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PROJECTED EFFECTS OF CO$_2$-INDUCED CLIMATE CHANGE ON THE PACIFIC HERRING (*CLUPEA HARENGUS PALLASI*) FISHERY IN THE NORTHEAST PACIFIC OCEAN

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1. INTRODUCTION

The worldwide combustion of fossil fuels, clearing of forests and changes in land use have created an increase in atmospheric CO_2. Concentrations are expected to double, from a pre-Industrial Revolution 270-290 ppm to about 600 ppm, in the 21^{st} Century (National Research Council [NRC] 1983). By conservative estimates, levels are now rising at about 2% per year (Palutikof et al. 1984). Increased CO_2 will create a greenhouse effect on the earth's surface, disrupting the global circulation system, with continuing climatic changes. If this occurs, global mean temperatures are likely to rise 2-4°C (Palutikof et al. 1984).

This study reviews existing literature pertinent to the potential effects of CO_2-induced climatic changes on herring (Clupea harengus pallasi) in the northeast Pacific Ocean. The geographical focus reflects the extent and historical importance, though not necessarily present size, of the fisheries and the outgrowth of research thereon. Most is from British Columbia; the rest, the eastern Bering Sea, Gulf of Alaska, Washington, Oregon and California (Figures 1 and 2). Where appropriate, information on Atlantic herring (Clupea harengus harengus) is included.

Production of herring (and other fishes) is a function of physical, chemical and biological processes and, where fisheries exist, economic factors and management (Sibley and Strickland 1985). Therefore, one would expect changes in the physical environment, even in "normal" times, to affect abundance. How this occurs is complex and still, to the frequent surprise of nonbiologists, largely unknown. To compound matters, herring pass through four major life history stages (egg, larva, juvenile, adult), and substages within those stages in different habitats.

Herring display wide interannual variability in abundance, making them well suited for study of interaction of their population dynamics and environment. Their comparatively early maturity and short life span reduce and may make more traceble the potential interactions with their environment. The short lag between environmental stimulus and fishery response - three years, on the average, for herring - will allow faster completion of future studies. Moreover, many studies have been conducted on the early life history stages, and they strongly suggest this period is crucial for determining adult stock abundance.

The coastal waters from Oregon to Alaska are among the most productive and heavily fished in the world (Bardach and Santerre 1981). Pacific herring is an important commercial species in this region. In addition, the fisheries data for herring are more extensive than for any other non-salmonid pelagic fish in the northeastern Pacific Ocean (Macy et al. 1978).

Pacific herring range from northern Baja California to the Beaufort Sea, and in commercial quantities from San Francisco to Western Alaska (Hart 1973). Early uses included bait and dry salting for export to the Orient. In the 1940's the dry salt market collapsed, and a reduction fishery producing oil and fishmeal soon developed (Hart 1973). A market developed in the 1970's for herring sac roe and roe on kelp, most exported to Japan. A small market persists for fresh, pickled and kippered herring. In the Northeast Pacific, commercial fishing on herring and other clupeoid fishes has been recorded for only the past hundred years.

Herring, like most fishes of the clupeoid family, are schooling plankton feeders. They are key links in the marine food chain, providing forage for larger apex or near apex carnivores (Murphy 1977). Pacific herring are like spring spawning Atlantic herring in most aspects of life history. Because of their similarities, some investigators consider them two races of the same species. Much of the extensive biological information on Atlantic herring is therefore applicable to Pacific herring. Atlantic herring usually spawn in spring or autumn on deep water gravel; different stocks are recognized according to spawning period. Pacific herring spawn in spring, primarily on subtidal or intertidal vegetation. Larvae are pelagic and tend to remain in nursery areas close to shore. Within several months

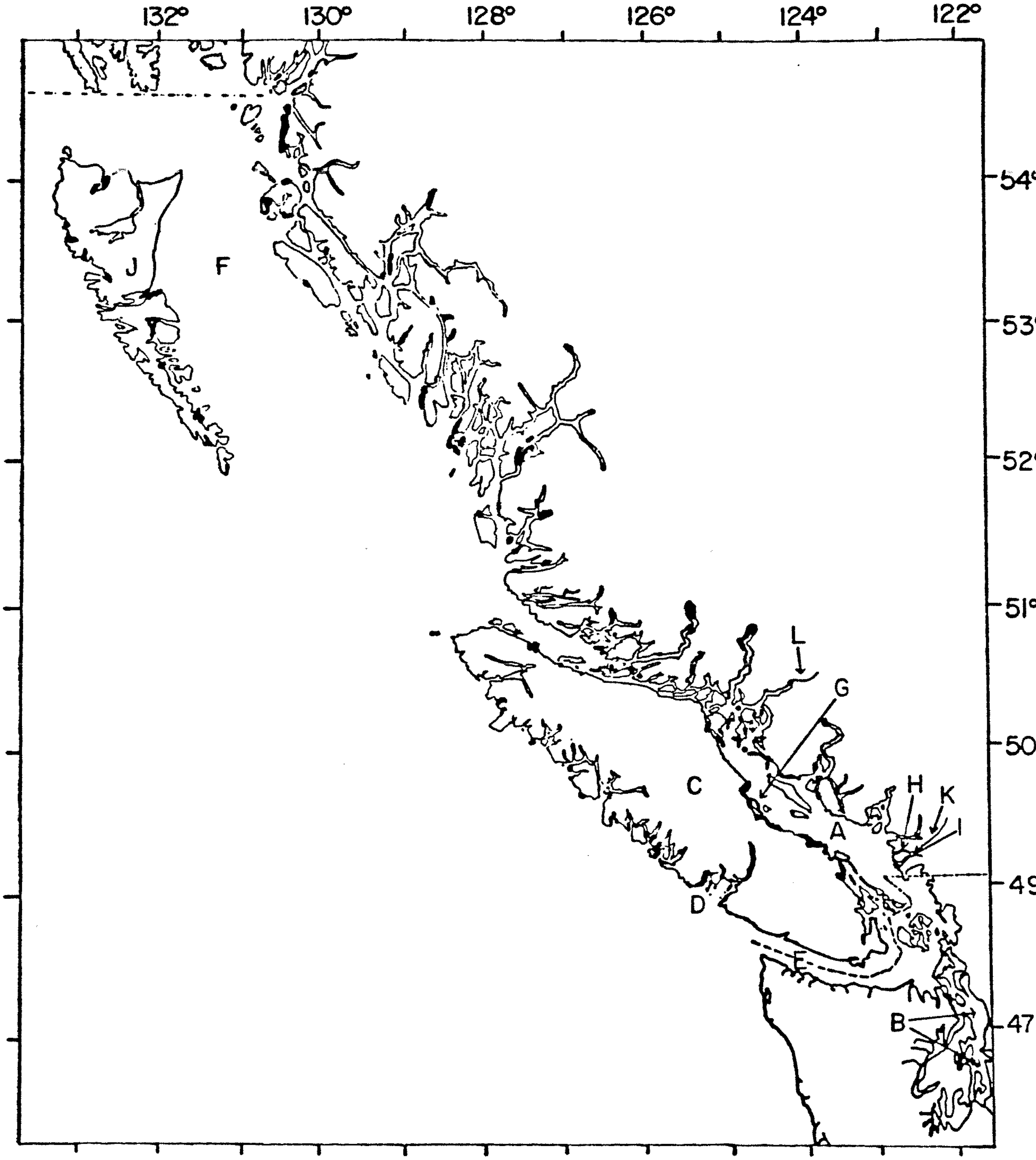


Figure 1. British Columbia. A. Strait of Georgia. B. Puget Sound. C. Vancouver Island. D. Barkley Sound. E. Strait of Juan de Fuca. F. Hecate Strait. G. Denman Island. H. Sturgeon Bank. I. Roberts Bank. J. Queen Charlotte Island. K. Fraser River. L. Squamish River.

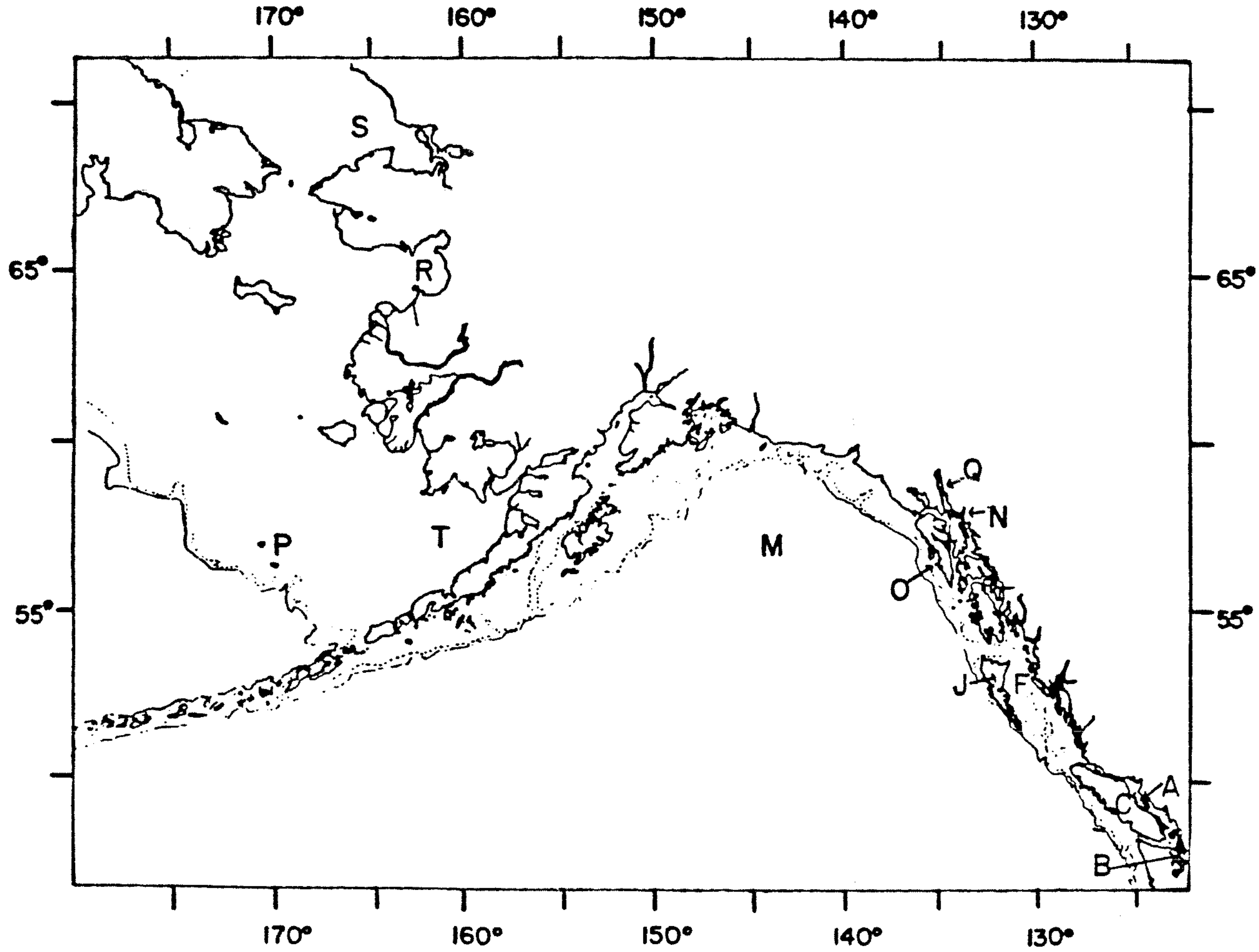


Figure 2. The northeast Pacific Ocean. A. Strait of Georgia. B. Puget Sound. C. Vancouver Island. F. Hecate Strait. J. Queen Charlotte Island. M. Gulf of Alaska. N. Auke Bay. O. Sitka. P. Pribiloff Islands. Q. Lynn Canal. R. Norton Sound. S. Chuckchi Sea. T. Bristol Bay.

they metamorphose into sexually immature juveniles resembling small adults, and gradually aggregate into schools. The majority migrate offshore, staying over the continental shelf. Sexual maturity and recruitment into the fishery occurs at 2-4 years. Although few live beyond age 9, Pacific herring can live to 15-16 years (Reid 1972).

1.1 HISTORICAL FLUCTUATIONS IN HERRING FISHERIES

A number of independent historical observations on Northern European herring fisheries suggest that large, long term fluctuations in herring abundance have been commonplace since 1100 (Cushing 1982). Fishing alone was probably not sufficiently intensive to create fluctuations of these magnitudes. Data from commercial Pacific herring catches began about 1920. Sometimes incomplete, these records are among the longest for any northeast Pacific species. Evidence from anchovy and sardine scales layered in sediment off California (Soutar and Isaacs 1974) suggests that these populations have large natural fluctuations. Herring, further north, are related clupeoid fishes, and similar fluctuations likely occurred in herring populations long before fishing by man. Several investigators (e.g. Wickett 1975) have attempted to link these fluctuations to climate, but no definitive relationships have yet been established.

Long term cycles in abundance have been reported in herring populations. Off the west coast of Sweden, fishery records begun about 1000 years ago show cycles of high and low abundances with an apparent 110 year (average) periodicity (Andersson 1942, in Halme 1952). A time series starting in the 17th century showed similar periodicities for stocks off the west coast of Norway, although with periods of high abundance opposite those of Swedish populations (Figure 3). Though there was no way of knowing then, the Scandanavian fluctuations seem more expansion and reduction of two stocks rather than back and forth migration of a single stock (Cushing 1982).

In 1926, Petterson noted that changes in internal waves in a Norwegian fjord coincided with changes in the herring catch from 1880-1920 (Cushing 1982). The periods in which Swedish herring flourished correlate with influxes of more saline water, transporting North Sea Bank herring into the Skagerrak area. The last abundant herring fishery in Sweden, 1878-1896, and the last in Norway, 1920-1950, occurred during a cold and warm phase, respectively (Figure 3). Beverton and Lee (1965) also link the beginning of the Norwegian fishery to reduced or expanded ice cover north of Iceland, consistent with Petterson's (1926, in Cushing 1982) observations of warm and cold Scandinavian weather.

Scandinavian temperatures may have been related to shifts between wind regimes (Cushing 1982). Coinciding with the recent warming period, when Norwegian herring were abundant, was a shift from westerly to southerly winds of less fetch, possibly more conducive to well-timed larval food production (Cushing 1982). Halme (1952) attributed the herring periodicity to oceanographic conditions affecting spawning grounds. He did not, however, identify responsible factors, and concluded that the role of climate in herring fluctuations was not clear.

High abundance of the Swedish herring populations coincides with cool climate and freezing of the Baltic (Petterson 1926, in Cushing 1982; Taning 1953). A large herring stock probably existed in the southern and western Baltic concurrent with the Swedish fishery. Cold winters accompanied by freezing in the western Baltic predominated during that time. High influxes of saltier Atlantic water into the Baltic, typical of cold periods, may have caused the less saline Baltic water to lie in a thinner layer on top and freeze more readily. Beverton and Lee (1965) suggested that water mass changes in the Baltic, and in shallow seas in general, may be due to atmospheric circulation patterns. Thus, the changes in climate may have caused both cooler weather and change in water inflows, and may have

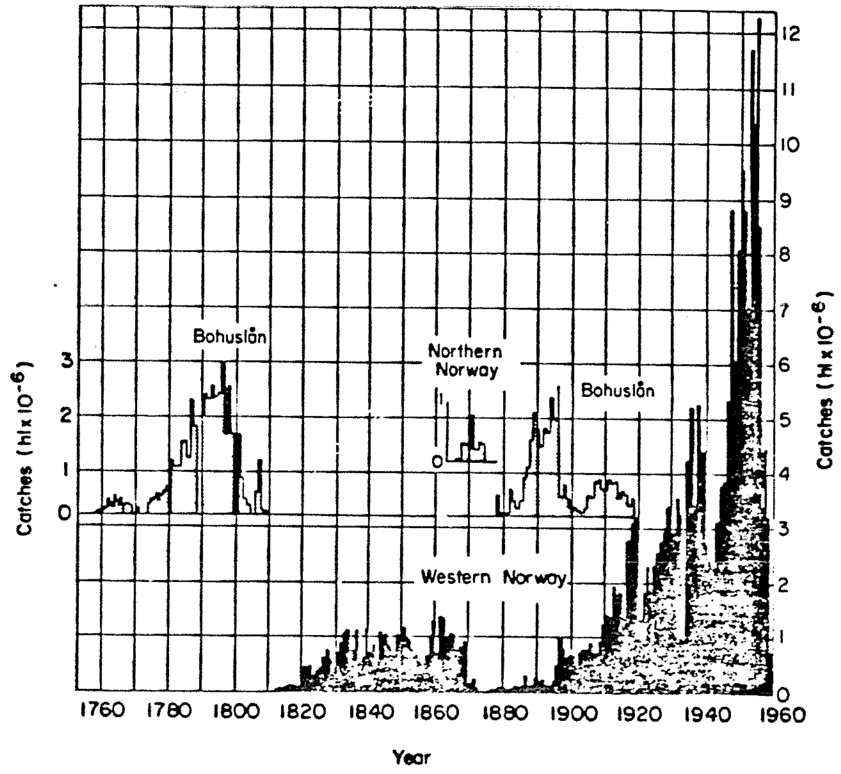


Figure 3. Catches of winter herring from the Swedish Bohulsan and the Norwegian fisheries from 1760 to 1960 (after Cushing 1982).

affected herring populations.

Halme (1952) also described changes in a herring fishery of the Turku archipelago in the Baltic Sea, where fish concentrations shifted on and off shore over the past 600 years. There, the last 50 year period of high nearshore concentrations, beginning in the late 19th Century, corresponded to a warm climatic period.

Bell and Pruter (1958), in reviewing climate-fisheries interactions, argued that increases in Norwegian and Baltic herring are probably not climate-related. Complex environmental changes other than climate per se may influence abundance, but they do not specify factors potentially responsible. Bell and Pruter (1958) used cumulative annual sea surface temperature from the European North Atlantic as a climate indicator. This may be too coarse a measure to identify interannual changes, although it would detect long term trends. Some abundant year classes occur during long term periods of low abundance. Bell and Pruter consider these events random and independent of climate.

Fishing practices also confound fisheries-climate interactions. The European herring fishery has been affected by various economic factors which are reflected in catch (Bell and Pruter 1958). Quantitative estimates of advances in fishing technology and how these affect catches are generally not available. Finally, historical estimates of abundance, on which Petterson's and others' conclusions were based, may be poor indicators of standing stock because of some disagreements over data.

Herring abundance fluctuates around long term trends (Cushing 1982). For example, fluctuations in Baltic and Norwegian herring since 1900 were not related to the general warming trends in European Seas that began in 1920 (Bell and Pruter 1958). Causes of short term fluctuations are uncertain.

The decline of herring in the North Sea between 1926 and 1966 coincided with a general warming trend in which (1) atmospheric and oceanic circulation increased; (2) strength of the upper westerlies diminished; (3) plankton abundance decreased, and an influx of northern indicator species, which may have entered as the rise in circulation tapered off, was observed, the most prominent being the replacement of one chaetognath species by another; (4) winter phosphorus concentration dropped; (5) all clupeoid fish abundances fell, and (6) pilchard, although relatively few in number, replaced herrings' traditional niche. This period (the Russell Cycle) reversed itself after 1966, and the fishery recovered (Russell 1973; Cushing and Dickson 1976).

Some fluctuations have been linked to climatic changes directly affecting marine environmental conditions. Cushing (1982) believes the important factors affect year class strengths by influencing survival during the first six months of life.

1.2 NORTHEASTERN PACIFIC HERRING FISHERIES

1.2.1 Unit Stocks

Washington

Individual stocks are not yet well defined in Washington (Buchanan 1983) although differences in growth rates among individual fishing groups suggest at least three stocks within Puget Sound (Gonyea and Trumble 1983). There may be, as well, some overlap of U.S. and Canadian stocks in the Strait of Georgia and off southeast Vancouver Island.

British Columbia

Nine herring stocks have been identified in British Columbia (Figure 4) among which Taylor (1964) reported up to 25% mixing. This figure is based on tag recovery of migrating herring, not from spawning grounds where stocks are probably more discrete.

Southeast Alaska

Two races of herring have been identified on the basis of genetic differences: an eastern race extends from Kodiak southward, and a western one extends into the Bering Sea (Grant 1979). Herring stocks in Auke Bay differ from those off Sitka and Craig and from most major stocks in southeast Alaska and British Columbia (Carlson 1980).

Eastern Bering Sea

Three major wintering grounds exist in the Bering Sea (figure 5) (Barton and Wespestad 1980). Each population has distinctive growth, maturation and age structures, suggesting separate stocks with little intermixing. Figure 6 shows locations, timing and magnitude of spawning in eastern Bering Sea spawning grounds.

1.2.2 The Fishery

Washington

Small fisheries for general purpose and bait have existed in Washington for decades (Trumble 1983). Washington herring fisheries, historically smaller than British Columbia's, were less than 500 tons until 1957 (Ketchen et al. 1983). With the development of a sac roe fishery, larger catches began in 1973 (figure 7).

British Columbia

Indians in British Columbia fished herring and herring spawn for at least 2800 years. The first commercial herring catch, 75 metric tons, was taken in 1877. From 1904 to 1934 a herring fishery for dry salting developed for export, taking 30,000-85,000 tons annually. In 1935 a fishery for reduction began (Hourston and Haegele 1980).

Annual fishing mortality rates of 75-90% in the 1950's did not cause noticable declines in the populations (Hourston 1980). In 1961 fewer age 0 herring were caught, and most stocks began declining in 1963 (Taylor and Wickett 1967; Hourston 1980) (Figure 4). Hourston (1980) attributed the decline to (1) poor recruitment for several years before and after the decline began, (2) improved fishing technology, (3) insensitive measurements of abundance, or all three. Environmental factors were not considered, and the cause of poor recruitment not known, but suspected to be overfishing.

The fishery was closed for four years beginning in 1967. By 1974 the southern stocks regained or surpassed previous levels; the northern stocks never regained more than half their earlier abundances (Hourston 1980; Webb 1983). The geographic variability in timing suggests the presence of several stocks whose declines were not simultaneous (Hourston 1980).

In the early 1970's the fishery changed as herring utilization shifted from meal and oil to roe. The fishery moved from migratory routes to spawning grounds. Large concentrations of spawners on the coast are easily and rapidly caught by seine and gill net fishermen (Hourston and Haegele 1980). Because spawners are so vulnerable to overfishing, the roe fishery is highly regulated. In some years low abundance prevents any fishing (Trumble 1983).

Southeast Alaska

Herring were first fished commercially in the Gulf of Alaska in the 1880's. A

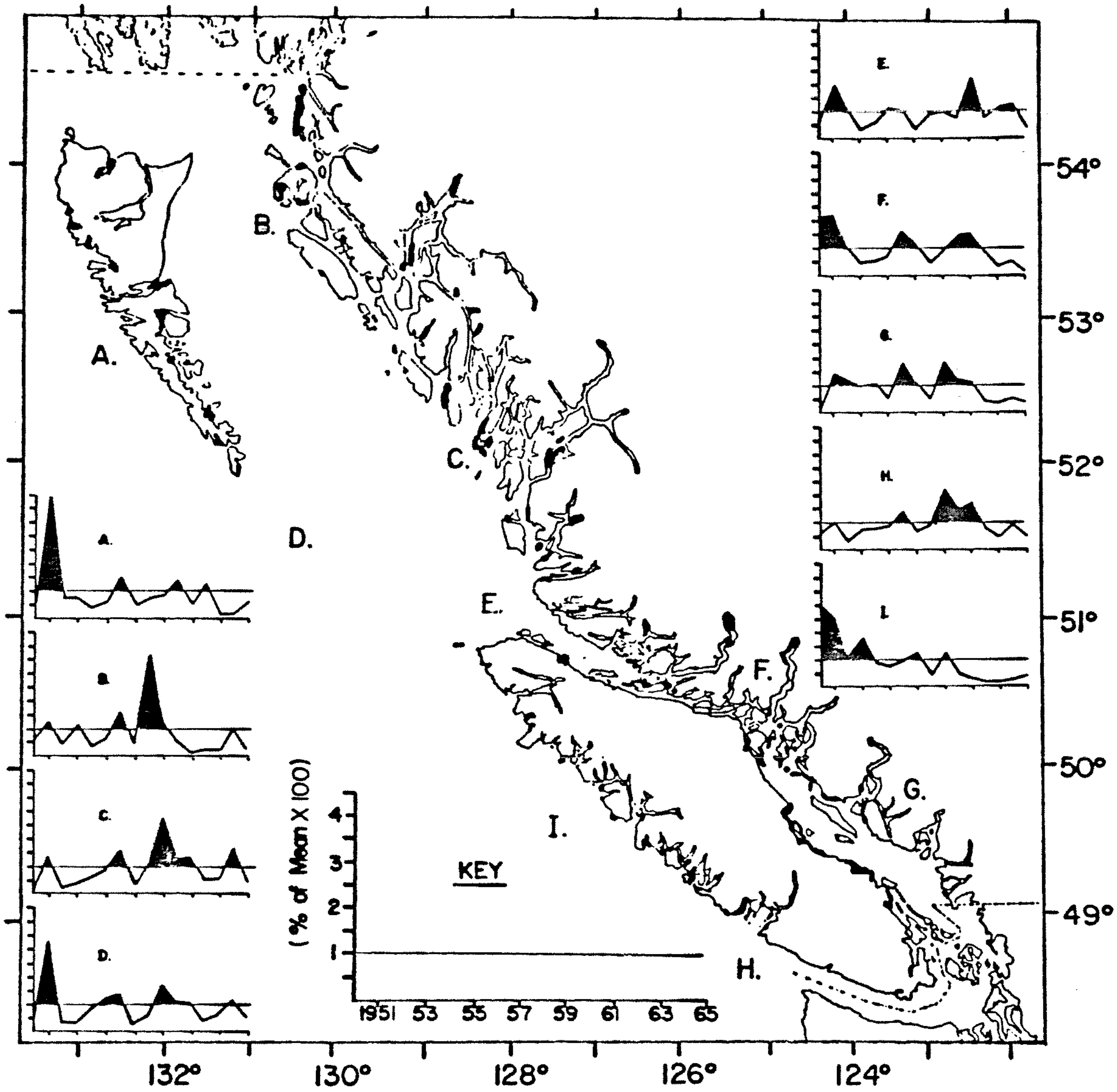


Figure 4. Estimated relative abundance of age 1 herring stocks of British Columbia. Major spawning grounds are also shown (after Hourston 1980).

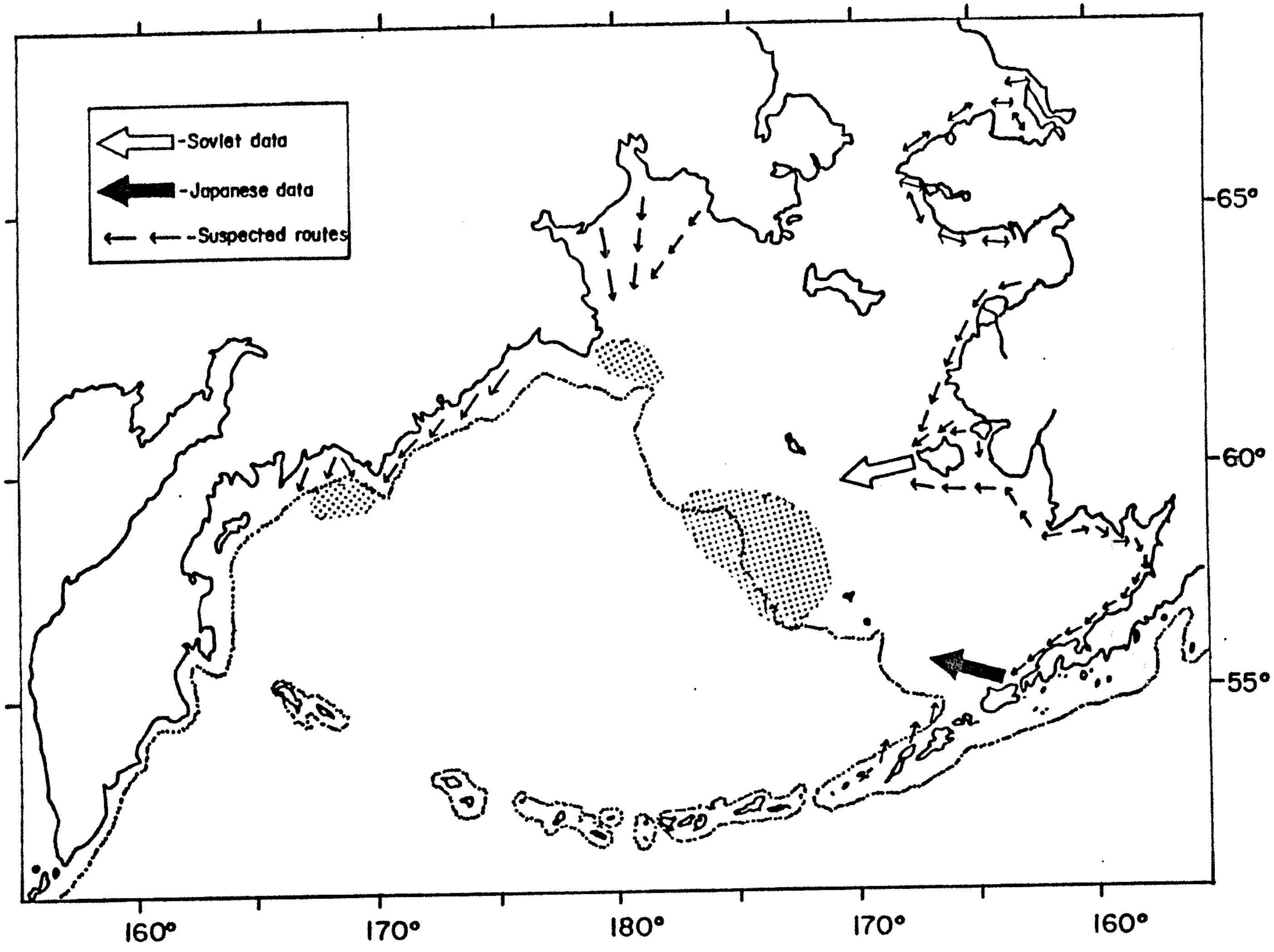


Figure 5. Herring migration routes to and from Bering Sea wintering grounds (after Wespestad and Barton 1981).

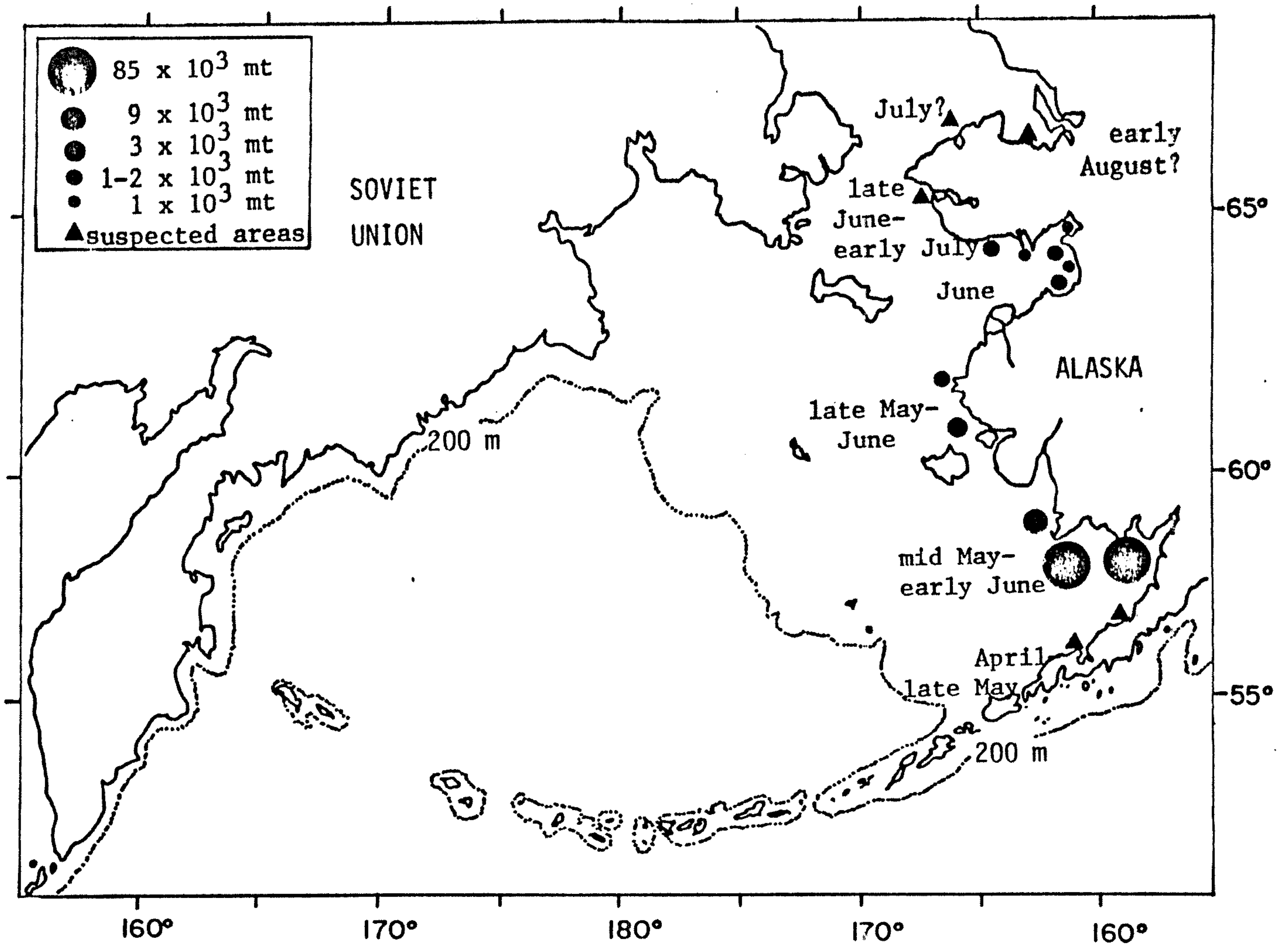


Figure 6. Distribution, average spawning time and relative abundance of herring on coastal spawning grounds in the eastern Bering Sea (after Wespestad and Barton 1981).

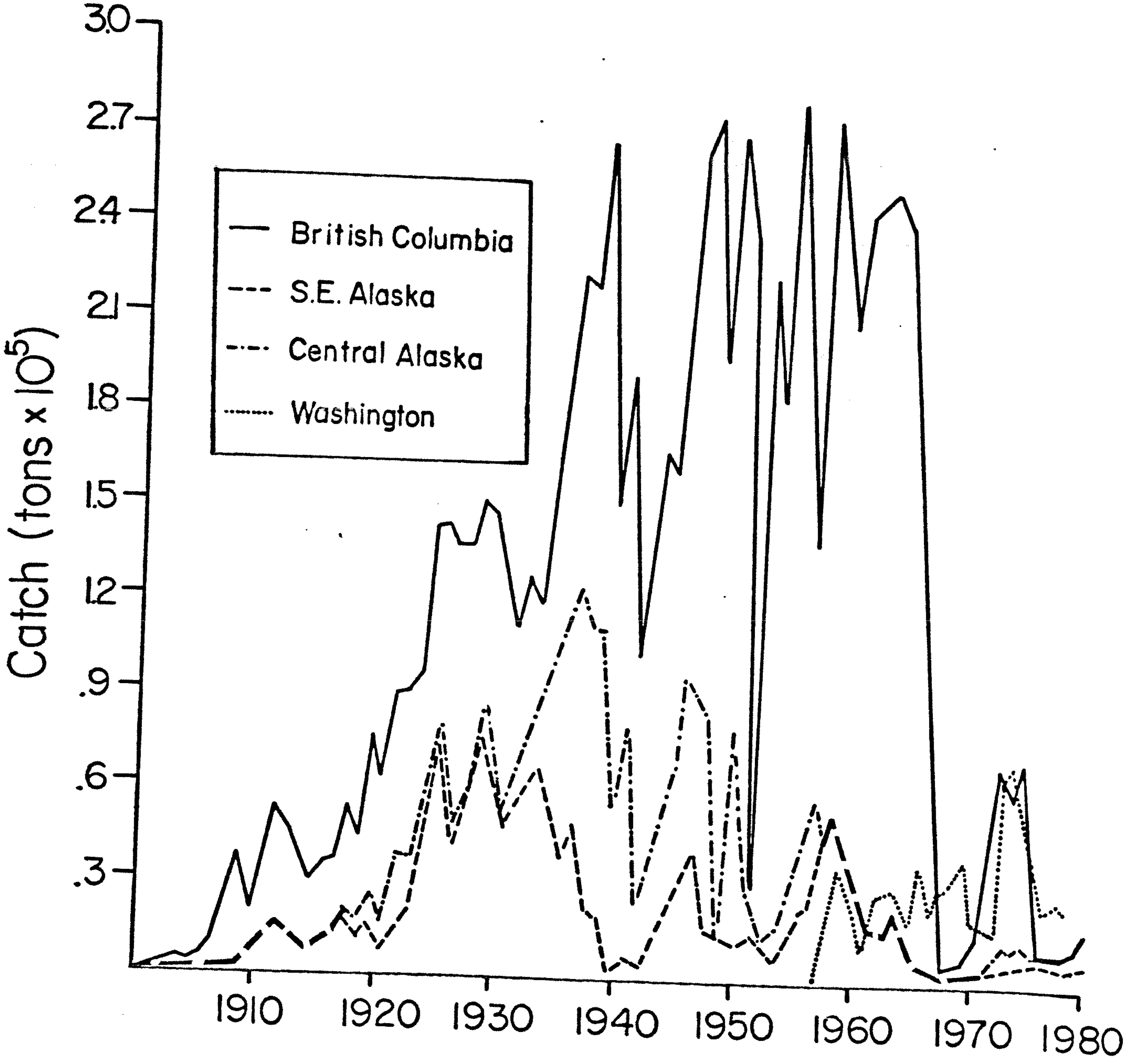


Figure 7. Herring catches in the northeastern Pacific Ocean, 1900-1980 (after Trumble 1980; Wespestad and Fried 1983).

fishery for reduction to fish meal peaked at 70,000 tons in 1929, but declined after the second World War and ended in the 1960's for economic reasons (Wespestad and Fried 1983). A sac roe and spawn on kelp fishery developed in the 1970's (Blankenbeckler 1980). Small food and bait fisheries continue. Average annual catch from the sac roe fishery was 5500 tons in the 1970's (Wespestad and Fried 1983).

Eastern Bering Sea

A fishery for herring to be salted existed in the eastern Bering Sea from 1928 through the 1940's that caught up to 3000 tons (Wespestad and Fried 1983). The Soviet Union began a trawl fishery in 1959, and was eventually joined by Japan. The catch peaked in 1970 at 140,000 tons, then declined due to lower abundance and government regulation. Americans began fishing in the late 1970's.

Catches in the late 1960's and early 1970's contained older, larger herring than catches in the late 1970's, suggesting that poor recruitment contributed to lower abundances. Recruitment has increased since 1972 (Wespestad and Barton 1981). However, current measures of abundance cannot be directly compared to earlier numbers because fishing intensity has increased. Therefore, it is difficult to assess catch and catch per unit effort (CPUE) data (Wespestad and Barton 1981). Furthermore, CPUE data are not available for most Alaskan herring stocks.

In a model of the eastern Bering Sea ecosystem, Laevastu and Favorite (1978) estimated a minimum of 2.75 million metric tons of herring necessary to maintain the system in equilibrium.

1.2.3 Current Status

Washington

Abundance was estimated at 14,000 tons in 1973-1974 but declined to 9000 tons by 1979, about 7% of British Columbia's. About 20% harvest is maintained (Trumble 1983).

British Columbia

Present annual catch is estimated at 30,000 metric tons (Webb 1983), and abundance about 116,000 mtons (Stocker et al. 1983). Total catches since 1900 are shown in Figure 7. Migratory routes and the absolute population size of British Columbia herring remain to be adequately determined.

Southeast Alaska

In 1979 the catch from sac roe, bait and food fisheries was 13,000 tons (Bankenbeckler 1980) and declined to 8000 tons in 1982.

Eastern Bering Sea

About 27,000 tons of herring were caught in 1982 (Wespestad and Fried 1983).

1.2.4 Age Composition

Washington

The fishery, generally dominated by four to six-year old fish, since 1980 has had a major component of two-year old herring. Subsequent observations (Buchanan 1983) show mean age, length and abundance decreasing, due not only to a loss of age 6 and older fish, but also to more younger individuals.

British Columbia

Taylor and Wickett (1967) found Vancouver Island stocks in the 1960's generally dominated (50-75%) by age 2 fish , and northern populations by a mixture of ages 2, 3 and 4 cohorts simultaneously. However, their information may have been based on oceanic stock rather than spawning area trawls, in which, through mixing, 1-2 year olds dominate (R. Trumble, Washington Dept. Fish., pers. comm.). More likely, southern populations were dominated by age 3 fish, and northern by age 3, 4 and older cohorts - so the pattern, but not the ages, was the same. This pattern continued in the north through the late 1970's, but the single cohort dominance in southern British Columbia gave way to additional, or in some years older, year class dominance (Hourston and Schweigert 1980). Most recent data suggest a return to the 1960's composition (Stocker et al. 1983). Because single year classes dominate southern populations, fluctuations are likely to be more abrupt in the south than in central or northern British Columbia (Taylor and Wickett 1967).

1.3 FISHERY DATA

Most data on herring stocks come from commercial catch records of adult fish. Age composition of a stock can reveal sizes of individual cohorts which comprise a catch. In Washington, estimates of spawning adults in Washington are calculated from spawning areas and spawner densities, and hydroacoustic surveys (Trumble et al 1982). Mortality rates are mostly determined by comparing the numbers in each age class for successive years (Taylor 1964).

The accuracy of fisheries estimates, especially during periods with changing fishing technology, is of major importance to any fishery study. Catch per unit effort (CPUE) measures, for example, are of questionable accuracy even in recent fisheries investigations; Clark (1975) suggests that CPUE can be inversely related to actual abundances when pelagic fish distributions are patchy.

2. BIOLOGY AND LIFE HISTORY

2.1 ADULTS

An average herring in British Columbia reaches sexual maturity and recruits into the adult fishery at age 3, at about 185 mm and 90 g (Hourston and Haegele 1980). Weight increases by only about 50% once mature. Cod and certain other species, in contrast, increase by an order of magnitude (Cushing 1982).

Spawning Behavior

Herring spawn once a year. Females lay about 100 eggs per spawning act, which they repeat several hundred times over a few days (Hourston and Haegele 1980).

Fecundity

Earliest maturing (age 2) and old (age 8) female Pacific herring lay about 9000 and 38,000 eggs, respectively (Hart 1973). Off British Columbia 190mm females contained 19,000 eggs, and 220mm females 29,000 eggs (Hart and Tester, 1934).

Fecundity of Pacific herring decreases from north to south, although this trend reverses in the Bering Sea (Barton and Wespestad 1980). The decrease is offset by an increase in mean length of mature females with latitude (Paulson and Smith 1977). Herring fecundity increases more than proportionally (i.e., nonlinearly) with body size. There is a slight trend toward smaller egg size with greater fecundity, but female growth rate and body size affect fecundity much more than egg size. Thus, smaller females produce fewer, not smaller and potentially less fit, eggs.

The relationship between spawner size and fecundity is similar among different stocks in British Columbia. No evidence exists that these factors are influenced by natural variations in abundance or environment (Ware 1984), at least on the small scale. However, regional differences in growth rates were attributed to available surplus energy for spawning adults (Ware 1984). The specific causes and consequences of these differences are not clear.

Density dependent effects on fecundity may have been found in North Sea herring. In 1933 the population was larger in number and less fecund than 23 years later (Nikolsky 1969). Fecundity is affected by growth, which in turn is influenced by food supply. It is unclear if population size of herring can alter the food supply. In the laboratory fecundity has not been affected by imposed environmental changes, including food (Blaxter and Hunter 1982) so the differences noted by Nikolsky (1969) may have been coincidental.

2.1.1 Distribution and Abundance

Large Scale

Adult Pacific herring are seasonally migratory, spawning inshore in spring, most moving offshore (but not beyond the continental shelf break) to feeding grounds in summer, and again to overwintering grounds. Their highly aggregate distribution may be in response to patchy food distributions or, being forage fish, to school so as to reduce predator effectiveness (Murphy 1977).

In April and May adult British Columbia herring move from spawning grounds to offshore feeding grounds off the Strait of Juan de Fuca in the south and Hecate Strait in the north (Hourston and Haegele 1980). Schools of 1-10,000 tons located off the Strait of Juan de Fuca, for example, totalled 200,000 tons, or about 19 billion fish. They are distributed on bank edges along a 160 km coastal stretch. In summer schools traverse the coast, presumably searching for or following food organisms (Hourston and Haegele 1980). From October to December adults stop feeding and concentrate into larger schools near inshore spawning grounds (Taylor 1964).

Data on exact migration routes in British Columbia are sparse. Timing of migrations varies from year to year and among populations (Taylor 1964). For example, inshore migration of lower east coast stocks generally occurs in late October and November, but upper west coast stocks migrate from December to February.

Herring distributions in southeast Alaska have similar patterns from year to year. They move in search of food during the summer, then migrate to and concentrate on overwintering areas (Carlson 1980). Wintering grounds of most major stocks are close to spawning grounds (Blankenbeckler 1977) but far from summer feeding areas (Kolloen and Smith 1953).

Fall migrations in southeast Alaska are linked to destratification of the water column. In autumn schools go deeper as air temperature, sea surface temperature and daylength decrease, and mean wind velocities increase. Storms, beginning in October, create more surface turbulence. The upwelling and water column destratification that often result (Bruce et al. 1977) create fairly uniform temperatures at all depths, and zooplankton quantity decreases (Carlson 1980). When this occurs, herring migrate from open passages to sheltered wintering grounds (e.g., Auke Bay and Fritz Cove). Destratification of the water column over a few days is probably a more important migration cues than are gradual environmental changes.

Migration patterns in the Bering Sea (Figure 5) are similar to, but longer than, migrations in southeast Alaska and British Columbia because distances from wintering grounds near the shelf edge to coastal spawning grounds are longer. Based on growth and behavioral differences, stocks north of Norton Sound probably stay there year round, overwintering under the ice in coastal lagoons and bays (Barton 1978).

Temperature. The summer distribution of herring in the eastern Bering Sea may be influenced by shelf temperature. Surveys in August show almost one order of magnitude more herring on the warm side of 4°C isotherms (Wespestad and Fried, unpublished data). During the summer adult herring prefer water warmer than 3°C, while juveniles are found usually in cooler water (Rumyantsev and Darda 1970). Nevertheless, herring are not limited physiologically to narrow temperature ranges. Dragesund (1970) found age 0 herring at temperatures from 0° to 8°C off Norway. Yet data from the Bering Sea (Wespestad and Fried 1983) suggest that some distributions are restricted to a smaller temperature range.

Water temperature may govern migration rates, because cold water decreases activity. Slightly later arrival of adults onto Bering Sea spawning grounds in cold years suggests slower migrations (Wespestad and Fried 1983). Alternatively, it may indicate delayed departure from wintering grounds.

Salinity. Salinity may also affect herring distribution. Bering Sea juveniles have been found in the autumn between 31-32ppt isohalines, and adults between 32-33ppt, with slight overlap (Wespestad and Barton 1981) (Figure 8). In the Gulf of Alaska, however, salinity has no discernable relation with herring distribution (Carlson 1980). Effects of salinity on British Columbia populations are unknown.

Pacific herring favor estuarine waters for spawning (Rabin 1977). Spawning in the Strait of Georgia is more extensive in the north, which may be attributable to lower salinities. Herring sperm remain motile longer in lower salinities, and brackish water may be preferred, in part, for that reason (Levings 1983a).

Phytoplankton blooms. Summer eastern Bering Sea herring distributions may be affected by phytoplankton blooms. Herring are generally found off the shelf in summer (Wespestad and Barton 1981), possibly to avoid heavy phytoplankton blooms

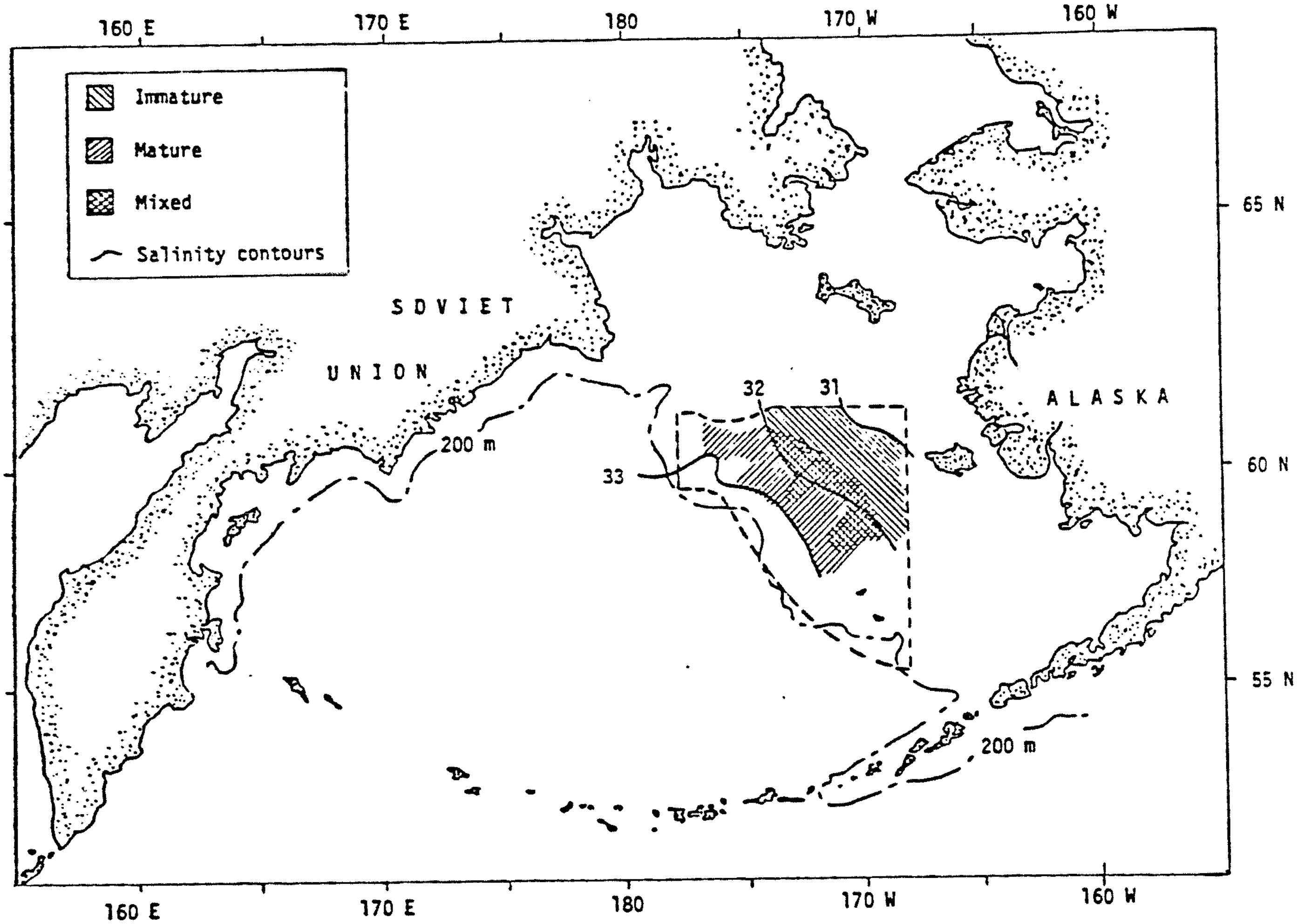


Figure 8. Distribution of eastern Bering Sea herring in October. Salinity isobars are in parts per thousand (after Wespestad and Barton 1981).

(1-3 g Carbon per m^3) which are associated with poor feeding and thought to clog gills (Rumyantsev and Darda 1970).

Ice. Icefishing surveys suggest that some Bering Sea herring stocks overwinter beneath the ice (Sheboneev 1965; Wespestad and Barton 1981). This behavior should reduce their vulnerability to some major predators that do not go under ice, such as adult pollock. Warmer air temperatures will likely reduce total ice cover in the Bering Sea.

Fronts. Horizontal migrations may be influenced by fronts between water masses. For example, North Sea migrations have a similar year to year pattern, but occasionally are altered by Atlantic Ocean water encroaching from the north and pushing the migrations southward.

The effect of fronts on herring distributions may be indirect. During the migrations herring may slow their movement or stop at food patches (Blaxter and Hunter 1982) often concentrated on fronts. The effects of climate changes on fronts in the eastern Pacific are difficult to predict.

Spawning locations. Pacific herring spawn intertidally or subtidally on a relatively small proportion of available coast (Hay 1984) in specific inshore habitats (Figure 4): on eelgrass in sheltered bays and open sand beaches, and on rockweed at rocky shores; almost never on exposed coast (Taylor 1964). No one coastline type seems favored. Some areas are used every year, others used intermittently.

Homing. Pacific herring tend to return to spawn in areas where they were spawned (Taylor 1964; Zijlstra 1969). Burd (1984) found year to year variability in spawning distribution, although herring making first spawning returns overlapped almost entirely their parents' distributions. In times of "anomalous environmental conditions" (no further detail given), however, European herring stocks have failed to return to regular spawning grounds and spawn elsewhere (Halme 1952). British Columbia herring may have spawned deeper than normal in 1978 during unusually warm water temperatures (Wickett, in Mclain and Ingraham 1980). The effects on abundance in either example, however, are unknown.

Spawning timing. Timing is fairly precise. The interannual variability in peak spawning times for individual herring populations is a one week standard deviation around the long-term mean (Cushing 1969; Wespestad and Fried 1983). There is controversy over which environmental variables control spawning timing. Cushing (1969) believes that fixed spawning times in temperate waters causes larvae to hatch, on the average, during periods with peak food production. Longer spawning periods with lattitude may dampen effects of interannual environmental variability (Cushing 1975). An environmentally driven food or growth resurgence may trigger spawning (Iles 1974), and peak spawning times may have evolved from larval food habits, subsequent growth rates or from seasonal changes in structure of zooplankton populations (Hunter 1981). One recent theory, at least for spring and autumn spawning Atlantic herring, is that spawning adapted to the mean characteristics of specific nursery areas, rather than to larger scale seasonal plankton blooms (Sinclair and Tremblay 1984).

Along the Pacific coast herring spawn later at higher latitude (Table 1). An exception is stocks on the Washington side of the Strait of Georgia, which spawn in April, one month later than stocks on the Vancouver Island side (Trumble 1980). Spawning in British Columbia is from mid-February to mid-June, most occurring in March, and peaks about 2 weeks later in the north than south (Taylor 1964). Higher mean temperatures in March result in earlier spawning in the Strait of Georgia, where each stock appears to have its own response to temperature (Hay 1984).

Spawning in San Fransisco and Tomales Bays, California peaked in February

Table 1. Herring spawning times and temperatures along the Pacific coast of North America (after Laevastu and Hayes 1981).

LOCATION	SPAWNING TIME	TEMPERATURE
California	January-April	8.0-10.0°
Oregon	January-April	3.8-12.3°
British Columbia	February-April	4.4-10.7°
Southeast Alaska	April-May	6.1-11.0°
Eastern Bering Sea	April-May	3.0-5.5°

until the late 1960's. By the late 1970's it occurred half a month early, for reasons unknown (Spratt 1983). Blaxter and Hunter (1982) suggest that spawners may control their ripeness and modify spawning time between years.

Cardwell and Koons (1981) believe that, because spawning in the Strait of Georgia can run from February to June, timing of peak spawning may vary considerably. Bimodal distributions of juvenile sizes have been found in some areas (e.g., Sturgeon Bank) in June, suggesting differences in age, hence spawning times, of up to three months. Alternatively, although unstudied, two different stocks may be spawning (R. Trumble, Wash. Dep. Fish., pers. comm.). Temperature and intrinsic developmental rate differences no doubt affect growth rates and, in turn, some of the size differences observed. Regardless why spawning spans such a wide interval, maturation cycles are unlikely controlled by just one set of photoperiod or thermal conditions for the whole species. Rather, different responses of groups or races to environmental conditions are possible (Blaxter and Hunter 1982).

Specific spawning locations and timing may be selected in part to enhance larval retention in nearshore areas (Stevenson 1962). Consequently, the production, timing and placement of larvae can be fairly precise (Cushing 1982; Blaxter and Hunter 1982).

Small Scale

Herring schools move back and forth with the tide along the shoreline of principal summer feeding areas. The longest axis of distribution lies in the direction of tidal currents (Bolster 1958).

Size, configuration and density of herring schools are highly variable. Variation occurs on seasonal, daily and hourly scales. Schooling breaks apart at night (Welsby et al. 1964) apparently in response to light intensity. No one shape or density is best suited for all purposes; variability may be adaptation to changing environments, or result from changes in physiological states of individual fishes (Blaxter and Hunter 1982).

Abundance

Oceanic stocks may comprise hundreds of thousands to millions of tons, inshore stocks hundreds to thousands of tons. Why herring schools are so variable in size is not known. Yet small stocks are apparantly as self-maintaining as larger ones (Blaxter and Hunter 1982).

Vertical Distribution

Adult herring in feeding grounds off the Strait of Juan de Fuca and Hecate Strait in British Columbia are found at depths of 100-150m, shallower than juveniles (Hourston and Haegele 1980).

Temperature, not salinity, is most likely controlling vertical distribution, especially in late summer (Carlson 1980). During the summer most adults in the Gulf of Alaska are at 5-37 m, 10-37 m in the latter half. Temperatures in southeast Alaska drop in November and December, and schools remain deep, close to bottom during the day, and rise and disperse at night. By January-February schools are at their deepest (50-80m). Bering Sea herring are deeper in winter than summer (Wespestad and Fried 1983). Depth segregation with age may occur in some months (Figure 9).

Depth preference is influenced by bottom depth, light intensity, and possibly turbidity (which also influences light intensity), temperature profile, food and predators (Blaxter and Hunter 1982). The role of light is complex. Light intensity is the principal trigger of vertical migration (Blaxter and Hunter 1982).

Spawning depths. Eggs are deposited intertidally and subtidally on marine vegetation from 1 m above sea level to 7 m below, and 5-12 m on worm tubes (Trumble 1983).

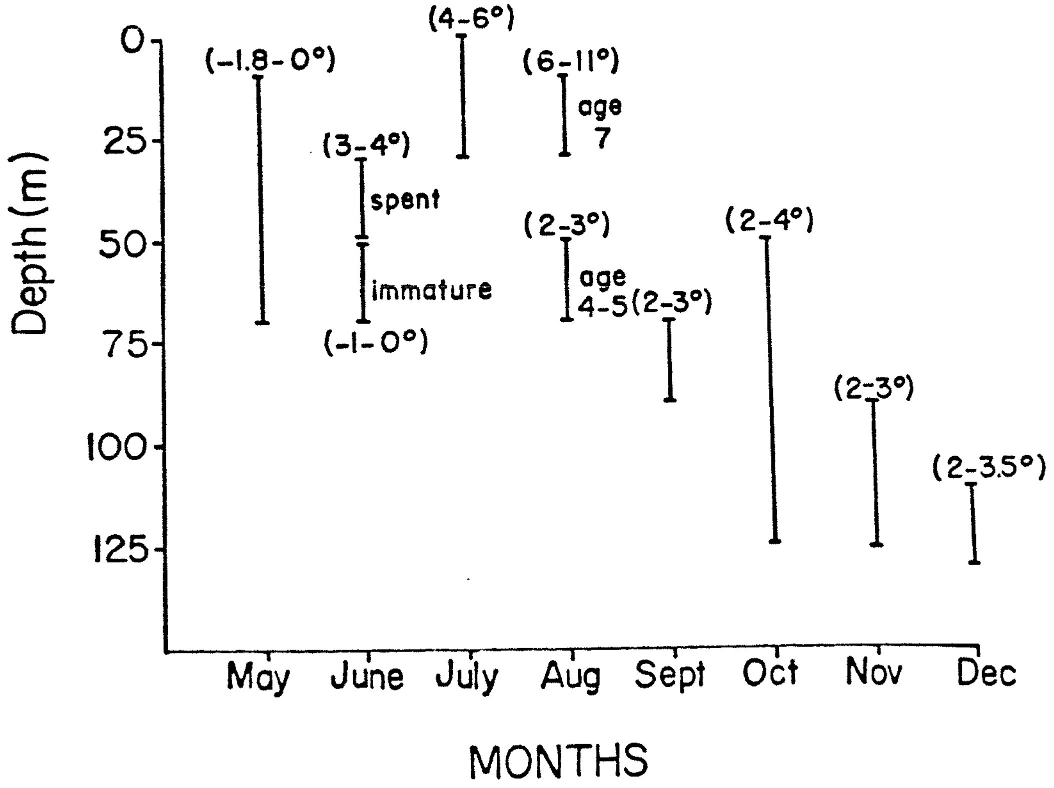


Figure 9. Monthly distribution of herring by depth and temperature in the eastern Bering Sea (after Wespestad and Barton 1981).

2.1.2 Feeding

Adults offshore of Washington and British Columbia consume mainly euphausiids and decapod larvae. Prey size increases as the individual grows (Fresh 1983). Adult herring feed by picking at relatively large food organisms in the water column. Filter feeding, seen in other clupeoid fishes, has been observed in the laboratory if herring have only very small particles to eat (Blaxter 1984).

Prey Abundance and Availability

The aggregation of prey organisms at sharp gradients, typically between water masses, where productivity is high, attracts herring. Cushing (1982) notes that herring and food organism distributions correspond. Around the British Isles, herring aggregate at fronts formed between stratified summer water masses and tide-driven currents (Pingree et al. 1975). Overwintering autumn spawning herring in the North Sea aggregate near the edge of the Baltic outflow to feed on krill. In turn, krill feed on increased productivity of smaller plankton (Steele 1961). Currents in the Gulf of Alaska are sufficiently strong to orient herring and carry in food, yet not so extreme as to displace them nor change their migrations upcurrent (Carlson 1980). The herring form, in effect, a biological front (Flierl 1983).

Changes in fronts between water masses, while of uncertain impact to Pacific herring, were attributed in part to the collapse of Icelandic and Norwegian fisheries in the 1960's (Jakobsson 1969). Calanus finmarchius, the principal food source, had previously concentrated in a polar front between Atlantic and Arctic Ocean water. In the mid 1960's, the front changed, and the distribution of Calanus populations was displaced. Coincidental with the change in fronts, Icelandic stocks decreased and Norwegian stocks migrated northward in the summers. By 1967-1968 the Norwegian fishery had concentrated 600-800 miles offshore of its prior location.

All life history stages of herring rise toward the surface to feed, and feeding peaks at dawn and dusk. At night they are inactive (Blaxter and Holliday 1963). Blaxter and Hunter (1982) postulated that the reduced feeding at night is accompanied by reduced metabolic energy consumption; whether they "sleep" isn't known. Feeding periods are controlled by light; they lengthen in summer at higher latitudes, and shorten in winter.

Food Limitation

Adult herring probably do not become food limited, for individual growth and reproduction rates don't increase when fishing is very intensive (Parrish et al. 1981). However, food may be limiting at high herring abundances. Haist and Stocker (1984) argue that they found a dome-shaped growth rate relative to abundance of British Columbia adults, suggesting, because of decreased individual growth at highest abundances, density dependent growth (see below). Incorporation of sea surface temperatures increased the model's fit.

Herring may be less density dependent than other species, and less prone to food limitation, due to their feeding on zooplankton, which have much shorter generations than food organisms (e.g., larger invertebrates, fishes) of many other fish species. Consequently any depleting effects of feeding by herring may not last as long (Ware 1980). Density dependence is discusses in more detail below.

Temporal Patterns of Energy Storage and Mobilization for Growth

Levings (1983b) found differences in condition, a relationship of length to weight, as strong within as between years in the Strait of Georgia, based on the data of Hourston (1957) and his own recent observations. By contrast, little year to year variation in length/weight ratios of Maine herring was noted from 1964-1968, but wide seasonal variations existed. Least variation was in January-February, when water temperatures and food supply were lowest (Chenoweth 1970).

In the eastern Bering Sea growth varies among individual herring stocks and from year to year. Stocks adjacent to one another show more similarity, although individual cohorts may show distinct patterns of growth within each stock. Differences in growth rates of herring spawned at different periods in the same year are usually less than growth rate differences between locations for individual year classes (Rowell 1983). In contrast to the general Pacific herring growth trend, herring in the Bering Sea have decreased growth rates from south to north. Smaller herring are found, for example, in Norton Sound and the Chuckchi Sea than in the southeast Bering Sea (Wespestad and Fried 1983). Age of sexual maturity and maximum length also increase with lattitude.

2.1.3 Predation

Dogfish are the major predators of adult and juvenile herring in the Strait of Georgia (Taylor and Wickett 1967). Fresh (1983) found that herring were greater than 50% (by weight) of adult and subadult chinook salmon prey in Puget Sound. Pollock and sperm whales are major adult herring predators in the eastern Bering Sea, where, variations in predation are hypothesized to cause changes in herring biomass (Laevastu and Favorite 1978).

Predation is high on spawning grounds; adults are shallow, concentrated and most vulnerable. Spawning ground predators in British Columbia include seals, sea lions, killer whales, gulls, cormorants and puffins, in addition to dogfish (Hourston and Haegele 1980).

2.1.4 Other Biotic Impacts

Epizootics. Effects of epizootics in marine fish populations have rarely been quantified. Epizootics of Pacific herring remain poorly studied, partly because they have never been identified as a major source of mortality. Some combinations of factors both environmental (e.g. temperature, salinity, vector and host availability, numbers infected) and intrinsic (e.g. nutritional state, disease resistance) may make populations more prone to widespread outbreaks or higher levels of infection of extant diseases (Sindermann 1965).

Six epizootics causing widespread mortality among herring in the northwest Atlantic have occurred since 1895 (Sindermann 1965). Little information is available on possible environmental correlations. Reductions in herring catches in the Gulf of St. Lawrence, from 11,340 metric tons in 1947 to 5443 tons in 1959, are attributed largely to infection by Ichthyosporidium, a fungus. Tibbo and Graham (1963) estimated that half the adult herring died in 1954-56 alone.

The effect of climatic changes, particularly temperature increases, on disease or parasite outbreaks in Pacific herring is difficult to predict. But conditions creating physiological stress increase the likelihood of epizootics.

2.1.5 Mortality Estimates

Annual natural mortality of British Columbia adult herring (probably caused by predation) is estimated to be 30%, and seems to increase with age, especially for males (Hourston and Haegele 1980). For example, in the Queen Charlotte Islands, Tester (1955) estimated 32%, 47% and 60% annual natural mortality for age 3-4, 4-5 and 5-9 herring, respectively. Yearly mortalities in Barkley Sound from 1910 to 1915, when fishing was negligible, was about 60% in age 6-9 herring (Taylor 1964).

Fishing removed about 60% of most British Columbia herring populations each year from 1953 until the mid 1960's (Taylor 1964). Natural mortalities were estimated at 15-20%, resulting in about 75-80% total mortality.

Separating short term natural and fishing mortality is difficult, because of the high interannual variability in recruitment. Variable age at recruitment, extending the recruitment of one year class over several years, often masks the effects of fishing.

Natural mortalities during the adult phase, with the exception of radical alteration of food supply due to changing fronts and epizootics of uncertain cause (both documented in Atlantic herring only), probably have little bearing on year class abundance and future recruitment. Fishing does, however, and so may unusually high numbers of predators.

2.2 EGGS AND INCUBATION

Eggs are demersal; their spatial and temporal patterns of distribution are fixed by spawning site selection. Pacific herring lay eggs on bottom vegetation, especially eelgrass and rockweed. Eggs are about 1.5 mm in diameter, weigh about .002 g and are sticky when laid (Hourston and Haegele 1980). Eggs are deposited in 1 to 4 layers.

Duration

Incubation time is 12 days at 10.6°C, and 20 days at 6.7°C (Taylor 1964).

Density

A typical 2 layer deposition on filamentous red algae covering 70% of the bottom would result in 8.15×10^5 eggs m^{-2}. On a typical large spawning ground in British Columbia 2000 m long by 100 m wide, 1.6×10^{11} eggs may be deposited (Hourston and Haegele 1980).

2.2.3 Predation

In British Columbia, gulls and diving ducks, mostly scoters, are major egg predators, causing 30-55% mortality (Taylor 1964). Marine birds, snails and amphipods are the most common predators in Washington (Palsson 1984).

2.2.4 Other Biotic Impacts

Eutrophication. Eutrophication can cause oxygen depletion through algal blooms. Egg mortalities in the Baltic Sea increased from the usual 10% to an estimated 70%, after blooms of filamentous algae in spawning areas (Aneer 1984). British Columbia and Washington waters, deeper and better circulated, are not likely to become this eutrophic.

Epizootics. Mortality to Pacific herring eggs from epizootics such as fungus is unstudied.

Changes over the spawning season. Eggs spawned later in the season are smaller, and incubation time is shorter as a result of warmer temperatures (Blaxter and Hunter 1982). The larger eggs spawned early in the season contain more yolk, and produce larger larvae. There is also longer yolk sac dependence in the colder early season (Blaxter and Hempel 1963). Female spawners producing smaller eggs later in the season may thus reduce their metabolic "cost" of reproduction, without compromising larval survival. Since 1980, late spawners in Washington have been smaller, younger individuals, often age 2 (Trumble 1983); this may also explain why eggs are smaller later in the season.

2.2.5 Other Abiotic Impacts

Temperature. Spawning ground temperatures are 3-20°C along their Pacific coast range, and 4.4-12°C (usually 10-12°C) in British Columbia (Hart 1973; Trumble 1983; Haegele and Schweigert 1984). Higher temperatures decrease incubation time and result in smaller larvae upon hatching. Optimum temperatures for Pacific herring eggs are 5-9°C (Alderdice and Velsen 1971).

Salinity. A neritic, reduced salinity environment is necessary for successful incubation (Alderdice et al. 1979). Pacific herring spawn in waters with salinities of 8-29 ppt; large mortalities of eggs and larvae occur above 30 ppt. Optimal salinity for Pacific herring eggs is 16 ppt (Alderdice et al 1979). Low salinities result in larger egg diameters, shorter incubation times and longer standard length at hatching in the Barents Sea and the northwest Pacific (Dushkina 1973).

Depth of spawning. Hatching success declines with water depth, though it is not certain why. Taylor (1971) reported that herring eggs at 18 m have 10-12% the hatching success of eggs near the surface. If warmer temperatures cause adults to spawn deeper (Wickett, in McLain and Ingraham 1980) those eggs may experience greater mortality.

Exposure to air. Exposure to air in the intertidal zone also reduces survival and raises temperatures (see above) (Jones 1972). Dessication can kill eggs (Palsson 1984).

Oxygen transport. Egg survival is dependent on adequate supply of oxygen and removal of CO_2 and metabolic waste by water flow around eggs. Therefore, hatching success is reduced because of smothering if eggs are more than four layers deep (Alderdice and Hourston 1984). Transport is a function of osmotic pressure within eggs, natural convection, wave surge and possibly vertical angle on the substrate, and is influenced by layering and density of eggs (Alderdice and Hourston 1984).

Storms and mechanical destruction. Storms can dislodge and wash ashore egg-covered eelgrass. Eggs in this condition do not usually survive to hatching (Hart and Tester 1934).

2.2.6 Mortality Estimates

Egg mortalities in British Columbia are estimated at 56-99%, depending on location. Bird predation, the largest cause, is fairly constant year to year, about 45%, 67% and 98% in protected, semi-protected and exposed areas, respectively, and is not considered a significant cause of year class variation (Taylor 1964).

Palsson (1984) estimates 95-99.5% egg mortalities in Washington from a combination of marine bird and invertebrate predation, removal by physical disturbance such as heavy wave action, and dessication in the upper portion of the intertidal zone. Eggs mortalities in the intertidal zone along the Oregon coast were 20% during cool, moist weather, but 50% in warmer, dry weather (Steinfeld 1972).

Dense spawning patches are believed advantageous because they minimize later larval dispersal and facilitate schooling, a necessary behavior for juvenile development (Shaw 1961; Stevenson 1962). However, clumping of eggs allows predators to feed selectively (Blaxter and Hunter 1982) and egg survival may be reduced if layering is overly thick. The higher mortality of fixed intertidal spawning is perhaps offset by precise larval siting and warming during exposure to accelerate incubation (Murphy 1977).

Climate changes may affect eggs exposed to air in the intertidal zone. If storminess increases, more eggs may be dislodged from turbulence. Bird predation is not likely to change, and the effect on other predators is difficult to predict.

2.3 LARVAE

On hatching, larvae are 4-6 mm long, transparent and posses a large yolk sac (Hourston and Haegele 1980).

Herring larvae in the Strait of Georgia grow at rates of 0.48-0.52 mm day^{-1} (Alderdice and Hourston 1983). Atlantic herring larvae grow slightly slower, up to 0.44 mm day^{-1} in laboratory conditions, 0.15-0.35 mm day^{-1} in plastic mesocosm enclosures (Oiestad and Moskness 1981) and 0.18-0.29 mm day^{-1} at sea (Gamble et al. 1981).

2.3.1 Distribution and Abundance

Horizontal Distribution

Larval herring nursery areas are close to spawning grounds, often directly offshore. Stevenson (in Hourston 1959) observed fewer larvae in the water column with distance from spawning grounds in British Columbia (numbers not given). Larvae in enclosed areas, where dispersal is slow, can be found in the vicinity of spawning grounds eight weeks after hatching (Trumble 1983).

Stevenson (1962) demonstrated that distribution of newly hatched larval herring in Barkley Sound, British Columbia, aside from very localized movement, was determined by tidal flow and net offshore advection. The ebbing tide carried larvae away from spawning grounds into an adjacent bay. However, flood tide did not necessarily return all larvae to shore because of counterflowing river runoff and, to a lesser extent, wind-driven currents (Ekman transport). Stevenson found that freshwater runoff at the time larvae were most susceptible to advection was more related to snowfall and spring melting than rainfall, and showed an inverse correlation between snowfall and eventual year class strength. Eddies, which elsewhere may return larvae inshore (Parrish et al. 1981) were negligible in Barkley Sound. Larvae retained near the spawning grounds survived and those carried offshore probably did not, but evidence is inferential. Although Stevenson could not demonstrate high mortality in larvae advected offshore - predation was evident but not high, starving larvae were not found and temperatures and salinities were within tolerable levels - only larvae which remained within the nursery area comprised the eventual cohort. Larvae advected offshore, Stevenson inferred, never rejoined the population.

In Bristol Bay a diffusion model depicted larval movement from spawning grounds (Checkley, in Wespestad and Fried 1983). Storms or their deviation from usual tracking can disrupt larval retention mechanisms, causing large advections from nursery grounds and resulting in poor year classes in the Bering Sea (Wespestad and Fried 1983).

Dispersal patterns may be important in determining year class strength in the St. Lawrence estuary (Hewitt 1981; Iles and Sinclair 1982). The belief is that, as in Barkley Sound, physical structure of the environment structures herring stocks. Larvae and zooplankton are retained by a gyre in St. Georges Bay in the Gulf of St. Lawrence (Lambert 1984). Areas of larval retention off the East Coast, driven by tidal currents, are thought to control larval survival and ultimately year class strength (Iles and Sinclair 1982). Larvae retained within the gyre were observed to thrive, whereas those on the outside presumably perished. Smaller retention areas resulted in fewer surviving larvae. Differences in prey and predator abundances within or outside retention areas were unreported. Survival in these retention areas maybe related to simulanteous retention of prey (see below).

The offshore distribution and transport of larvae is believed to have a significant effect on their survival. Most northeastern Pacific fish species spawn in late winter-early spring, and their larvae may exploit Ekman transport, which is wind driven and extends to a depth of about 25 m off Washington and British Columbia. Surface water movement is largely landward in winter and weakly seaward in summer. Landward transport causes surface water to accumulate and downwell on the coast. Surface water advected seaward causes compensatory upwelling of deeper water (Parrish et al. 1981). Larvae thus hatch into an environment of low ocean temperatures and the beginnings of coastal upwelling which brings nutrients to the surface. However, they hatch before offshore transport is very strong, a result of timing and location of spawning (Parrish et al. 1981).

Duration

The yolk sac is absorbed within 6 days of hatching (Hourston 1980) after which exogenous feeding begins. At this point larvae are about 9 mm long (Stevenson 1962). Within 2 months they grow to 2.5-4 cm and metamorphose into juveniles. Metamorphosis is accompanied by weight increases (up to threefold) and scale development (Stevenson 1962).

Abundance

Alderdice and Hourston (1984) estimate that an average of 5 billion larvae hatch annually in the Strait of Georgia. Little information on larval densities is available.

Vertical Distribution

In British Columbia newly hatched larvae concentrate in the upper 2 m. They move deeper and aggregate less after yolk sac absorption (Stevenson 1962). Norwegian herring larvae are most abundant at 20-40 m during the day, and above 20 m at night (Dragesund 1970). At night most move up and become vertically diffused. Older larvae undergo greater vertical "excursions" than younger ones at night, and are more often seen at the surface (Blaxter and Hunter 1982). Atlantic herring can make diurnal migrations to 75-100 m. These become regular once feeding begins (Seliverstov, in Parrish et al. 1981).

Depth distribution can influence offshore transport of larvae, as a result of horizontal current velocity, which is dependent on depth and tidal stage, and buoyancy. In the Gulf of St. Lawrence, yolk sac larvae are most abundant near the bottom, and older, post yolk sac larvae are buoyant and more dispersed throughout the water column (Henri and Dodson 1984). Due to the mean landward tidal flow below and mean seaward flow near the surface, larvae are retained during the yolk sac stage. Dispersion occurs after the yolk sac stage, when they are more buoyant and subject to vertical rise and horizontal drift into the estuary (Henri and Dodson 1984). Tidal action produces larval aggregations up to several km from spawning grounds. An inverse correlation exists between tidal current velocity and larval abundance in the water column. This pattern should remove all post yolk sac larvae from the estuary. However, Henri and Dodson did not account for this discrepancy.

2.3.2 Feeding

Prey Species

Young larvae eat many kinds of organisms. Copepods are the main food organisms, and phytoplankton, tintinnids, ciliates, fish and copepod eggs and mollusc larvae are also consumed (e.g. Wailes 1936; Bainbridge and Forsythe 1971) (Figures 10 and 11). As larvae grow they take larger prey, ranging in size from naupliar to adult stages of copepods (0.2-2 mm) (Beyer 1980).

Studies of gut fullness suggest that larval herring feed during the day (Bainbridge and Forsythe 1971). Lower limits of visual acuity are equivalent to

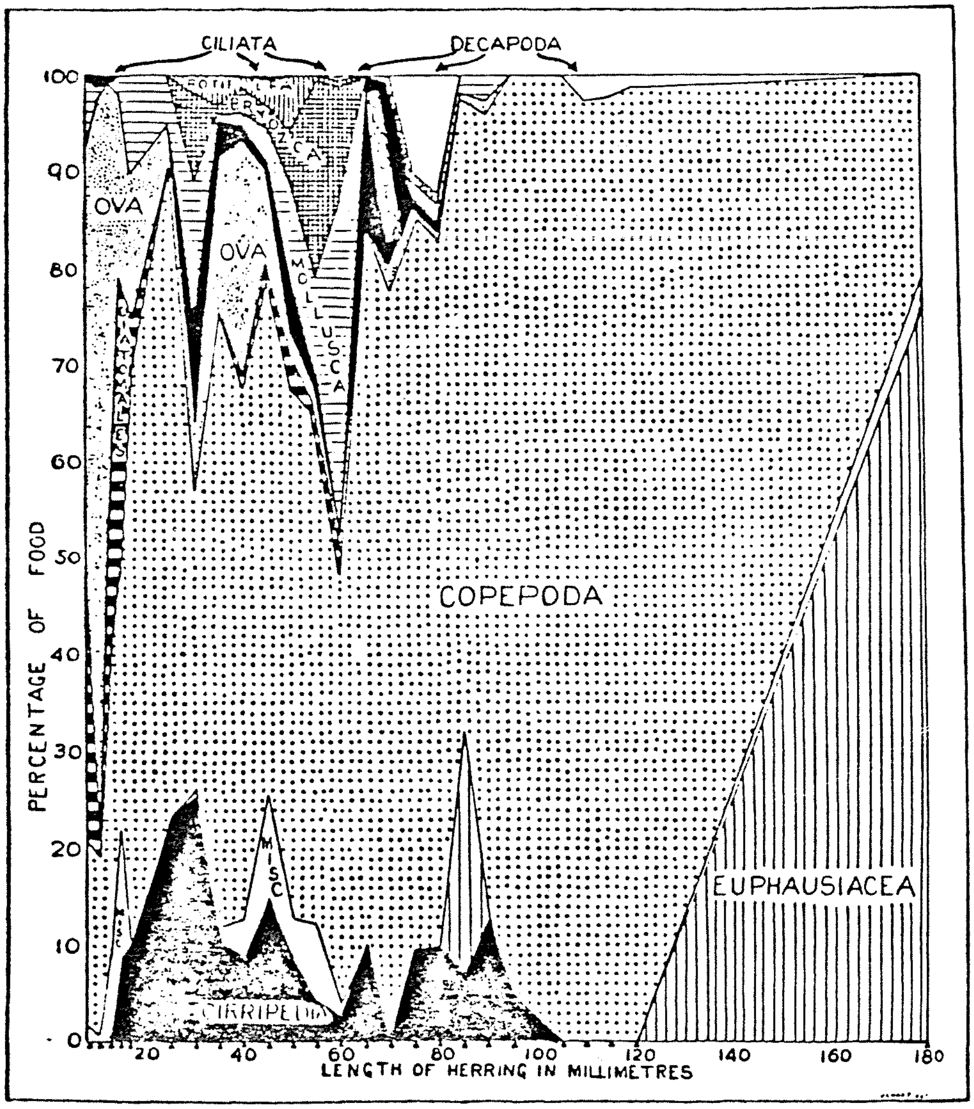


Figure 10. Relative consumption of major groups of food organisms of herring at all stages of development, in British Columbia (after Wailes 1936).

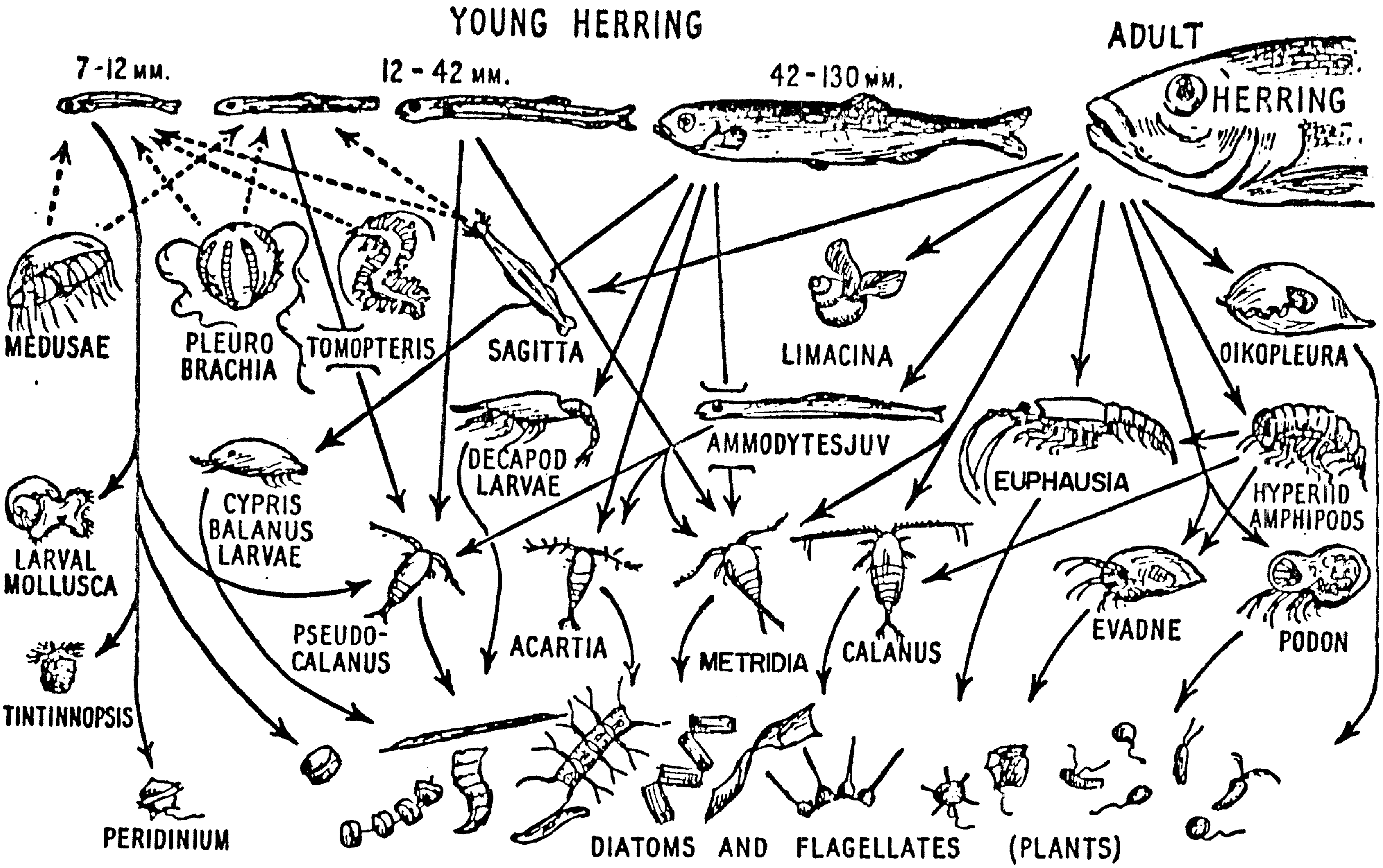


Figure 11. A sketch showing feeding relationships between Pacific herring of different ages and plankton (after Hardy 1965).

light levels at late dusk or early dawn. Visual acuity improves with growth (Blaxter and Hunter 1982), as does feeding success. At the onset of feeding, success of striking at food is only 2-6%, improving to near 100% in seven weeks (Blaxter and Staines 1971).

Larvae possess teeth but no functional gill rakers for straining. The gut is a simple straight tube. Transition to an adult feeding morphology happens gradually during the larval and juvenile stages (Blaxter and Hunter 1982).

Significant numbers of herring larvae regurgitate when handled roughly in capture (Kjelson et al. 1975) and in preservation (Blaxter and Hunter 1982). Therefore, larval gut analyses may underestimate gut fullness and misrepresent the actual diet.

Prey Abundance and Availability

Ninety percent of zooplankton production in the Strait of Georgia takes place from March to May. Interannual differences in zooplankton production are high, but smaller than seasonal changes (Harrison at al. 1983).

Small copepods such as *Pseudocalanus* spp. are the dominant zooplankton in surface waters of the Strait of Georgia during winter, especially in nearshore areas, although absolute abundances are small. and *Neocalanus* spp. are dominant in spring (Figure 12). *Neocalanus* is not as abundant to the south, where shallow depths (<200 m) and greater mixing are a barrier to the deep water adult stage. Most herring larvae feed in the euphotic zone, above 20 m (see section 7.1.2).

Nearshore zooplankton assemblages, on which larval herring feed, are more variable than in the middle of the Strait because of more dynamic hydrography, such as flushing of bays. Nearshore regions are also more subject to large, intermittent increases in abundance of meroplankton, planktonic larvae of organisms (shrimp, crab) that do'nt remain long in the plankton and of which, though consumed by larval herring, little is known of distributions or food web interactions (Harrison et al. 1983).

Most estimates of zooplankton standing stock, spatially averaged and probably underestimated, are far lower than necessary to support herring larvae in the laboratory. Often there is spatial heterogeneity - patchiness - in abundance, such as around fronts, where physical, biological and chemical gradients concentrate phytoplankton and other zooplankton prey. Zooplankton concentrations in patches have been observed to exceed 60,000 m^{-3} (0.06/ml), which approach the minimum densities that support herring larvae in the laboratory (Werner and Blaxter 1980). However, recent observations from field enclosures suggest that laboratory estimates of necessary food densities may be an order of magnitude too high (Oiestad 1984).

During years of reduced upwelling, lower plankton productivity that can be detrimental to adult pelagic fishes results when fewer nutrients are brought to the surface (Parrish et al. 1981). But reduced upwelling also results in a more stable water column, which can benefit larvae, as Lasker (1978) proposed for anchovies. Rothschild (1983) hypothesized that stability governs the spatial heterogeneity of prey, and that intermediate water column stabilities are best suited for larvae. Under very stable conditions the distribution of prey may be highly contagious and encounters with patches of food organisms may be too few, on the average; under unstable conditions, such as those that follow a storm, prey would be too widely dispersed for efficient foraging.

The onset of larval feeding generally coincides with peak zooplankton abundance in the water column (Cushing 1982). Cushing (1969, 1975) hypothesized a "match/mismatch" relationship between most larvae and their food organisms. According to this hypothesis, if peak larval abundance coincides with peak zooplankton production (match), larval survival will be far better than if timing did not coincide (mismatch), though this has never been demonstrated. Sinclair and Tremblay (1984) argue against match/mismatch, suggesting instead that, because

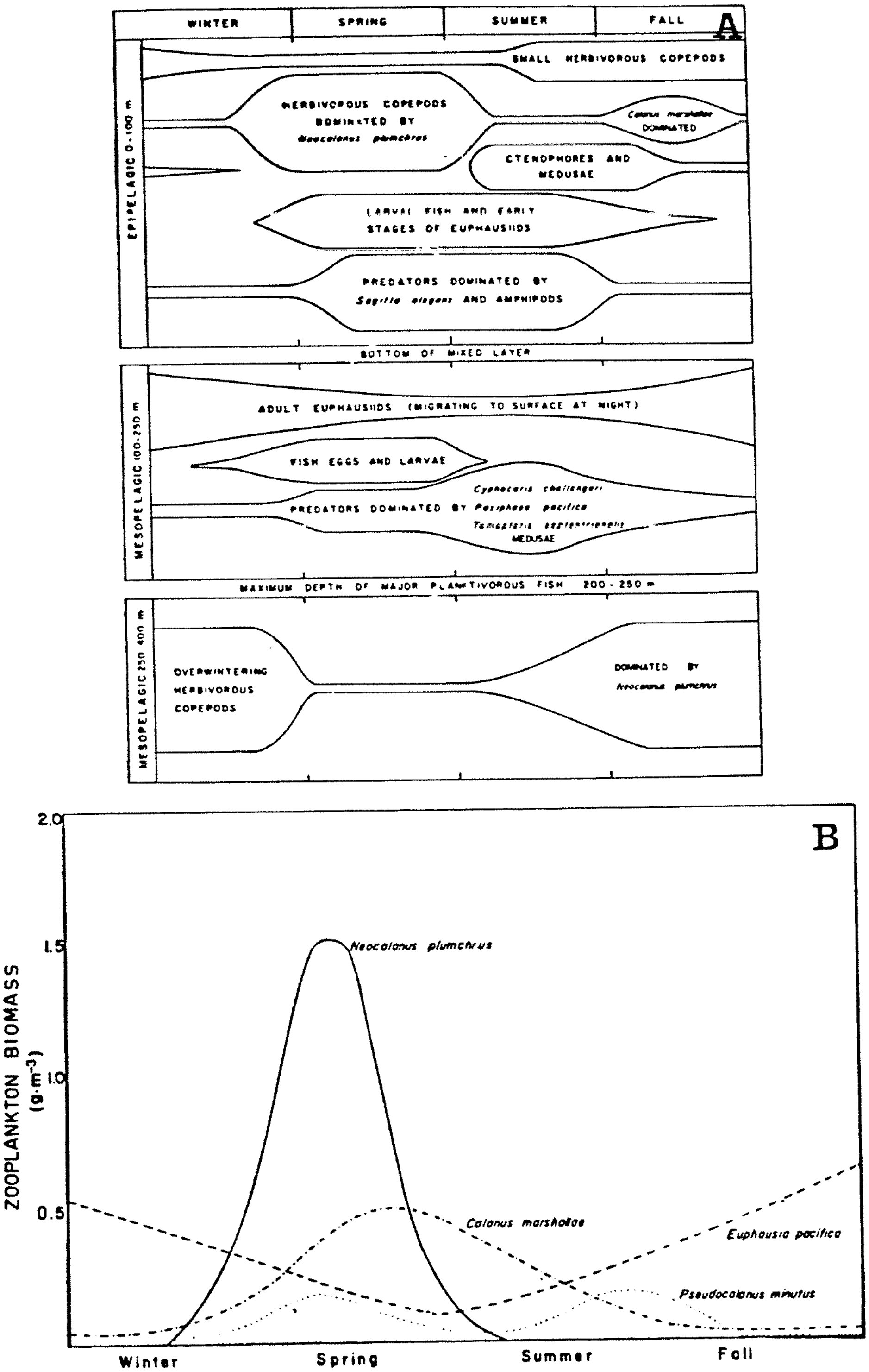


Figure 12. Generalized schematic representation of the zooplankton assemblage structure for the Strait of Georgia. A. Changes in relative abundance with season. The biomass contours indicate major population trends and not quantitative estimates. B. Seasonal changes in biomass of dominant species inhabiting the upper 20-50 m of the water column (after Harrison et al. 1983).

some herring (Atlantic) are spawned in well-mixed areas with few peaks in plankton abundance, duration of the larval phase has adapted evolutionarily to compensate for uncertain or less productive environments. This phenomenon might not apply in areas such as the Strait of Georgia, where there are definite peaks in zooplankton abundance.

Competition

Though other larval fishes and zooplankton consume the same food organisms and may have considerable temporal and spatial overlap with herring larvae, competition for food has not been demonstrated. Several empirical correlations suggest the possibility of competition, however. The relationship of Gulf of Maine herring year class abundance to temperature (see section 6.3.2) is apparently influenced by abundance of co-occurring mackerel larvae that may compete with larval herring (Skud 1982). Smith (1978), however, found similarities in year class fluctuations among fish species (including clupeoid) in the California current that are potential competitors as larvae; much more coherence, in fact, than among species that potentially compete as adults.

Food Limitation

Herring larvae must begin feeding within a few days of yolk sac absorption or they perish. The larger the larva and yolk sac, the longer death from starvation can be postponed. However, there is a point beyond which a starving larva cannot recover even if fed, because of overly depleted body reserves. "Point of no return" for newly feeding herring larvae occurs after about 40% of time from initial starvation to death elapses (Blaxter and Ehrlich 1974). Hickey (1982) noted that wounds took longer to heal in starving Atlantic herring larvae than in fed larvae. Starvation may either kill larvae outright or make them more susceptible to predators and disease in the wild, but this is difficult to demonstrate.

Opinion is divided on whether starvation is a critical factor in clupeoid (and other) larval survival in nature. No abrupt mortality occurs that would provide evidence of critical periods (Lasker 1984). Evidence of direct mortality from starvation is lacking, but indirectly, slower growth leaves starving larvae in the field of predation longer than fed larvae.

Many larvae captured in the wild weigh (dry) less than starved laboratory-reared larvae, strongly suggesting starvation (Hay 1983). But Blaxter (1975) cautions that comparative determination of condition factors and nutritional state of reared and wild larvae may be inadequate.

Alderdice and Hourston (1984) found no evidence of starvation in British Columbia herring larvae. About half the larvae sampled had food in their guts. However, O'Connel (1981) found evidence for starvation in a related clupeoid, the northern anchovy, in the Los Angeles Bight, and felt that food patchiness played an important role in survival. But the incidence of starvation was less than expected from prey densities. O'Connel asessed starvation histologically, which may have revealed changes overlooked by more conventional methods such as length or morphological comparisons.

Prey Density

Prey densities for successful larval feeding have been determined in laboratory studies only. Werner and Blaxter (1980) found that Atlantic herring larvae reared with brine shrimp densities above 0.3 ml^{-1} showed greater growth and survival than at lower food densities. At high prey densities survival was above 40% over the first five weeks of feeding. Haegele and Outram (1978) observed slightly lower survival of Pacific herring, about 35% over the same period. Both studies found asymptotic growth and survival curves, flattening out at high prey concentrations. Werner and Blaxter (1980) calculated a threshold prey density of 0.171 brine shrimp ml^{-1}, far greater than average zooplankton concentrations in nature, for herring larvae to survive with 10% weekly mortality, and felt that this threshold value might be low. Zooplankton distributions and densities in nature are not uniform; herring probably must encounter concentrated prey aggregations in order to survive.

Food organisms may be more abundant within areas hypothesized to retain larvae. Although likely, it is not known if currents retaining herring larvae have the same effect on zooplankton. But in general, nursery areas tend to be regions of abundant plankton (Cushing 1982). Due to their placement, larvae may grow coincidentally with zooplankton and have a better chance of successful feeding encounters because of higher zooplankton concentrations.

2.3.3 Predation

As larval herring grow they are subject first to predation by filter feeders such as anchovies, then by entrappers such as gelatinous zooplankton (Stevenson 1962) and hyperiid amphipods (Westernhagen et al. 1979) (Figure 11). In Barkley Sound, major larval predators were, in decreasing order, ctenophores, jellyfishes and chaetognaths (Stevenson 1962).

Predation on clupeoid yolk sac larvae is probably high, because high natural mortality could not be due simply to starvation (Blaxter and Hunter 1982). Predators have the potential to consume significant numbers of (if not all) larval herring (Lasker 1984), but no direct evidence implicates predation on larvae as the major cause of mortality. Alderdice and Hourston (1984), in ruling out starvation and higher than tolerable salinities as major causes for the high larval mortalities they observed in the Strait of Georgia, hold predation, by default, responsible. A match/mismatch phenomenon with predators, analagous to one for larvae and their food supply, has been hypothesized by Lasker (1984). Although cannibalism on larvae by juveniles and adults can occur in laboratory aquaria, and is sometimes observed in nature, it is probably a limited and insignificant phenomenon in nature (Hourston et al. 1981).

2.3.4 Other Biotic Impacts

Schooling. Large mortalities among larvae advected offshore may result from visual separation, which inhibits the ability to school and may be a stressor, even if adequate food organisms are present and predation not overwhelming (Shaw 1961; Stevenson 1962; Hunter 1981). No larvae of other herring stocks in the Pacific or Atlantic are known to survive in the open sea (e.g. Iles and Sinclair 1982)

Epizootics. Parasites are known to infect Atlantic herring larvae, but have not been described in Pacific herring. Parasites can be region and age specific. Immunity generally increases with age. Outbreaks of two parasites in the northwest Atlantic, a myxosporidium and a trematode infecting herring less than 6 months old, were directly correlated with summer water temperature (Sindermann 1965). But direct mortalities from these outbreaks are not known.

2.3.5 Other Abiotic Impacts

Salinity. Alderdice and Hourston (1984) argue that salinity probably has little direct effect on larval mortality in the Strait of Georgia. They determined a lethal upper boundary salinity of 27.5-31.7 ppt for Pacific herring larvae. Salinities in the Strait of Georgia are below this, in the range 2-28 ppt. Atlantic herring larvae can survive 24 hours in salinities of 1.4-60 ppt, and 7 days at 2.5-52.5 ppt. Fujita and Kokudo (1927) reported best survival of Japanese herring larvae at 25 ppt. Salinity tolerance of herring may be influenced by incubation conditions. The variability reported in the published literature matches that in larvae incubated under different conditions (Alderdice and Hourston 1984).

Temperature. Yolk sac duration is influenced by metabolic rate, largely a function of temperature and size. At 8°C larvae from large and small eggs survived 28 and 15 days after hatching, respectively, when no food was provided (Blaxter and Hunter 1982). Larger size at hatching and faster growth at higher temperatures reduces the period of high vulnerability to predation.

Combined factors. Anomalously high or low temperatures are reported to reduce salinity tolerance of herring larvae (Alderdice and Hourston 1984).

2.3.6 Mortality Estimates

Mortality during the larval stage is about 99% (Hourston 1980). Mortality rates in the Strait of Georgia are probably 70-80% per week in the first few weeks following hatching (Alderdice and Hourston 1984). Stevenson (1962) found that daily larval mortality rates in Barkley Sound, calculated from numbers of larvae found over time, decreased as the season progressed, from 34% in April to 22% in May. Neither the causes nor the variability of mortality is understood, nor are the relative contributions of possible mortality factors known.

2.4 JUVENILES

Following metamorphosis from larvae, juvenile Pacific herring resemble small adults, and grow from about 35 mm and 5 g to 70-100 mm and about 40 g by the end of their first summer. They grow little during the following winter (Hourston 1959). By the end of their second summer, they have grown to about 150 mm and weigh 60 g (Hourston and Haegele 1980).

Some investigators (e.g. Hourston and Haegele 1980) divide the juvenile phase into two parts. The latter part of the first year, July to March, is defined as the juvenile stage, and the second year is the immature stage. Sexual maturity is usually reached at age 3, and small proportions of immature age 3 and 4 fish are found among juvenile schools in British Columbia (Taylor 1964). Average age of sexual maturity of Pacific herring increases with latitude: 2 years for herring off San Francisco, 2 and 3 years in Washington, 3 years in British Columbia and the Gulf of Alaska, and 4 years in the Bering Sea (Trumble 1983; Wespestad and Fried 1983).

2.4.1 Distribution and Abundance

Horizontal Distribution

The horizontal distribution of juvenile herring is determined by active swimming, rather than by passive drift more characteristic of larvae (Hourston 1959). In southeast Barkley Sound, British Columbia, juveniles form large schools, away from spawning grounds. This aggregation results from gradual dispersion and reconcentration rather than from simple migration (Hourston and Haegele 1980).

Juveniles form increasingly larger schools and remain in inshore feeding areas (Hourston 1959). In fall they move offshore and deeper (Hourston 1959) and remain on offshore feeding grounds several to tens of kilometers from the outer coast at depths of 100-200 m at edges of banks (Taylor 1964). A small percentage stay close to shore year round. Major offshore grounds in the south are off the Strait of Juan de Fuca mouth, and Hecate Strait in the north (Hourston and Haegele 1980). Juvenile schools on offshore wintering grounds off British Columbia consist of millions of individuals (Hourston and Haegele 1980). Unrecruited juveniles (1, 2 and some 3 year olds) outnumber recruited adults (Taylor 1964). Not much information on interannual variability is available.

Very little is known of the eastern Bering Sea herring distribution during their first 2-3 years (Wespestad and Barton 1980). They feed close to the coast in summer and move deeper by winter (Wespestad and Fried 1983). In both eastern and western Bering Sea 0 and 1 age herring were found in areas of lower temperatures, inshore of adults (Prokhorov 1968; Wespestad and Fried 1983).

Ambient temperatures and salinities probably do not directly affect survival of juvenile herring, but may affect their distributions. Such effects may occur in the Bering Sea, where juveniles are found in lower salinities than adults (Wespestad and Fried 1983). Juveniles can survive at 5-6 ppt to 40-50 ppt (Blaxter and Holliday 1963).

Vertical water column stability and reduced turbulence, associated with areas sheltered from prevailing winds and currents, characterize juvenile rearing grounds (Hourston 1959). Hourston (1959) found no consistent trends in temperature, salinity or food resources among nursery grounds, though he noted that salinities in most areas were below 28 ppt. However, his data on food supply may be incomplete. Levings (1983b) found that juvenile abundances in the Fraser River estuary may be influenced by salinity and food supply.

Haist and Stocker (1984) found some evidence of density dependent growth (discussed below) among juvenile (age 2) herring on the west coast of Vancouver Island, although much of the variation in growth rates and abundance was explained by spring sea surface temperature. They found no correlations between growth and other environmental variables (such as Ekman transport or sea level).

Vertical Distribution

Juveniles inhabiting inshore nursery areas of British Columbia occur at depths of 3-15 m during the day and 1-7 m at dawn and dusk. Age 1 juveniles on offshore feeding grounds remain at 150-200 m. Age 2 juveniles are shallower, 100-150 m, and are more likely to mix with adults (Hourston 1959). In the Bering Sea juvenile herring are generally found deeper in the water in winter than in summer (Figure 9).

2.4.2 Feeding

Prey

Following metamorphosis, herring in British Columbia prey mostly on small zooplankton such as barnacle and mollusc larvae, bryozoans, rotifers, larval fishes and copepods (Figures 10 and 11). Copepods remain the predominant food organism throughout the juvenile stage in British Columbia (Barraclough 1967). Juvenile herring in shallow sublittoral and nearshore pelagic areas of Pugest Sound are known to consume copepods, decapod larvae and euphausiid shrimp (Fresh 1983).

Prey Abundance and Availability

Zooplankton productivity and distribution will affect their availability to juvenile herring. Inshore areas with bottom vegetation, such as found in the Fraser estuary, support higher standing stocks of zooplankton than areas with little vegetation (Levings 1983b). Zooplankton are most concentrated and visible at dawn and dusk. Most rise toward the surface at dusk, and begin to sink at dawn (Hourston 1959). Juvenile herring, which are strong swimmers, rise and feed at dawn and dusk.

Food Limitation

No evidence of food limitation exists in juveniles. Sufficient food probably exists both inshore and on offshore feeding grounds (Hourston and Haegele 1980). However, in years of very abundant herring larvae, there may not be sufficient food when they become juveniles and, though evidence is lacking, juvenile abundance may be food-limited (Hourston 1959). Maturation rate may also be associated with food supply, and has been accelerated in the laboratory by increasing food supply (Hay 1984) but has never been verified in nature.

Geographical separation (Wespestad and Fried 1983) may minimize competition for prey between juveniles and adults. Fresh (1983) believes that herring could outcompete and possibly adversely affect juvenile coho salmon in Puget Sound because of the high diet overlap. Competition has never been documented in juveniles, nor is it known how competition would be affected by changes in the physical or biological environment.

2.4.3 Predation

Predation on juvenile and adult herring by dogfish (Squalus acanthias) is well documented. Herring are the main winter food item of dogfish in the Strait of Georgia and off the west coast of Vancouver Island (Taylor and Wickett 1967). Schools of dogfish are known to track and aggregate beneath migrating herring schools.

Estimates of dogfish predation run to greater than 40% of total herring stock in British Columbia. No close relationships between herring and dogfish abundances have been documented; perhaps because, as an added complexity, dogfish also prey on herring predators such as hake (Taylor and Wickett 1967). Other inshore predators include fishes such as salmon (Oncorhynchus sp.) and sea perch (Sebastes spp.), seals, gulls (Larus sp.) and diving ducks. Offshore, herring are fed on by any birds, fish and mammals capable of capturing and swallowing them. Juveniles soon outgrow size ranges of smaller predators, such as perch, but may fall prey to larger organisms such as salmon (Hourston and Haegele 1980).

Unlike larvae, juveniles and adults are strong swimmers and can avoid predation and unfavorable environments to some extent (Taylor 1964).

2.4.6 Mortality Estimates

Little information is available on natural mortality rates of juvenile herring. Mortality rates are believed to be lower for juveniles than for larvae, and are probably comparable to those of adults (Taylor 1964). Extent of predation on juveniles is, like with larvae, though unknown, not believed to have major impact on adult abundance. Hourston and Haegele (1980) estimate 20% mortality of first year juveniles.

3. FACTORS AFFECTING ABUNDANCE

3.1 DENSITY DEPENDENCE

Factors that affect the population dynamics of a species and vary with population density are termed density dependent. These tend to be biological processes such as disease, food limitation or predation. Competition for non-biological resources such as nesting sites may also be density dependent. Over the long run, density dependent factors are usually compensatory or homeostatic, acting to regulate the population. In fish populations the effects of density dependence may appear as changes in growth rates (suggesting food limitation) or in fecundity. If the number of recruits per spawner changes with spawner density, recruitment is considered density dependent.

No apparent relationship exists between the abundances of spawning herring adults and those of recruits. Therefore, within usual levels, abundance of herring is thought to fluctuate independently of spawning adult number. Resource limited spawner-recruit models, such as the Ricker curve, cannot apply, at least from year to year with respect to recruitment (Murphy 1977). Fishery managers in British Columbia found that these models underestimate actual abundance of Pacific herring at high population levels, and have not worked well for managing the fishery since 1970 (Stocker et al. 1984).

Clupeoids display extreme natural variations in abundance and are highly susceptible to overexploitation. Blaxter and Hunter (1982) speculate that the absence of density dependent responses reduces the ability of these fishes to stabilize populations. Such instability would leave herring more sensitive to overfishing and environmental change than species with more stable populations.

Weak year classes of Pacific herring frequently follow strong ones. There has been a 400% difference between lowest and highest year classes since 1949 in British Columbia (Stocker et al. 1984). Why this happens is not known. Little relation exists between egg number and year class strength of herring. Declines in British Columbia have not been related to reduced spawning (Taylor and Wickett 1967), although inconclusive evidence suggests partial dependence on spawner number in northern and lower east coast populations (Taylor 1964). Obviously some lower spawning population threshold must exist, as collapses following overfishing happen, even in otherwise "density independent" fish stocks (Ricker 1963). In fact, the very flatness of the yield per recruit curve may have led to the false conclusion that overfishing was impossible in British Columbia (Murphy 1977).

Population fluctuations from other causes sometimes mimic the effects of density dependence. For example, if herring populations were influenced by density dependent factors, we would expect an increase in individual growth rates with less numerous populations. This ostensibly occurred in the North Sea in the early 1950's: when the number of older fish declined, younger herring grew faster and matured earlier, suggesting density dependence (Cushing and Burd 1957). By maturing younger they entered the fishery sooner. As a result of earlier exploitation, the number of older fish fell even more. However, the increased growth in younger fish was probably caused by a two or threefold increase in Calanus copepods (unrelated to changes in predation by herring) rather than decreased density of herring (Cushing and Burd 1957). Another North Sea stock sharing the same nursery area in the eastern North Sea also grew faster. Both populations matured earlier and changed recruitment patterns, probably altering their vulnerability to fishing. Calanus were not related directly to herring recruitment but to faster growth rates. The Calanus increase was speculated as arising from an invasion of Atlantic oceanic water into the North Sea (Cushing 1982).

Iles (1968) suggested that some growth increase of North Sea herring at that time was density dependent, but has since found it difficult to demonstrate density dependent growth in that or any fish species (Iles 1984). For example, the 1904 North Atlantic year class was 30 times larger than those of 1903 or 1905, yet growth rates remained unchanged (Iles 1983).

3.2 HOW YEAR CLASS STRENGTH IS SET

Pacific herring year class abundance is probably established shortly after metamorphosis, while juveniles are still inshore (Hourston 1959). This conclusion is based on correlations of juvenile to later adult abundances. For clupeoids in general year class strength appears to be set within the first six months (Smith 1984). Hay (1983) believes larval survival might not determine year class strength in British Columbia herring because, despite high variability in location and timing of hatching, there is much coherence in relative abundance among stocks (Figure 4). If larval survival determined year class strength, then abundance should vary with location. His argument does not consider actual mortality in different regions, spatial or temporal variation among regions within a single year, or stock intermixing. Also, time of hatching may have little bearing on larval survival.

The difference between abundant and poor years for larvae may be due to small, subtle factors rather than large ones (Houde 1983). As a theoretical example. Alderdice and Hourston (1984) considered inshore and offshore mortalities in the Strait of Georgia, 70 and 78% respectively, to be very close. However, those mortality rates would result in more than eightfold differences in abundance after only four weeks (Figure 13) if mortality rates remained constant. Equally subtle are the effects of time spent at a highly vulnerable stage. Faster growing larvae pass through periods of heaviest mortality faster, and may have an advantage over slower growing ones. Bad food conditions coupled with slightly greater predation, or longer time spent in either situation, could be disastrous (Houde 1983). Taylor (1964) estimated that, in British Columbia, 99% larval mortality would leave 1 billion surviving larvae, and produce a strong year class. A weak year class would ensue in years with 99.9% mortality, in which only 100 million larvae would survive.

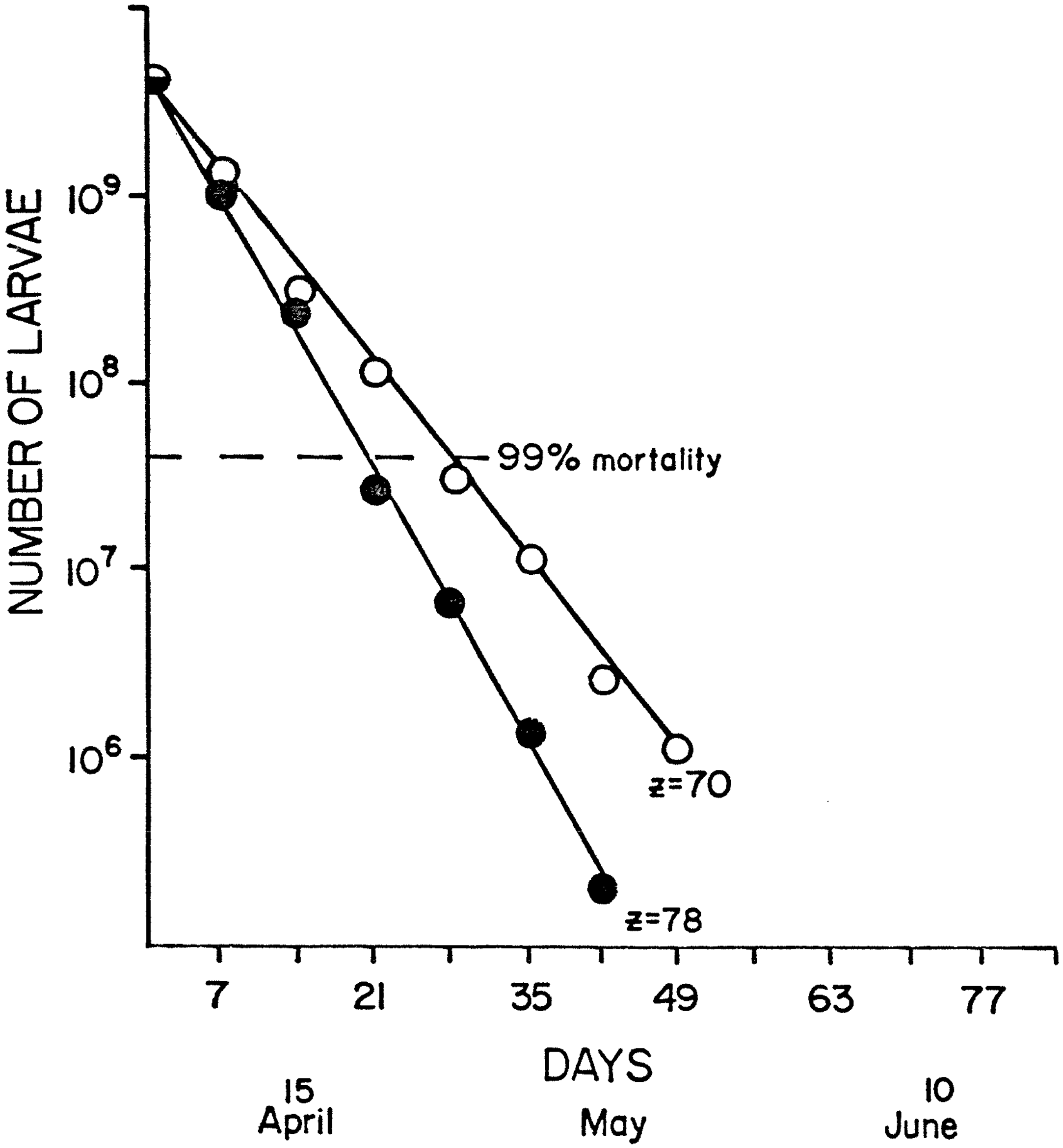
Population maintenance is not due entirely to larval survival in any one region. Immigration from other stocks may be as high as 25% in some British Columbia populations (Taylor 1964), which undoubtedly contributes to and may explain some of the coherence in year class fluctuations.

3.3 EMPIRICAL CORRELATIONS WITH ENVIRONMENTAL FACTORS

Long-term large scale events seem likely to affect herring in the Northeast Pacific, but data on interannual differences are insufficient to draw adequate conclusions. Though many large scale correlations between environmental factors and herring abundance have been identified (Table 2), the mechanisms connecting them are incompletely studied; investigations have been few, brief and localized.

3.3.1 Pacific Herring

Taylor and Wickett (1967) found year class strength of British Columbia herring associated with onshore transport. They developed an index of water movement based on a combination of oceanographic factors off British Columbia. Average north-south component of onshore wind-driven surface water from December to March was their measure of amount and direction of onshore current. The index increases as onshore transport becmes more rapid. Due to the angle of the coastline relative to direction of transport, water is held against the coast (onshore transport) when net movement is northward, and water moves offshore when net movement is southward. Two indices were developed, one for the southern area (upper and lower west coast and lower and middle west coast of



NUMBER OF LARVAE

Date	Offshore, 70% mortality	Inshore, 78% mortality	
April 1	5 billion	5 billion	
April 7	3.5 billion	1.1 billion	
April 14	1.05 billion	242 million	
April 21	315 million	55 million	◄ 1% of initial number
April 28	95 million	12 million	

Figure 13. Predicted changes in the population of larval herring with time, inshore and offshore in the Strait of Georgia, based on mortality rate estimates of Alderdice and Hourston (1984). For this example, 5 billion larvae are assumed to hatch on April 1.

Table 2. Empirical correlations of environmental factors and herring stocks.

REGION	BIOLOGICAL VARIABLE	ENVIRONMENTAL FACTOR	RELATIONSHIP	COMMENTS	SOURCE
I. PACIFIC HERRING					
British Columbia (lower West Coast of Vancouver Island)	Year class strength	Snowfall	Inverse. Lack of snow and little snowmelt favorable	Data from 1936-1950 Mechanisms tied to run-off, offshore advection of larvae.	Stevenson 1962
British Columbia	Year class strength	Onshore and offshore transport (advection)	Onshore - strong year classes Offshore- weak year classes	Based on wind-driven surface water movement Indices developed for northern and southern British Columbia.	Taylor and Wickett 1967
British Columbia	Year class strength	January-February salinity at station "P" in year spawned	Direct. Greater salinity favorable	r^2=.85. Salinity a water column stability proxy. Less stability, greater mixing, more food for offshore-migrating 2 year old fish.	Wickett 1975
British Columbia	Year class strength	Baroclinic waves	Low frequency, northward moving Kelvin waves, causing raised sea surface temperatures, salinities, sea levels. Direct.	Cross-spectral analysis of herring abundance trends and wave cycles (roughly 6 year).	Mysak et al. 1982
British Columbia	Year class strength	March sea surface temperature	Indirect	r^2=.3. Some strong cohorts in cold years.	Ketchen et al. 1983
Southeast Alaska	Year class strength	Winter and spring sea surface temperatures.	Direct.		Favorite and McLain 1973
Southeast Alaska (Prince William Sound)	Year class strength	Mean March-June air temperature.	Direct. Air temperature correlated highly with sea surface temperature.	r^2=.73 Period covered 1 month on either side of spawning period.	Rounsefell 1930
Eastern Bering Sea	Year class strength	Pollock predation; sea surface temperature in water.	Inverse with predation; direct with temperature.	Temperature, by increasing pollock growth rates, raises predator biomass.	Lavestu and Favorite 1978
II. ATLANTIC HERRING					
Gulf of Maine	Catches	Mean February-March sea surface temperature.	Strong, direct before 1960. Looser, inverse after 1960.	Stocks more abundant before 1960. Temperature effect likely modified by presence of other fish larve.	Anthony et al. 1984

Table 2 (cont.)

REGION	BIOLOGICAL VARIABLE	ENVIRONMENTAL FACTOR	RELATIONSHIP	COMMENTS	SOURCE
St. Lawrence Estuary	Year class strength	Gyres driven by tidal currents	Direct with gyre size	Gyres retain larvae. The larger the gyre, the more larvae survive, and the larger the year class.	Iles and Sinclair 1982
North Sea (East Anglia, Downs herring stock)	Year class strength	Wind strength in March	Direct with prolonged easterly wind	Randomly generated wind values gave equally strong relationships, especially with nonlinear functions (Gulland 1953).	Carruthers 1938
North Sea	Catches	General warming trend associated with increased atmospheric, oceanic circulation, decreased upper westerlies.	Inverse. Plankton species, winter phosphorus declined.	All fish species declined. Pilchard replaced herring niche. Event began after 1926, ended 1966.	Russell 1973
Irish Sea	Catches	Sea surface temperature	Direct in 4-5 year cycles. Inverse in 9-12 year cycles.	Temperature, salinity probably proxies for factors affecting larval advection.	Grainger 1978
Sweden (Bohuslan coast)	Catches	Cool climate, Baltic freezing.	Direct	Saltier North Sea Bank influxes may have brought in herring.	Petterson 1926 (in Cushing 1982)
Norway	Catches	Warming, reduced ice cover north of Iceland.	Direct	Warming possibly associated with shifts from westerly to southerly winds, delaying coastal zooplankton production. Out of phase with Swedish fishery. Data since 17th Century.	Cushing 1982
White Sea	Year class strength	1) Spring atmoshperic regime	Anticyclonic - strong year classes Cyclonic - weak year classes	Frequent storms, cold inflows associated with cyclonic regime, lowering sea surface temperatures lowering productivity and delaying spawning. 9 years of data.	Azernikova 1967
		2) Depth of >0° water June-August	Direct	Warm water layer related to spring ice conditions - vertical distribution may set temperature of photoactive layer, influencing development of zooplankton.	Azernikova 1967

Vancouver Island) and one for the north (northern and upper central groups). Central regions showed more variation than did the north or south, and no index was developed there.

Wickett (1975) hypothesized that reduced offshore upwelling was responsible for decreases in British Columbia herring abundances in the late 1960's. During the 1960's "the marine climate [was] less favorable to fishes...less fertilizer was being stirred up into the upper layers where sunlight penetrates". Conditions reversed in the 1970's and upwelling increased. Wickett used salinities at Ocean Weather Station Papa (50°N, 145°W) and the Queen Charlotte Islands lagged nine months as an indicator of water column stability. These are "proxy" data (Austin and Ingham 1978) but Wickett argues that they are appropriate because there is sufficient similarity between offshore British Columbia and the Gulf of Alaska. Zooplankton biomasses at Station P were greater in years of more upwelling (Fulton 1978). Eighty-five percent of the variance in annual mean year class strength was explained by mean January-December salinity of that year (Figure 14) and is attributed to yearly changes in availability of food resources for age 2 herring. Seasonal variations within a single year were not evaluated. Wickett hypothesized that recruitment of herring is determined at age 2 during the first offshore migration. If events in earlier life history stages were crucial, Wickett would expect an inverse relationship between recruitment and salinity, since more frequent and intense storms would cause greater runoff and advect larvae offshore. However, he finds a direct relationship, and concludes that the number of recruits is determined at later life stages. To be a legitimate counterargument, salinities during larval rather than juvenile stages should be used. Wickett also assumes a priori that decreased growth in fishes leads to smaller populations.

Ketchen et al. (1983) correlated weak year classes in British Columbia herring with high March sea surface temperatures ($r^2 = 0.3$) and found some strong year classes in cold years. They speculated that water temperatures or some related factors at time of spawning influence egg to larval survival.

Year class strength of Alaskan herring around Prince William Sound correlated with average mean March-June air temperatures ($r^2 = 0.73$), a period extending from one month before spawning to one month after hatching (Rounsefell 1930). Air temperature was highly correlated with sea surface temperature. Rounsefell could only speculate on the underlying mechanism, although he did not believe it resulted from direct effect on eggs. The period examined spanned four months; the effects could be associated with food supply or predators. Temperature probably did not exceed larval tolerances and may have been a proxy for offshore advection (Anthony et al. 1984).

Pacific herring year class abundance has been correlated both directly (e.g., southeast Alaskan herring, Figure 15) (Favorite and McLain 1973) and inversely (e.g., Hokkaido herring, Uda 1952) with winter and spring temperature. Temperature is thought to be a proxy for hydrographic processes in both situations.

Year class strength of herring in the eastern Bering Sea has been related to temperature and predation by pollock (Laevastu and Favorite 1978; Laevastu 1983). Herring stock size (but not year class strength) also has been related to available spawning area (Wespestad and Fried 1983). One Bering Sea ecosystem model (Lavestu 1983), hypothesizes temperature to affect pollock directly and herring indirectly. Warmer temperatures are thought to increase pollock biomass by accelerating growth, thereby inducing greater predation on herring. Anomalously low temperatures would have the reverse effect. This proposed mechanism presupposes no direct effect of temperature on growth or biomass of herring which, considering they too are poikilotherms (cold-blooded), seems unlikely. Wespestad and Fried (1983) believe that advection of larvae from nursery grounds may be the principal determinant of year class strength in the eastern Bering Sea. The effects are probably large scale, for most major stocks in this region undergo similar variations in abundance on interannual time scales (Fried et al. 1982).

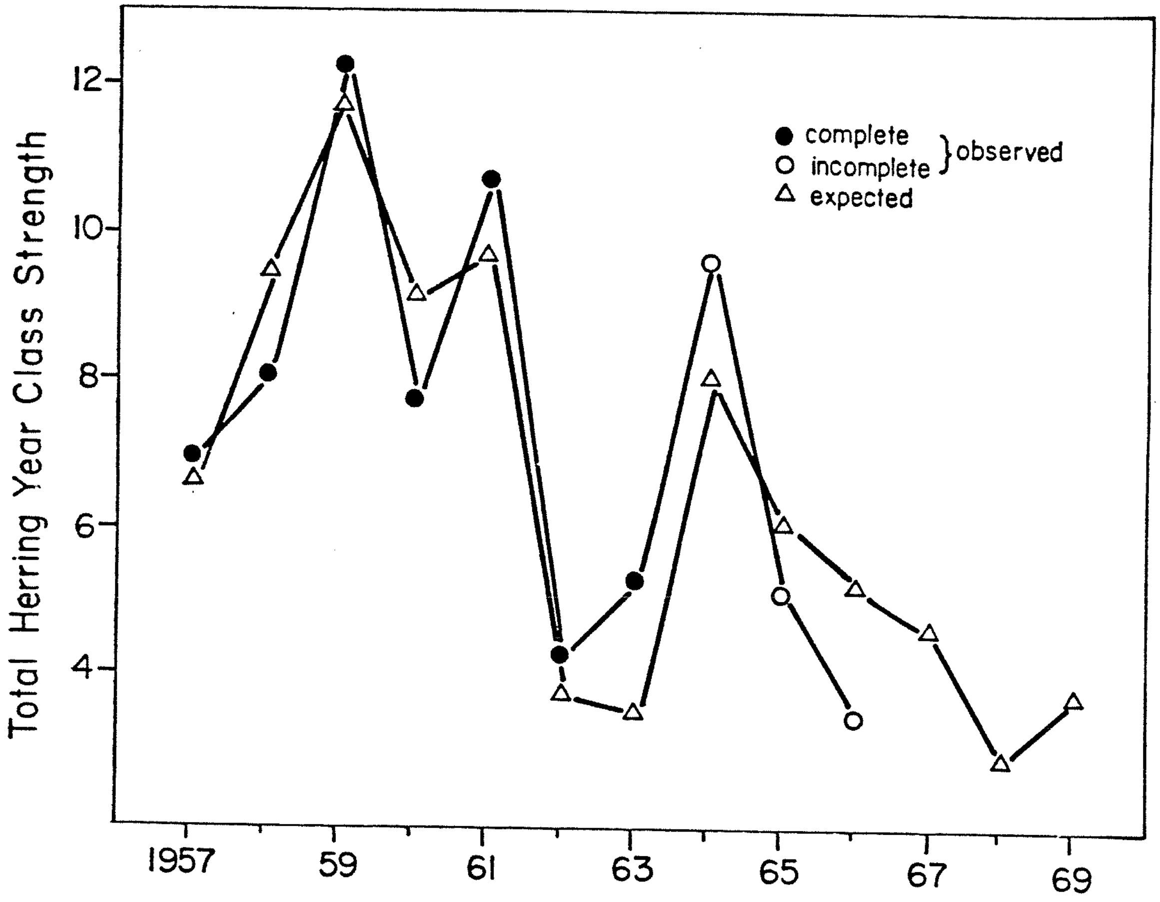


Figure 14. Combined year class strength of eight British Columbia herring stocks, observed and expected from the equation

$$y = 29.255x - 947.872$$

where x = mean February-January surface salinity at Station "Papa" in year of spawning (after Wickett 1975).

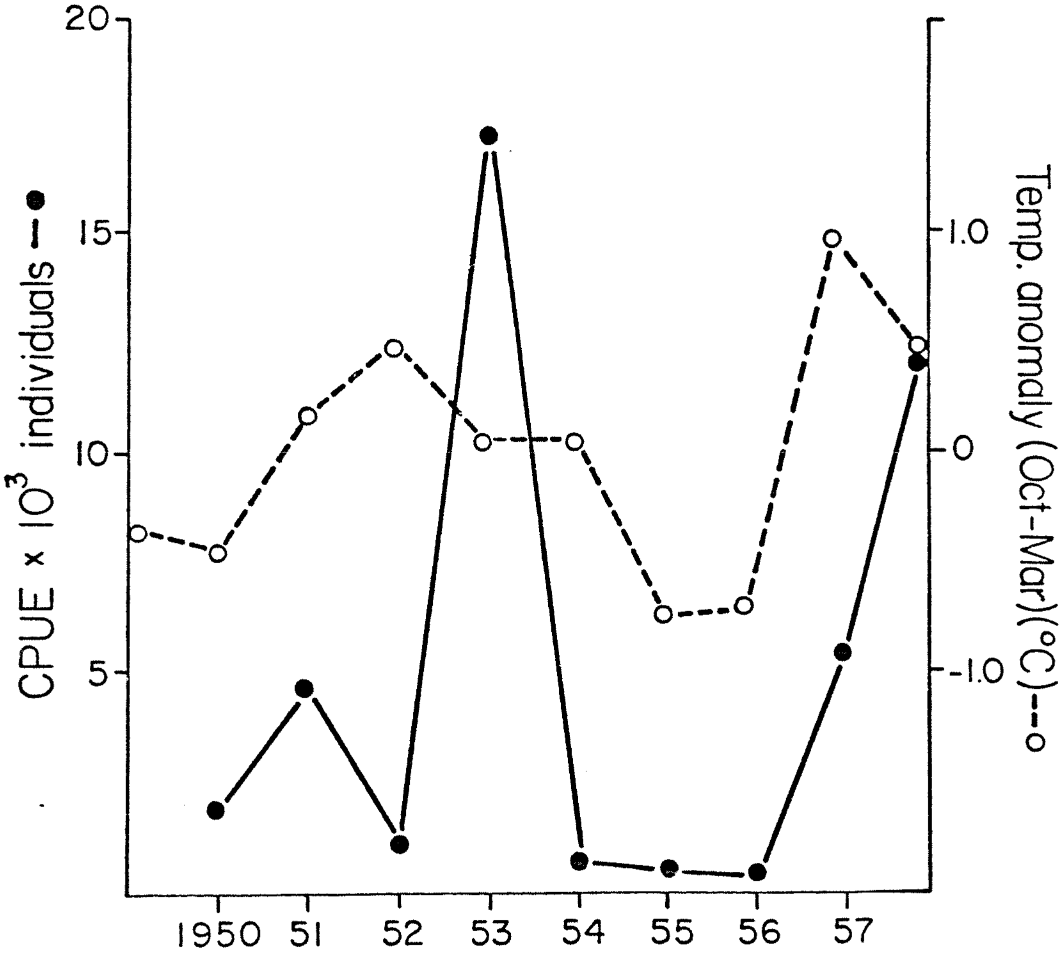


Figure 15. Relative herring year class abundance in southeastern Alaska and mean October-March sea surface temperature anomalies (after Favorite and McLain 1973).

Pearcy (1983) suggests a correlation between El Nino Southern Oscillation events and abundant herring year classes in the northeastern Pacific. During El Nino, altered equatorial Trade Winds cause the normal coastal upwelling off South America to cease, and warm water masses are propagated northward up the Pacific coast. The 1926, 1929, 1939-40, 1951 and 1953 year classes in southeast Alaska, and 1957 and 1958 year classes there and in the Bering Sea were strong, and all were produced in El Nino years. However, according to O'Brien (1978), 1929, 1939-40, 1951 and 1953 were not major El Nino years. A 5-6 year cycle of 12 month running mean sea level from Astoria, Oregon to Kodiak, Alaska, in phase with 5-6 year temperature sea surface temperature maxima, usually peaks in El Nino years (Pearcy 1983). Mysak et al. (1982) support this idea, arguing that baroclinic waves driven by cycles in the Southern Oscillation affect the entire northeastern Pacific and its biota. Widespread high sea levels and warmer sea surface temperatures associated with long (six year) Kelvin wave cycles, correlate with high herring abundances in British Columbia.

The proposed mechanism of Mysak et al., like that of Stevenson (1962), has climate ultimately affecting herring abundance, but the pathways have little in common: Stevenson's is driven by coastal climate from the preceeding winter affecting onshore/offshore advection, and is more localized, whereas the theory of Mysak et al. envisions large scale, longer term atmospherically forced currents parallel to shore creating good or bad environments. Nonetheless, high sea levels are associated with onshore convergence and reduced offshore transport (Pearcy 1983), conditions advantageous to herring according to both theories.

3.3.2 Atlantic Herring

Lough et al. (1981) found no relationship among overwintering larval abundance, growth and mortality, and eventual year class abundance of Georges Bank herring. Nor was year class strength related to spawning stock size. Such relationships would have indicated some density dependence. Lough et al. (1981) provide a time series model that suggests sufficient larvae were produced in most years to yield abundant year classes, given the right environment, although the stock on east Georges Bank collapsed after 1976. Although specific factors governing recruitment were not identified, it was believed that they are complex processes which operate throughout winter.

Ten-year cycles in herring catches were inversely correlated to sea surface temperature cycles of 9-12 years in areas south and west of Ireland (Muir 1977). But shorter term (4-5 year) herring fluctuations were positively correlated to temperature (Kelly 1975; Grainger 1978). The effect on short term cycles may not be temperature-dependent, but influenced by other associated hydrographic factors. Fishing was ruled out as a cause for the ten year cycle of abundance, and suitable fishing weather, another potential cause for such similarities, was not as well correlated with catches as temperature. Regular fluctuations in catch suggest the influence of some recurring environmental factor(s) during the first year of life.

Variable time lags in successive years are likely in relationships between environmental factors and abundance because age distributions vary with abundance. This may explain why short term catch fluctuations are sometimes out of phase with long time series temperature data (Grainger 1978).

The correlation between salinity in the western Irish Sea and 4-5 year catches suggests that hydrographic conditions associated with salinity changes in winter affect herring abundances when they recruit into the adult population three to four years later. Salinity and temperature may be measures of winter hydrographic conditions (e.g., currents, runoff) that affect larval drift in late October-March, following October spawning (Grainger 1978).

Abundant White Sea herring year classes are correlated with warm springs, high runoff, clear skies and normal sea levels (Azernikova 1967). Clear skies and light winds prevail in spring anticyclonic (high pressure) atmospheric regimes. Cyclonic (low pressure) regimes are associated with frequent storms and cold inflows. The cause of poor year classes, Azernikova postulates, is frequent recurrence of spring cyclones bringing cloudiness, low light and strong winds. These factors produce low sea surface temperatures and delay spawning, cause mechanical destruction of eggs, reduce phytoplankton growth and reduce larval and juvenile growth. Spring ice cover is an indicator of temperature and illumination. A correlation between April ice cover and subsequent herring yield had a $r^2 = 0.72$ for nine years of data.

Carruthers (1938) correlated wind strength and year class strength of the North Sea Downs herring stock. A prolonged easterly wind in March may have caused larvae to drift out of nursery areas. The effect of wind on subsequent recruitment was less apparent (Saville 1965). But Gulland (1953), using Carruther's data, showed that randomly generated wind values yielded as strong a relationship with recruitment as the observed wind values, especially when nonlinear functions were used.

Catches in the Gulf of Maine may be related directly or inversely to temperature, although for data after 1960, when both the adult fishery and decline in stock began, correlation is weaker (Anthony et al. 1984). Zooplankton abundance had not changed in 80 years, and increases in herring abundance prior to 1960 may have been temperature related. However, possible changes in species composition of zooplankton were not considered. Anthony et al. (1984) noted that increased recruitment in recent years was correlated with colder temperatures in February and March ($r^2 = 0.8$) in contrast to earlier years when higher temperatures were associated with good year classes. Skud (1982) believes that the paradoxical reversal of the relationship between year class strength and temperature depends on abundance of other fish larvae, such as mackerel. High temperatures may affect herring larvae more during periods of low abundances of other larvae, and less when those abundances are high.

3.3.3 Coherence Among Populations

If stocks in different locations have coherent population fluctuations, large scale events are likely responsible (Pearcy 1983). Examples in addition to those above include (1) the coherence among British Columbia stocks (Figure 4); (2) strong year classes in 1926 and 1931 in southeastern Alaska, Prince William Sound and Kodiak (Dahlgren and Kolloen 1943); (3) weak year classes in the 1960's followed strong ones in the late 1950's in northern British Columbia, southeast Alaska and the Bering Sea (Pearcy 1983); and (4) similar fluctuations in Atlantic herring stocks in Nova Scotia, the western Gulf of Maine and Georges Banks (Anthony et al. 1984). Tempting though it is to attribute all coherences to large scale environmental events, simultaneous utilization of new fishing techniques (Hourston 1980; Jakobsson 1984) or mixing among stocks (e.g., British Columbia) may be equally important.

With a sufficiently long time series of biological data (i.e. abundance) and a variety of physical environmental factors for comparison, correlation with at least one variable is likely. Often the best possible r^2 values are sought, regardless of the possibility of a mechanism, and frequently with statistical problems inherent (McCaughran 1983). If correlations are more than spurious, they may suggest possible interactions, generate testable hypotheses and, to the benefit of fisheries management, provide some prediction of future abundances. The next logical step is to explain causal mechanism(s). Otherwise, we have no additional understanding of the system.

4. POTENTIAL EFFECTS OF CO_2-INDUCED CLIMATIC CHANGE ON HERRING

4.1 ENVIRONMENTAL CHANGES

4.1.1 Direct

Few if any direct effects on fishes are likely to occur from the projected CO_2 increases alone. To the oceans, the only direct effect to the oceans may be a balance shift in dissolved carbonate, decreasing pH by about 0.3 (Sibley and Strickland 1985). Lower pH may increase primary productivity; even if not, timing and magnitude of production and species composition may change, with possible impact on fishes through the food web.

4.1.2 Indirect

Atmospheric Changes

Increased CO_2 is predicted to cause a greenhouse effect on the earth's surface, increasing atmospheric heat retention, in turn influencing pressure systems and changing atmospheric circulation patterns. A doubling of present atmospheric CO_2 is projected to cause a 1.5-4°C increase in air temperatures (Palutikof et al. 1984), higher at the poles. The change in air pressure systems may increase precipitation by 20% at higher latitudes. The handful of existing climate simulation models and projections from paleoclimatic and historical climate records (NRC 1983) hesitatingly agree on these general predictions but differ widely on more specific seasonal and geographical changes. Nevertheless, for British Columbia Palutikof et al. (1984) predict a decrease in air temperature variability in summer and winter, and greater varibility in spring and fall. Storm severity may decrease, and offset some of the lowered temperature variability in summer and winter. Winters and springs are expected to be warmer, summers and falls drier, a higher sea level pressure will be centered over British Columbia year round and, in general, greater variability in coastal precipitation, especially in spring.

Physical Oceanographic Changes

The projected climatic changes will influence ocean temperatures, surface salinity and currents, all of which, directly or indirectly, have biological implications.

At present, the Gulf of Alaska and offshore British Columbia waters are fairly cool, with relatively constant temperature conditions: 3-4°C in winter, 13-14°C in summer (Strickland and Sibley 1984). The Strait of Georgia, where the bulk of British Columbia's herring originate, is well mixed by winds in the north to a uniform temperature of about 7°C in winter, and stratified from surface heating in summer. In the more complex southern Strait, stability remains higher due to low salinity Fraser River surface runoff (Harrison et al. 1983). In the Bering Sea, by contrast, one finds both temperate and polar environments, with severe cold and extensive ice cover in winter (Strickland and Sibley 1984). Its transitional nature and high lattitude suggest a greater sensitivity, relative to other large water bodies, to climatic changes. Salinity is lower off British Columbia and Alaska than other oceanic waters because of large amounts of precipitation and runoff. The northeast Pacific Ocean is characterized by strong currents and weak stratification. Prevailing winds and runoff create downwelling offshore of British Columbia and in the Gulf of Alaska in winter, and in the eastern Gulf year round (Strickland and Sibley 1984).

Within each major area, shelf and shallow coastal waters, estuaries especially, environments perhaps most sensitive to the vagaries of climate. Far from the buffering effects of deeper water heat sinks, these areas are more susceptible to atmospheric heating, more subject to greater advective and mixing effects because of their shallowness and, because of proximity to rivers and terrestrial runoff, more subject to turbidity and salinity changes (Harrison et al. 1983; Sibley and Strickland 1985).

With higher air temperatures, offshore ocean temperature increases may be less in the northeast Pacific, because currents transport much heat from the south, than in the eastern Bering Sea, where most heat transfer is across the air sea interface. Higher atmospheric temperatures will reduce or eliminate winter ice cover in the Bering Sea, and the resulting lower vertical stability of the surface water may, by mixing, offset some surface temperature increase.

Salinity will generally decrease if net precipitation and runoff increase. Higher surface temperatures and lower salinities may increase stability by increasing vertical density gradients, decreasing depth of vertical mixing and pychnocline depth, reducing turbulent exchange between surface and deeper waters, and increasing the seasonal duration of stratification. However, if the prevailing North Pacific storm track, now centered over the Aleutian Islands in summer and the Gulf of Alaska in winter, moves northward, surface turbulence in the Bering Sea and the northeast Pacific may increase and further decrease, respectively (Strickland and Sibley 1984).

Increases in local wind magnitude and duration associated with a northward shift in storm tracks could create significant horizontal advection, especially in a Bering Sea with reduced ice cover, where little now exists. However, a general global decrease in wind strength is projected to accompany global warming (NRC 1983). A northward shift of atmospheric pressure patterns may increase the frequency, magnitude, and seasonal and areal extent of coastal upwelling and offshore transport in the northeastern Pacific, and offset the general increase in temperature and decrease in surface salinity in coastal areas (Sibley and Strickland 1985).

Phytoplankton Changes

Primary productivity, mostly controlled by light, depth of mixed layer and vertical advection (Beverton and Lee 1965), may be affected by changes in turbulence, winds and cloudiness. Spring primary productivity in the northeastern Pacific Ocean may change if the greater than optimal present level of turbulence reduces. If wind shifts favor greater upwelling in the Gulf of Alaska and off British Columbia, primary productivity in those regions will also increase due to more nutrients brought towards the surface (Sibley and Strickland 1985). At present, average annual primary productivity in the Strait of Georgia is 2-4 times greater than the open northeast Pacific (Harrison et al. 1983), and probably more limited by light than nutrients. Therefore its productivity may not increase substantially. Increased storm frequency may reduce productivity in spring because of water column destabilization, but enhance it in summer, as Sambrotto and Goering (1983) found in the Bering Sea.

Phytoplankton species compostion changes rather than northward shifts are likely because the taxa are fairly ubiquitous. In general, excluding extreme conditions, diatoms dominate in well mixed regimes, flagellates in more stable regimes. Increases or decreases in turbulence and runoff are likely to favor one flora over the other. Flagellate dominated systems are usually less productive overall than ones dominated by diatoms, although early spring flagellate blooms may be greater (Strickland 1983). Timing of blooms, too, may alter, as higher temperatures result in earlier stratification. Salinity changes per se, other than being associated with runoff and turbulence, appear not to affect phytoplankton (Harrison et al. 1983). Turbidity, however, can affect primary productivity. Production is generally low near river mouths; anomalously high turbidities in the Squamish River Estuary, British Columbia reduced light penetration by one order of magnitude, primary productivity by 35% (Harrison et al. 1983). Such occurrences may become more commonplace with the greater runoff predicted.

Zooplankton Changes

Higher temperatures alone will probably not alter zooplankton species composition, but zooplankton growth rates and abundance could be affected, especially small zooplankton. Changes in primary productivity are likely to have more impact on composition and growth rates (Sibley and Strickland 1985); thus, the availability of prey for herring. It usually takes about a quarter year for zooplankton to react to changes in phytoplankton (Strickland 1983).

Flagellates, more dominant in stratified conditions, favor smaller zooplankton species including microzooplankton (Strickland 1983). British Columbia waters experiencing greater runoff and temperatures are likely to become more stratified, favoring a greater proportion of smaller zooplankton. If that happens, early life history stages of herring may benefit, possibly at the expense of later stages, all else equal. Greater stability also creates more spatial patchiness of organisms. However, a direct link between plankton productivity and larval fishes, an important assumption, has not been studied extensively (Smith and Eppley 1982) and is not well established.

4.2 CHANGES TO HERRING

To predict how climatic changes will affect herring abundance and distribution, one must first determine the present causes of year to year variability. This is far from clear. Most evidence, though inferential, suggests that processes in the early life stages determine future abundance, and act independently of spawner abundance unless stocks are overfished. And good years, which herring are able to exploit, are infrequent, from which it is inferred that herring are evolutionarily adapted to some degree of environmental uncertainty. Their very adaptation to highly variable brackish and estuarine environments may actually lessen the impact of some environmental changes (Bardach and Santerre 1981).

In all years, even those with strong year classes, large mortalities of eggs and larvae occur. Therefore two important questions remain: (1) What conditions result in good or bad year classes? (2) Are the causes of variation the same in good and bad years, and in consecutive years?

The nursery environment near spawning grounds is important because larval herring are more or less passively subject to processes occurring therein. Evidence for a defined critical period for starvation or large mortalities directly or indirectly due to starvation is lacking. Adult condition, affecting egg number more than egg size or quality, has little bearing on number of larvae surviving to metamorphosis. Predation may be the greatest source of mortality, but remains unquantified. The few studies specifically investigating predation on larvae are mostly qualitative. Furthermore, predation may remove starving and less fit larvae that would otherwise die from other causes.

Several investigators hypothesize that passive drift of larvae by surface currents from productive nursery areas has the greatest effect on larval survival and later recruitment. As the nursery environment is generally nearshore, changes in coastal physical processes are likely to have most impact on young herring. Despite limited control, larvae drift passively and are more likely to be affected by adverse environmental conditions than more actively swimming juveniles and adults.

The following potential effects to Pacific herring are summarized in Table 3. Certain physical phenomena in the environment (photoperiod, tide) with direct or indirect effects on phytoplankton, zooplankton or herring, will not be influenced by climatic changes.

Table 3. Potential effects of CO_2 and CO_2-induced climatic change on herring.

	SECONDARY EFFECT ON ENVIRONMENT	EFFECT ON HERRING[1]
I. DIRECT EFFECT		
Increased atmospheric CO_2	1. Greenhouse effect, reduced and particulates, leading to increased photosynthesis and UV radiation	a. Increased phytoplankton production, affecting larvae and later stages?
Increased oceanic CO_2	1. Shift in carbonate balance, pH?	a. Changed phytoplankton production, affecting larvae and later stages? b. Changed algae and rooted vegetation production, necessary egg substrata in spawning areas?
II. CLIMATIC CHANGE		
Warmer air temperature	1. Interdidal heating, dessicstion	a. Warm, dry weather - greater mortality to intertidal eggs than cool, moist weather.
	2. Less snowfall, decreased runoff in late spring	a. Reduced offshore advection of larvae, better survival.[2] b. If extreme, salinity may exceed larval tolerances, though not affect other stages.
	3. Warmer water temperatures	a. Range, center of abundance, shift northward . b. Earlier spawning (slight). c. Faster incubation. Earlier hatching environment may be uncertain. Peak in food organism production may not coincide if linked to different environmental cues. d. Summer horizontal distributions of adults affected. e. Vertical distribution affected. f. In long term, eggs may become smaller, and incubation and time at greatest vulnerability reduced (as happens now later in season). A genetic change?[3] g. Increased diseases, parasites? h. Failure to spawn in usual grounds, a geographical change. Uncertain for larvae.
	4. Deeper thermoclines (also affected by mixing)	a. Deeper summer vertical distribution (partial cause).
	5. Phytoplankton, zooplankton changes? Increased zooplankton production (favoring neritic species)?[4]	a. Uncertain effect on all life history stages. a. Faster growth, all else equal. Fish may mature earlier, resulting in earlier recruitment, more eggs per fish of given age. Thus, greater proportion of population subject to fishing.
	6. Decreased ice cover	a. Herring not directly affected? May influence predator, competitor and food organism distributions. b. Changes in regions of plankton productivity. Uncertain effect on herring. c. Shifts in horizontal fronts may bound distributions of adults. and juveniles.

Table 3 (cont.)

I. CLIMATIC CHANGE	SECONDARY EFFECT ON ENVIRONMENT	EFFECT ON HERRING[1]
Wind shifts	1. Change in onshore or offshore transport (If increased Ekman transport of warm surface water from the southwest and coastal water convergence and sinking, the warmer bottom temperatures - British Columbia.)	a. Increased or decreased transport of larvae from nursery grounds, better or worse survival. b. Deeper spawning; poor egg survival; uncertain larval environment.
	2. Change in upwelling (averaged over the year)	a. Increased or decreased nutrient supply to upper layers, greater or lesser plankton productivity, better or worse larval juvenile?) survival. Changes in prey, predator, competitor distributions. b. Advanced or delayed plankton production peak, possibly unsynchronized with larvae.
	3. Changes in mixing. Deeper thermocline (also affected by temperature)?	a. Similar to effects of upwelling changes. Vertical distributions and migration trigger affected?
Change in storm intensity, tracks	1. Water column stability affected	a. Initiates, may alter timing of, fall migrations? b. Changes in food organism, larvae and predator distributions, patchiness. Could be advantageous or disadvantageous.
	2. Changes in onshore or offshore transport	a. Change in advection of larvae from nursery areas.
	3. Increased wave action	a. Mechanical destruction of eggs.
Increased precipitation	1. Increased runoff, offshore transport	a. Increased advection of larvae from nursery grounds.
	2. Lower coastal salinities	a. Larger egg sizes, shorter incubation, greater length at hatching.
Changes in water mass intrusions	1. Changes in horizontal fronts	a. Bounding horizontal distributions, influencing and bounding summer migrations (Bering Sea)? b. Bounding food organism distributions, which adults and juveniles may follow.

NOTES:

1. Intensive fishing may reduce a stock's ability to withstand changes.
2. Larval retention areas may be largely tidally controlled (Gulf of Maine), yet much year to year variation. Causes, if not runoff, are uncertain.
3. No demonstrated direct effect of changing conditions on fecundity or egg size. However, size of fish effects fecundity, and growth is affected by temperature.
4. Food organisms have comparatively short life cycles. Climate-induced changes may be more quickly felt, overgrazing not.

4.2.1 Warming

Within any region warmer water temperatures may cause herring to spawn a week or more early. Coupled with shorter incubation times, earlier spawning will result in earlier hatching. If zooplankton production relies on a different set of environmental factors, and is not similarly advanced, herring larvae may hatch before peak food production. A simliar decoupling of peak predator and herring abundance may benefit larval herring.

Slight increases in temperature may not have major impacts on herring growth rates. For most fishes optimal feeding and growth temperatures correspond to temperatures at which they normally exist (Brett and Groves 1979). Although higher temperatures may cause herring to eat more, growth efficiency may actually decrease because a greater percentage of food consumed is used for routine metabolism rather than growth (Brett and Groves 1979). It is not known if faster growth and developmental rates in early stages due to increased temperatures will produce greater mortality at later stages, as has been suggested for pollock (Strickland and Sibley 1984).

If warming in the eastern Bering Sea diminishes the ice cover, adult herring that overwinter part of the time under ice might become more vulnerable to pollock, a predator that may not venture beneath ice (Favorite and Lavestu 1981).

General warming may shift the center of herring abundance northward. However, this shift may result from attrition of southern stocks and strengthening of northern ones, rather than by relocation of individual populations. Homing to spawn probably roots herring to one location despite their wide migrations.

Warmer waters may extend the center of abundance of two related clupeoid fishes, northern anchovy and Pacific sardine, northward into areas with existing herring concentrations (Ketchen et al. 1983). Remnants of the once abundant sardine and anchovy populations off Washington and British Columbia are still present in these regions (Hart 1973).

Increased epizootic outbreaks may result from higher than normal water temperatures.

4.2.2 Increased Storminess

Storms cause egg mortalities through physical destruction by increased wave action. Increased storminess during the 2-3 week incubation could result in higher intertidal egg loss. Larvae spawned early might also be at a disadvantage if increased storminess prevented high production of prey organisms, but these conditions could favor larvae spawned later by maintaining productivity higher than would occur under more stable conditions. The eventual effect of these changes could be the evolution to a later spawning population, a genetic change. However, herring succes has only been linked to stability in one study (Wickett et al. 1975) which found greater abundance with increased upwelling during the second year of life.

Timing of fall migrations is believed initiated by vertical destratification of the water column. Therefore changes in the location and intensity storm tracks might alter fall migrations, but to what extent it is difficult to predict.

4.2.3 Increased Precipitation

Salinities in estuaries may drop below normal with increased runoff from precipitation. Lower salinities affect herring by increasing egg diameters and siae at hatching, and reducing incubation time. How these changes relate to survival is unknown.

4.2.4 Water Mass Changes

Migrations and distributions of adults and juveniles may shift because of changed water mass characteristics directly or from changes in the distribution of food organisms. Changes in distribution may result in stocks mixing, but does not seem to affect abundance; there is no evidence that return to spawning grounds is affected. Herring may spawn deeper, and may make small changes in the horizontal, but these are thought rare or minor events. However, migratory shifts may change established balances with prey, competitors and predators, including susceptibility to fishing.

4.2.5 Combined Factors

Onshore and offshore advection - transport away from nursery grounds - is caused by tidal currents, wind and freshwater runoff. Although tides will probably not be affected by changing climate, winds and runoff may be. Generally, increased precipitation and runoff increase offshore transport, especially in British Columbia during late spring from snowmelt. If increased winter temperatures result in less snow, then runoff at the time when larvae are most vulnerable, late spring, would be reduced despite increased annual precipitation.

Egg mortality in the intertidal zone is higher in warm, dry weather than during cool moist conditions. Warmer and moister weather is predicted to result from greater atmospheric CO_2; however, it is uncertain what effect this may have on egg dessication. Even were the effects known, investigations have not linked fluctuations in egg mortalities with year class abundance.

4.2.6 Increased Variability

Herring, and fishes in general, are likely better able to cope with slow (decadal) changes than more abrupt ones. Their response to variable interannual environmental conditions is to maximize the long term probability of occurrence of good conditions, though these may be infrequent and fortuitous. Even if variability reduces, and "ideal" conditions arise with greater frequency, standing stocks may not increase, because variability may be necessary to maintain balance and diversity in the ecosystem. However, small increases in frequency of good conditions may increase populations with marginal reproductive success, and vice versa (Sibley and Strickland 1985).

4.3 EL NINO

The consequences of the 1982-1983 El Nino, in which northeastern Pacific coastal temperatures increased 2-5°C, may provide a partial glimpse of what permanent climatic changes could bring. Granted, many of the mechanisms producing temperature increases differ and, unless varibility increases, effects of CO_2-induced changes may be less severe (Sibley and Strickland 1985). Preliminary data suggest that catches of salmon and other species in the Pacific Northwest decreased, and many southern species were displaced northward (Fluharty 1984). The data are correlative, not cause and effect, and some effects are inconsistent. Herring caught off California in 1984 were smaller than normal, 25% lighter for a given length, and about 6% shorter (J. Spratt, Cal. Fish. and Game, pers. comm.), though sizes of Washington herring were virtually normal (R. Trumble, Wash. Dept. Fisheries, pers. comm.). But abundances were normal in California, despite reduced biomass, and below normal in Washington.

Consequences to herring cohorts spawned in 1982-83 may not be fully evident until after 1985, when recruitment into the fishery begins. Preliminary surveys show strong 1982 and average 1983 California herring cohorts (J. Spratt, pers.

comm.). Primary productivity for the entire northeast Pacific was lower in 1982-83. Reduced upwelling probably had more effect on phytoplankton and zooplankton than did raised temperatures (Sibley and Strickland 1985). Why California herring appear unaffected may be explained by the sheltering of early stages in San Fransisco Bay, more affected by local runoff than the greater oceanic environment (J. Spratt, pers. comm.).

4.4 CONSIDERATIONS

Predicting possible changes in herring predators or actual or potential competitors is hampered by uncertainties in their responses to climatic changes. Even were the changes predictable, the effects on herring might not be clear. As one example, fluctuations in the abundance of dogfish, the major predator of juvenile and adult herring in the Strait of Georgia, seem to have little relation to herring number. As another example, the recent recovery of British Columbia herring stocks (Hourston 1980) may have been accelerated by the absence of ecologically similar competitors, as well as reduced fishing while populations were still relatively large (Murphy 1977).

Often a single strong year class interspersed among weaker ones will dominate and sustain a fishery for several years. To some extent, the presence of other year classes will buffer the effects of one poor year class on a fishery. This is typical in northern British Columbia, where age 3, 4 and sometimes older herring may dominate the herring populations (Stocker et al. 1984). In southern locations, where age 3 fish usually dominate, populations are more prone to fluctuate with abundance of a single cohort. But several consecutive year strong or weak year classes can cause prolonged and substantial increases or decreases in catches. Low recruitment of two or more successive year classes is considered serious to Washington herring (Trumble 1983).

The biomass of very early life stages of herring, the period when abundance is probably set, is small in comparison to later, when the much greater biomass is affected by fishing. Very intense fishing, however, may reduce a population's ability to withstand environmental changes (Bardach and Santerre 1981). Fishing not only reduces numbers of adults, but also causes changes in population structure. Overfishing can remove disproportionate numbers of larger, older fishes, leaving behind younger ones, and reduce the buffer of several dominant cohorts. Herring appear more vulnerable to overfishing than other fishes. Of low fecundity (pollock, by contrast, are one or two orders of magnitude more fecund), they are more vulnerable to recruitment failure (Cushing 1982), naturally or fishing caused.

Herring stocks contract their feeding and spawning ranges if the population is reduced. The effects of this behavior may be detrimental to the population because it reduces the ability of compensation, and, though more a problem at present with other clupeoid fishes, fishermen respond by contracting their area of operation, increasing fishing mortality (Murphy 1977).

Unfortunately, with present management practices, many changes in herring abundance are discovered only in retrospect. But for fisheries biological production is only part of the picture. In Washington, stock availability is more determined by migration to and mixing with British Columbia stocks (Trumble 1983). Even a small northward shift in distribution, while not much affecting British Columbia fisheries, could seriously affect those of Washington. In the meantime, the effects of climatic change on herring remain to be seen.

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