

**A SYNTHESIS OF THE FOOD HABITS
AND FEEDING ECOLOGY OF SALMONIDS
IN MARINE WATERS OF THE NORTH PACIFIC**

by

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ABSTRACT

Available information on the food habits and feeding ecology of the six species of salmon and two species of trout in the Genus *Oncorhynchus* found in marine waters of the North Pacific is presented and discussed. Three distinct life history stages are examined: (1) the pelagic juvenile phase in coastal waters, (2) the maturing phase in oceanic waters, and (3) the mature adult phase in coastal waters prior to the spawning migration. For each phase, the following features of feeding are examined: (1) general food habits, (2) geographic variations, (3) temporal variations, (4) selectivity, and (5) daily ration and variations in feeding intensity.

Sockeye and pink salmon subsist mainly on small zooplankton but will consume small nekton (fishes and squids) especially at a larger size. Chum salmon generally consume small crustaceans but often consume pteropods and gelatinous species and their diet is often most unique among all the salmonids. Coho salmon and steelhead trout exhibit a mixed diet of fish and invertebrates. Masu and chinook salmon and cutthroat trout are mainly piscivorous in all phases of their marine existence. Euphausiids, decapod larvae, amphipods and young fishes are the predominant prey items of most species in coastal areas whereas fish, squid and amphipods are important foods in more oceanic waters. Despite the differences in general food habits among the various salmon species, most species appear to be non-selective feeders within a preferred size range of prey organisms. Most geographic or temporal variations in feeding appear to be attributable to variations in prey resources. Although the types of food consumed by all phases are reasonably well-known for most species, relatively little is known concerning quantitative aspects of salmon feeding such as daily ration and environmental effects on feeding success.

INTRODUCTION

The anadromous Pacific salmon and trout of the Genus *Oncorhynchus* are renowned for their dramatic migrations as they return to natal streams to spawn. At this time, most salmon occur in large concentrations and are relatively accessible to many types of fishing gear. Hence they have supported major fishery operations for centuries around much of the Pacific rim from Japan to California. The tremendous cultural and economic importance of salmonids has prompted much research this century into understanding the ecology of the spawning fish and how it may be affected by human activities. In addition, the early life history stages of salmon and trout rearing in streams, rivers and lakes have received much scientific attention because of concerns over habitat degradation resulting from forestry and agricultural practices, wetland destruction, and hydroelectric power demands of rapidly-expanding populations. For these reasons, Pacific salmon may be among the most well-studied fishes on earth.

Although the ecological importance of the freshwater environment is recognized, the marine phase of their life history has received considerably less attention in the North Pacific (Percy in press) and may be attributed in part to the difficulties in sampling salmon in the vast oceanic domain that they inhabit. For most salmonid species, however, their marine existence occupies a significant part of or, for some species such as chum and pink salmon, the majority of their life cycle. Productivity is relatively low in freshwater and in order to achieve the large terminal size needed to produce large numbers of offspring, most salmonid populations undertake long migrations in order to exploit rich oceanic feeding grounds. In fact, the majority of the final weight of most salmon is gained in the ocean, where growth continues until they begin their spawning run (Brett 1983).

In order to maintain such rapid and sustained growth rates in the ocean, salmon must feed often and successfully. They initially must adapt to rapidly changing biotic and abiotic conditions when they first enter the ocean and migrate to new areas when food resources are not sufficient to sustain them. They generally exploit the resources of the coastal zone for several months as they undergo a major growth spurt (Cooney 1984). Upon leaving the coastal environment, salmon congregate in large numbers in the open ocean feeding grounds where they mingle with fish from other stocks as well as other species (Peterman and Wong 1984) and represent the majority of the fish biomass in the Subarctic Domain (Ware and McFarlane 1989). Here again they must adapt to new prey taxa that have evolved mechanisms (e.g., vertical migration) to avoid capture. Finally, the salmon must reenter coastal waters and continue to accrue the energy reserves needed to make their spawning migration. Therefore, feeding is an important, if not critical, aspect of all phases of the marine life of a salmon.

Despite the availability of many studies on the food and feeding ecology of salmon in the ocean dating back over the last fifty years, we are still a long way from complete understanding of all the processes linked to salmon feeding in the ocean. The existing data are widely scattered in both the refereed and informal literature and are presented in a number of different languages and formats. The only attempts to review the literature to date have been the single species summaries in International North Pacific Fisheries Bulletins (e.g., Godfrey et al. 1975, French et al. 1976, Neave et al. 1976, Major et al. 1978, Takagi et al. 1981) but these are of varying completeness. It is my intent in this paper to review many of these food habits studies and synthesize the results so that a clearer picture of the feeding ecology of salmon in the ocean may emerge.

SCOPE OF COVERAGE

I will review aspects of the food habits and feeding ecology of the six species of Pacific salmon and two species of anadromous trout commonly occurring in the North Pacific Ocean. Included among these are sockeye (*Oncorhynchus nerka*), chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), chinook (*O. tshawytscha*) and masu (*O. masou*) salmon and steelhead (*O. mykiss*; formerly *Salmo gairdneri*) and cutthroat (*O. clarki*; formerly *S. clarki*). The Kamchatka trout (formerly *S. mykiss*) has been found to be the same species as the North American steelhead (Smith and Stearly 1989) and in this review shall be treated together with steelhead under *O. mykiss*.

The life history phases covered by this review include (a) the juvenile period when they enter open coastal waters, (b) the maturing stage when they are found offshore in open ocean waters, and (c) the mature stage when they reenter coastal waters to spawn. I have excluded the estuarine and near-shore (i.e., accessible to beach seines) existence of salmon from the first phase since salmon feed mainly upon epibenthos at this time (see reviews by Healey 1982a, Simenstad and Wissmar 1984) and therefore are subject to different constraints than the pelagic-feeding individuals I intend to focus upon in this review.

For each species and life history phase, I will discuss, when data are available, the following aspects of feeding: (1) general food habits, (2) geographic variability, (3) temporal (interannual, seasonal and diel) variability, (4) selectivity of size and type of prey, (5) daily ration and factors affecting feeding intensity. I will consider also the overlap in diet among salmon species collected from the same area. Finally, I will discuss some of the biases associated with inferring food habits from stomach sampling and point out critical areas where information is still lacking.

SOCKEYE SALMON

JUVENILE COASTAL PHASE

General food habits

Juvenile sockeye salmon consume a wide variety of prey organisms in the coastal environment including euphausiids, hyperiid amphipods, copepods, pteropods, larval and juvenile fishes, and, to a lesser extent, squid and decapod larvae.

Geographic variability

Off Oregon and Washington, juvenile sockeye consumed mainly larval fishes (Osmeridae) and euphausiids, but a high diversity of prey was found in the limited number of stomachs examined (Brodeur and Pearcy 1990). Healey (1980) found that sockeye smolts in the Fraser River Plume consumed mainly insects, copepods and euphausiids whereas fish caught in the Strait of Georgia fed mainly upon amphipods. In contrast, sockeye off Northern British Columbia and Southeast Alaska ate mostly teleosts, larvaceans (*Oikopleura*), euphausiids and copepods (Manzer 1969, Andrews 1970, Jaenicke et al. 1984, Healey MS, Landingham and Mothershead MS).

Dell (1963) reported that immature sockeye (age .0) ate mainly fishes, squid, amphipods, and euphausiids south of the Aleutian Islands and euphausiids and fish (sand lance) in Bristol Bay. Juvenile sockeye examined from the Eastern Bering Sea north of the Alaska Peninsula consumed mainly copepods, euphausiids and fish, but a substantial regional variability was apparent (Andrews 1970, Carlson 1976, Straty and Jaenicke 1980, Craig 1987).

The food habits of sockeye juveniles in the Western Bering Sea and in Kamchatkan waters are fairly well described. Copepods, hyperiids, fish and decapod larvae, euphausiids, chaetognaths, and cladocerans were all found to be important in various studies from this area (Snykova 1951; Andrievskaya 1968, 1970; Karpenko 1980; Karpenko and Piskunova 1984). Karpenko (1980) found that their diets changed dramatically as sockeye moved offshore.

Temporal variability

Healey (1980) found that crab fish larvae were important foods in 1975 whereas copepods and ctenophores were the main foods in 1986, a difference he attributed to differences in food availability. Juvenile sockeye diets collected in Hecate Strait during two years differed only slightly; the main difference being that larvaceans were replaced in part by copepods in the second year (Healey MS). Landingham and Mothershead (MS) found major differences in prey composition (i.e., more fish and less invertebrate taxa) between two years of sampling off Southeast Alaska, which they attribute to a change in oceanographic conditions. Andrews (1970) found few interannual differences in overall diet from fish collected over a broad area of the North Pacific, but he did find pronounced diel differences in food composition in many areas. Sockeye smolts in the Bering Sea caught in two areas switched their diets on a seasonal basis from euphausiids in June to fish (sand lance) and cladocera in July and August (Straty and Jaenicke 1980).

Selectivity

Healey (1980) suggested that sockeye juveniles prefer copepods and insects, but will eat euphausiids, amphipods and fish larvae when these become available. Sockeye salmon showed more positive selection for organisms found in the neuston than those found throughout the water column (Landingham and Mothershead MS). Comparisons between zooplankton and juvenile sockeye food in Bristol Bay in the Eastern Bering Sea revealed that sockeye preyed opportunistically on the most abundant large plankton available but switched to smaller prey when large prey were not available (Straty and Jaenicke 1980). Similar comparisons in the Western Bering Sea suggested that sockeye consumed amphipods and euphausiids in higher proportions than their available biomass while the opposite was true for copepods (Karpenko and Piskunova 1984).

Daily ration and feeding intensity

Feeding by juvenile sockeye tended to increase through the daylight hours and amounted to a total ration of between 1.24 and 2.33% of their body weight consumed daily (Healey MS). Andrews (1970) found substantial variability in sockeye feeding at all times of the day but sockeye showed a greater tendency to feed in early morning after sunrise or in the evening. Straty (1974) found that juvenile sockeye stomachs collected offshore were generally fuller late in the summer suggesting that food may be limiting inshore in the early summer.

MATURING OCEANIC PHASE

General food habits

Maturing sockeye in the open ocean consume mainly euphausiids, hyperiid amphipods, fish and squid but they are also known to consume copepods, pteropods, crustacean larvae and pelagic polychaetes.

Geographic variability

The oceanic feeding habits of sockeye salmon have been well-studied in a number of geographic areas of the North Pacific. In the Gulf of Alaska, LeBrasseur (1966) examined sockeye from several oceanic domains. Fish caught in the Subarctic region consumed mainly squid whereas fish caught in more coastal regions and the Transition domain consumed mostly euphausiids, amphipods and fish. Manzer (1968) found the majority of the volume of sockeye stomach contents consisted of lantern fish and squid. Percy et al. (1988) examined both meridional and zonal variations in feeding of sockeye salmon collected in gill nets in the open Gulf of Alaska. They generally found that along North-South transects, euphausiids, fish, and amphipods were the dominant food in fish collected in the Alaska Current and Ridge Domain but the diet changed dramatically to almost a complete reliance on squid, with amphipods of secondary importance in the Subarctic Region. This shift was most apparent in larger fish, which had as the majority (> 82% by volume) of their food at all stations the large squid, *Berryteuthis anonychus*. The diets were more varied along the East-West transects and were dominated at various stations by euphausiids, squid, fish, amphipods, pteropods and pelagic polychaetes. There were few discernable trends in food composition with longitude of collection.

Similar inshore-offshore differences in feeding of sockeye were observed in the Bering Sea with squid being the dominant food consumed in more oceanic areas and with euphausiids, amphipods and fish larvae being the dominant foods on slope and outer shelf regions (Favorite 1970, Nishiyama 1970, Kanno and Hamai 1972, Takeuchi 1972). South of the Eastern Aleutian Islands, a wide variety of foods were taken by sockeye including copepods, euphausiids, hyperiids, euphausiids, pteropods, fish and squid (Maeda 1954, Allen 1956a, Allen and Aron 1958, Dell 1963, Ito 1964). East of the Kamchatka Peninsula, the diet of sockeye consisted mainly of amphipods in one study (Allen 1956a, Allen and Aron 1958) whereas a greater variety of foods, including also euphausiids, hyperiids, medusae, pteropods, squid and fish, was reported by other researchers (Andrievskaya 1958, Ueno et al. 1969). The latter authors found substantial differences in food composition in fish collected only 60 miles (96 km) apart on the same day. Finally, Takeuchi (1972) found that most individual prey taxa showed significant differences in occurrence among three different areas examined but these differences were less pronounced than those seen for other salmon caught at the same time.

Temporal variability

In sampling successive years along the same transects in the Gulf of Alaska, Percy et al. (1988) observed major interannual variations in food habits of sockeye. For example, during 1983, pteropods were a very important component of the diet at several stations while in 1982, they were important at only one station and absent from several. Although other examples are available, interannual differences appear to be less significant than regional differences in this species. Ito (1964) found an interesting biennial shift in sockeye stomach contents with an emphasis on large prey (fish and squid) during even years and small prey (euphausiids, amphipods and copepods) during odd years.

Seasonal and diel differences in adult sockeye food habits have been reported in only a few studies. Manzer (1968) compared his own data collected in winter to LeBrasseur's (1966) data collected in early summer and found a shift in the main food from fish to squid between the two seasons. However, other factors such as yearly differences and gear selectivity could account for the differences found. Takeuchi (1972) found relatively minor monthly variations in major prey taxa consumed with less than half of the prey showing significant variation. Adult sockeye,

however, did show distinct diel variations with euphausiids becoming increasingly important during the night (Pearcy et al. 1984).

Selectivity

Few studies are available that have examined food selectivity in adult sockeye in oceanic waters. Although several studies suggest that sockeye are indiscriminate feeders, consuming whatever prey is abundant at the time of feeding (Takeuchi 1972, Pearcy et al. 1984), there is some evidence that they may consume certain midwater fish and large squid in higher proportions than would be expected based on availability (Pearcy et al. 1988).

Daily ration and feeding intensity

The diel feeding cycle of sockeye salmon collected in gill nets has been examined in both the open North Pacific and the Bering Sea. Pearcy et al. (1984) found that the fewest empty stomachs and the highest stomach content weights occurred during nighttime and early morning collections when sockeye were in surface waters. This contrasts with the findings of Machidori (1968) that showed feeding indices to be higher during the day than at night. Azuma (1989), based on the relative fullness and condition of stomach contents of sockeye caught in the Bering Sea, concluded that there was an increase in feeding activity twice a day; in the evening before sunset and after sunrise.

Nishiyama (1970, 1974, 1977) conducted one of the most complete studies to date on the energetics of adult sockeye salmon. For fish caught in the open Bering Sea seaward of the continental shelf, Nishiyama (1970) estimated a daily ration of 1.8-2.0% BW for females and 2.1-2.3% BW for males. He found that mean stomach content weights progressively increased as fish neared the shelf region (Nishiyama 1977).

MATURE COASTAL PHASE

General food habits

Sockeye adults in coastal waters are mainly zooplanktivorous, feeding predominantly upon euphausiids, hyperiid amphipods, and decapod larvae with some contribution from small squids and fishes.

Geographic variability

Euphausiids, hyperiids and crab larvae were numerically the dominant prey of mature sockeye returning along the southern coast of Vancouver Island, with sand lance and mysids eaten occasionally (Beacham 1986). Mature sockeye salmon collected in the coastal region in the northeast Gulf of Alaska consumed mostly euphausiids with fish being of secondary importance whereas in the Alaska Stream, the relative importance of these two prey groups was reversed (LeBrasseur 1966). In the Bering Sea, euphausiids were the predominant food (79% by weight) of mature sockeye returning to Bristol Bay (Nishiyama 1970, Craig 1977).

The diet of maturing sockeye in coastal waters of the Western North Pacific have been extensively studied. Snykova (1951) and Andrievskaya (1957, 1958) studied salmon feeding in Kamchatkan coastal waters and found that euphausiids, amphipods, crab larvae and young fish were the dominant food items eaten although other presumably less desirable prey (jelly fish and seaweeds) were also eaten. Sockeye collected in Autumn off Kamchatka and in the Okhotsk Sea consumed mainly young squid, but fish, decapod larvae and euphausiids also contributed substantially to the overall diet (Andrievskaya 1966). Allen and Aron (1958) examined sockeye collected in the Okhotsk Sea and found that their diet consisted mainly of amphipods (64.6% by

volume) and crustacean larvae (26%). Mishima and Tokusa (1977) observed marked geographic variations in the diet of mature sockeye. Those collected on the eastern side were found to consume mainly lanternfishes, euphausiids and squid while those on the Okhotsk Sea side consumed mainly euphausiids.

Temporal variability

Most studies analyzing temporal variability in sockeye feeding in coastal waters have emphasized interannual differences since mature fish are generally in coastal waters for only a short period of time. For example, Nishiyama (1970) examined sockeye collected in Bristol Bay during two years of sampling and found only minor differences in the diets compared to the interannual differences observed in more oceanic waters. Dietary differences were also relatively minor in two years of sockeye feeding examined by Mishima and Tokusa (1977) in the Okhotsk Sea.

Selectivity

No data are available on the food selection of adult sockeye relative to food availability. Beacham (1986) showed that the average size of invertebrate prey decreased and fish prey increased with increasing size of sockeye, which suggested that the largest individuals of each prey type were not necessarily selected by these predators.

Daily ration and feeding intensity

Nishiyama (1970) estimated the daily ration of adult sockeye in Bristol Bay to be about 1.6% and 1.8% of the body weight for females and males, respectively.

CHUM SALMON

JUVENILE COASTAL PHASE

General food habits

Chum salmon juveniles begin to move offshore as inshore prey resources decline and at a size that they are able to feed on many larger pelagic resources. The most important planktonic prey groups consumed tend to be calanoid copepods, euphausiids, hyperiid amphipods, larvaceans, chaetognaths, decapod larvae and fish larvae at this time.

Geographic variability

At the southern end of their range in the Northeast Pacific, chum juveniles (97-237 mm) feed on euphausiids with fish larvae, hyperiids and chaetognaths of lesser importance (Peterson et al. 1982, Brodeur and Percy 1990). In the Georgia Strait, British Columbia, Healey (1978, 1980) found that chum fed upon decapod larvae, hyperiid amphipods, euphausiids and fish, although regional differences in diets were pronounced. Off northern Vancouver Island, Black and Low (1983) found ctenophores to be a major component of the diet of juvenile (70-170 mm) chum. In northern British Columbia (Hecate Strait), Healey (MS) found that the major part by weight (64-81%) of the diet of juvenile chum consisted of larvaceans (*Oikopleura dioica*) with euphausiid and copepods being of minor importance. Manzer (1969) also found larvaceans to be the major food (51%) of chum salmon collected from Chatham Sound with copepods being more important in the southern part of the sound. Off Southeast Alaska, euphausiid larvae were the main food of juvenile chum collected in gillnets but most of the food was well digested and unable to be identified to any major prey category (Jaenicke et al. 1984). Fishes were the dominant prey by weight off northern British Columbia and southeastern Alaska, but hyperiids and larvaceans were important numerically. In the Alaska Stream south of Kodiak Island, chum salmon consumed mainly the pteropod, *Limacina* and several unidentified fish (LeBrasseur 1966). Little is known

about the food habits of chum salmon through the remainder of Alaskan waters with the exception of a study by Craig (1987), which found that fish, decapod larvae, amphipods and insects were consumed by chum collected off the Alaska Peninsula in the Eastern Bering Sea.

The feeding of juvenile chum salmon in Western Bering Sea and Sea of Okhotsk has been intensely studied for decades. Snykova (1951) found copepods, hyperiids, euphausiids and fish to be the most frequently found prey of several age groups (including juveniles) of chum. The hyperiid amphipod *Parathemisto* was the dominant food item in juvenile chum stomachs collected in both the eastern (Kamchatka) and western (Sakhalin) sides of the Sea of Okhotsk (Andrievskaya 1968, 1970). Fish larvae, especially sand lance (*Ammodytes*), were also important in some areas.

Okada and Taniguchi (1971) found mainly copepods, euphausiids, insects and hyperiids to be important prey of chum juveniles sampled off the coast of Hokkaido Island, Japan. These authors reported a major change in prey size consumed between chum salmon less than and greater than 55 mm. Off Otsuchi Bay on Honshu Island, Terazaki and Iwata (1983) showed that larger chum feed mainly on hyperiids, cladocerans, copepods and euphausiids. Many of these same prey, with the addition of sand lance juveniles (*Ammodytes personatus*), were identified by Kaeriyama (1986) in pelagic waters off the Sanriku coast.

Temporal variability

Chum salmon juveniles exhibited substantial diet variability among the five summers examined by Brodeur and Pearcy (1990) off Oregon and Washington. Euphausiids were most important during two years whereas fishes and chaetognaths were dominant during two other years and copepods in the last year. There were also seasonal shifts from chaetognaths being the main prey early in the summer to euphausiids and copepods late in the summer (Brodeur, unpubl. data). Healey (MS) found few differences in the diet of chum collected during two years of his study but Landingham and Mothershead (MS) noted a major shift from euphausiids and hyperiids to mostly teleosts for the same two months one year apart.

Karpenko (1980, 1982) found major differences in stomach fullness and taxonomic composition of the diets of chum during the course of several days of diel sampling. He attributes much of this variation to differences in prey availability due to tidal variations during the diel cycle. Karpenko and Nikolaeva (1989) showed that the diel pattern of feeding was different during different years and that chum juveniles generally cease feeding at night except during nights when there is a substantial amount of moonlight. Juvenile chum off Japan showed a seasonal shift in diet composition from *Parathemisto* and sand lance in May to other coastal zooplankton in June and July (Kaeriyama 1986).

Selectivity

Healey (1980) speculated that chum salmon juveniles have a preference for larvaceans (*Oikopleura* spp.) and euphausiids over other prey items but does not provide data to show this. Chum juveniles off Southeast Alaska showed preference for hyperiids and larvaceans relative to their abundance in the neuston or plankton (Landingham and Mothershead MS). Chum salmon juveniles in the Bering Sea consumed *Themisto japonica* in higher proportions than those available in the plankton although the opposite pattern was evident for copepods and euphausiids (Karpenko and Pushkinova 1984). Similarly, Terazaki (1983) found that amphipods were positively selected for and copepods selected against by chum salmon in the outer part of Otsuchi Bay, Japan. Kaeriyama (1986) also found hyperiids were consumed preferentially in relation to their abundance in the plankton, and copepods and cladocerans appeared not to be consumed in relation to their abundance.

Daily ration and feeding intensity

Healey (1980) found chum salmon stomach contents as a percentage of body weight decreased from April (3-5%) through July (1-2%) which was associated with chum emigration out of Georgia Strait. In Hecate Strait, chum juveniles showed a significant increase in stomach content weight over the diel cycle and consumed a ration of 2.91-3.83 %BW day⁻¹ (Healey MS).

In the Okhotsk Sea, Gorbatenko and Chuchukalo (1989) estimated daily rations of 4.2-6.8 %BW, and found that chum fed most intensely during the morning and evening periods. Karpenko and Nikolaeva (1989) found similar peak feeding periods but their estimates of daily ration were much higher ranging from 3.7-9.7 %BW at the mouth of the Kamchatka River to 6.7-16.5 %BW at the mouth of the Anapka River.

MATURING OCEANIC PHASE

General food habits

The dominant food organisms consumed by chum salmon in the open ocean are amphipods, euphausiids, pteropods, fishes and, to a lesser extent, copepods. The stomachs of chum frequently contain unidentifiable material, which may be a mixture of gelatinous forms that are quickly digested relative to most crustacean, mollusk, or fish prey.

Geographic variability

In the Gulf of Alaska and Northeast Pacific, maturing chum reportedly feed upon euphausiids, amphipods, and pteropods and gelatinous zooplankton (LeBrasseur 1966, Pearcy et al. 1988). In the Subarctic Current Region south of 50 °N, midwater fishes and squid are predominant particularly in larger individuals (Pearcy et al. 1988).

In the Western North Pacific, chum diets have been studied extensively. Fishes, amphipods, copepods and euphausiids were all dominant prey items at different collection sites in an early study by Maeda (1954). In the more oceanic regions studied by Allen (1956b) and Allen and Aron (1958), euphausiids constituted half the volume but pteropods, copepods and fishes were also major prey in gill-net caught chum. Chum were the only salmon species to consume decapod larvae in this area. Ito (1964) observed that pteropods (*Limacina* and *Clione*) and euphausiids were dominant foods of chum caught on the high seas but gelatinous zooplankton also appear to be important. Ueno (1969) found myctophid fishes, squids, euphausiids, amphipods and pteropods mainly in the stomachs of chum salmon and that many of these stomachs were well stratified, suggesting that chum feed on concentrated prey patches.

Takeuchi (1972) found that euphausiids, pteropods and amphipods were the main prey by weight and frequency of occurrence south of the Aleutian Islands, and in the Sea of Okhotsk and the Bering Sea. All but one of the 11 most important prey taxa showed significant areal differences in occurrence. Adult chum diets in the Bering Sea were highly variable and consisted of euphausiids, amphipods, pteropods and copepods but, in contrast to the other salmon species collected, chum salmon generally did not consume squid (Kanno and Hamai 1972). These authors were able to identify four different feeding areas in the Bering Sea, depending on the major prey taxa consumed.

Temporal variability.

Interannual variations in stomach contents of maturing chum in the North Pacific were summarized by Neave et al. (1976) from the studies of LeBrasseur and Doidge (1966) and Ito

(1964). In the Northeast Pacific, chum diets varied greatly from year to year with different taxa being important during consecutive years. In the Northwest Pacific, pteropods were ranked first or second in importance during six of the eight years examined by Ito (1964).

Although a high percentage of the stomach contents of chum examined by Percy et al. (1988) was unidentified material, there was also substantial variation between years for the transects that were sampled two years in a row. For example, euphausiids and amphipods were dominant foods during 1984 but polychaetes and other miscellaneous prey were most important the next year at the same stations.

Seasonal differences were reported by Takeuchi (1972), who found that the species composition of the prey of chum salmon changed considerably from April to July in the Northwestern Pacific. Significant differences were found for ten of eleven prey taxa he examined. On a diel basis, chum stomachs were also highly variable containing mainly salps in the late afternoon and euphausiids and fish at night (Percy et al. 1984).

Selectivity

Percy et al. (1984, 1988) suggest that chum salmon feed opportunistically at the surface on aggregations of prey such as polychaetes, euphausiids and gelatinous zooplankton. The latter prey were often the dominant taxa in the biomass of midwater trawls at the same stations but chum were often the only salmonid species to utilize these abundant prey resources. Similarly, Takeuchi (1972) found much similarity between chum diets and zooplankton composition in the same area and found no evidence of selective feeding. Contrary to most other salmonids, chum salmon generally do not consume squid in open waters of the North Pacific.

Daily ration and feeding intensity

Several studies have examined diel variations in feeding intensity of chum salmon. Ueno et al. (1969) report that chum feed most actively from the early night to early morning. No discernable diel trend in feeding of chum salmon was found by Percy et al. (1984), with both full and empty stomachs found at all times of the day. Azuma (1989) also found relatively minor differences in stomach fullness and the percentage of empty stomachs during the diel cycle with some indication that feeding peaks from sunset to midnight.

Takeuchi (1972) provided one of the few studies that examined regional variations in stomach fullness of adult chum salmon and found that the weight of stomach contents and percentage of empty stomachs was significantly different in four regions of the Bering Sea.

MATURE COASTAL PHASE

General food habits

Adult chum in coastal waters consume a wide variety of organisms of various sizes including euphausiids, amphipods, crustacean larvae, pteropod larvae and small fish and squid.

Geographic variability

There is a general dearth of knowledge concerning the feeding of mature chum salmon in the Eastern North Pacific. A limited number of chum salmon were examined along the north side of the Alaska Peninsula by Craig (1987) who found that fish, decapod larvae, amphipods and copepods were the main foods eaten.

Extensive data are available on adult chum feeding in the Northwest Pacific, particularly in the vicinity of the Kamchatka Peninsula and in the Sea of Okhotsk. Allen and Aron (1958) found

somewhat similar diets for chum collected on the east and west sides of the Kamchatka Peninsula. They found that euphausiids and amphipods were relatively more important on the east side whereas crustacean larvae and pteropods were substantially more important on the west (Okhotsk Sea) side. The main foods off Kamchatka during five years of sampling were euphausiids, copepods and amphipods whereas off the Kuril Islands, crab larvae were also important (Snykova 1951). Andrievskaya (1957) found many different prey in adult chum stomachs among which pteropods, fish larvae, hyperiids, crab larvae and mysids were most important. Mishima and Tokusa (1977) report that jellyfish were the most frequently occurring prey in both the North Pacific and Okhotsk Sea adjacent to the Kuril Islands. Euphausiids and myctophid fishes were also relatively important components of the diet. Finally, Gorbatenko and Chuchukalo (1989) found pollock and capelin juveniles to be the most important food of trawl-caught chum off Kamchatka and zooplankton, mainly (98.7%) euphausiids, was most important off Sakhalin Island.

Temporal variability

The diets of mature chum off the Kuril Islands differed little between two years examined by Mishima and Tokusa (1977). However, myctophids were less important and euphausiids more important during the second year of the study. Snykova (1951) examined changes in chum diets from one location between May and August. She found relatively minor changes in the diet over these four months but her sample size in several months was rather small. The diet of chum was examined during three seasons by Andrievskaya (1966) and also varied relatively little from spring through autumn. Pteropods were the dominant prey taxa during all three seasons but the second most important prey shifted from euphausiids in the spring to a mixture of euphausiids and amphipods in summer to young cod in autumn.

Diel variations in mature chum salmon at two stations in the Okhotsk Sea was examined by Shimazaki and Mishima (1969). Amphipods were most important during the evening and early morning but the remaining prey did not show any consistent diel trends.

Selectivity

Little is known about the feeding selectivity of adult chum salmon in coastal waters. Shimazaki and Mishima (1969) found large numbers of hyperiids in plankton tows in surface waters at the same time hyperiids were a dominant food item in the diet of chum salmon. The occurrence of mysids, benthic sponges and seaweeds in chum salmon stomachs examined by Andrievskaya (1957) suggest that chum adults may feed close to the bottom layer in coastal waters.

Daily ration and feeding intensity

Diel differences in feeding intensity were observed by Shimazaki and Mishima (1969) with peak feeding occurring shortly after sunset and sunrise. Stomach fullness was lowest around midnight and during midday. The daily ration of mature chum salmon was estimated to be approximately 7% of the body weight in the Okhotsk Sea (Gorbatenko and Chuchukalo 1989).

PINK SALMON

JUVENILE COASTAL PHASE

General food habits

Juvenile pink salmon grow rapidly in marine waters, which requires a relatively rapid movement offshore to obtain the necessary food resources. Once offshore, they feed mainly upon

fish, copepods, amphipods, euphausiids, pteropods and chaetognaths in coastal waters of various parts of the North Pacific.

Geographic variability

Calanoid copepods are the dominant food of juvenile pinks in the Fraser River plume and these prey continue to be important as they move offshore, supplemented by amphipods, larvacea, insects, chaetognaths and euphausiid eggs (Healey 1980). Larvaceans, fishes, copepods, euphausiids and decapod larvae are the main prey consumed by juvenile pinks off northern British Columbia and off Southeast Alaska (LeBrasseur and Barner 1964, Manzer 1969, Jaenicke et al. 1984, Healey MS, Landingham and Mothershead MS). Larvaceans replaced copepods as the dominant prey as one moved northward within Chatham Strait, British Columbia (Manzer 1969). Amphipods, copepods and decapod larvae were the main foods of pink salmon juveniles collected in the Eastern Bering Sea (Craig 1987).

In the Western Bering Sea, pink juveniles (160-195 mm) feed mainly (> 83% by weight) upon pteropods (*Limacina helicina*) according to Andrievskaya (1968). Andrievskaya (1968, 1970), however, found the majority of juvenile pink salmon diet in the Okhotsk Sea to consist of copepods and hyperiid amphipods, although the relative proportions of these prey varied according to capture location. Other studies (e.g., Karpenko 1980, Karpenko and Piskunova 1984, Karpenko and Safronov 1985, Gorbatenko and Chuchukalo 1989) in the Okhotsk Sea and off Kamchatka Peninsula found a wide variety of prey organisms to be important. In addition to copepods and amphipods, these authors found mysids, insects, pteropods and chaetognaths also to be important food organisms. Snykova (1951) found juvenile fish (sand lance and cod) to be the dominant food of young pink salmon off Kamchatka and the Kurile Islands. Okada and Taniguchi (1971) found juvenile (40-70 mm) pink salmon to feed mainly upon copepods, amphipods, fish larvae and insects off southern Hokkaido, Japan.

Temporal variability

Healey (1980) found substantial differences in juvenile pink salmon feeding between two collection years in Georgia Strait when the dominant prey taxa switched from copepods and amphipods to euphausiid eggs. In Hecate Strait, the differences were even more dramatic as the diet changed from mainly larvaceans (> 80% by weight) to a more mixed diet of crab larvae, euphausiids, copepods, and larvaceans (Healey MS). Landingham and Mothershead (MS), however, did not find major seasonal or interannual differences in pink salmon diets off Southeast Alaska.

In the Bering Sea, the diets of pink salmon change seasonally as the fish grow in length from mainly small zooplankton in July and August to larger zooplankton (euphausiids, hyperiids and large copepods) by September (Karpenko and Piskunova 1984). Off Kamchatka, Karpenko (1980) found that pink salmon switched from eating mainly copepods and mysids in June and July to juvenile fishes and crab larvae during August and September.

Selectivity

Juvenile pink salmon appear to feed preferentially on smaller prey organisms (copepods and invertebrate eggs), especially compared with other juvenile salmon, and consume larger prey when these prey become less available (Healey 1980). Landingham and Mothershead (MS), however, showed that larger juvenile pink salmon feed preferentially on hyperiids and euphausiids and avoid copepods. There appears to be a dramatic shift in the size composition of prey when pink salmon reach 55-60 mm (Okada and Taniguchi 1971), which suggests a behavioral (or habitat) change rather than a more gradual morphological change.

Karpenko and Piskunova (1984) found that the dominant food by weight (a species of euphausiid) of pink salmon in one area of their study was also the dominant species by biomass represented in the plankton. The main food in the other area (*Themisto japonica*) was not very abundant but tended to be found in high density patches, which may be utilized by these juveniles. Karpenko and Safronov (1985) compared the diet of pink juveniles to the near-surface (neuston) composition and found some similarities between the two, suggesting that they may feed near the surface.

Daily ration and feeding intensity

Estimated daily rations of juvenile pink salmon vary from 3.2-4.1 % BW off British Columbia (Healey MS) to 1.9-7.2 % BW in the Okhotsk Sea (Andrievskaya 1988, Gorbatenko and Chuchukalo 1989). Feeding intensity of juvenile pink salmon off British Columbia peaked in early June (3.5 % body weight) and then dropped off later in the summer (0.5-1.0 %), which did not appear to correlate with food availability (Healey 1980). Stomach contents increased significantly during daylight hours but feeding intensity did not appear to be related to the abundance of salmon during any time period (Healey MS).

MATURING OCEANIC PHASE

General food habits

Pink salmon in offshore waters consume predominantly fishes, hyperiid amphipods, euphausiids, and squid and also secondarily consume pteropods, copepods, and polychaetes.

Geographic variability

The food habits of maturing pink salmon in the Northeast Pacific and Gulf of Alaska are highly variable. Manzer (1968) found that pink salmon caught on longlines fed almost exclusively (97% by weight) on hyperiid amphipods, although his sample size was limited. A more diverse diet was reported by LeBrasseur (1966) for the Subarctic and Transition Domains and included, in addition to hyperiids, euphausiids, copepods, pteropods, squid, and fish. Squid were particularly important in the Subarctic Domain, comprising almost 75% of the total weight. Regional north-south differences were also apparent in the study by Percy et al. (1988) which found that euphausiids and fishes were the dominant prey in the northern Gulf of Alaska and squid and amphipods assume predominance in the Subarctic Current region. Along east-west transects, squid and amphipods were the dominant prey items at most stations but occasionally, pteropods, fish, or copepods were important.

In the Western North Pacific south of the Aleutians, euphausiids and fishes were the principal components of the diet of gillnet-caught pink salmon with a minor contribution from squid, copepods, pteropods and hyperiid amphipods (Maeda 1954, Ito 1964). Squid were particularly important in the stations south of 48 °N. Andrievskaya (1966) found that four prey groups, namely fishes, euphausiids, squid and amphipods, were the primary foods of pink salmon in oceanic waters. In contrast, Allen and Aron (1958) found copepods to be over twice as important by volume as the next major prey category. In samples collected from the Western North Pacific, Takeuchi (1972) observed that pink salmon consumed mainly euphausiids, squid, copepods and amphipods whereas samples collected the same year in the Bering Sea contained appreciably more fish and euphausiids and less squid and amphipods. Most major prey taxa showed substantial variation by area of collection. Pink salmon followed a pattern similar to sockeye salmon in the geographical consumption of major prey in the Bering Sea (Kanno and Hamai 1971). Offshore in the central Bering Sea, squids were almost exclusively (> 91% by weight) the dominant prey

consumed but on the Bering Sea shelf to the north and west, fishes, amphipods and euphausiids were the major prey and squid were not represented at all in the diet.

Temporal variability

Although the dominant prey consumed by pink salmon in the study by Pearcy et al. (1988) were consistent in sampling of the same transect in consecutive years, some major anomalies occurred. For instance, euphausiids and squid were more important during 1982 than the warm year of 1983 when euphausiids were almost totally absent and squid were consumed only in the colder water mass in the western Gulf of Alaska. Ito (1964) observed a cyclic feeding pattern with squid of major importance only during even-numbered years and euphausiids and copepods high in alternate years. Takeuchi (1972) also found more squid in the stomachs during the two even-numbered years as opposed to the intervening odd year, but the same areas were not sampled all three years.

A seasonal shift in adult pink salmon diets observed by Andrievskaya (1966) from a spring diet consisting mainly of amphipods to a more mixed diet also containing fish and euphausiids. Takeuchi (1972) found that some prey (particularly euphausiids, copepods, and pteropods) of adult pink salmon showed substantial variation from April to July in the Northwest Pacific. Diel changes in food composition were pronounced for pink salmon caught in one location over a 24 h period (Pearcy et al. 1984). Euphausiids were most important during nighttime while squid were important only in the evening hours. Fish and amphipods were a major food shortly after sunrise.

Selectivity

Pink salmon appear to be mostly nonselective feeders based on the geographic covariation in their food habits and major prey distributions (Takeuchi 1972). Pearcy et al. (1988) noted few similarities between the diet of adult pink salmon and midwater trawl catches especially in the case of cephalopods, which were seldom found in the trawl catches, and gelatinous zooplankton, which were rarely identified in the stomachs.

Daily ration and feeding intensity

The greatest number of full stomachs observed during the diel cycle occurred at night and in the early morning but some empty stomachs were present at all sampling times (Pearcy et al. 1984). Pearcy et al. (1988) and Kanno and Hamai (1972) generally found fuller stomachs in pink salmon collected offshore, which coincided with an increased reliance on squid in their diet. Ito (1964) also found interannual variations in stomach fullness, which he attributed to increased consumption of squid during the better feeding years. Feeding also declined in general during the winter months in the Northeast Pacific (Manzer 1968).

MATURE COASTAL PHASE

General food habits

Pink salmon adults in coastal waters are known to eat a variety of food items with euphausiids, amphipods and fishes being of primary importance and squid, copepods, pteropods and decapod larvae of generally less importance.

Geographic variability

The pelagic gastropod, *Limacina*, was the dominant food overall in the limited number (n=9 with food) of pink stomachs analyzed by Brodeur et al. (1987a) off Washington and Oregon. Fresh et al. (1981) reported that four adult pink stomachs collected off the Columbia River contained mainly northern anchovy and crab larvae.

Off Vancouver Island, British Columbia, pink salmon adults consumed mainly euphausiids, amphipods and fishes (Beacham 1986). Smaller individuals ate more herring while larger individuals ate proportionally more crab larvae. Although little quantitative data are given, Wing (1985) provides species lists of prey items found in troll-caught pink salmon off Southeast Alaska. Myctophids and juvenile walleye pollock were the most common fish species represented. Euphausiids, decapod larvae and pteropods were the most frequently encountered invertebrate prey. There appears to be no other information on the diet of pink salmon adults in Alaskan waters.

Many studies have examined adult pink salmon food habits in the Western North Pacific. The diets of pink adults collected off the Kuril Islands consisted of young fish, hyperiids (*Themisto*), crab larvae and euphausiids with insects and mysids becoming more important closer to shore (Pushkareva 1951, Snykova 1951, Andrievskaya 1958). Pink salmon collected in marine bays off Kamchatka by Snykova consume almost exclusively (80-92 % by weight) small fishes, notably sand lance, capelin, cottids and agonids. Hyperiid amphipods, followed by fish and decapod larvae, were the main food item of pinks collected on both coasts of the Kamchatka Peninsula (Allen and Aron 1958). Gorbatenko and Chuchukalo (1989) found nekton (walleye pollock, capelin, sand lance and squid) to be the predominant food of trawl-caught pink salmon adults in the Okhotsk Sea. In the Sea of Japan, Fukataki (1967) found that hyperiid amphipods (mainly *Themisto*) and euphausiids (*Thysanoessa longipes*) comprised over 80% of the diet of adult pinks collected offshore. Fishes, copepods and pteropods were rare in these stomachs while squid and decapod larvae were important in some months.

Temporal variability

The amount of data on interannual variations in adult pink salmon diets is very limited since most studies have samples from only one or two years. Puskareva (1951) sampled the same area during two consecutive years and found young fish to be of greater importance the first year and mysids and insects to be more important the second year. The diet varied greatly even among four consecutive 10 day periods in the same year. Similar intraseasonal variation was found by Fukutaki (1967) for 10 day periods from the beginning of March through the end of May. The diet progressed from consisting mainly of hyperiids in March to a more mixed situation containing hyperiids, euphausiids and squid. When Fukataki (1967) compared this study done in 1965 to previous work done in 1959 and 1960, he found remarkably few interannual differences in frequency of occurrence of the dominant prey taxa. Diel differences in prey composition of adult pink salmon were examined by Shimazaki and Mishima (1969). They found that amphipods and squid tended to be consumed before sunset or during nighttime but feeding on fish larvae tended to be spread out over several parts of the day.

Selectivity

Few studies have directly examined the relationship between the prey consumed by adult pink salmon and those available to them. Beacham (1986) has shown that pink salmon generally consume larger prey than sockeye but smaller prey than coho or chinook salmon, which agrees well with morphological differences. There appeared to be a close correspondence between the diel cycle of prey composition of adult pink salmon and the composition of plankton nets towed close to the surface, particularly with respect to hyperiid amphipods (Shimazaki and Mishima 1969).

Daily ration and feeding intensity

Several studies have reported a reduction in feeding intensity of adult pink salmon associated with maturation and spawning (Pushkareva 1951, Fukataki 1967). Shimazaki and Mishima (1969) found a distinct diel periodicity in pink salmon feeding intensity at two stations in the Okhotsk Sea. Both the percentage of stomachs containing food and the absolute amount of food in the stomachs was highest after sunset, although they found a second peak in feeding intensity in the late morning was found at one station. Pre-spawning pink salmon (40-55 cm) were estimated to consume between 5.8 and 6.4% of the body weight per day by three different methods employed by Gorbatenko and Chuchukalo (1989).

COHO SALMON

JUVENILE COASTAL PHASE

General food habits

Juvenile coho salmon are relatively large when they enter coastal waters and consume a mixed diet of fishes and several invertebrate taxa, including euphausiids, decapod larvae, hyperiid amphipods, pteropods, insects, and calanoid copepods.

Geographic variability

The diet of juvenile coho had been examined in several studies off Oregon and Washington. Peterson et al. (1982) found that fishes, mainly sand lance and rockfishes (*Sebastes* spp.), euphausiids, and hyperiid amphipods comprised the bulk of food consumed by juvenile coho (94-134 mm) off Oregon. Emmett et al. (1986) examined coho collected near the mouth of the Columbia River and also found these same three major prey taxa along with pteropods to be important foods. A high diversity of prey taxa were identified from juvenile coho collected over a six year period by Brodeur and Pearcy (1990) but the dominant prey by weight (72 %) were larval and juvenile fishes (sand lance, rockfishes and northern anchovy). The diets were relatively similar among the three latitudinal and inshore-offshore subareas examined.

In Georgia Strait, British Columbia, juvenile coho consumed mainly fish, amphipods and crab megalopae by volume, but there were substantial regional differences (Healey 1980). Crab larvae and fish decreased in importance and amphipods and most other invertebrates increased in importance toward the northern part of the strait. Manzer (1969) found coho to be primarily piscivorous in Chatham Sound, consuming mainly sand lance and herring larvae.

Off Southeast Alaska, coho fed almost entirely upon fish (sand lance, rockfishes and gadids), with decapod larvae, euphausiids, and hyperiids of minor importance (Jaenike et al. 1984, Landingham and Mothershead MS). Decapod larvae were relatively more important inshore whereas euphausiids were most important offshore.

Little is known about the feeding habits of coho juveniles in coastal waters of the Northern Gulf of Alaska and Eastern Bering Sea. Craig (1987) examined 26 coho stomachs collected from various locations in the Bering Sea and found fishes (mainly sand lance) to be the only important prey item. In the Western Bering Sea, coho juveniles consumed primarily juvenile greenlings, whereas in the Sea of Okhotsk, they consumed other fishes (walleye pollock and sand lance) and hyperiids (Andrievskaya 1968). A greater variety of prey were identified from coho stomachs collected during other studies in the Sea of Okhotsk and off the Kamchatka Peninsula (Andrievskaya 1970, Karpenko 1980, Gorbatenko and Chuchukalo 1989). Squid, crab larvae,

fish, mysids and amphipods were among the major prey identified in these studies. Hyperiid (mainly *Themisto japonica*) and squid were much more important to fish captured farther offshore, comprising over 90% of the diet of these fish (Andrievskaya 1968, 1970).

Temporal variability

Juvenile coho diets varied markedly on a seasonal and interannual basis off Washington and Oregon. Their diets consisted primarily of fishes early in the summer (May-June) and then switched to predominantly invertebrates (hyperiid, euphausiid, and pteropods) by later in the summer (Emmett et al. 1986). Although a similar pattern emerged in the study by Brodeur and Pearcy (1990), fish were also important gravimetrically but not numerically in September because of the consumption of several large northern anchovy juveniles. Variability was great among the 15 cruises examined, which was due to both seasonal and yearly differences in prey availability. Fish, however, made up over half the diet in all but two cruises, when pteropods (July 1981) and insects (July 1984) were the main foods. This latter occurrence was due to anomalous offshore wind patterns that occurred that month (Brodeur et al. 1987b, Brodeur 1989). Diets varied greatly on an interannual basis due to anomalous oceanographic conditions (Pearcy et al. 1985, Brodeur and Pearcy 1990) but did not follow any consistent pattern on a diel basis (Peterson et al. 1982).

Healey (1980) found some interannual differences in the diets of coho in Georgia Strait that paralleled those found in other species of juvenile salmon, reflecting somewhat the overall changes in prey availability. Temporal variations in feeding appear to have been poorly studied throughout the remainder of the distribution of coho salmon.

Selectivity

Most studies suggest that juvenile coho are mostly opportunistic feeders, consuming mainly the most abundant prey available. Peterson et al. (1982), however, suggest that coho consume hyperiid more and copepods less than would be expected based on their abundances. These authors attribute this apparent selection to the higher visibility and activity levels of hyperiid. There was an overall resemblance between the diets of juvenile coho and the catches of neuston nets, suggesting that coho forage mainly in surface waters (Brodeur et al. 1987b, Brodeur 1989). Large prey (crab megalops, euphausiid, most fish) appeared to be preferred over smaller prey (mostly small insects and copepods) by juvenile coho (Brodeur et al. 1987b). There was a significant relationship between the size of fish and euphausiid prey consumed and coho predator size, but there were substantial differences in prey size consumed by year and month of collection (Peterson et al. 1982, Brodeur 1990a).

Juvenile coho off Alaska show a strong preference for euphausiid and fish and decapod larvae and an avoidance of copepod prey (Landingham and Mothershead MS). Healey (1980) also suggests that coho prefer euphausiid over most other available prey.

Daily ration and feeding intensity

Juvenile coho caught off Oregon showed a bimodal diel feeding cycle, with peaks occurring during the crepuscular periods (Brodeur and Pearcy 1987). These authors estimated the daily ration of coho to be between 2.4 and 3.7 % BW, depending on fish size and temperature. Brodeur (1990b) examined a number of factors that may influence the feeding success of juvenile coho and found that the feeding intensity was affected by year and month (but not area) of collection but was generally not related to environmental or food availability indices. Healey (1980, 1982b) found stomach fullness to be positively related to coho abundance, suggesting that they congregate in good feeding areas.

MATURING OCEANIC PHASE

General food habits

Coho salmon collected in oceanic waters consume mainly fish and squid although other prey, such as euphausiids, amphipods and pteropods, may be important, particularly in fish collected closer to the continental shelves.

Geographic variability

Adult coho collected offshore in the coastal domain of the Eastern North Pacific fed upon a variety of foods including euphausiids, fishes, squid and decapods, but the diet consisted chiefly of squid further offshore (LeBrasseur 1966, Manzer 1968). Percy et al. (1988) examined coho collected in gill nets during six years along North-South and East-West transects in the Gulf of Alaska and Central North Pacific. They found gonatid squid to be the dominant prey in the Subarctic Current region but diets were more mixed with the addition of euphausiids and myctophid fishes in the Alaska Current and Ridge Domain along the North-South transects. Few trends were apparent along the longitudinal transects with various squid, fish and euphausiids the dominant foods at different stations.

In the Western North Pacific, squid, fish and euphausiids comprised the majority of the diet of coho caught in the mothership fishery, but the relative proportions of each varied greatly by location of catch (Maeda 1954, Ito 1964, Machidori 1972). North of 50 °N, euphausiids and, to a lesser extent myctophid fishes, were the dominant food items recorded whereas squid were almost exclusively consumed in more southern waters.

Temporal variability

Ito (1964) reported that the proportion of the diet consisting of squid varied from 4.5% to 93% during the seven years of his study although in all but one year they made up over half the diet. A seasonal shift in the diet from euphausiids in early July to squid in late July and August may have occurred, but these differences may be confounded by geographic changes in sampling.

Between years in which the same locations were sampled, Percy et al. (1988) found some notable differences in prey consumption by adult coho. Euphausiids appeared to be particularly variable being important prey in some years (e.g., 1982) but not others (1983) whereas fishes exhibited the opposite pattern.

Selectivity

Percy et al. (1988) observed that the species composition of midwater fishes in the diets of coho and midwater trawls differed substantially. They suggest that many salmon, including coho, feed on organisms that reside in deep (> 150-200 m) water during the day and on neustonic organisms at night.

Daily ration and feeding intensity

Coho salmon collected in gill nets over a 24 h period consumed mainly euphausiids at night in surface waters and squid during the day when coho occurred in deeper waters (Percy et al. 1984). Stomach fullness was highly variable over the diel period but a gradual increase in food was observed during the night although few coho were caught in daylight hours. In general, Percy et al. (1988) found a lower percentage of empty stomachs and a higher overall feeding intensity with increasing distance offshore which could be attributed mainly to the increased consumption of large squid offshore.

MATURE COASTAL PHASE

General food habits

About half the diet of adult coho consists of various fish species, with euphausiids, crab larvae, amphipods and squid making up the majority of the remaining diet.

Geographic variability

Euphausiids were by far the dominant food of coho salmon collected in the commercial squid fishery in Monterey Bay off central California (Morejohn et al. 1978). Off southern Washington and Oregon, adult coho consume mainly fishes (herring, northern anchovy, smelt, and rockfishes) and, to a lesser extent, euphausiids and crab megalopae (Heg and Van Hynning 1951, Reimers 1964, Fresh et al. 1981, Brodeur et al. 1987a).

Off northern Washington and British Columbia, euphausiids and other species of fish (i.e., sardines and sand lance) become more important while anchovy and crab larvae diminish in importance to the diet of coho adults (Chapman 1936, Silliman 1941, Pritchard and Tester 1944, Prakash 1962, Beacham 1986, Brodeur et al. 1987a). Regional differences in diets were observed by Prakash (1962) who found herring to comprise the bulk of troll-caught coho diets on the outer coast of Vancouver Island whereas euphausiids and decapod larvae were important in Georgia Strait.

In the inland and coastal waters of Southeast Alaska, fish were the dominant prey consumed by troll-caught coho, including herring, sand lance, prowlfish, sablefish, capelin and rockfishes (Reid 1961, Wing 1985). Euphausiids, crab larvae and amphipods were secondarily important in these studies. Off Kamchatka, adult coho consumed mainly juvenile fish (mainly walleye pollock) but also ate crab larvae, hyperiids, euphausiids, squid and, to a lesser extent, copepods (Snykova 1951, Andrievskaya 1957).

Temporal variability

Adult coho display substantial temporal variations in their diet on both a seasonal and interannual basis. Off British Columbia, Pritchard and Tester (1944) found the species composition of fishes consumed to change greatly during the three years of their study although the invertebrate prey were not as variable. Prakash (1962) showed seasonal differences in the diet of troll-caught coho but the same patterns were not evident in both areas examined.

Off Oregon and Washington, fish generally become more important and euphausiids and decapod larvae become less important in the diet of adult coho salmon toward the latter part of the summer (Heg and Van Hynning 1951, Reimers 1964, Brodeur et al. 1987a). Crab larvae tend to peak in importance in June and become scarce in the diet by September when most of the species settle out to a benthic habitat. The dominant food items of adult coho often varied during different years probably as a result of highly variable oceanographic conditions affecting prey abundances (Brodeur et al. 1987a, Brodeur 1990b). Euphausiids tended to be more important during strong upwelling years and decapod larvae were more important during weak upwelling years. A high diversity of prey was encountered during an anomalous El Niño event, including many species not found normally in the diet of coho (Brodeur 1990b).

Interannual differences were less pronounced than regional differences in the stomachs examined off Alaska by Reid (1961), but the importance of prey was based only on their frequency

of occurrence. Finally, Wing (1985) also reported some unusual occurrences of prey (saury, squid) in coho stomachs during an unusually warm year.

Selectivity

Most researchers tend to agree that coho are highly opportunistic feeders consuming prey of a wide size range that may be available in near surface waters (Heg and Van Hying 1951, Reimers 1964, Brodeur et al. 1987a). They generally exploit either the most abundant prey available or prey that are highly aggregated as the stomachs frequently contain only one or two prey items (Brodeur 1989, pers. obs.). The size of both fish and invertebrate prey tended to increase with increasing coho predator size (Beacham 1986).

Daily ration and feeding intensity

Nothing is known about the daily ration of adult coho salmon in coastal waters. Prakash and Milne (1958) suggested that the differences in growth rate and size of return as adult coho between those returning in the Georgia Strait and those on the west coast of Vancouver Island were probably related to differences in type and overall food consumption between these fish. They observed that adult coho on the west coast ate mainly fish and had stomach volumes over twice that of fish collected on the east coast. They also observed that peak feeding occurred much later in the year in the west coast fish.

CHINOOK SALMON

JUVENILE COASTAL PHASE

General food habits

Juvenile chinook salmon are predominantly piscivorous in coastal waters. Other important prey taxa besides fishes include euphausiids, hyperiid amphipods, cephalopods, copepods, and pteropods.

Geographic variability

Juvenile chinook salmon collected off Oregon and southern Washington consumed large numbers of euphausiids, crab larvae and amphipods, but almost half their diet by weight was made up of fish (Peterson et al. 1982, Emmett et al. 1986). The dominant fish taxa consumed by chinook included northern anchovy, rockfishes, sand lance, and juvenile cottids, but their importance varied by geographical regions off Washington and Oregon (Brodeur and Percy 1990). Geographic (both cross-shelf and latitudinal) variations in major prey consumed were not important.

Similar patterns were observed by Healey (1980) in Georgia Strait, British Columbia, where fish (mainly herring) were the dominant food of juvenile chinook, followed by crab megalops, amphipods, euphausiids and insects. Fish were much less important to chinook collected further north in the strait. Although euphausiids were most important numerically, fish comprised over 99% of the stomach contents by weight off Southeast Alaska (Landingham and Mothershead MS).

Little information exists on the food habits of chinook throughout much of the rest of their geographic range in the North Pacific. Snykova (1951) reported that juvenile chinook fed upon copepods, euphausiids, amphipods and osmerid larvae in marine waters. Off Kamchatka, Karpenko (1980) found that chinook juveniles consumed mainly adult insects and mysids, although fish and crab larvae were also important. Finally, Gorbatenko and Chuchukalo (1989) found squid and small fishes to be the major food of juvenile chinook caught in the Okhotsk Sea.

Temporal variability

Emmett et al. (1986) documented both a change in major taxa and individual species consumed by juvenile chinook from late May through early September. There was a general decrease in the proportion of the diet made up of fishes and an increase in decapod larvae and hyperiids. Somewhat similar trends were observed by Brodeur and Percy (1990), although both seasonal and interannual differences were not all that striking. Healey (1980) reported distinct interannual differences in chinook diets in Georgia Strait over a two-year period.

Selectivity

According to Healey (1980), chinook prefer fish (especially herring) but will consume larger invertebrates (amphipods, crab larvae, and euphausiids) when these become available. Juvenile chinook in enclosures feeding on natural prey assemblages fed mainly on the larger and more visually contrasting prey taxa (English 1983). Although juvenile chinook consumed many of the dominant organisms found in neuston samples collected in the same general area, they did not show as much similarity in species composition overall as found for juvenile coho (Brodeur 1989). Chinook consumed prey between 5 and 40% of their body length during their first summer in the ocean and there was a significant relationship between prey size and predator size (Brodeur 1990a).

Daily ration and feeding intensity

No studies are available that document the diel feeding cycle or estimate daily ration of juvenile chinook salmon in the coastal environment. Healey (1980, 1982b) reported that a significant relationship existed between chinook feeding success and overall abundance, suggesting that they aggregate in high density food patches. The feeding success of chinook juveniles off Washington and Oregon was related to the geographic area but not to the year or month of capture (Brodeur 1990b). Although there was some relationship between feeding intensity and several environmental variables measured at the time of collection, most of these relationships were insignificant.

MATURING OCEANIC PHASE

General food habits

The diet of chinook salmon on the high seas consists mainly of squid and, to a lesser extent, fish, euphausiids and pteropods.

Geographic variability

Only a few studies have examined the diet of chinook salmon in the pelagic regions of the North Pacific Ocean and the number of fish examined in these studies is generally low. Hence, these results should be considered tentative pending more research. Maeda (1954) and Ito (1964) examined stomach contents of chinook salmon captured in the driftnet fishery in the Western North Pacific and found that they consumed mainly squid (*Gonatus*), but would occasionally eat fish (laternfish, saury, and walleye pollock) and euphausiids. In the Eastern North Pacific, Percy et al. (1988) observed that adult chinook also consumed mostly gonatid squid but at some stations, euphausiids and midwater fish were also important.

Temporal variability

The proportion of the diet made up of squid varied among the four years examined in the study by Ito (1964) from 87.5% in 1958, 98.6% in 1960, 73.4% in 1962, and only 23.3% in 1963.

Selectivity

Ito (1964) observed that the larvae of one species of squid (*Gonatopsis borealis*), which were extremely abundant in plankton sampling, was not observed in chinook salmon diets. Euphausiids were important in the diet of chinook only at the stations where they were the major food of other salmonids (Pearcy et al. 1988), suggesting that chinook consume euphausiids opportunistically.

Daily ration and feeding intensity

No data are available on daily ration or variations in feeding intensity of chinook salmon in the open ocean.

MATURE COASTAL PHASE

General food habits

The diet of adult chinook salmon in coastal waters consists primarily of various fish taxa, but they will also consume euphausiids, decapod larvae and cephalopods.

Geographic variability

In contrast to the open ocean phase, the food habits of chinook salmon in coastal waters have been extensively studied throughout much of their range. Merkel (1957) examined over 1000 adult chinook salmon stomachs collected by sport fishing party boats in the vicinity of San Francisco Bay. Northern anchovy and rockfishes comprised over half the diet. Euphausiids, squid, herring and other fishes contributed the bulk of the remaining diet. The main fish prey varied according to location and depth of capture. Rockfishes and herring were most important offshore but northern anchovy were predominant inshore. Adams et al. (MS) found similar results in chinook adults collected from the same general area but found that the main prey varied between inshore (herring and northern anchovy) and offshore (rockfishes and euphausiids) areas of collection.

The study of Chapman (1936) was probably the first of many to examine the diets of chinook salmon off British Columbia, Washington and Oregon. He found that the diet of both purse seine and troll-caught chinook consisted mainly of sardines (*Sardinops caerulea*) but herring and euphausiids were also important in the stomachs of fish caught by purse seine. Silliman (1941) found that sardines, herring, anchovies, and euphausiids were the main foods of chinook caught in the commercial troll fishery off Washington and Vancouver Island. Pritchard and Tester (1944) studied the diets of troll-caught chinook over much of the marine waters of British Columbia. They reported that herring, sardines and sand lance were the dominant food items overall but euphausiids were also important near Barkley Sound on the outer coast of Vancouver Island. Off the Oregon Coast, fishes (mostly herring and anchovies) made up the bulk of the diet of troll- and sport-caught chinook with euphausiids of minor importance (Heg and Van Hyning 1951). Although euphausiids were important in some areas during certain months, the diet of troll-caught chinook collected on the east and west coast of Vancouver Island consisted mainly of herring and sand lance (Prakash 1962).

In more recent studies, Fresh et al. (1981) found sport-caught chinook at the mouth of the Columbia River were feeding mainly on northern anchovy and smelt by weight. Sand lance, herring and rockfish were the dominant fish prey and euphausiids the dominant invertebrate prey of troll-caught chinook collected off southern Vancouver Island (Beacham 1986). Brodeur et al. (1987a) described the food habits of adult chinook collected in purse seines off Washington and Oregon. Although many prey taxa were identified, the bulk of the diet consisted of herring and

northern anchovy by weight and euphausiids and crab larvae by number. Euphausiids were particularly important off the Washington coast.

In the inland and coastal waters of Southeast Alaska, Reid (1961) found herring to be the most common prey of troll-caught chinook but sand lance, capelin and squid were also important in some areas. Wing (1985) reported on the prey identified in troll-caught chinook off Southeast Alaska. Although herring and sand lance were the most common fish prey identified, numerous other fish and invertebrate (especially squid and euphausiids) species were identified.

Information on adult chinook feeding in the remainder of the North Pacific is limited. Andrievskaya (1957) reported on a limited number (17) stomachs of chinook collected off Kamchatka and found them to contain juvenile fishes, squid, amphipods, euphausiids and crab larvae, but no quantitative information is provided. Chinook collected off the Kuril Islands consumed mainly lanternfish and squid (Mishima and Tokusa 1977).

Temporal variability

Several studies have examined the seasonal cycle of feeding in adult chinook salmon. Prakash (1962) found a shift in the diets of chinook caught off Vancouver from eating mostly euphausiids and sand lance in May and June to mostly herring and other fishes from July through September. Merkel (1957) found herring, rockfishes and northern anchovy to be the dominant prey throughout much of the year but euphausiids, crab larvae and squid were important during the spring (March through June). Similar results were reported by Brodeur et al. (1987a) who found that the proportion of invertebrate prey decreased from May through September. The seasonal change in chinook diets appears to be related to seasonal inshore-offshore movements of individuals (Silliman 1941, Prakash 1962, Adams et al. MS).

Interannual differences in adult chinook diets are generally less pronounced than seasonal ones. Reid (1961) found the occurrences of fish prey to be similar over both years of sampling but the occurrence of squid and shrimp differed substantially. Pritchard and Tester (1944) found similar volume proportions of prey overall during three years of study, but when examined by geographic area, the importance of some prey (e.g., sardines, sand lance and euphausiids) fluctuated greatly. Fish were the dominant prey during all years of sampling in the study by Brodeur et al. (1987a) but the importance of individual fish, euphausiid and decapod species varied greatly among the six years of their study. Adams et al. (MS) noted a major disruption in the normal feeding cycle of chinook adults during the El Niño year of 1983 when several of their normal prey (anchovy, rockfishes and euphausiids) were unavailable.

Selectivity

Chinook salmon tend to consume the largest prey available in comparison to other salmon species, which may be related to the morphological differences between species but also may be related to differing depth distributions (Beacham 1986). The dominant food items found in the stomachs of chinook were also the same that dominated the catch of pelagic trawls off Central California (Adams et al. MS).

Daily ration and feeding intensity

The diel feeding cycle of adult chinook has not been examined in any detail. In regard to feeding intensity, Prakash (1962) found larger quantities of food on the west coast of Vancouver Island compared to the Strait of Georgia but that feeding peaked in August in both areas. The decline later in the summer could probably be attributed to cessation of feeding in sexually mature fishes preparing to spawn. Merkel (1957) also found the highest feeding intensity in chinook

preparing to spawn but still residing in the ocean while almost no feeding occurred once they reached San Francisco Bay.

MASU SALMON

JUVENILE COASTAL PHASE

General food habits

Juvenile masu salmon enter the ocean at a relatively large size (12-20 cm) and feed mostly on young fishes and squid with some contribution from euphausiids, copepods, amphipods, and insects.

Geographic variability

In coastal waters off Honshu Island, Japan, Kiso and Takeuchi (1985) found juvenile masu fed upon mainly hyperiids (*Themisto japonica*), euphausiids and small fishes. Euphausiids were important only in the northern part of their study area. Off Sakhalin Island, young masu salmon consumed mainly crustaceans and insects and young fishes, such as Atka mackerel, sand lance, smelt and herring (Dvinin 1956, Semko 1956). Gorbatenko and Chuchukalo (1989) reported that masu collected off Sakhalin consumed many different species of fish and squid whereas off the West Kamchatkan shelf, they fed chiefly on walleye pollock and sand lance.

Temporal variability

Little information is available on temporal variations in the diet of juvenile masu salmon. Tanaka (1965) summarizes some seasonal sampling carried out off the west coast of Hokkaido, which showed that masu consumed mainly amphipods and euphausiids in April but switched to mainly fish and squid in May when these prey became available.

Selectivity

Tanaka (1965) suggests that masu will feed on whatever small fish are available but will switch to large planktonic crustaceans when fish are unavailable.

Daily ration and feeding intensity

No data are available on either daily ration or variations in feeding intensity of juvenile masu in coastal waters.

MATURING OCEANIC AND MATURE COASTAL PHASES

General food habits

Masu salmon do not migrate very far into open waters of the North Pacific Ocean but instead are found mainly in coastal seas such as the Sea of Japan. Here, masu salmon appear to feed mainly upon small nekton (fish and squid) and large zooplankton (euphausiids and hyperiids) with some minor consumption of copepods and decapod larvae.

Geographic variability

Some regional variation in the types of prey consumed by adult masu are described by Machidori and Kato (1984). Hyperiid amphipods were the dominant food eaten by masu in the southern Sea of Japan and were replaced by euphausiids (mainly *Thysanoessa longipes*) further north. Copepods were also consumed off Sakhalin. Fish species composition also varies depending on area of capture. In the open waters of the Sea of Japan, the main fish species consumed were Atka mackerel and the Japanese pearlside. In coastal waters, adult masu fed mainly upon sand lance and anchovies. Adult masu in coastal waters of Sakhalin consumed many

of these same species but also herring and saury (Dvinin 1956). Off the Kamchatkan coast, capelin and saffron cod were the main components of adult masu diets (Semko 1956).

Temporal variability

Seasonally, the diets of adult masu collected offshore in the Sea of Japan varied substantially from being comprised mainly of hyperiids in early March to a more varied diet of fishes, squid and euphausiids by late May and early June (Fukutaki 1969). The dominant fish species also varied by season in that Japanese pearlides and sandfish were important only up to the end of April and Atka mackerel became dominant only after this time.

Selectivity

Machidori and Kato (1984), in comparing the diets of pink and masu salmon caught together, suggest that masu consume fish preferentially over zooplankton, and will generally eat the latter when fish are unavailable.

Daily ration and feeding intensity

No information is available on these subjects for adult masu salmon.

STEELHEAD

JUVENILE COASTAL PHASE

General food habits

In contrast to all other salmonids in the North Pacific, juvenile steelhead apparently spend little time in coastal waters and migrate directly offshore to the open ocean. While migrating through coastal waters, they consume mainly fishes and euphausiids, with some contribution by smaller crustaceans.

Geographic variability

In the only detailed study to date that analyzed the marine food of juvenile steelhead, Percy et al. (1990) found many types of fishes (mainly juvenile rockfishes) and euphausiids to be important prey by weight, although decapod and barnacle larvae and hyperiid amphipods were important numerically. Virtually nothing is known about the diet of juvenile steelhead originating from the Asian continent.

Temporal variability

Euphausiids tend to dominate the diet of steelhead when they are abundant (such as in strong upwelling years) while fishes tend to dominate in other years (Brodeur 1990b).

Selectivity

The occurrence of insects, barnacle larvae, and some fish taxa associated with the neustonic layer in the diet of juvenile steelhead suggests that this species forages to some extent in the surface layer on large or heavily-pigmented organisms (Brodeur 1989). There was no relationship between predator size and size of fish prey consumed by juvenile steelhead (Percy et al. 1990).

Daily ration and feeding intensity

Nothing is known about the daily ration or variations in feeding intensity of juvenile steelhead.

MATURING OCEANIC AND MATURE COASTAL PHASES

General food habits

Steelhead trout consume mainly large nekton, such as fish and squid, but will also eat euphausiids, amphipods, pteropods, and pelagic polychaetes.

Geographic variability

Taylor and LeBrasseur (1957) examined steelhead stomachs collected primarily in the eastern half of the Gulf of Alaska and found them to contain mostly (63% by volume) fish and squid (31%), with shrimp and amphipods of minor importance. Manzer (1968) reported that the stomach contents of four steelhead collected in open waters of the North Pacific off Washington and Oregon contained mostly cephalopods (81% by volume) and fish (10%). Lebrasseur (1966) stratified his collections of steelhead according to oceanic domains. Fishes were the dominant food in the coastal domain, squid were most important in the Subarctic domain, and a more mixed diet was found in transitional waters. Amphipods were the only other prey that occurred frequently.

In the most detailed study of adult steelhead trout food habits to date, Light (1985) examined over 600 stomachs collected during two years in the Gulf of Alaska and western North Pacific. The main components of the diet by weight were fish, squid, polychaetes and crustaceans. Fishes were dominant in the Alaskan stream close to the coastal zone and during one year of sampling in the Western Subarctic. Cephalopods were dominant in all other areas of sampling. Hyperiid and polychaetes were important numerically in some areas. The majority of fish identified were Atka mackerel although sticklebacks and laternfish were occasionally important. The squid were mainly gonatids, especially *Berriteuthis magister*.

Pearcy et al. (1988) examined steelhead stomachs taken in gillnet collections from three years of north-south transects and one year along an east-west transect in the Gulf of Alaska. The major foods identified in this study included fish, squid, euphausiids, amphipods and polychaetes. In general, squid increase and fish and polychaetes decrease in importance with decreasing latitude along one transect. The change in diet was quite abrupt when crossing the Subarctic Boundary. Few consistent patterns emerged in the east-west transect but there was a shift from euphausiids being an important prey in the western gulf and amphipods being important in the eastern gulf.

In one of the few studies to examine adult steelhead diets in coastal waters, Fresh et al. (1981) found that almost all the food items identified were fishes, including northern anchovy, chinook salmon and smelt. Crab larvae was the only invertebrate prey identified.

Temporal variability

Light (1985) found major changes in steelhead diets in collections from the same area (Western Subarctic Domain) taken during two years. Squid were predominant (92% by weight) the first year whereas fishes made up the bulk (> 68%) of the diet the second year. In the two years sampling along 145 °W by Pearcy et al. (1988), squid became more important above and fish below the Subarctic Boundary during the second year.

Selectivity

The diets of steelhead trout caught in open waters of the North Pacific more closely resembled the composition of neuston rather than oblique midwater hauls, suggesting to Pearcy et al. (1988) that they forage at the surface at night. Steelhead apparently seek out actively swimming and

visually contrasting nekton and do not consume gelatinous zooplankton, which often makes up the majority of the plankton biomass.

Daily ration and feeding intensity

Light (1985) found that steelhead stomach fullness as a percentage of the total body weight peaked in June. Stomach fullness was also highest in the more oceanic waters of the Central and Western Subarctic and the Transitional regions and lower in the Gulf of Alaska and Alaska Stream regions. Pearcy et al. (1988) also generally found fuller stomachs and a higher percentage of stomachs containing food in the stomachs collected furthest from land, especially south of the Subarctic Boundary. There is no available information on the diel feeding or daily ration of adult steelhead in oceanic or coastal waters.

CUTTHROAT TROUT

ALL PHASES

General food habits

Since cutthroat trout spend generally only a few months at sea, they remain within the coastal zone throughout their marine existence but may migrate some distance from their river of origin (Pearcy et al. 1990). Fish caught at sea may be either juveniles, maturing adults or adults that had spawned at least once and have return to the ocean (Trotter 1989). These fish will be combined in the present analysis.

Sea-run cutthroat consume mainly fish in marine waters. In a study off the Columbia River, Loch and Miller (1988) found that almost 83% of the diet by weight of juvenile cutthroat was fishes, mainly northern anchovy and cabezon. Similarly, Pearcy et al. (1990) observed that cutthroat off Oregon and Washington were feeding mainly on fish (> 75 %) identified mostly as rockfish and hexagramid juveniles and northern anchovy. Euphausiids and decapod larvae were of secondary importance. Larger (> 300 mm) and presumably more mature cutthroat from the same collections consumed almost exclusively fish of the same taxa as the smaller individuals with the addition of juvenile salmon (Brodeur et al. 1987a).

Geographic variability

No data are available on geographic variations in cutthroat trout diets in marine waters.

Temporal variability

Brodeur (1990b) found different fish taxa to be important during three hydrographically different summers. Northern anchovies were most important during 1981, greenlings during 1982, and juvenile rockfish and sculpins during 1983.

Selectivity

Brodeur (1989) suggested that juvenile cutthroat may forage mainly in the neustonic layer based on similarities between the diet of cutthroat and neuston collections.

Daily ration and feeding intensity

No data are available on variations in feeding intensity or daily ration for cutthroat in coastal waters.

DIETARY OVERLAP

Researchers have observed for some time similarities in the diets of salmonids based on subjective groupings of food types. For instance, Maeda (1954) and Ito (1964) observed that the salmon species caught on the high seas fall into three general categories based on food type: 1) a coho-chinook group that feeds mainly on fish and squid, 2) a sockeye-pink group that consumes both nektonic and planktonic organisms, and 3) a chum group that consumes mainly crustacean and gelatinous zooplankton. In these, and many other studies that examined the diets of several co-occurring salmon, no attempt was made to quantitatively assess the degree of similarity or dissimilarity in the diets of these species.

Studies that measure diet overlap often have different objectives. The most common is to measure intraspecific overlap among sympatric salmonid species to understand potential competition among species. Another purpose might be to look at variations among collection sites, geographic areas or collection times by examining intraspecific overlap for a single or several species. Finally, diet overlap can be measured between salmon and other co-occurring species to examine potential competitive interactions and elucidate the position of salmon in a marine ecosystem. This latter type of study is extremely rare.

In this section, I will review studies that have attempted to measure diet overlap and will consider only studies that have compared the composition of food and not the similarity in overall amount of food eaten. The same three life history phases will be considered although, in some cases, this may be somewhat limiting since juvenile and adult salmon may often temporally and spatially co-occur in the coastal marine environment. In most studies, diet overlaps that exceed 60% are generally considered significant, and this convention will be followed here.

JUVENILE COASTAL PHASE

Several studies have examined diet overlap among two or more species of juvenile salmon along the coast of Oregon and Washington (Peterson et al. 1982, Emmett et al. 1986, Brodeur 1990b, Brodeur and Percy 1990, Percy et al. 1990). These studies show that juvenile coho and chinook salmon generally have the most similar diets of all the salmonids, although the degree of overlap can vary between years and months. Emmett et al. (1986) found overlaps between 71% and 91% for three cruises in one summer off the Columbia River. Brodeur and Percy (1990) found within-cruise diet overlap to vary between 20% and more than 80% for 15 cruises over a six year span, with an overall diet overlap of 54%. They found that diet overlap may often be higher between species at one station than within species at adjacent stations and suggested that juvenile salmon may be highly opportunistic, feeding on whatever prey were available at a particular time and place. Diet overlap between juveniles of these two species was generally higher than between either species and adult salmon and other associated species (Brodeur 1990b). Cutthroat trout showed substantial diet similarity with several other salmonid species during several years.

Healey (MS) examined in detail the diet overlap among juvenile chum, pink and sockeye salmon off Northern British Columbia. He found diet overlaps among the species to be high (64-100%) within a given year but much lower between years. An exception to this was chum salmon, which utilized the larvacean (*Oikopleura*) in both years of the study. Diets were most similar in replicate samples (most > 70%) and became more dissimilar with increasing time or distance between the collections. Landingham and Mothershed (MS) examined these same species with the

addition of juvenile coho salmon in coastal waters of British Columbia and Southeast Alaska with respect to temporal and geographic variations in diet overlap. Pink and sockeye juveniles showed the greatest similarity, followed by pink and chum, chum and sockeye, and finally coho combined with all other species. Diet overlaps were generally higher offshore than in coastal waters.

In the Okhotsk Sea, the food of pink and chum was most similar, particularly at collections away from the coastal zone, with the diet overlap exceeding 95% due to the common utilization of hyperiid amphipods (Andrievskaya 1970). Chum and sockeye exhibited the least similar diets. Karpenko (1980) found generally insignificant diet overlaps among pink, chum, coho and chinook salmon at different locations. The one significant overlap occurred between pink and chum salmon in one bay where both species preyed upon calanoid copepods.

MATURING OCEANIC PHASE

Diet overlap, using only the four dominant prey taxa, was highest (78%) between maturing sockeye and pink salmon and lowest between chum salmon and each of the other species (sockeye, pink and coho salmon) examined at one diel series of collections in the North Pacific (Percy et al. 1984). Similar findings were reported by Percy et al. (1988) for these same species (plus steelhead) from a large number of collections in the Gulf of Alaska and eastern North Pacific. They found the highest interspecific overlaps by cruise between steelhead and coho, sockeye and pink and between sockeye and coho salmon. Overlap was particularly high in one year when most species fed on squids. Chum salmon was generally an exception with low intraspecific overlap. Diet overlap within species but among stations was occasionally high, but was generally lower than among species at the same station, which may indicate generalized feeding patterns.

Light (1985) examined diet overlap among steelhead trout collected in different oceanographic domains and different months within the same domain. He found generally low diet overlaps among the domains but higher overlaps occurred between months in the same domains. This suggests that temporal variations in prey composition may be less than regional variations. Diet overlaps among chum, sockeye and pink adults in Bering Sea were analyzed by Kanno and Hamai (1972) who found the highest overlap (95%) between pink and sockeye and the lowest between chum and pink salmon.

MATURE COASTAL PHASE

Diet overlap among adult salmon has received little attention in coastal waters of the Eastern North Pacific. Brodeur (1990b) examined the overlap in diets of adult coho and chinook salmon and with juveniles of these species as well as other pelagic nekton and found highly variable results. During two years, adult coho and chinook salmon showed the highest overlap (71% and 73%) of all possible combinations of species and life history stages. Both species also showed high overlaps with juvenile and adult cutthroat trout during the first year and coho had high overlap with herring (*Clupea pallasii*) and black rockfish (*Sebastes melanops*) the second year. During two other years, diet overlap between coho and chinook was relatively low (28% and 37%), as was overlap between these two species and all other predators.

Andrievskaya (1957) examined diet overlap among pink, chum, sockeye and coho salmon during their pre-spawning migrations. She found the highest overlaps between sockeye and pink salmon and the lowest between coho and sockeye, but all values were insignificant. Diet overlaps among pink, chum and sockeye salmon were examined for two years and three seasons in later studies (Andrievskaya 1958, 1966). She found higher overlaps (47- 77%) among these species in one year than in the previous year (29-52%), but these differences could be attributed to different

levels of taxonomic detail to which the stomachs were examined during the two years. Diet overlap was generally higher during even years than during odd years over a period of seven years, with chum salmon showing the most variability between odd and even years (Andrievskaya 1966). Food similarity was the greatest in the summer (32-64%) and least in the autumn (13-61%).

RECOMMENDATIONS FOR FUTURE STUDIES

With the exception of a few geographic areas (i.e., coastal northern Gulf of Alaska and Bering Sea) and life history stages (pre-spawning adults of most species), we have available some data on the general food habits and variability in the diet with respect to year, season or geographic area of collection for most salmonid species. Based on the available data, it appears that most salmon species are fairly opportunistic in their feeding, with most temporal or areal differences within species resulting from variations in prey availability. Differences among species collected in the same area at the same time may reflect differences in swimming depth or minor morphological differences between species that may restrict the total availability of prey capable of being consumed (Beacham 1986, Brodeur 1989). Between-species differences in feeding behavior may be validated only by controlled laboratory experiments which are difficult, especially for adult fishes.

A number of researchers have noted much more unique food items and generally poor condition of stomach contents in chum salmon compared to the other salmonid species (Allen and Aron 1958, Ito 1964, LeBrasseur 1966, Percy et al. 1988). These differences may be the result of a morphological and physiological adaptation on the part of chum salmon to feed on organisms of relatively low trophic level at a continuous level throughout the diel period (Azuma 1989). The factors which differentiate chum feeding should be examined in detail

Future studies in salmon feeding ecology in the ocean should progress from the descriptive stage to the more analytical stage. We need to do rigorous studies of the diet selection with respect to available prey items and also the relationship between feeding success and various physical and biological parameters measured at the time of collection. Since salmon feeding appears to be so dynamic and variable in both spatial and temporal scales, specimens used in these studies should be selected from among those which have only recently fed. We need to determine the daily ration of most species of salmon and how this ration changes with age or physiological state of the individual and date or location of capture. Ambient temperature, predator size and food concentrations are likely to be important factors affecting the maximum ration size. The effects of varying ocean conditions on the diet and food consumption of salmon (Fulton and LeBrasseur 1985, Brodeur 1990b) is an area that will some increased attention in the coming years, particularly with the potential of large-scale global warming on the horizon.

Finally, it may be necessary to further study salmon in the context of the entire pelagic ecosystem since they seldom occur alone in most systems (Brodeur 1988, 1990b). We may gain some valuable insight from understanding predator-prey and competitive interactions among salmonids and between salmonids and other organisms in the pelagic ecosystem. Thus we may be in a better position to understand natural or anthropogenic changes in ecosystems and how these affect salmonid production.

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