line of pigment spots along both finfold margins. The ventral margin of the gut is pigmented, as well as the tip of the lower jaw, but the head in general is lacking in pigmentation. Along the body, pigment is located in bands along the border of the central trunk musculature which more or less line up with the finfold spots. These spots persist and can be found on demersal young (Hagerman 1952).

Eye migration begins during notochord formation and reaches the dorsal ridge of the head in 30-40 mm larvae and may not be complete by 48 mm (Pearcy et al. 1977; Hagerman 1952). The larval stage of Dover sole is protracted compared to other flatfish, and larvae may spend over a year in the plankton and reach a size of 50-65 mm before transformation (Pearcy et al. 1977)(Table 49.1).

Off Oregon, Dover sole larvae are most common in oceanic waters beyond the continental slope and in the upper 50 m of the water column (Pearcy et al. 1977). Off California, Dover sole have been taken up to 450 km offshore (Hagerman 1952).

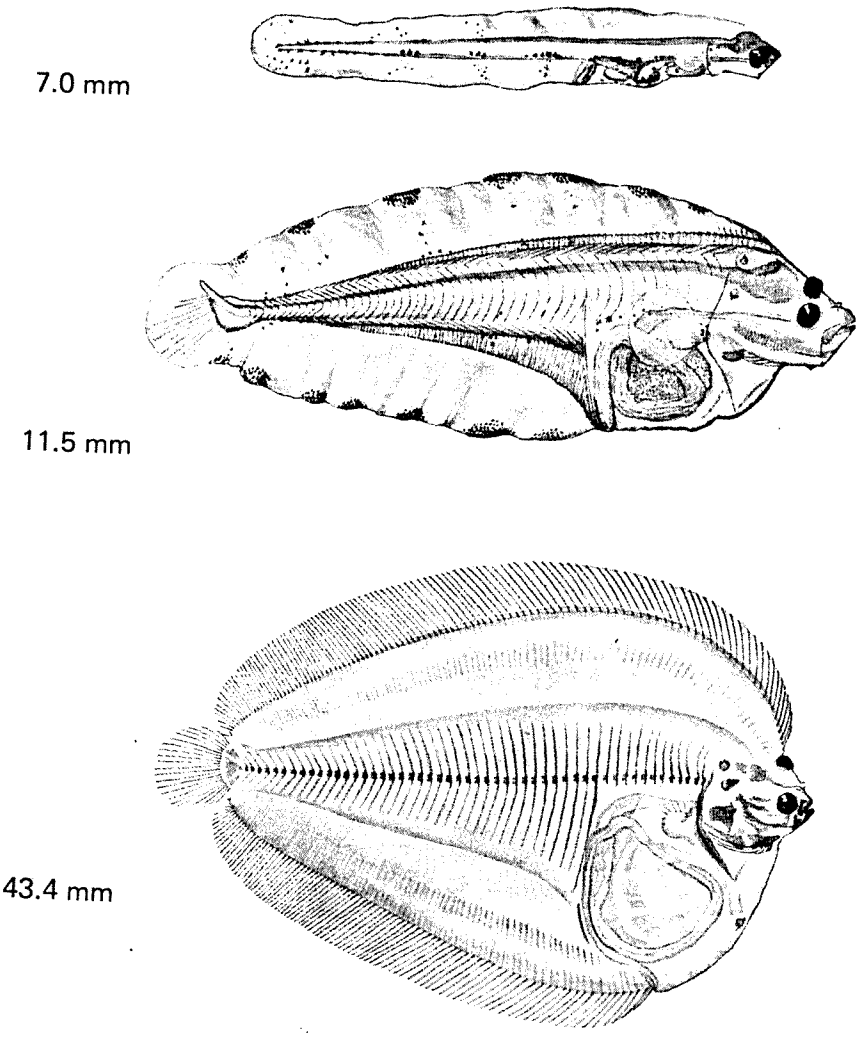


Fig. 49.24. Larval stages of Dover sole, Microstomus pacificus. (Source: Ahlstrom and Moser 1975).

Parophrys vetulus - English sole

Range: Baja California to Unimak Island, Alaska

Occurrence in Puget Sound: common

Adult habitat: demersal, moderate depths

Spawning habitat: demersal

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

English sole range from Baja California to Unimak Island, Alaska (Hart 1973) and are the most abundant of the flatfishes in Puget Sound. Along the coast, adults are found at moderate depths and out as deep as 550 m, with commercial quantities at less than 128 m (Alverson 1960). In Puget Sound, English sole are found primarily between 15-110 m and are commercially abundant between 26 and 50 m. They frequently occur on soft sand or mud bottoms (Smith 1936).

On the basis of observations of ripe and spawning fish from California to British Columbia, the spawning season of English sole is protracted and variable, although there is no obvious north-south trend (Table 49.12). Fish in a spawning condition have been taken as early as October and as late as May, with peak spawning between December and April. In Puget Sound, English sole are in a spawning condition from at least January to April with most fish spawning in February to March (Smith 1936). The protracted spawning of English sole in Puget Sound was also documented by catches of recently metamorphosed juveniles in almost all months of the year (Kendall 1966).

English sole reach sexual maturity at 21 cm and two years of age for males and 26 cm and three years of age for females. Off Oregon, only a small percentage of females are mature at 16 cm, but 50% are mature at 31 cm and all females over 35 cm are mature. Some males as small as 21 cm are mature, 75% are mature by 26 cm, and almost all are mature at lengths over 29 cm (Harry 1959). According to Smith (1936) for English sole in Puget Sound, all age group II males were mature, but only a small percentage of age group III females were mature and were not all mature until age group IV. In British Columbia, 50% of females mature at lengths of 295 mm which is reached by most females at the end of their third year. Males mature earlier, as in Puget Sound, at two years of age (Ketchen 1947, 1956).

Table 49.12. Spawning season for English sole, *Parophrys vetulus*, from California to British Columbia.

Reference	Area	Spawning[1] Season	Spawning[1] Peak
Villadolid 1927	California (Bodega Bay - Point Montara)	Dec-Apr	Jan-Feb
Budd 1940	Monterey Bay	Jan-May	Mar-Apr
Jow 1969	Santa Monica Bay - Santa Barbara Channel off San Francisco	Dec-Apr	
	Eureka-Oregon border	Oct-May	
Harry 1959	Oregon	Nov-May	Dec-Jan
Smith 1936	Puget Sound	Jan-Apr	Feb-Mar
Ketchen 1956	Hecate Strait, B.C.	late Dec-early Apr	Feb

[1]Based on fish in a ripe condition.

The fecundity of English sole increases with length and age of the female. A female of age III and 30 cm in length produces between 150,000 and 300,000 eggs and at age X at an average size of 43.7 cm produces close to 2 million eggs (Table 49.13; Fig. 49.25).

In British Columbia, there is evidence of both inshore and offshore spawning of English sole. The inshore populations have definite spawning grounds, and in the Strait of Georgia, there are two important areas of spawning along the east side of Vancouver Island and one of lesser importance at the entrance to Burrard Inlet (Ketchen and Forrester 1955; Taylor 1946). Minor spawning grounds are also found in four or five inlets bordering on the more exposed parts of the British Columbia coast. All these grounds lie in relatively sheltered water in channels or bights, at depths of 55-70 m, and over soft mud (Ketchen 1956). Offshore spawning of English sole is thought to occur in the lower region of Hecate Strait or Queen Charlotte Sound in deep water (Ketchen 1956).

English sole off the coasts of Washington and British Columbia have been shown to exhibit a northward post-spawning migration in spring months to summer feeding grounds, with a southerly or return movement in early fall. Extensive migrations are unusual for English sole, but are more characteristic of females than males (Ketchen 1956; Pattie 1969). In central Puget Sound, tagged and displaced sole showed a homing tendency and non-displaced fish remained in the same area. Recaptures of tagged fish were lowest during fall-winter implying there was some migration of English sole out of the area and/or depths of sampling at that time (Day 1976).

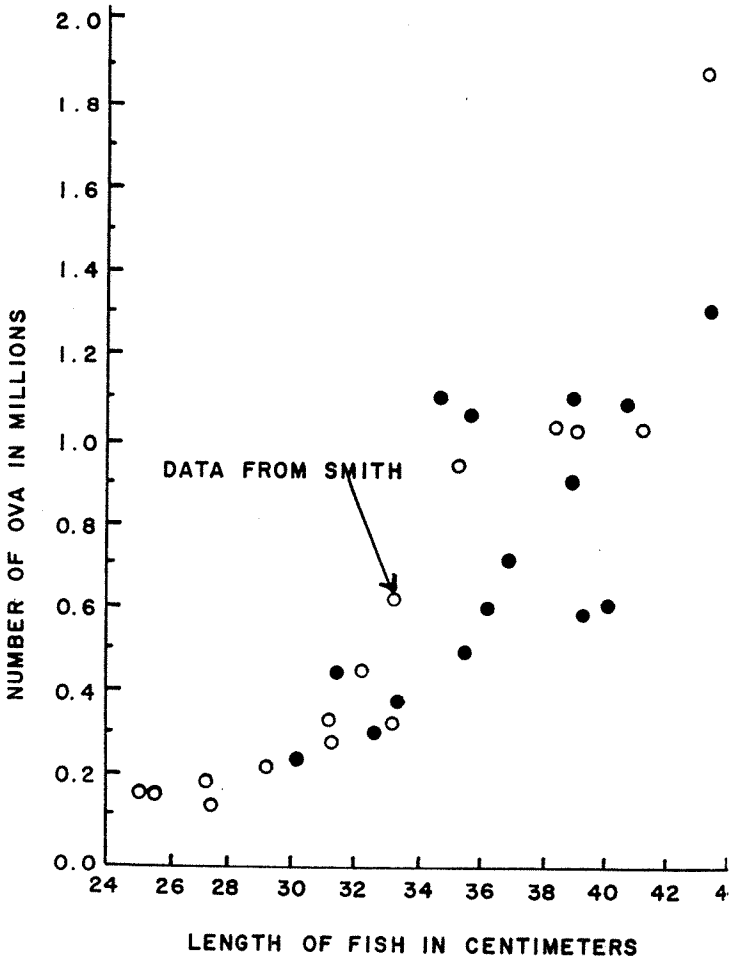
Mature, unfertilized eggs of English sole are spherical, transparent, and lack oil globules and pigment. They range in size from 0.91-1.04 mm ($\bar{x}$ = 0.98 mm). The egg membrane is covered by numerous small wrinkles and is pierced by many fine pores arranged in a regular, even pattern and the micropyle is visible as a shallow depression measuring 0.032 mm in diameter. The cytoplasm sheathing the yolk contains many small clear oil droplets linked into chains (Orsi 1968; Budd 1940).

After fertilization, eggs average 0.99 mm (0.93-1.05 mm) and float with the animal pole (area of blastodisc formation) downward. The perivitelline space is small (Orsi 1968).

The development of English sole eggs has been traced by Budd (1940), and Orsi (1968) who studied the development of organs through embryology. At 10.6°C, cleavage begins 2 hours after fertilization and conforms to the typical teleost pattern; cleavages continue at about one-hour intervals. No segmentation cavity exists because the periblast remains attached to the lower surface of the blastomeres. At 25 hr, gastrulation is complete, resulting in a large, sub-germinal cavity. At 48-49 hr, the blastopore closes and the embryo possesses eye vesicles, olfactory sacs, neural cord, notochord, Kupffer's vesicle, and 11

Table 49.13. Approximate fecundity, by length and age, of English sole, Parophrys vetulus, from British Columbia. (Source: Ketchen 1947).

Age	Average length, mm	Approximate number of eggs
III	300	150,000
IV	330	500,000
V	355	850,000
VI	382	1,200,000
VII	402	1,500,000
VIII	416	1,700,000
IX	431	1,850,000
X	437	1,950,000



English Sole	
Length of Fish (cm.)	*Number of Ova*
30.0	327,600
31.5	557,300
32.5	369,000
33.0	484,400
34.5	1,266,100
35.5	638,200
35.5	1,181,800
36.0	712,300
36.5	811,300
38.5	986,900
38.5	1,251,400
39.0	706,900
40.0	751,900
40.5	1,292,900
43.0	1,566,200

Fig. 49.25. Fecundity-length data for English sole, Parophrys vetulus, captured off Oregon. (Source: Harry 1959, also Smith 1936, unpublished data).

somites. Also at this time, an unusual caudal vesicle appears and becomes located behind Kupffer's vesicle. With development, it moves toward Kupffers's vesicle, but doesn't fuse with it, and eventually dwindles in size, disappearing between 67-78 hr (Table 49.14; Fig. 49.26).

At 12°C, development requires 3.5 days, and 4-4.5 days at 10.6°C, 5.6 days at 8.8°C, 8 days at 6.2°C, and 11.8 days at 4°C (Alderdice and Forrester 1968; Orsi 1968; Ketchen 1956). Alderdice and Forrester (1968) found that temperatures of 2°C were lethal to developing eggs and optimum conditions of devleopment and survival were at 25-28°/oo and 8-9°C. At 30°/oo and 6°C, eggs floated for most of the incubation period, but sank just prior to hatching.

Larval English sole were hatched and reared for 9 days to a size of 4.0 mm by Budd (1940) and for 14 days, to 4.2 mm, by Orsi (1968). At hatching, larvae are about 2.8 mm TL with a large yolk sac which causes them to float at the surface. Some swimming is accomplished by flutterings of the transparent, fan-like pectoral fins and tail. No mouth is present at hatching and the eyes are well-formed, but unpigmented. Pigmentation consists of scattered groups of melanophores on the head, sides, and at the anus. There is no pigment on the yolk sac or finfolds. A definite band of amber chromotopheres encircles the tail about midway from the anus to the tail tip, and amber color is present at the posterior border of the eye, at the anus, and on the body directly about the anus (Fig. 49.27). In 3-4 days, larvae grow to about 4 mm, the eyes are pigmented, and jaws are developed. There are two separate bands of yellowish pigment around the tail and a third band above the hind gut. Amber pigment is also located at the pectoral fin level. Melanophores are distributed over the dorsal and ventral body surfaces, with more melanophores along the ventral surface. After about 6 days, melanophores appear on the ventral margin of the yolk sac, which is almost absorbed and fin rays are developing in the caudal region. With development, there is generally a reduction of melanophores until metamorphosis.

According to Ahlstrom and Moser (1975), a 6.3 mm larva illustrated by Budd (1940) is not that of English sole. They briefly describe later stages of larval English sole from the plankton off California. Larvae of 13 and 16 mm are only moderately pigmented. Melanophores are distributed along the anal pterygiophores and along the ventral margin of the head and gut, and at the base of the caudal fin. Pigment outlines some of the ventral myomeres on the tail and scattered, but distinct melanophores, are located on the dorsal body surface, on the gut, and on the head (Fig. 49.28). Metamorphosing and early juveniles of English sole (20-26 mm) were photographed by Misitano (1976).

Eggs and larvae of English sole are pelagic. Ketchen (1956) estimated the total time spent in the pelagic stage to be 6-10 weeks in British Columbia. However, estimates of the pelagic life of English sole off Oregon is longer, possibly 18-22 weeks (Laroche and Richardson

Table 49.14. Development of eggs of English sole, Parophrys vetulus at 10.6°C. (Source: Orsi 1968).

Time (from fertilization)	Developmental event
2 hr, 20 min.	Two-cells formed in blastodisc
3 hr, 14 min.	Four-cells formed
4 hr, 10 min.	Eight-cells formed
5 hr, 8 min.	Sixteen-cells formed
6 hr	Thirty-two cells formed
15 hr	Blastodermal cap reaches maximum height
25 hr	Germ ring formation and invagination begins
41 hr	Notochord becomes distinct
42 hr	Eye vesicles arise as lateral swellings
44 hr	Somites start to form
46 hr	Kupffer's vesicle appears
47 hr	Olfactory sacs forming
48-49 hr	Blastopore closure
60 hr	Auditory vesicle appears
62 hr	Heart begins to form
66 hr	Lenses of eye form
60-73 hr	Disappearance of Kupffer's vesicle
74 hr	Weak heart beats
79 hr	Subdivision of brain into fore-, mid-, and hindbrain complete
83 hr	Strong heart contractions, otoliths arise
85 hr	Pectoral fins appear

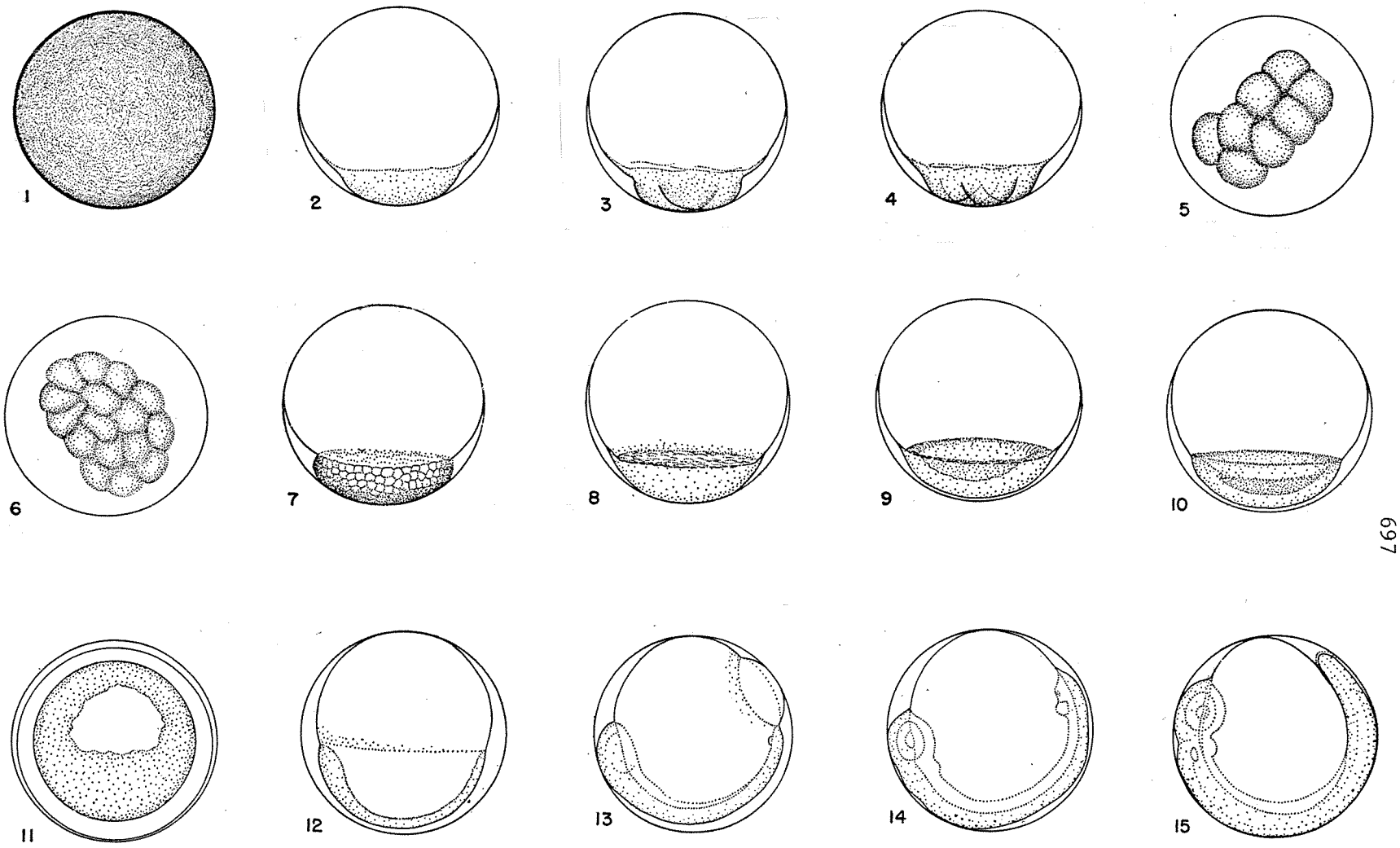


Fig. 49.26. Development of eggs of English sole, Parophrys vetulus: 1) Unfertilized egg; 2) blastodisc, 1 hr; 3) two-cell, 2 hr; 4) four-cell, 3 hr; 5) eight-cell, 4 hr; 6) sixteen-cell, 5 hr; 7) early blastodermal cap, 10 hr; 8) completed blastodermal cap, 23 hr; 9) segmentation cavity, 25 hr; 10) early germ ring, 27 hr; 11) embryonic shield, 28 hr; 12) germ ring nearly equatorial, 30 hr; 13) blastopore nearly closed, 40 hr; 14) blastopore closed, 50 hr; 15) advanced embryo, 70 hr. (Source: Budd 1940).

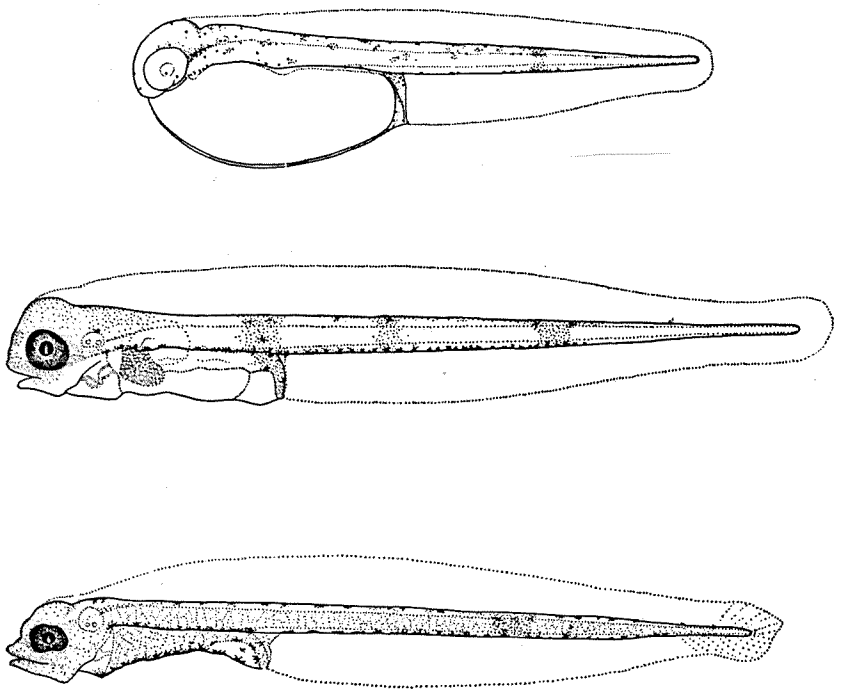


Fig. 49.27. Early larvae of English sole, Parophrys vetulus. Top) yolk sac larva just after hatching, 2.8 mm; middle) 4-day larva, 3.8 mm; bottom) 9-day larva, 4.0 mm. (Source: Budd 1940).

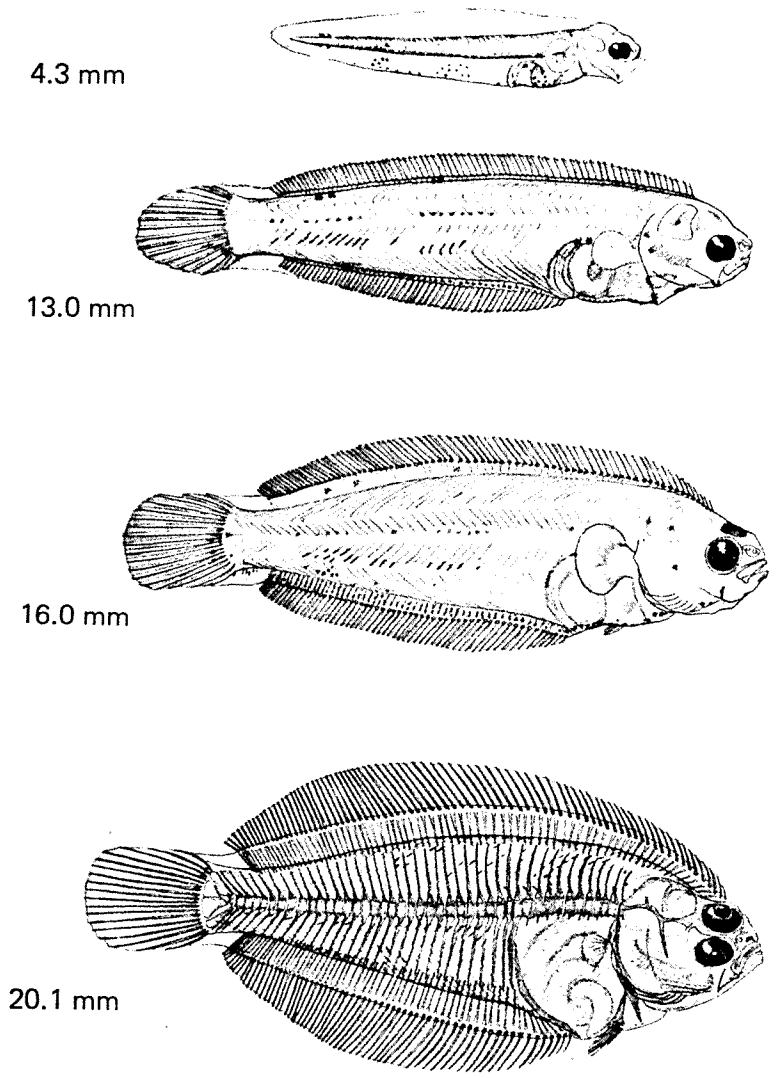


Fig. 49.28. Larval stages of English sole, Parophrys vetulus. (Source: Ahlstrom and Moser 1975).

1979). Age-at-length estimates for pelagic larvae were estimated by Laroche and Richardson (1979):

Length, mm SL	Age, weeks (excluding duration of egg stage)
5.5	2.3
7.5	4.1
9.5	5.9
11.5	8.7
13.5	13.4
15.5	17.6
17.5	21.9

During their pelagic stage, larvae are transported to inshore nursery areas such as the intertidal zone, bays, or estuaries where they undergo metamorphosis and remain until the fall of their first year. In Humboldt Bay, California, young English sole are recuited from oceanic spawning grounds into the bay at sizes of 19-26 mm TL with most sole between 20-22 mm TL undergoing metamorphosis (Misitano 1976). Similarly, English sole also appear to use estuaries along the Oregon coast as nursery areas. Young-of-the-year first appear in Yaquina Bay in February and are abundant from April to September with most emmigrating to offshore areas in October (Olson and Pratt 1973). In British Columbia, young English sole are in the shallow intertidal zone in late spring and summer and move deeper by November (Ketchen 1947).

In Puget Sound, English sole were the most abundant juvenile flatfish caught on two sandy beaches and were present in the intertidal zone during all months, although they were found in greatest abundance during July (Kendall 1966). Peak months of settlement of English sole in the San Juan Islands were January-March and June-July. In the Straits of Juan de Fuca, the highest settlements were observed in late summer and early winter (Thornburgh 1978).

Juveniles that are recently metamorphosed, appear on the beach at about 18 mm. By fall, most juveniles reach 110-130 mm and probably soon leave the intertidal zone for deeper water. Growth rates of the juveniles during their intertidal stage range from 0.5-0.7 mm/day (Kendall 1966).

Platichthys stellatus - Starry flounder

Range: southern California to Beaufort Sea; Kamchatka to Sea of Japan

Occurrence in Puget Sound: common

Adult habitat: demersal, shallow water

Spawning habitat: unknown

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

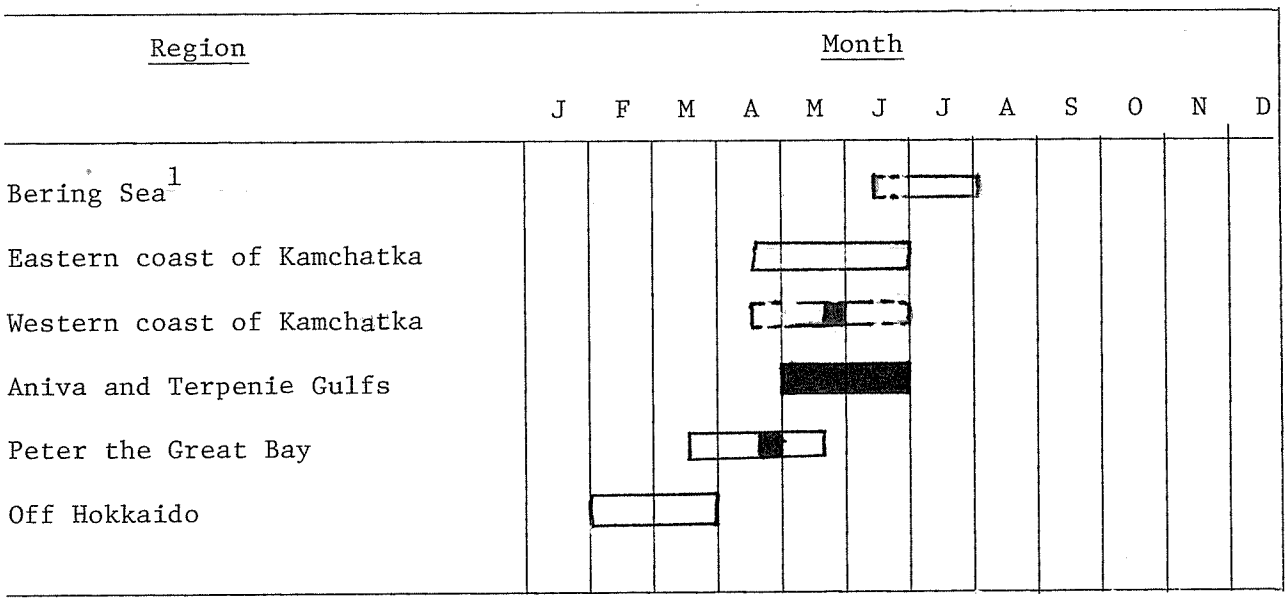
Starry flounder are found on both sides of the Pacific Ocean, ranging from southern California to the Beaufort Sea and along the Aleutian chain to the Commander Islands, Kamchatka Peninsula, and southward along Asia to Japan, including the Sea of Okhotsk and Japan Sea. There appears to be no record of starry flounder occurring along the Arctic coast of Asia (Orcutt 1950). In Puget Sound they are common and widely distributed (Miller and Borton 1980).

Adults are usually encountered in shallow water and on a variety of substrates, excluding rock. They are taken on gravel, clean shifting sand, hard stable sand, or mud, and may move from one type to another in search of food. Adults and juveniles are euryhaline and often occur around river mouths, in estuaries, and can penetrate fresh water rivers to several miles from the sea (Orcutt 1950).

Starry flounder differ from most pleuronectid flatfishes in having a high degree of sinistrality or "left-sidedness" (Forrester 1969b). They are also unusual in being able to form hybrids with other flat fishes such as Kareius bicoloratus in Japanese waters and with Parophrys vetulus in the eastern Pacific (Hart 1973; Orcutt 1950).

Starry flounder spawn once a year throughout their range and at a definite and relatively short spawning period. In California, spawning takes place from November to February with peak spawning in December and Janaury (Orcutt 1950). Starry flounder spawn later in the year in Puget Sound and British Columbia, with most spawning occurring between February and April (Smith 1936; Hart 1973). Southeast Bering Sea populations spawn in May and June (Fadeev 1965). Off the Soviet coast, the spawning period lasts for 2.5 to 3.5 months and spawning also occurs later in the northern areas (Table 49.15)(Pertseva-Ostroumova 1961).

Table 49.15. Summary of spawning times of starry flounder, Platichthys stellatus from the western Pacific Ocean. (Source: Pertseva-Ostroumova 1961).



[1]In text, claimed spawning season was from middle and end of May to middle and end of June.

Spawning may take place in shallow water (< 45 m), although it has not been well-documented (Orcutt 1950). Off the Soviet coast, spawning has been reported at depths of less than 25 to 30 m at temperatures below 0°C (Moiseev 1953) and Pertseva-Ostroumova (1961) found early stage eggs over water depths of 20-70 m and at temperatures near 0°C.

Males reach sexual maturity during the winter of their second year at lengths of 220-276 mm, and all males are mature at three years of age. Females may reach sexual maturity at three years of age and at lengths of 239-362 mm, and all are mature by age four (Orcutt 1950; Smith 1936).

Starry flounder show no outstanding sexual dimorphism or noticeable secondary sex characteristics. However, during the breeding season, mature females can be differentiated by a distension of the body posterior to the origin of the anal fin caused by enlargement of the ovaries with ripening eggs. Sex can be determined in fish $\geq$ 20 mm by dissection to reveal the gonads (Orcutt 1950).

Fecundity of starry flounder has not been well-examined. Orcutt (1950) reported that a 565 mm SL specimen from California contained ovaries which measured 262 mm in length and produced 11,000,000 eggs. In the Bering Sea, Fadeev (1965) found starry flounder between 380 and 480 mm yielded between 900,000 and 2,500,000 ova.

Starry flounder eggs have been well-described (Yusa 1957; Orcutt 1950). The unfertilized eggs are spherical, transparent, colorless or pale orange-pink and do not contain oil globules. They are nonadhesive and pelagic, floating at or near the surface. Off California, unfertilized eggs are 0.89-0.94 (Orcutt 1950), but are 0.97-1.01 mm ($\bar{x}$ = 0.991 mm) off Hokkaido (Yusa 1957), and planktonic eggs collected by Pertseva-Ostroumova (1961) were 1.00-1.28 mm ($\bar{x}$ = 0.92). The chorion is thin, transparent, and unsculptured, but a fine vermiculated pattern caused by minute wrinkles on the egg surface may appear in unfertilized eggs (Orcutt 1950). Descriptions and illustrations of egg development are given by Yusa (1957)(Table 49.16), Orcutt (1950)(Fig. 49.29), and Pertseva-Ostroumova (1961). Development ranges from 353 hours at 2.0-5.4°C to 168 hours at 7-8°C (Pertseva-Ostroumova 1961), 110 hours at 10.5°C and 68 hours at 12.5°C (Table 49.17).

Early stage eggs of starry flounder cannot be separated from those of English sole, butter sole, or sand sole, but late stages can be identified when embryos become pigmented (Richardson et al. 1980). In starry flounder embryos, pigment appears as an extensive irregular series of melanophores on the dorsal surface of the body and as a scattered series dorsal and anterior to Kupffer's vesicle. With further development, melanophores begin to appear about the eyes and nasal capsules, and xanthophores appear dorsal and posterior to the auditory capsules (Fig. 49.30) (Orcutt 1950). Pertseva-Ostroumova (1961) showed late stage embryos with pigment in the finfold.

Table 49.16. Development of starry flounder, Platichthys stellatus, eggs at 2-5.4°C. (Source: Yusa 1957).

Time (hours from fertilization)	Developmental event
4	Blastodisc
6	2-cell stage
8	4-cell stage
11.3	8-cell stage
13.25	16-cell stage
22	Early morula stage
27	Morula stage
55	Blastula stage
65	First gastrula stage
99	Germinal ring nearly at equatorial plane
122	Germinal ring reaches more than 3/4 of the egg surface.
138	Head of embryo well formed, optic vesicles appear.
161	Embryo distinguishable
186	Blastopore closed, embryo with ∿ 6 pairs of somites, Kupffer's vesicle appears.
210	Embryo with 10-16 pairs of somites, minute specks of pigment appear on all parts of the body except on yolk sac, olfactory capsules appear, heart forming.
224	Embryo with 18-20 pairs of somites, intestine appears.
247	Embryo with 25 pairs of mesodermal somites, chromatophores become more pronounced at the dorsal portion of the posterior end of the embryo.
257	Kupffer's vesicle disappears, tail lifts from yolk
270	Embryo with 30-32 somites, embryo extends about 3/4 of way around yolk.
305	Black pigment spots on the head become large and stellate, heart beat.
332	About 40 somites, otoliths present, embryo almost encircles yolk, increase of melanophores along dorsal surface of body.
353	Hatching begins.

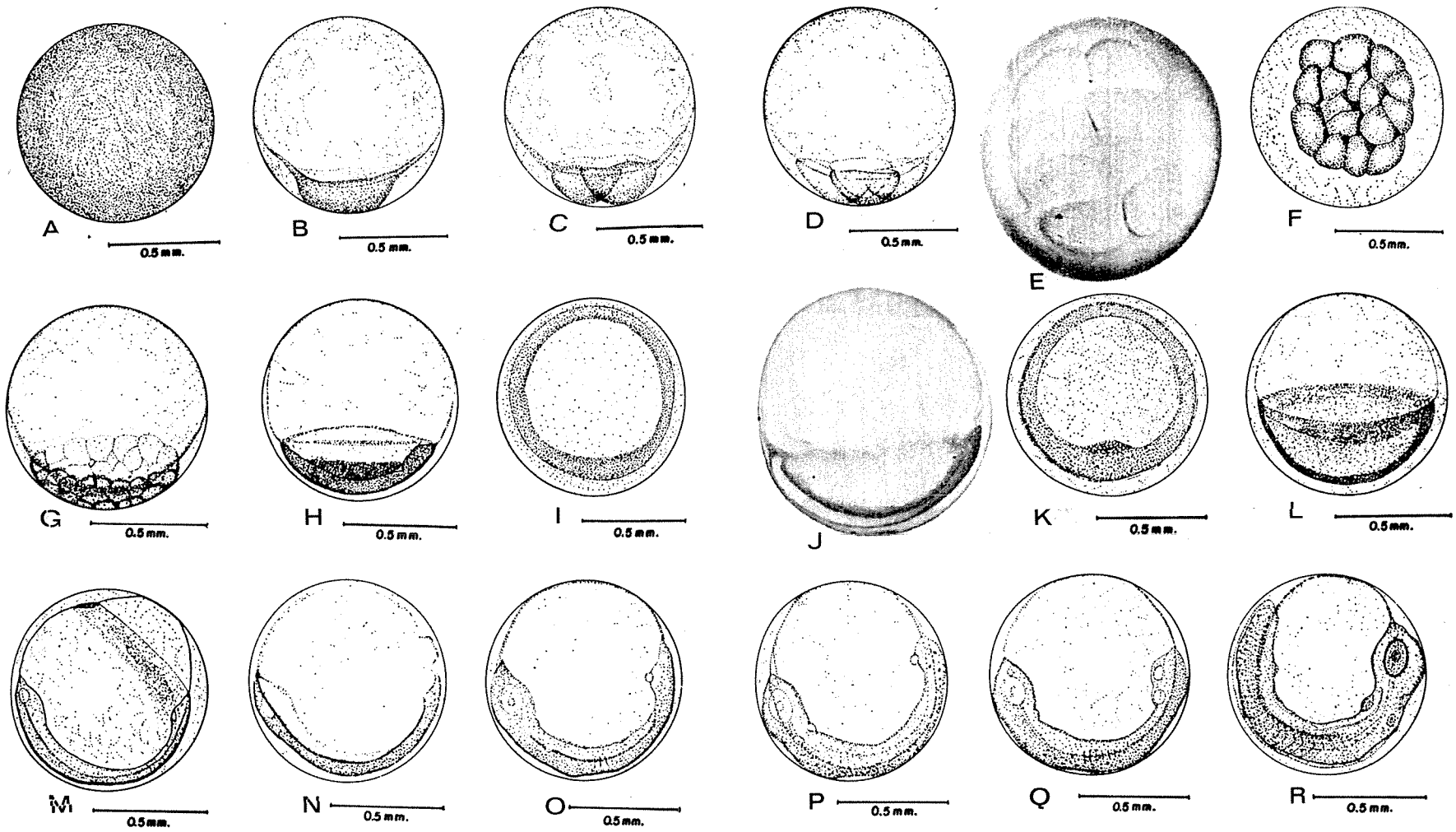


Fig. 49.29. Development of eggs of starry flounder, Platichthys stellatus, at 12.5°C. A) Ripe unfertilized egg; B) blastodisc, 1 hr after fertilization; C) two cells, 2 hr; D) four cells, 3 hr; E) eight cells, 4 hr; F) sixteen cells, 5 hr; G) blastodermal cap, 7.5 hr; H) enlarged segmentation cap, 18 hr; I) same, dorsal view; J) early germ ring, 19 hr; K) embryonic shield, 20 hr; L) germ ring nearly equatorial, 20 hr; M) 30-hr embryo; N) 31-hr embryo; O) 35-hr embryo; P) 43-hr embryo; Q) 43-hr embryo; R) 52-hr embryo. (Source: Orcutt 1950).

Table 49.17. Time required to reach various stages of development at different temperatures for starry flounder, Platichthys stellatus, eggs. (Sources: Yusa 1957; Orcutt 1950).

Developmental event	Time of fertilization (hours)		
	2.0-5.4°C[1]	10.5°C[2]	12.5°C[2]
First cleavage	6	2.5	2.5
Second cleavage	8	3.5	3
Third cleavage	11.3	5	4
Germ ring nearly equatorial	99	23	18
Kupffer's vesicle appears	186		28.5
Optic vesicles appear	138		29
Blastopore closure	186		32
Olfactory capsules	210		35
Heart appears	210	70	35
Pigmentation appears	210		40
Embryo with 16-17 pairs of somites	210		42
Gut appears	224		47
Disappearance of Kupffer's vesicle	257		52
Embryo extends 3/4 of way around the yolk	270		52
Heart beat	305		57
Embryo moves		93	53
Hatching	353	110	68

[1]Yusa (1957).

[2]Orcutt (1950).

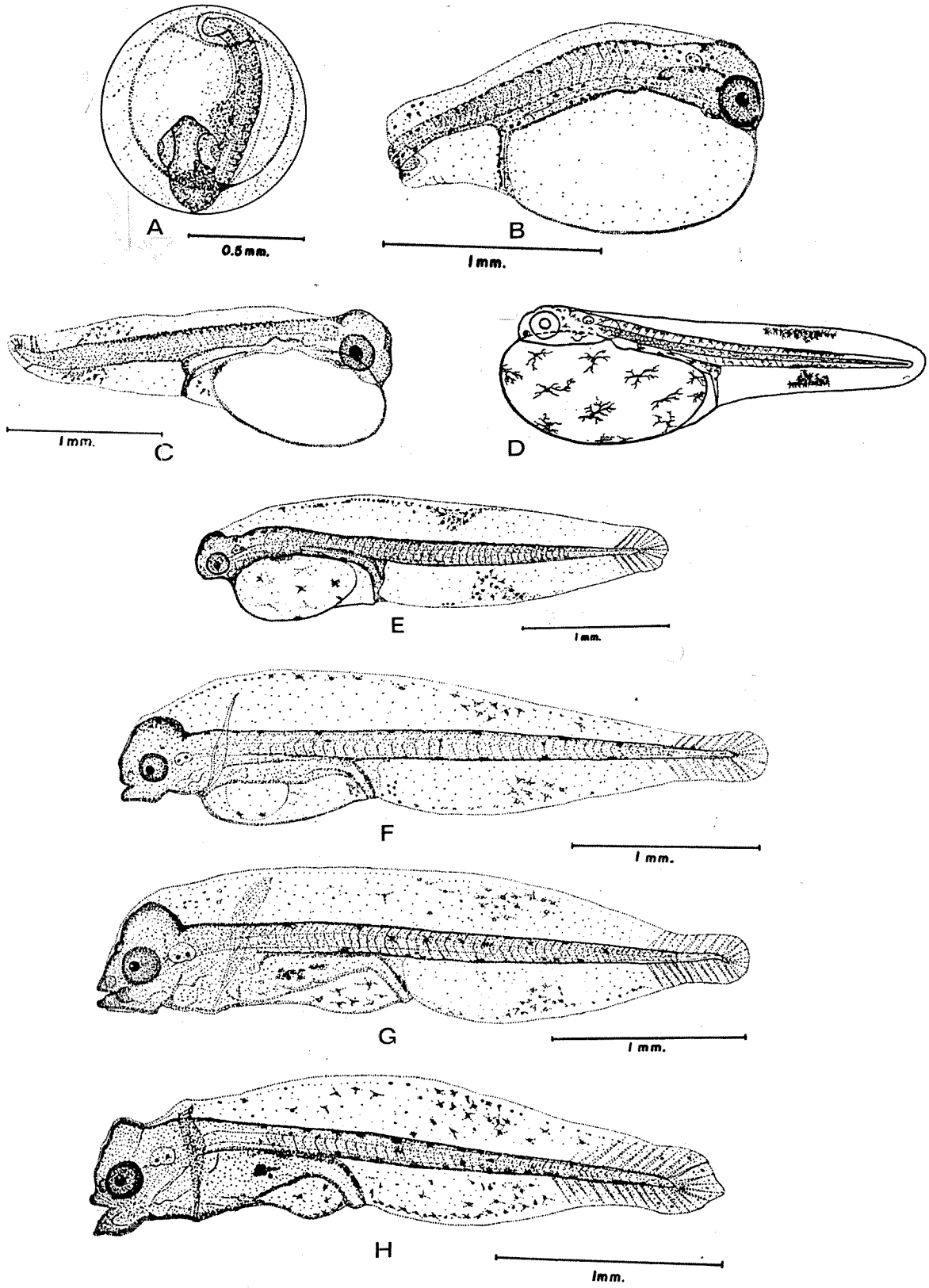


Fig. 49.30. Late stage egg and early larvae of starry flounder, Platichthys stellatus: A) 63-hr embryo; B) newly hatched larva; C) 12-hr yolk sac larva; D) yolk sac larva; E) 2-day larva; F) 4-day larva; G) 7-day larva; H) 10-day larva. (Source: A-C, E-H, Orcutt 1950; D, Yusa 1957).

Larvae are liberated from the eggs by vigorous twitching of their tails and exit either head or tail first (Yusa 1957; Orcutt 1950). Early stage larvae have been described , but Yusa (1957) and Orcutt (1950) were unable to obtain starry flounder larvae greater than about 4.5 mm. Pertseva-Ostroumova (1961) described larvae up to 8.0 mm SL from the plankton in the western Pacific. At hatching, larvae are 1.93-2.08 (Orcutt 1950) or larger, 2.58-3.36 mm TL (Yusa 1957) and are relatively undeveloped. They are slender, delicate, and transparent. Mouth and jaws are unformed at hatching but develop after several days. The yolk sac is large and buoyant, causing the larva to float upside-down, although newly hatched larvae can swim in the normal position for short periods by beating their pectoral fins and fluttering the tail (Orcutt 1950; Yusa 1957).

Early larvae (~ 2-4 mm) are characterized by melanophores and xanthophores which are most dense along the dorsal body surface and on the posterior portion of the gut. Large melanophores are also grouped on the dorsal and ventral finfold about half way from the anus to the tip of the tail, and xanthophores are located on the yolk sac. At 4.5-4.6 mm, larvae are characterized by a group of scattered melanophores in the middle of the tail, two parallel rows of melanophores on the lower edge of the tail, an irregular row of internal spots along the notochord, a compact row along the lower half of the abdomen, and a few stellate cells in front of the pectoral fins and on the lower jaw (Fig. 49.30). Pigmentation remains relatively unchanged in larvae through 8.0 mm, except there is a tendency toward a reduction in the number of melanophores on the surface of the tail and the abdomen, and large pigment cells appear on the upper edge of the rear half of the tail (Fig. 49.31) (Pertseva-Ostroumova 1961).

The onset of flexion and the development of the caudal fin begins at small sizes. Thickening in the region of the hypural plate is observed in 2.58 mm larvae (Orcutt 1950) and flexion and rudiments of the caudal fin rays are observed in ~ 5 mm larvae. Pterygiophores form at the bases of dorsal and anal fins, and rudiments of these fin rays appear at 6.6-8.0 mm SL larvae (Pertseva-Ostroumova 1961). Body height increases to 11-18.4% by 8.0 mm (Pertsova-Ostroumova 1961) and it is possible that metamorphosis is complete by 10.5 mm (Orcutt 1950). Descriptions of metamorphosing larvae are lacking.

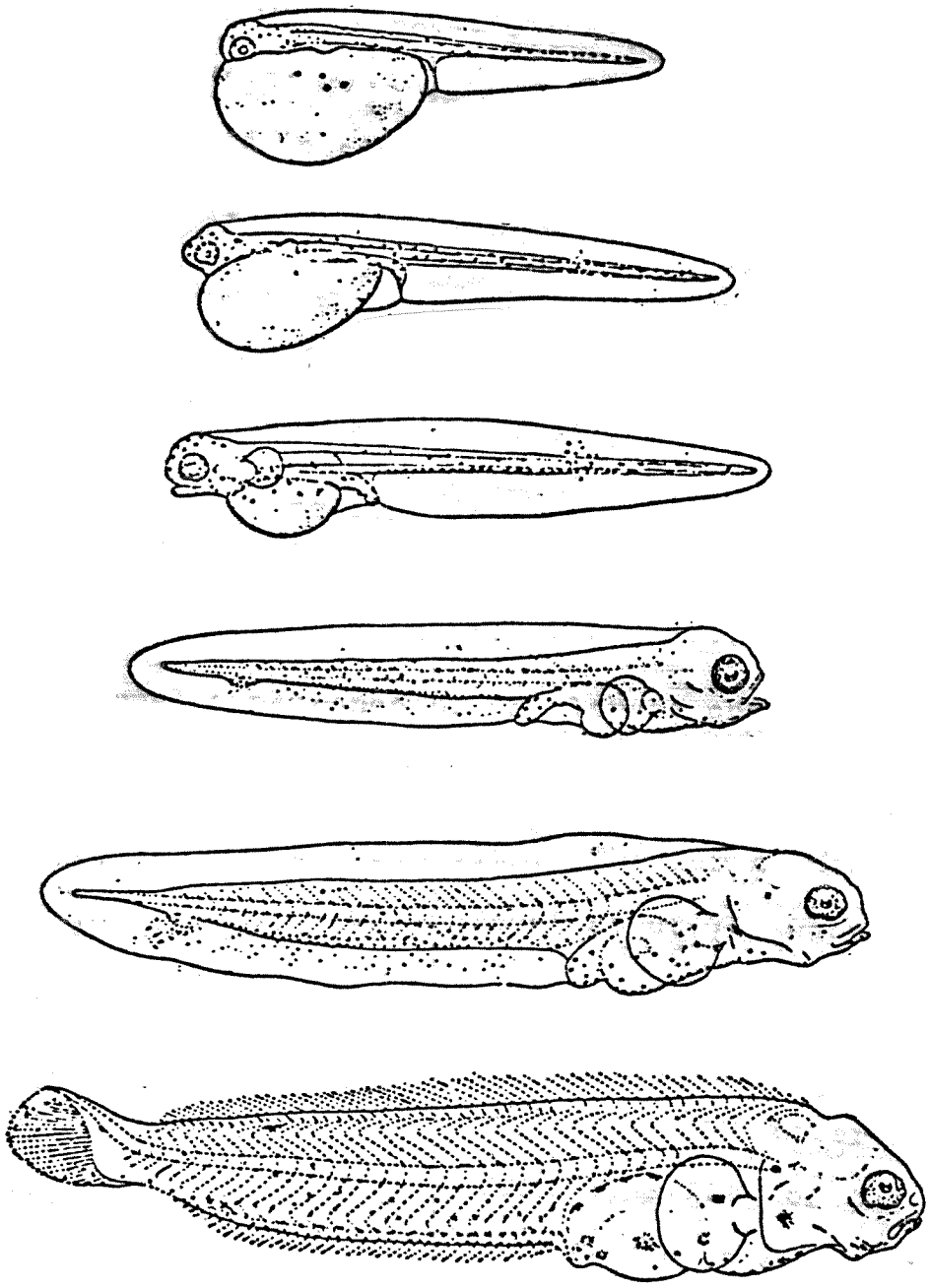


Fig. 49.31. Development of larvae of starry flounder, Platichthys stellatus, 2.4 mm, 3.0 mm, 3.22 mm, 4.6 mm, 5.9 mm, and 6.6 mm. (Source: Pertseva-Ostroumova 1961).

Pleuronichthys coenosus - C-O sole

Range: Baja California to southeast Alaska

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: winter-spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

C-O sole are distributed from Alaska to Baja California (Hart 1973), where the collection of eggs and larvae by Sumida et al. (1979) extended their range southward to Point Abreojos on the central Baja peninsula. In Puget Sound, C-O sole are common and generally widely distributed (Smith 1936; Miller and Borton 1980).

Spawning history of C-O sole is not well documented. Smith (1936) reported capturing a single mature male in Puget Sound during March, but found no mature females at this time. However, an examination of ovaries in January revealed that eggs were enlarged and approaching maturity. C-O sole spawn from March to August in California (Budd 1940).

The eggs and early larvae (3.88, 4.35, 4.62 and 4.72 mm) of C-O sole were first described by Budd (1940), but were inaccurately identified as Pleuronichthys decurrens (Sumida et al. 1979). The eggs, which have a homogenous yolk, but no oil globules, are characterized by a hexagonal sculpturing of the shell (Fig. 49.32). This type of ornamentation is unique to the genus Pleuronichthys among flatfishes, but similar patterning is found in eggs of fishes in other families (Sumida et al. 1979, p. 107). The arrangement of the polygons in C-O sole eggs is fairly uniform and the greatest distance across a polygon averages about 0.035 mm. Eggs are pelagic and range in diameter from 1.20 to 1.56 mm (Sumida et al. 1979).

Development of C-O sole eggs, (identified as "P. decurrens"), was described for eggs collected from the plankton and incubated at 13.8°C. The youngest stage found was that of early blastodermal cap (Fig. 49.33A) which reached its full growth 14 hours later (Fig. 49.33B). The segmentation cavity developed 22 hours after formation of the blastocap (Fig. 49.33C), and the germ ring began to migrate and reached the equatorial position after 34 hours (Fig. 49.33D). At 42 hours after formation of the blastocap, the eyes and Kupffer's vesicle appeared

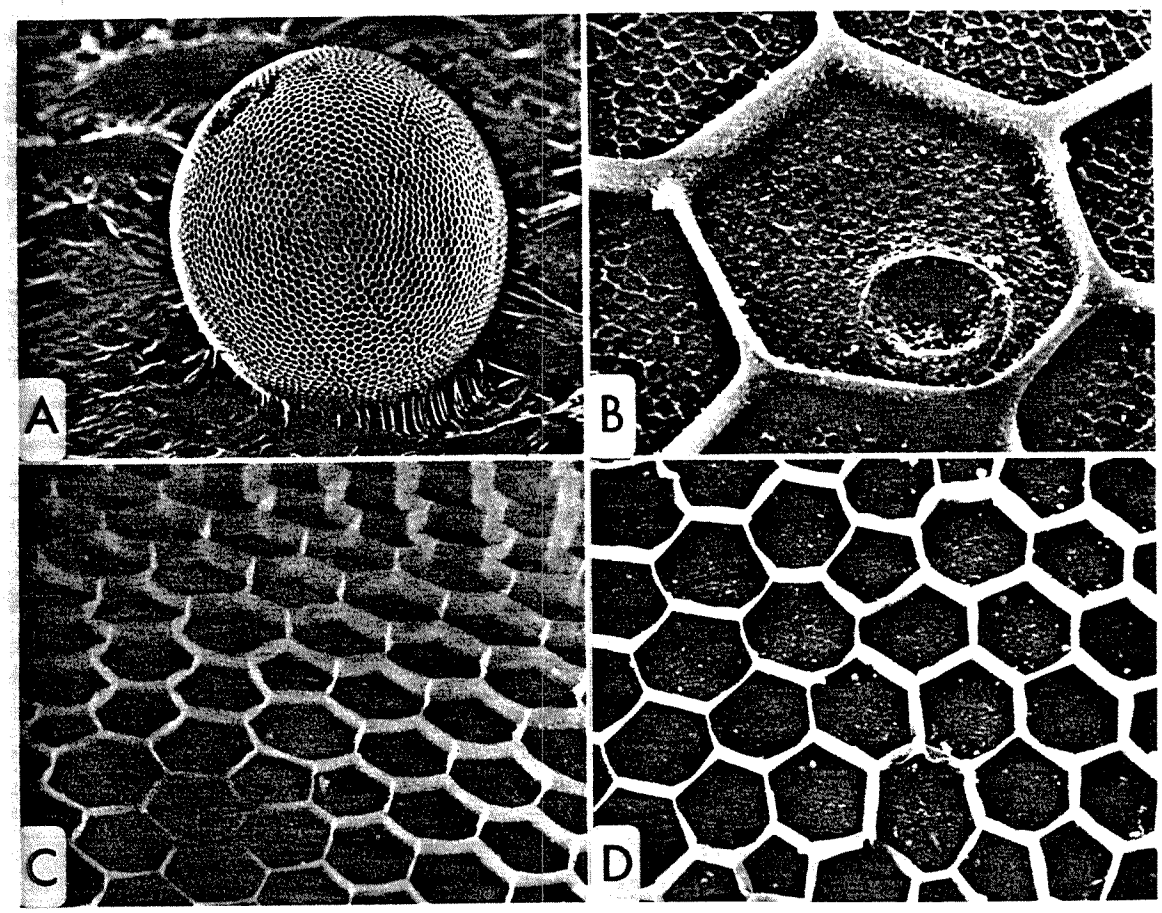


Fig. 49.32. Scanning electron micrograph of eggs of C-O sole, Pleuronichthys coenosus: A) Entire egg, 40x; B) single polygon showing micropyle and texture of chorion surface, 1,880x; C) and D), side and face views showing regular arrangement of hexagons. (Source: Sumida et al. 1979).

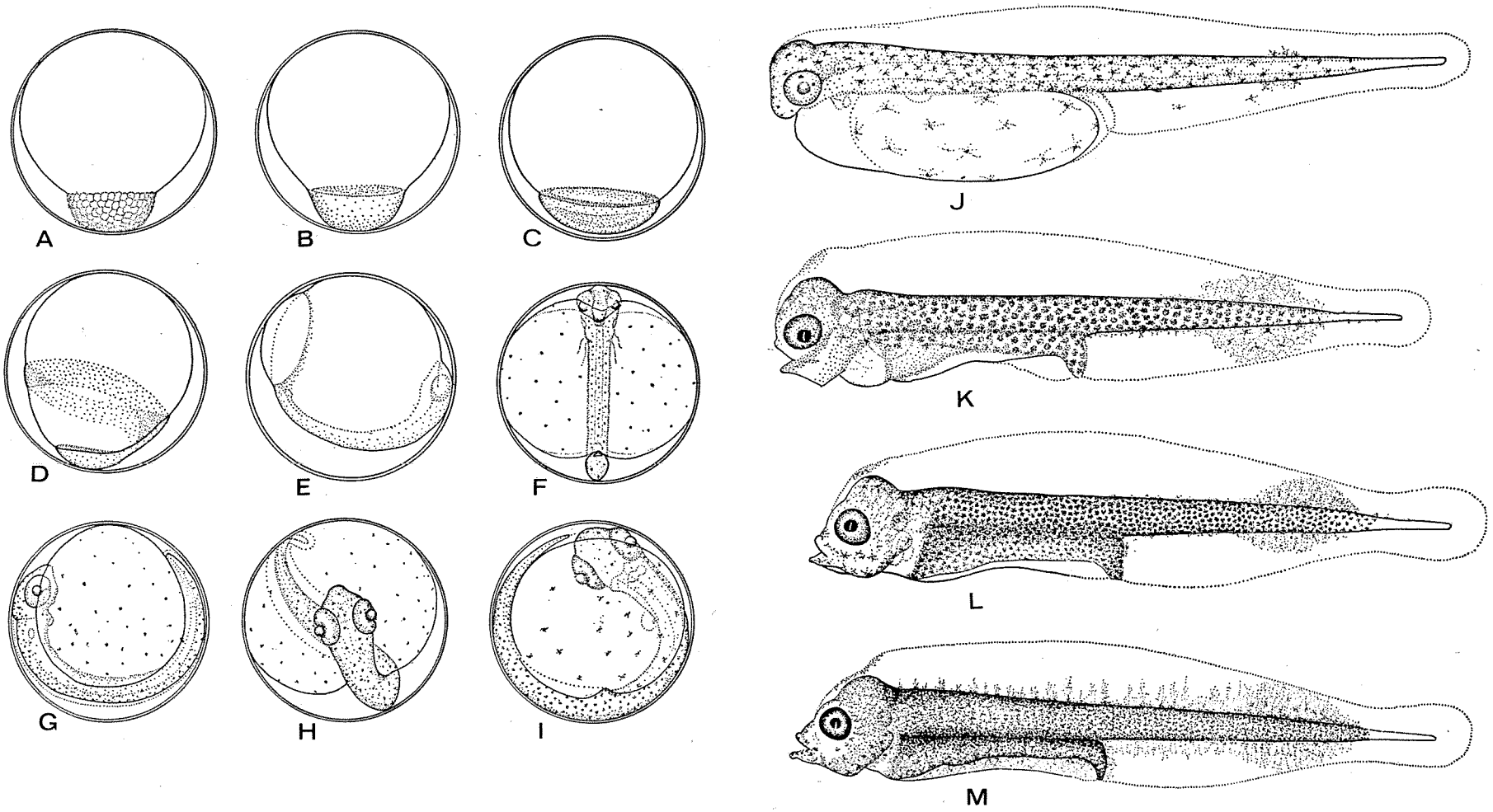


Fig. 49.33. Egg development and early larvae of C-O sole, Pleuronichthys coenosus. A) Early blastodermal cap; B) completed blastodermal cap, 14 hr; C) segmentation cavity and early germ ring, 22 hr; D) germ ring nearly equatorial, 34 hr; E) germ ring past equatorial position, 42 hr; F) shortly after blastopore closure, 62 hr; g) tail free of yolk sac, 86 hr; H) tail encircling yolk sac, 114 hr; I) late stage embryo, 140 hr. (Times given are hours from early blastodermal cap stage). J) Larva just after hatching, 3.88 mm; K) 4-day larva, 4.35 mm; L) 7-day larva, 4.62 mm; M) 9-day larva, 4.72 mm. (Source: Budd 1940, who identified the series as Pleuronichthys decurrens).

(Fig. 49.33E) and by 62 hours, tiny pigment spots appeared on the body and yolk sac (Fig. 49.33F). Yellow chromatophores appeared on the body by 86 hours (Fig. 49.33G). When near hatching, the embryo formed a complete circle around the yolk and was almost completely covered by an even coating of yellow and black chromatophores with a sparse scattering of chromatophores on the yolk sac (Fig. 49.33I). Two-thirds of the way along the tail, a trace of color occurred at the base of the finfold. At 13.8°C, hatching began at 150 hours after early blastodermal cap and probably about 160 hours after fertilization (Budd 1940).

Newly hatched larvae are 3.88 mm SL and active, although movements are erratic due to the large, buoyant yolk sac. The body is well-covered with melanophores, except for the tip of the tail and the yolk sac which has a scattering of pigment cells. Near the end of the tail, melanophores appear to "stray" into the dorsal and ventral finfolds (Fig. 49.33K). In early larvae (3.7 mm) described by Sumida et al. (1979), several small melanophores are present on the margin of the posterior tip of the tail and the lower half of the head is relatively unpigmented (Fig. 49.34).

Reared larvae measure about 4.35 mm after four days from hatching, and the yolk sac is almost entirely absorbed, eyes are very dark and mouth and jaws are formed (Fig. 49.33K).

Flexion occurs when larvae are 6.2-7.8 mm NL (notochord length) and postflexion larvae are characterized by increased pigmentation in the dorsal and ventral finfolds and on the lower part of the head (Fig. 49.34C). With development of anal and dorsal rays, pigment in the finfold aligns along the fin rays (Fig. 49.34D) and later becomes compacted into a narrow band adjacent to the fin bases (Fig. 49.34E).

The gut begins to coil at 5.5-6.0 mm SL and larvae are undergoing caudal fin formation at sizes of 6.2 to 8.5 mm NL with the full count of caudal rays developed on a postflexion specimen of 8.2 mm SL. Dorsal and anal fin formation takes place at about the same time as caudal fin formation. Pectoral fin buds are present, but without rays through 11.4 mm, but rays are present by 17.0 mm. Pelvic fin buds are present during notochord flexion and reach full count of rays by 9.6 mm SL. Eye migration may begin at sizes of 8.2 mm SL and is nearly complete in a 11.4 mm Sl transforming specimen (Sumida et al. 1979).

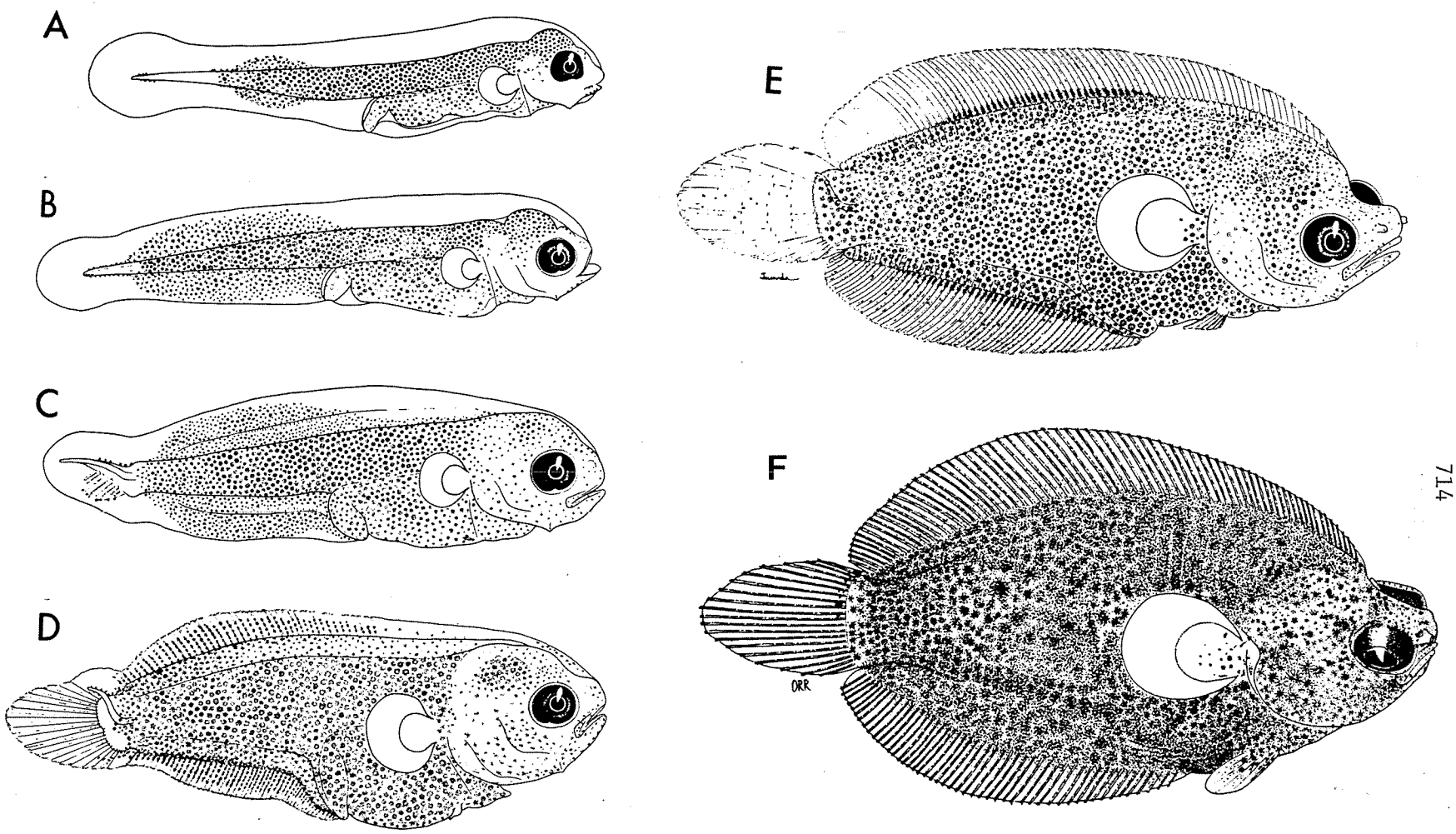


Fig. 49.34. Larval stages of C-O sole, Pleuronichthys coenosus: A) 3.7 mm; B) 5.9 mm; C) 6.1 mm; D) 7.8 mm; E) 8.9 mm; F) 10.0 mm, transforming. (Source: Sumida et al., 1979).

Psettichthys melanostictus - Sand sole

Range: southern California to Bering Sea

Occurrence in Puget Sound: common

Adult habitat: demersal

Spawning habitat: unknown

Spawning season: late winter-spring

Mode of reproduction: oviparous

Eggs: pelagic

Larvae: pelagic

Sand sole are found from southern California to the Bering Sea (Hart 1973) and are generally distributed along the inner continental shelf at depths less than 180 m and usually $\leq$ 35 m (Alverson et al. 1964). In Puget Sound, sand sole are common and wide-spread (Miller and Borton 1980), and have been commercially abundant in Bellingham Bay and Washington Harbor. In Puget Sound, adults are found between 20 and 30 m over sand-mud bottoms (Smith 1936).

Sand sole spawn in late winter to spring and possibly through summer. Smith (1936) found ripe females in Bellingham Bay during February through April. Hickman (1959) and English (1961) collected maximum abundances of eggs from Puget Sound in January through March. Spawning fish have been collected as late as July in Sydney Inlet on the west coast of Vancouver Island (Manzer 1947).

In Puget Sound, all age-group II males and age-group III females are mature, with some age-group II females also reaching maturity (Smith 1936). In B.C., Manzer (1947) reported finding two immature females which were completing their fourth year.

No information on fecundity of sand sole is currently available.

Sand sole eggs are pelagic, spherical and about 1.0 mm in diameter. They are colorless and contain no oil globules, chorion sculpturing, or other distinctive characteristics (Hickman 1959). Early stage eggs cannot be separated from those of starry flounder, English sole, or butter sole (English 1961; Richardson et al. 1980).

Development times range from 5-7 days at 7.5^{o}C, decreasing to about 3.5 days at ~ 12^{o}C (Table 49.18). Times to reach major developmental stages at 7.5^{o}C are summarized in Table 49.19.

Table 49.18. Development times of eggs of sand sole, Psettichthys melanostictus, at various temperatures.

Reference	Temperature °C	Development time (hours)
Smith 1940	7.5	126.2[1]
	9.1	126.75
	10.8	97.5
	12.0	80.75
	14.7	68.5
	16.8	60
Hickman 1959	7-9	∿120
English 1961	7.5	157[2]
	10.0	108
	12.3	84

[1]Times to first hatch
[2]Times to 50% of eggs hatched

Table 49.19. Developmental stages of artificially fertilized sand sole eggs incubated at 7.5°C. (Source: English 1961).

Developmental stage		Duration (hours)	Cumulative hours
Early embryo	I Cell cap	28	28
Middle embryo	II Early epiboly	11	39
	III Half epiboly	20	59
	IV Yolk plug	4	63
	V Blastopore	9	72
Late embryo	VI Closed, diffuse	16	88
	VII Closed, well	19	107
	VIII Tail bud	17	124
	IX Tail bud free	7	131
	X Tail bud thin	4	135
	XI Tail bud medium	12	147
	XII Tail bud wide	8	153
	one-half hatched	4	157

Larval and early juvenile stages of sand sole have been well-described and illustrated (Hickman 1959; Sommani 1969). Sand sole hatch at about 2.8 mm in an undeveloped condition, and contain a large oval yolk sac characteristic of flatfish larvae. There is no sign of the mouth or jaws, but within 24 hours of hatching an indentation at the mouth appears. The anus is also undifferentiated at hatching, but becomes visible after 24 hours. The optic cups and lens are well-formed, but only lightly pigmented in one-day old larvae. At hatching, pigmentation consists of melanophores scattered over the body surface and in characteristic areas. Rows of melanophores are present along the dorsal and ventral finfold margins and persist throughout the larval period. Midway between the anus and tip of the tail, a concentration of melanophores overlies the trunk musculature and extends dorsally and ventrally into the finfolds. Another concentration of melanophores overlies the gut. Thirty-seven to thirty-nine myomeres are evident (Fig. 49.35A).

In later stage larve, 3 to about 10 mm, pigment along the trunk becomes concentrated in several groups along the dorsal and ventral surfaces and along the ventral surfaces of the yolk sac, and lower jaw, eventually forming a row along the ventral midline from the anus to the mouth (Figs. 49.35B-F). In larvae > 8.0 mm, the trunk chromatophore groups gradually disappear, except for the most posterior group which remains prominent throughout the larval period (Figs. 49.35, 49.36). Chromatophores on the gut become prominent and expanded after 7 mm and persist until metamophorsis.

Live sand sole larvae are characterized by brown melanophores which appear black after preservation. Also, in live material shortly following yolk sac absorption (10-12 d), the brown chromatophores become overshadowed by a bright orange carotenoid pigment, which is also destroyed by preservation.

The gut begins to coil at 4.6-4.9 mm and is complete in larvae $\geq$ 5.5 mm. The body also begins to deepen noticeably at this stage. Caudal fin rays first appear at 6.0 mm and at 7.5 mm a slight swelling in the posteroventral tip of the tail indicates the first hypural cartilages are forming. Radial elements first appear on the dorsal and anal fins at ~ 8.0 mm and caudal fin rays have begun to appear. Flexion of the notochord commences at 9 mm and fin rays of the dorsal and anal fins begin to appear. Ossification occurs first in the dermal bones of the 8.0 mm larva in the skull, particularly the jaw bones, and in the cleithrum. The pectoral fins which are undifferentiated at hatching, become large and fan-like with small scattered melanophores at 6 days, and are the last fins to acquire fin rays.

Eye migration and the resulting shift to asymmetry begins at about 13-14 mm and the left eye reaches the dorsal surface of the head by 20-24 mm, and may reach the adult position in larvae of ~ 22-23 mm. During the stages of eye migration, pigmentation is added in groups scattered over the body, and on the head some appear as streaks

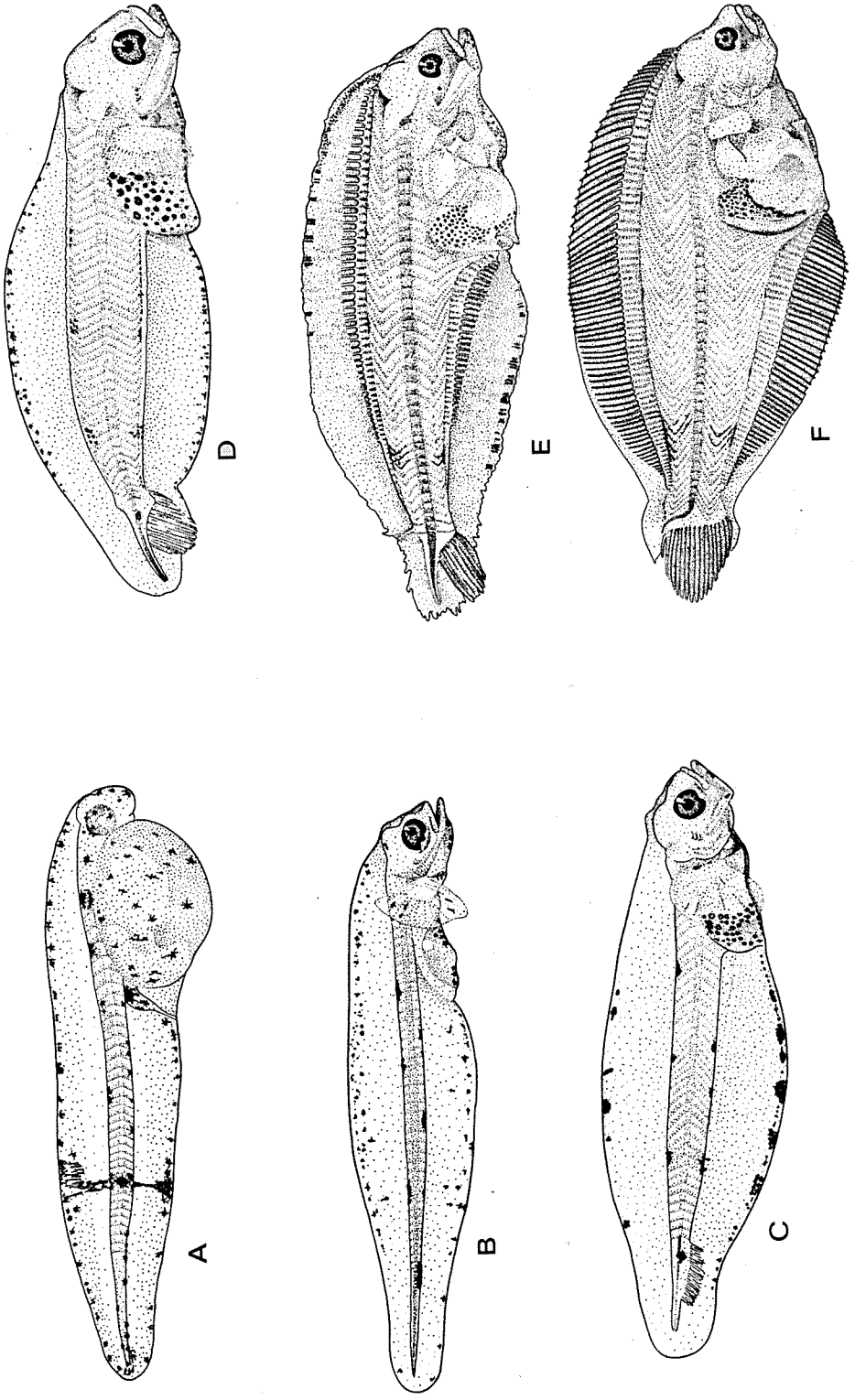


Fig. 49.35. Larval stages of sand sole, Psettichthys melanostictus: A) yolk sac larva, 3.0 mm, one-day-old; B) 4.0 mm, ten days old; C) 7.5 mm; D) 8.5 mm; E) 11.0 mm; F) 14.5 mm. (Source: Hickman 1959).

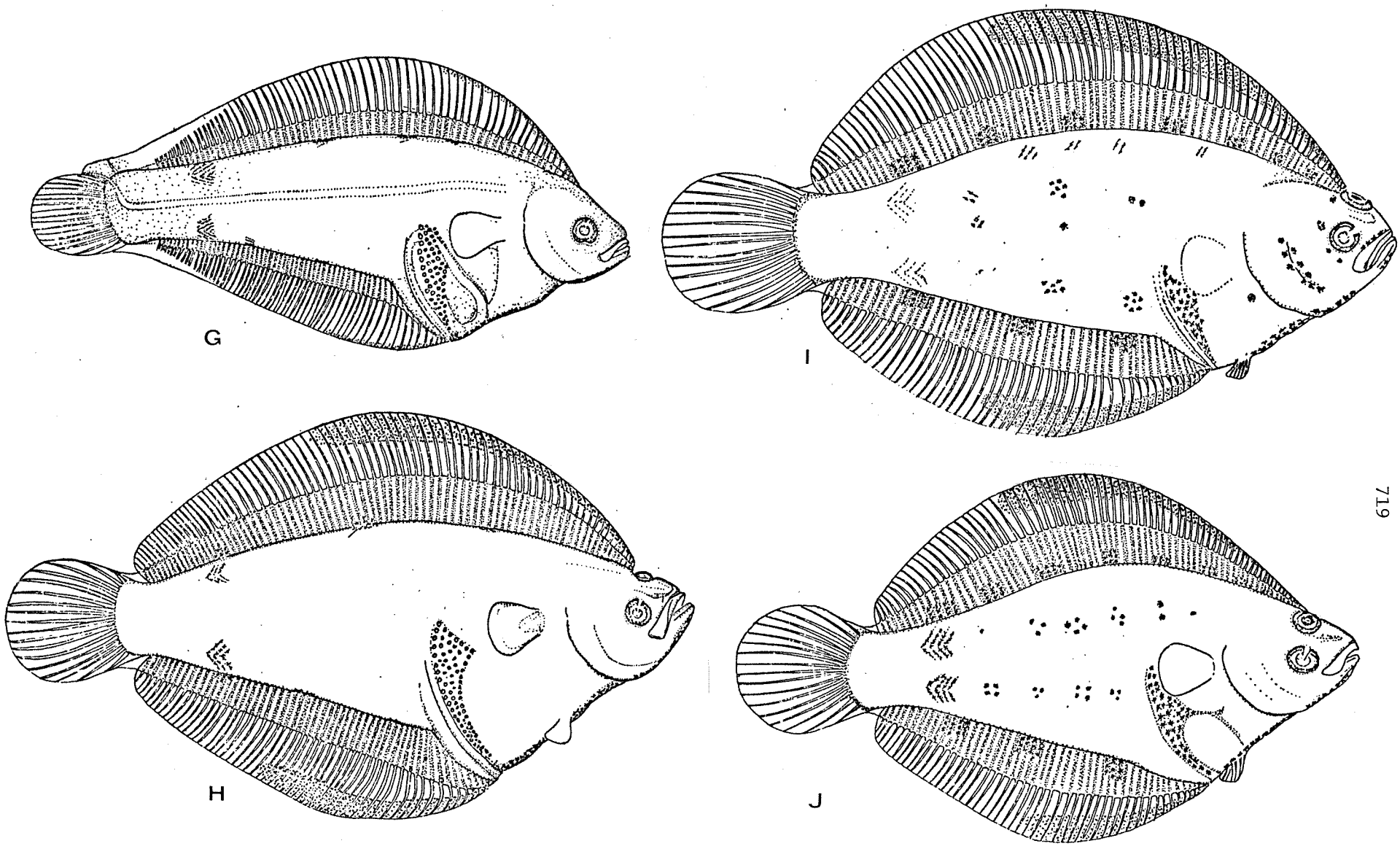


Fig. 49.35 (cont.'d) Larval stages of sand sole, Psettichthys melanostictus: G) 15.38 mm; H) 21.76 mm; I) 23.33 mm; and J) 26.41 mm. (Source: Sommani 1969).

overlying the myocommata. Patches of stellate melanophores on the bases of the anal and dorsal fin ray supports have increased to seven dorsally and three ventrally. Metamorphosis to juvenile coloration is complete by 25-27 mm.

Small larvae have been collected from the plankton in Puget Sound from April to August and are relatively abundant at depths of 5-20 m (Sommani 1969). Settlement of sand sole juveniles occurs over an extended time period. In the Straits of Juan de Fuca and in the San Juan Islands, the arrival of metamorphosed sand sole on beaches occurs from summer through winter, although the heaviest settlement occurs in summer (Thornburgh 1978).

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50. MOLIDAE

Mola mola - Ocean sunfish

(Available literature not reviewed)

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