FEEDING ECOLOGY OF JUVENILE PACIFIC SALMONIDS IN ESTUARIES: A REVIEW OF THE RECENT LITERATURE

Joseph M. Hiss
Fishery Management Biologist

Ralph S. Boomer
Project Leader

Fisheries Assistance Office
U.S. Fish and Wildlife Service
Olympia, Washington

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The purpose of this review is to synthesize the recent literature on the importance of estuarine areas as feeding grounds for juvenile Pacific salmonids. This review fulfills a contract with the U.S. Army Corps of Engineers, Seattle District, to provide background information for a proposed study of the impact of a beach nourishment project in the vicinity of Seattle, Washington. For this reason the review will emphasize research relevant to the nearshore marine waters of Puget Sound. Meyer's (1979) review of juvenile salmonid ecology in estuaries was chosen as a reference point because it too was compiled in response to proposed shoreline developments in the Seattle area.

Questions addressed here include: (1) At what time of the year are juvenile salmonids present in the inshore marine areas of Puget Sound and Hood Canal in western Washington? (2) What is their preferred habitat within this region? (3) At what time of year do these fish depend on epibenthic zooplankton for prey? (Epibenthic zooplankton can be defined as the fauna between 2mm and 0.2mm in size, which are associated with the surface of the bottom (Sibert, 1981).) (4) At what time of year is the epibenthos most available to the fish? (5) To what degree do juvenile salmonids selectively feed on certain components of the epibenthos? (6) What features of the habitat are favorable to epibenthic prey? (7) How long does it take for the epibenthic community to recolonize a disturbed habitat?

Types of Pacific Northwest Estuaries

In terms of salmonid feeding ecology, it is helpful to distinguish between two types of estuaries: river estuaries, and nearshore marine areas. River estuaries generally consist of distinct channels with relatively strong freshwater discharge and predominantly fine sediments. Nearshore marine areas display relatively weak influence of freshwater runoff and more variable substrate types.

While river estuaries are not the main concern of this review, recent studies will be listed here for the sake of completeness. Examples of this type of estuary are the lower Columbia River, Grays Harbor, and the deltas of the Nisqually and Skagit Rivers in Washington and the Fraser River delta in British Columbia. Typical food resources are those associated with brackish water and generally not available in other estuarine habitats. Examples are larvae, pupae, and adults of certain dipteran families, and cladocera (primarily *Daphnia* spp).

River estuaries that have been studied for juvenile salmonid feeding ecology or for epibenthic zooplankton include the Columbia River estuary (Jones and Herring, 1984; Simenstad, 1984), Grays Harbor (Cordell and Simenstad, 1981; Albright, 1977) and the Quillayute estuary of coastal Washington (Simenstad and Buechner, 1981), the Nisqually Delta (Pearce et al., 1982) and the Duwamish estuary of Puget Sound (Meyer et al., 1980b), and the Fraser River delta (Levy and Northcote, 1981) and Nanaimo estuary of British Columbia (Sibert, 1979).

Nearshore marine habitats are the principal subject of this review. They include most of the Hood Canal and Puget Sound shorelines, such as Nisqually Reach, Commencement Bay, Elliott Bay, and Port Gardner. Substrate ranges from mud to cobble. Attached algae may occur in the intertidal and subtidal zones. Some areas that have been studied for salmonid prey availability include Nisqually Reach (Fresh et al., 1979), Commencement Bay (Blaylock and Houghton, 1981; Meyer et al., 1980a), Elliott Bay (Weitkamp and Schadt, 1982), Port Gardner (Schadt and Weitkamp, 1985), Hood Canal (Simenstad, 1980), and the Straits of Juan de Fuca (Simenstad et al., 1980).

The salmonid feeding habitat in the nearshore marine area can be divided into the epibenthic and neritic zones. This distinction is important because certain species of juvenile salmonids make a gradual transition in their feeding habits from epibenthic to neritic prey. The epibenthic zone is typified by a distinct community of zooplankton, especially harpacticoid copepods and gammarid amphipods. This zone may extend several centimeters above the substrate, depending on turbulence and sediment type.

The neritic zone is characterized by the availability of zooplankton types that are not directly dependent on the benthic or epibenthic environment. These include calanoid copepods, larvaceans (primarily Oikopleura spp), marine species of cyclopoid copepod, hyperiid amphipods, and euphausiids.

Migrational Characteristics of Juvenile Salmonids

A synthesis of the reviews by Meyer (1979), Simenstad et al. (1982), and Healey (1982) suggests the following period of nearshore marine residence for juvenile salmon in British Columbia, Washington, and Oregon estuaries: Chum fry, chinook fry, chinook yearling smolts, coho smolts, pink fry, and sockeye smolts are most abundant in April, May, and June. However, chum may enter the estuary as early as February in some locations (Bax and Whitmus, 1980; Fresh et al., 1979). Sockeye fry are present mainly in June, July, and August. Chinook that migrate as subyearling smolts are most abundant in May, June, and July, but may persist until October in some systems.

Meyer's (1979) review of estuarine residence suggested that chum and chinook were the most estuary-oriented species. In contrast, data cited by Simenstad et al. (1982) suggests that the average estuarine residence time of most species of salmon is 11 or 12 weeks. Individual residence times ranged from 6 to 189 days for chinook, 4 to 32 days for chum, and 6 to 40 days for coho, depending on the location studied.

A more distinct difference between the species' estuarine dependence is indicated by their relative abundance in experimental beach seine and purse seine catches. Recent studies of juvenile salmonid abundance in Washington estuaries indicate that chum (Pearce et al., 1982; Bax and Whitmus, 1980; Meyer et al., 1985) or chinook (Meyer et al., 1980a, 1981; Weitkamp and Schadt, 1982) are usually most abundant in terms of catch per effort. Pink salmon may be about as abundant as chum or chinook in even-numbered years

Copepod larvae are sometimes an important prey item, but because they may be produced by either epibenthic or neritic-dwelling species they cannot be attributed to a particular zone.

Simenstad et al., (1982) reviewed prey spectra of juvenile salmonids in sixteen estuaries in Washington. He used the Index of Relative Importance for thirteen basic prey categories that encompassed brackish-water and neritic prey, as well as epibenthic prey. He generalized that juvenile chum prey consisted of epibenthic crustaceans (harpacticoid copepods, gammarid amphipods, and isopods) for smaller (less than 50-60mm long) fish collected in shallow water habitats. In salt marshes, emergent insects such as chironomids were eaten. The preferred prey in the shallow sublittoral zone was harpacticoids, especially Harpacticus spp. Larger chum gradually shifted their diet to include more prey of neritic origin.

Juvenile chinook fry and subyearling smolts in shallow water habitats preyed principally on emergent insects and epibenthic crustaceans such as gammarid amphipods, mysids, and cumaceans. Juvenile pink salmon fed almost exclusively upon neritic zooplankton (calanoid copepods, copepod nauplii, and larvaceans) even when these juvenile salmon were found in shallow sublittoral habitats. Juvenile coho fed primarily on large neritic zooplankton, although some epibenthic organisms, especially gammarids, were consumed. Healey's (1982) review of Canadian data generally agreed with Simenstad's, with the exception that pink fry captured in the Nanaimo River estuary had fed mainly on harpacticoids and amphipods.

Recent data from the Puget Sound area (Table 1) suggested that only harpacticoids, gammarids, cumaceans, and mysids were important epibenthic prey; isopods were virtually absent from the diets of juvenile salmonids. Chum clearly relied primarily on harpacticoids, and secondarily on gammarids, but to varying degrees depending on the location. Chinook foods were roughly similar to those of coho, but the absence of harpacticoids at all locations was not expected. Coho emphasized gammarids, to a surprising degree considering their reported reliance on neritic prey. Cumaceans and mysids were more important for this species of predator than for the others. Epibenthic foods made a surprisingly large contribution to the prey spectrum of pink salmon fry in contrast to the findings presented in previous reviews. However, this did not occur consistently among locations or between years. Harpacticoids were of primary importance, followed by gammarids.

Seasonal Change in Diet

Meyer (1979) described a shift in the diet of chum from epibenthic to neritic prey upon reaching a size of 50 to 80mm. This shift was well documented for a variety of areas, but the critical length varies considerably. On account of this, it was difficult to predict, on the basis of mean fish size, at what time during the season chum cease to rely primarily on the epibenthos.

Healey (1982) documented a seasonal food shift in chum at Nitinat Lake, British Columbia, from epibenthos (gammarids) and adult insects in April to cladocera in mid-May and June. He also described a similarly-timed, but more gradual decline in the importance of epibenthos in the diet of chinook.

Table 1. Epibenthic prey of four juvenile salmonid species in the shallow sublittoral zone of Puget sound and Hood Canal.

Species	Site (a)	Year	% Index of Relative Importance (b)			
			Harpacticoid	Gammarid	Cumacean	Mysid
Chum	HC	77-79	24	4	0	0
	NR	77	85	12	1	0
	NR	78	34	1	0	3
	EB	80	26	7	0	0
	Ev	80	22	41	5	0
Chinook	Ev	80	0	54	19	0
	NR	78	0	35	0	1
	EB	80	0	0	0	2
Pink	HC	78	5	0	0	0
	NR	78	47	0	1	8
	EB/Du	80	79	0	1	0
	Ev	80	26	36	4	0
Coho	NR	77	18	45	7	4
	NR	78	3	29	1	8

(a) HC = Hood Canal. Source: Simenstad, 1980.
NR = Nisqually Reach. Sources: Fresh et al., 1979; Pearce et al., 1982.
EB = Elliott Bay. Source: Weitkamp and Schadt, 1982.
Ev = Everett Harbor. Source: Schadt and Weitkamp, 1985.
Du = Duwamish River. Source: Meyer et al., 1980b; Weitkamp and Schadt, 1982.

(b) Percent of total index of relative importance; only data for epibenthic prey categories are presented here.

The data of Simenstad (1980) for Hood Canal and Fresh et al. (1979) for Nisqually Reach indicate the range in time during which the diet shift in chum and chinook may take place. Table 2 shows that importance of epibenthos for Nisqually Reach chum had declined greatly by the end of May, but that a similar decline did not occur until mid-June in Hood Canal. A shift from epibenthic to neritic prey over time was also documented for Nisqually Reach chinook. These fish continued to rely heavily on epibenthic prey until the end of May, after which time the prey was primarily of neritic origin.

Variability in Abundance of Epibenthos

Abundance of epibenthos may exhibit marked changes over a given season. Density and biomass have been reported to build to a peak in late March or mid-April in Hood Canal (Simenstad and Kinney, 1979), or early May in some British Columbia estuaries (Sibert, 1979). Thom et al. (1984) reported large seasonal fluctuations in central Puget Sound, reaching maximum values in early spring in one study year and early summer in another. According to the

Table 2. Seasonal changes in importance of epibenthic prey in the diet of Puget Sound and Hood Canal juvenile chum and chinook salmon.

Species	Location	% Contribution of Epibenthic Prey			
		March	April	May	June
Chum	Nisqually Reach(a)	89	65	14	4
Chinook	Nisqually Reach	(b)	81	63	2

Species	Location	April 20-May 19	May 20-June 19	June 20-July 19
Chum	Hood Canal (c)	26	52	15

(a) Source: Fresh et al., 1979.
(b) Insufficient samples available for analysis.
(c) Source: Simenstad, 1980.

theory set forth by Simenstad et al. (1980) and supported by Healey (1982), high epibenthic prey abundance is an incentive for migrating chum juveniles to reside in a particular area during their outmigration. However, high rates of predation by this species reduces the prey density over a matter of weeks or months, and leads to either seaward migration along the shallow sublittoral zone or migration into the deeper waters and heavier reliance on neritic prey.

Species composition of the epibenthos can undergo rapid changes over a short interval. Simenstad et al. (1980) reported large monthly shifts in relative abundance of major categories of epibenthos in Hood Canal. On the other hand, Thom et al. (1984) concluded that the taxonomic structure of a given site was apparently stable and habitat-specific enough to be a potentially sensitive predictor of changes in the nearshore environment.

Selectivity of Salmonid Feeding on Epibenthos

Selective feeding on particular epibenthic taxa has been demonstrated only for chum salmon. Simenstad and Kinney (1979) cited many earlier studies showing the selectivity of chum fry for harpacticoid copepods in Alaska, the Straits of Georgia (British Columbia), and Puget Sound. The data of these authors for Hood Canal additionally suggested selectivity for gammarid amphipods. Selective feeding by chum fry on a particular species of harpacticoid, *Harpacticus uniremis*, was suggested by the occurrence of large numbers of this organism in stomach contents and the relative scarcity of this species in the environment.

(Sibert, 1979) in the Nanaimo Estuary in British Columbia. Seasonal chum fry abundance in the Nanaimo River estuary corresponded to the seasonal abundance of *H. uniremis*. Furthermore, chum fry emigration from the estuary occurred as the population of this copepod decreased.

Selective feeding with respect to size of prey has been demonstrated for juvenile chum. Simenstad and Kinney (1979) suggested that "as the chum fry grow during outmigration, they exploit a changing size continuum of epibenthic harpacticoids, showing selection for smaller organisms when first in the estuary (30-40 mm chum fry length), for large size fractions later (when 40-55 mm in length), and eventually for larger planktonic prey (when over 55 mm in length)." They cite a study performed in Puget Sound documenting selection for the smaller fraction of the available prey size distribution, where chum of relatively small size were examined. In contrast, selectivity for larger prey organisms documented in Hood Canal, where the largest individual harpacticoids were selected, even though they were relatively scarce, even at times absent, from the pump samples (Simenstad and Kinney, 1979). In a subsequent report, Simenstad (1980) documented selection for the larger gammarid genera (Calliopiella, Pontogeneia, and Ischyrocerus) in preference to the more abundant genera which had smaller individuals.

Epibenthic Ecology

Many factors have been proposed to explain the abundance and species composition of the epibenthos. The relative exposure of a beach to prevailing winds and wave action is likely to be associated with the relative dominance of gammarids, but protected areas are likely to have more abundant harpacticoids (Simenstad et al., 1980). Exposure has also been related to the the species composition of harpacticoids, gammarids, and other epibenthic invertebrate groups (Thom et al., 1984).

Stability of the substrate has been suggested as a key factor in promoting high densities of harpacticoids, gammarids, and cumaceans in a recent experiment in Elliott Bay (Parametrix, 1985). Recently placed sand and gravel were sampled two, four, and six months after placement. The artificially-placed sand was not well colonized apparently because of its tendency to shift with the currents. In comparison, artificially placed pea gravel and a natural, stable sand flat, both supported relatively high densities of epibenthic zooplankton.

Texture of the substrate may be important in determining species composition and abundance. For instance, coarse sand was generally better than fine sand for abundance of harpacticoids (Hicks and Coull, 1983). Pea gravel was better than coarse gravel for density of epibenthic harpacticoids (Parametrix, 1985). Epibenthic harpacticoid species composition at five locations in the vicinity of Lincoln Park Beach was influenced by substrate texture (Thom et al., 1984). Densities being higher over sandy substrates than over cobble. For gammarids, a cobbly substrate may be more suitable than bare sand, since the cobbles act as a detritus trap. Detritus is the main food source for most species of gammarids, and for the epibenthic food chain in general (Miller et al., 1980).

Zonation of the epibenthic community by tidal elevation has been reported or implied in several studies (Table 3). Measures of epibenthic abundance were usually higher at 0 or at +3 than at +6 feet from mean lower low water. Exceptional cases of higher numbers or biomass per unit area at +6 feet than at +3 or 0 were supposed by Cordell and Simenstad (1981) to be the result of wave action maintaining crustaceans in suspension so they did not become part

Table 3. Zonation in vertical distribution of epibenthos in three estuaries of western Washington.

Location	Bottom type(a)	Season	Gear	Min. size (mm)	Taxon	Density (b) by tidal elevation (c)		
						0	+3	+6
Commencement Bay (d)	S,G	Apr. & Nov.	Pump	0.25	All	146	153	92
Commencement Bay (d)	S,G	Apr. & Nov.	Pump	0.50	All	8.6	7.3	3.9
Grays Harbor (e)	(f)	May	Pump	0.13	All	58,000	(f)	3 2,000
Grays Harbor (e)	(f)	May	Pump	(f)	Harp.	10,100	(f)	5,600
Nisqually Delta (g)	M,S,G,C	Apr.	Core	1.00	Gamm.	486	832	524

(a) M=mud, S=sand, G=gravel, C=cobble.
(b) Number per sample at Commencement Bay; number per square meter at other locations.
(c) Feet above mean lower low water.
(d) Source: Blaylock and Houghton, 1981. Data presented here is averaged from 8 transects presented separately in report cited.
(e) Source: Cordell and Simenstad, 1981. Data presented here is averaged from 5 transects presented separately in report cited.
(f) Not specified.
(g) Source: Wisseman et al., 1978. Data presented here is averaged from 5 transects presented separately in report cited.

of the infauna. The general trend of lower abundance with higher elevation was further supported by the graphic data of Albright (1977), who indicated very low abundance of gammarids, and Corophium spp in particular, at tidal elevations of +7 or above.

Information on the tidal zonation of harpacticoid species of particular interest as salmonid prey did not appear in the literature reviewed here. However, tidal zonation of infaunal harpacticoids has been shown by several authors in the European literature reviewed by Hicks and Coull (1983). Three or four distinct species assemblages were suggested. However, no inference as to the relative value of the respective elevations was possible, since the genera consistently differed from those of importance as salmonid prey in the Pacific Northwest.

Recovery of Epibenthos from Disturbance

Reestablishment of the epibenthos after disturbance of large shoreline areas has been studied at only a few locations in Washington. In Grays Harbor, reestablishment of Corophium spp populations did not occur after intertidal deposition of dredged material at Moon Island (Albright 1977). The failure was attributed to a permanent rise in the tidal elevation of the disposal area from about +4 feet to about +8 feet above mean lower low water. Virtually no Corophium were encountered above tidal elevation +7. Generalizing from this and other epibenthic studies in Grays Harbor, Cordell and Simenstad (1981) stated that the composition of the epibenthic community following disturbance by dredging and disposal could not be predicted given the existing state of knowledge.

Recolonization may not be so inhibited when no change in elevation is involved. For example, areas affected by intertidal log rafting on the Snohomish delta were studied by Smith (1977). He concluded that for the salt-marsh-mudflat benthic infauna, including species of Anisogammarus and Corophium, recolonization after a rafting event occurred quickly after removal of rafts. Logs were impacting the study area by denying crustaceans access to the underlying substrate during low tide when the logs were resting on the bottom. After the rafts were removed, populations statistically indistinguishable from control areas were established within two months.

Recolonization by epibenthic harpacticoids was apparently inhibited by placement of unstable substrate, in a study conducted for the the Port of Seattle (Schadt and Weitkamp, 1985). Covering a subtidal riprapped bank with fine sand resulted in lower densities of harpacticoids and cumaceans compared to a nearby naturally-occurring sand flat. Lower densities were attributed to the instability of the artificially-placed sand during the five-month post-project study period.

Depression in both the density and diversity of the benthic infauna occurred after subtidal dredge spoil disposal in Elliott Bay (Bingham, 1978). The effect lasted at least nine months after disposal had ceased. The implications for salmonid prey are not clear because the investigation focused on large deposit-feeding polychaetes, do not contribute significantly to the salmonid food chain.

Recolonization by harpacticoids and other copepods in very small (less than 50 foot square) patches of disturbed habitat may occur over the range of one day to several months. In one experiment (Sherman and Coull, 1980), an intertidal mudflat in North Carolina was depopulated by overturning mud down to the anoxic zone over a five meter square area. Total copepod density (infauna plus epibenthos) returned to levels comparable to those of an undisturbed control plot after twelve hours.

In another experiment, conducted in Scotland (Hockin and Ollason, 1981), screened containers about the size of a shoe box were filled with sterilized sand and partially buried in a beach of similar texture. Recolonization, as measured by stability of species composition in the infauna, was complete after five weeks. Harpacticoids dominated the infauna.

In the Baltic Sea off Germany, boxes of sand, gravel, and cobble placed in the subtidal zone were colonized by harpacticoids and nematodes (Scheibel, 1974). Size of boxes was not specified. Colonization by the infauna was considered complete in two to five months.

Rapid repopulation of polychaete worm cases by harpacticoids was reported by Bell and Coen (1982) for a Florida subtidal area. Sand-and-detritus cases constructed by large burrowing worms were removed from the substrate, sterilized, and replanted. Densities of harpacticoids on the cases reached pre-disturbance levels in one to five days.

SUMMARY

1. Juvenile salmonids may be expected in the intertidal waters of Puget Sound as early as March. In this zone, chum, chinook, and pink salmon are the most likely species to occur. Coho are usually less abundant, while juvenile steelhead, cutthroat trout, and sockeye occur only infrequently.

2. During their residence in the shallow nearshore waters, juvenile chum, chinook, pink, and coho depend in varying degrees on prey produced in the epibenthos. Chum apparently depend more than other salmonids on epibenthic prey. Chinook occupy an intermediate position, while coho and pink usually are least dependent. In all species, this dependence is greatly decreased by the end of June, when neritic organisms dominate the prey.

3. Epibenthic prey consists primarily of harpacticoid copepods (especially of the genera Harpacticus and Tisbe) and gammarid amphipods (Anisogammarus and Corophium being the genera most commonly consumed, although other genera may be locally important).

4. Juvenile chum have been shown to feed selectively for certain sizes and species of epibenthic prey. The size of prey may be larger or smaller than what is represented by samples taken with an epibenthic pump. Size selectivity appears to depend on the size and growth rate of the fish, with progressively larger prey consumed over the season. Selective feeding for certain prey species is at least in part due to selection for a particular prey size. Feeding selectivity of other juvenile salmon species has apparently not been examined.

5. The density of epibenthic zooplankton may vary widely over the season during which salmonids are in the nearshore area. Substantial variation also occurrs between years. However, the abundance of certain groups of crustacean species at certain sites is relatively stable over the seasons.

6. The key environmental factors influencing density of epibenthic zooplankton appear to be the tidal elevation and the stability of the substrate. The species composition depends on the texture of the substrate and the exposure of the site to wave action. All these elements affect and are affected by the degree of cover provided by attached algae or eelgrass.

7. Projects which raised the tidal elevation, destabilized the substrate, or changed its composition led to long-term depression of the density of certain potential salmonid prey categories, and changed the species composition. In contrast, experiments measuring recovery from defaunation in small areas in which the elevation, stability, or texture of the substrate were not changed have suggested recovery within several months. No evaluation of the specific effect of beach nourishment on availability of salmonid prey was revealed in our literature review.

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