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ANALYSES OF FEEDING IN TWO MARINE COPEPODS FROM SANTA MONICA BAY, CALIFORNIA

Understanding the feeding strategies of herbivorous, planktonic copepods is an important step in determining how primary production is partitioned in coastal marine food webs. The conditions under which selective feeding occurs among these animals vary, and are defined both by the species and the environment (Poulet 1974; Poulet and Marsot 1980; Donaghay 1980).

Although it is desirable to study feeding behavior in natural zooplankton assemblages, this is often difficult. Identification of phytoplankton in the gut by standard dissection and microscopic techniques is labor intensive, and usually qualitative. Furthermore, it is impossible to identify many of the soft-bodied organisms which might have been consumed. For this reason, much of the work on food selection in copepods has been restricted to the laboratory, where cultivated foods (Frost 1972) or natural particles (Poulet 1978) have been offered to the animals. While such studies have provided valuable information, they have been limited by the variety of foods which can be offered and by other technical problems (Mullin 1963; Harbison and McAlister 1980). Studies employing gut contents analysis of animals collected in the field using gut fullness (Hayward 1980; Huntley 1980) or chlorophyll a fluorescence as an estimate of total phytoplankton biomass in the gut (Mackas and Bohrer 1976; Boyd et al. 1980) have answered questions about when and where certain zooplankton feed, but usually provide only indirect data on the kinds of phytoplankton actually ingested. Dagg and Grill (1980) showed that the rate of particle ingestion is often not solely a function of concentration and suggested that food quality may be important in explaining the variability observed in the relation between feeding rate and particle concentration.

To understand the processes involved in food selection it is necessary to determine directly the types of materials in the guts of the copepods being studied. Such an analysis must be capable of detecting soft-bodied phytoplankton as well as diatoms and armored dinoflagellates, and of providing some indication of the relative importance of different taxa in the diet at a given time. We have been especially interested in the importance of the green algae to zooplankton feeding in coastal waters. Information in this area is rela-

tively scarce despite the periodic importance of green algae in the coastal flora (C. Lorenzen unpubl. data).

In September 1980, the cyst (phycoma) stage of *Halosphaera* sp. (Prasinophyceae) was observed in Santa Monica Bay, Calif., providing an opportunity to study its importance in the feeding of two calanoid copepods, *Acartia tonsa* and *Calanus pacificus*. Since chlorophyll b is present only in the green algae (Chlorophyceae, Prasinophyceae, Euglenophyceae) and chlorophyll c is present in the diatoms, dinoflagellates, chrysomonads, Haptophyceae, and Cryptophyceae (Meeks 1974; Parsons et al. 1977), we sought to compare water column concentrations of chlorophyll pigments with those in the guts of animals collected in various parts of the bay.

Methods

Samples were collected at two of three stations in Santa Monica Bay (Fig. 1) on 12 and 26 September 1980. On 12 September, stations 7B and N6 were sampled. On 26 September, stations 7B and N4 were occupied. All samples were taken between 0700 and 1200 h.

Depth integrated water samples were collected by lowering a submersible pump through the water column (to the same depth as zooplankton were collected; see below) at a constant rate and by pumping into a 122 l plastic container. The contents were mixed thoroughly, and 1 l samples were withdrawn and fixed in 3% buffered Formalin[1] for phytoplankton counting and identification, using the method of Palmer and Maloney (1954). Five hundred ml water samples were frozen for pigment analysis. In the laboratory, these were passed through 0.45 μm filters (Nucleopore) at low vacuum (<100 mm Hg), and pro-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

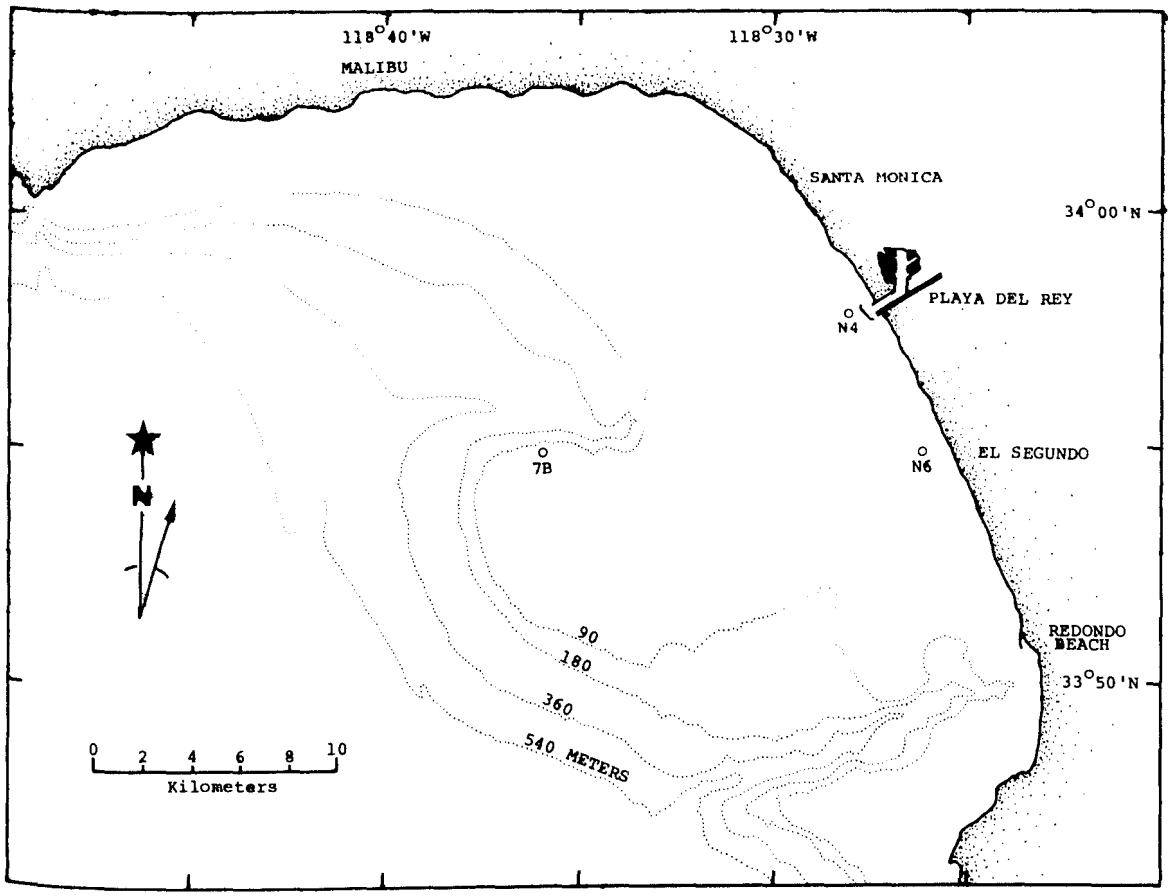

FIGURE 1.—Station locations.

cessed for chlorophylls a, b, and c by the trichromatic method (Strickland and Parsons 1972), using the equations of Parsons and Strickland (1963). Unfortunately, these equations do not give accurate estimates of chlorophyll b or c, and despite numerous attempts to improve their accuracy, no set of equations has been completely satisfactory (Jeffrey 1968, 1981; Jeffrey and Humphrey 1975). However, if the errors for gut and water samples are assumed to be the same, then comparisons can be made between pigment concentrations in guts and water. To test this, *Acartia tonsa* were starved for 24 h and a sample of animals was examined microscopically to ensure that the guts were empty. Pure cultures of the diatom *Thalassiosira fluviatilis* were added to half of the flasks containing the copepods. The animals in the remaining flasks were not fed. After 4 h, the animals in all of the flasks were processed for chlorophyll pigments as described below. We chose to feed a diatom in this experiment to find out if chlorophyll a or c might, during digestion, be converted into a product absorbing at the wavelengths used in measuring chlorophyll b (not found in diatoms). Table 1 suggests that this did not occur. Low levels of chlorophyll b were detected both in the culture and the fed animals but not in the starved animals, indicating that there was some contaminant in the culture or a small error in the equation at high chlorophylls a and c concentrations. Pigment ratios in the culture and the guts of animals fed from the culture were fairly stable.

Copepods for gut contents analysis were collected from 7 to 10 vertical tows of a CalCOFI vertical tow net (335 μm mesh). Tows were made from 70 m at station 7B and from near-bottom at stations N4 and N6. The tows took 2-3 min each to complete and were made in rapid succession. The ship was kept on station during the entire sampling period. On the cruise of 12 September, adult *A. tonsa* and *C. pacificus* were immediately separated from the rest of the catch. Half of each sample was washed in filtered (0.5 μm) seawater and frozen, and the other half was maintained in aerated, filtered seawater for 24 h allowing them to clear their guts of food prior to freezing. This empty gut group was used to detect absorbance at wavelengths used in chlorophyll analysis that was not due to chlorophyll. On 26 September, collections were made in a similar manner, except that half of the entire catch was washed with filtered seawater and frozen and the other half was maintained alive for 24 h in filtered seawater prior to freezing. Specimens for analysis were separated from the rest of the catch in the laboratory.

TABLE 1.—Ratios of chlorophyll pigments in a culture of *Thalassiosira fluviatilis* and in *Acartia* guts when the animals were starved or fed the phytoplankton culture.

Chlorophyll pigments	Culture	*Acartia* guts	
		Starved	Fed
a/b[1]	56.91	ND	60.00
a/c	1.21	0.30	1.09
b/c	0.02	0	0.02

[1]Chlorophyll a levels per milliliter of culture = 0.24 μg; per animal = 12 ng.
ND = a ratio that could not be computed, since chlorophyll b was not detected.

Chlorophyll a analysis of gut contents was conducted by macerating 50-200 animals of each species of full and empty gut groups in 90% acetone and by reading absorbances in triplicate at wavelengths of 750, 665, 645, and 630 nm on a Beckman model 34 spectrophotometer. Chlorophylls a, b, and c concentrations were computed by the trichromatic equations of Parsons and Strickland (1963). Chlorophyll degradation products (pheopigments) in the gut contents were computed as described by Strickland and Parsons (1972) and were considered as part of the total chlorophyll because the processing of food in the gut rapidly degrades chlorophylls. Since our interest was in how much plant material was present and not in the rate of food processing, we include both chlorophyll and its degradation products as a single indication of plant biomass in the gut.

Gut fullness was estimated in *A. tonsa* collected on 26 September. The animals were "cleared" by immersion in 85% lactic acid for 30 min and then examined under 25× magnification (Hayward 1980). Gut fullness was estimated independently by each author and the average of the two estimates was recorded. Attempts were made to estimate gut fullness in *C. pacificus*, but there was disagreement between estimates because the lactic acid did not clear the animals well.

Results

Phytoplankton density and community structure were similar at station 7B on both sampling dates. Cell density averaged 8-10 × 10^3 cells/l. The majority of phytoplankton species found were dinoflagellates (35% of the community), dominated by *Gymnodinium* spp., and diatoms

(35% of the community), dominated by *Skeletonema costatum*. Cysts of *Halosphaera* sp. composed about 20% of the community on both dates; the motile form was not detected. Coccolithophorids composed about 10% of the cells counted. Mean chlorophyll a concentrations at the station were 0.56 and 1.16 μg/l on 12 and 26 September, respectively.

At stations N4 and N6 there were about 10^5 phytoplankton/l on each occasion. About 60% of the phytoplankton in the samples were diatoms of the genus *Chaetoceros*. Other diatom species composed about 25% of the community, and dinoflagellates made up 10%. *Halosphaera* cysts, small unidentifiable spherical cells (some of which probably contained chlorophyll b) and coccolithophorids made up about 5% of the community. Mean chlorophyll a concentrations were 1.54 and 1.92 μg/l on 12 and 26 September, respectively.

Figure 2a, b summarizes gut fullness estimates for 50 *A. tonsa* from stations N4 and 7B. At station N4 (Fig. 2a), 70% of the animals exhibited >40% gut fullness; mean gut fullness was 55.5%. At station 7B (Fig. 2b), about 20% of the animals exhibited >40% gut fullness; the mean was 31% fullness.

Gut chlorophyll a concentrations (corrected for the absorbance of empty gut animals) are shown in Table 2. Comparative water column data are also provided. The concentration of chlorophyll a in the gut contents of *A. tonsa* increased with seaward distance. Animals collected at station 7B had, on average, 40 times more chlorophyll in their guts than the same species at nearshore locations.

The chlorophyll b and c content of the water column diminished slightly with distance from shore (Fig. 3a). In the guts of *Acartia* these pigments increased sharply from nearshore to offshore stations (Fig. 3b).

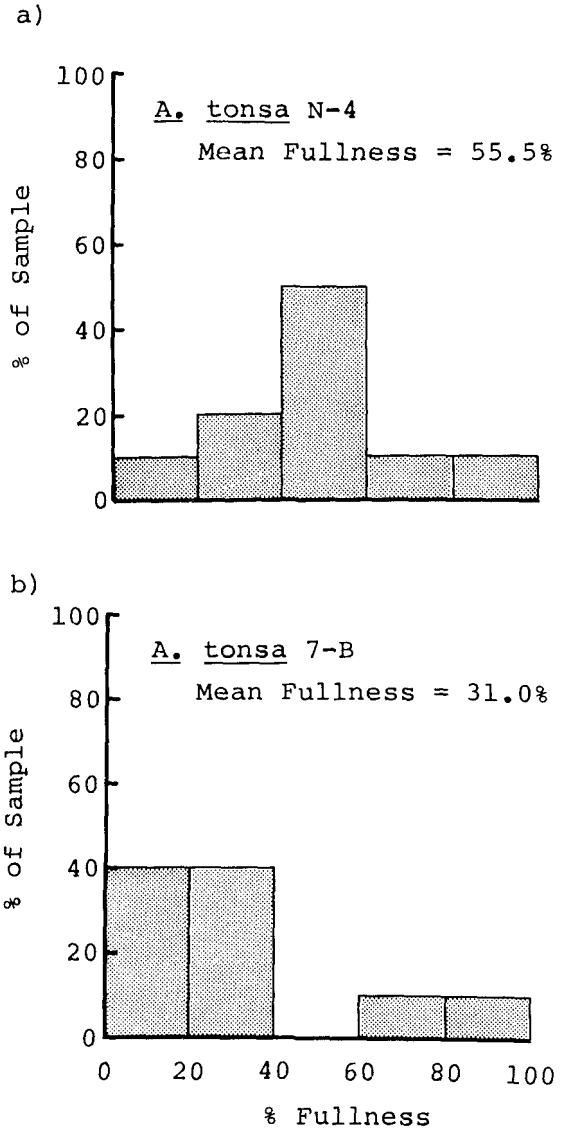

FIGURE 2.—Percent gut fullness of *Acartia tonsa* at stations a) N4 and b) 7B on 26 September 1980. $N = 50$.

TABLE 2.—Chlorophyll a in two copepod species, *Acartia tonsa* and *Calanus pacificus*, at stations of varying distances from shore, with comparative water column[1] values.

Station	Distance from shore (km)	Species (sample size)	Chlorophyll a		
			Gut (±SD) (ng per animal)	Background (ng per animal)	Water (±SD) (μg per liter)
[2]N4	0.6	*A. tonsa* (200)	0.12 (0.01)	0.16	1.92 (0.36)
[3]N6	0.9	*A. tonsa* (160)	0.18 (0.01)	0	1.54
[3]7B	18.0	*A. tonsa* (200)	6.10 (0.003)	0	1.16 (0.15)
[2]7B	18.0	[4]*C. pacificus* (55)	13.24 (0.003)	0.001	0.56

[1]Water column chlorophyll a values are mean ± standard deviation (in parentheses) from water column composite samples. On 12 September only one sample was analyzed; on 26 September, 5 subsamples of the water column composite were analyzed.
[2]Data from cruise on 26 September 1980.
[3]Data from cruise on 12 September 1980.
[4]Numbers of *C. pacificus* at the nearshore stations were too low (<5 animals/tow) for the analysis to be conducted.

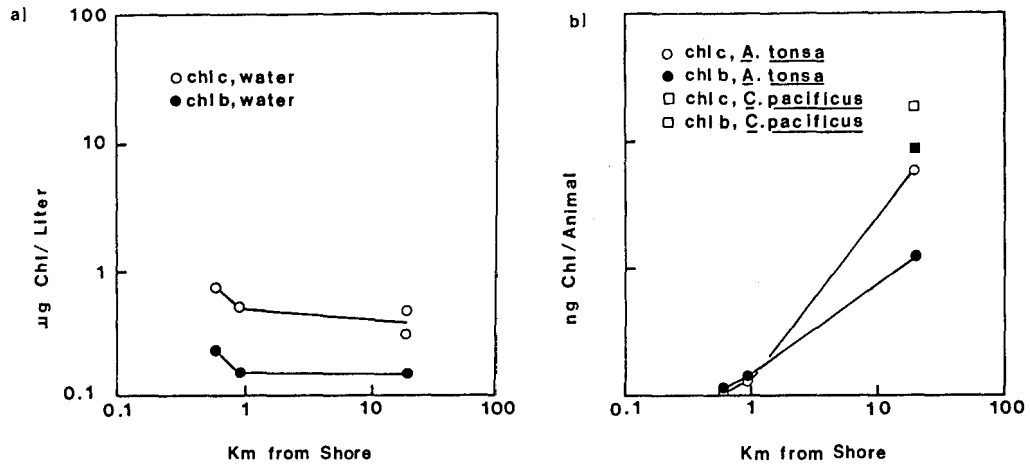

FIGURE 3.—a) Mean chlorophyll b and c concentrations in water samples plotted relative to distance from shore. b) As in a) but for pigments in the gut contents of *Acartia tonsa* and *Calanus pacificus*.

If the ratio of the chlorophyll b or c to its sum, T (= b + c), is the same in the gut of a copepod as it is in the water, then it might be reasoned that feeding on phytoplankton was not selective. Variations from unity would be interpreted as an indication of food selectivity. We define relative selectivity indices for chlorophyll b (RSI_b) and chlorophyll c (RSI_c) as:

$$RSI_b = \frac{(b/T)_g}{(b/T)_w} \quad (1)$$

$$RSI_c = \frac{(c/T)_g}{(c/T)_w} \quad (2)$$

where g and w represent the ratios in the gut and water, respectively.

RSI values, presented in Table 3, indicate selectivity for chlorophyll b-bearing organisms by *Acartia* at stations N4 and N6. At station 7B, *Acartia* evidenced a weak selection of chlorophyll c-bearing organisms and *Calanus pacificus* selected for chlorophyll b-bearing organisms.

TABLE 3.—Relative selectivity indices for chlorophyll b (RSI_b) and chlorophyll c (RSI_c) by *Acartia tonsa* and *Calanus pacificus*.

Station	Species	RSI_b	RSI_c
[1]N4	*A. tonsa*	2.04	0.62
[2]N6	*A. tonsa*	2.48	0.61
[2]7B	*A. tonsa*	0.73	1.08
[1]7B	*C. pacificus*	1.20	0.93

[1]Data from cruise on 26 September 1980.
[2]Data from cruise on 12 September 1980.

Discussion

There were clear differences in the gut contents of *Acartia* from near- and offshore locations. Gut fullness was higher in copepods from nearshore than from those offshore (Fig. 2), but the amount of chlorophyll a in the guts of animals collected nearshore was substantially lower than in the guts of animals from offshore locations (Table 2). Apparently materials other than phytoplankton composed a relatively large portion of the diet of the nearshore animals. Evidence from laboratory studies (Poulet 1973; Heinle and Flemer 1975; Richman et al. 1977; Roman 1977) suggests the possibility of a detrital or animal component in the diet of *Acartia* when these foods are available.

The RSI indicates that *C. pacificus* was feeding selectively on phytoplankton containing chlorophyll b at station 7B. The only green alga detected by microscopic analysis of water samples at this location was *Halosphaera* sp. Although it is possible, even likely, that other green algae were present, the typical chlorophytes and euglenoids were not observed, and, unlike the nearshore stations, nanoplanktonic green algae appeared to be absent. We assume, therefore, that *Halosphaera* was at least the dominant source of chlorophyll b in the water, and constituted the greater portion of the chlorophyll b signal in the *C. pacificus* gut. Since we cannot test this assumption, what follows must be considered somewhat speculative. However, we suggest that under the conditions observed in Santa Monica Bay at the time, selective feeding by *Calanus* on *Halosphaera* cysts

would be energetically advantageous to the animal.

Although many calanoid copepods, including *C. pacificus*, are recognized omnivores (Landry 1980), there have been numerous reports that *C. pacificus* will remove certain types of particles from the water, apparently in preference to others (Gifford et al. 1981). Therefore, the indication of selective feeding is not surprising. It is difficult, however, to explain the mechanisms driving this selection. It has been held that food selection is often passive in nature. For instance, the intersetal distance may facilitate the capture of certain-sized particles over others (Frost 1972; Wilson 1973), and accidental encounter may result in the most abundant particles being most commonly ingested (Poulet 1974). However, explanations based on passive feeding modes have been inadequate in several situations (Huntley 1980), and the work of Poulet and Marsot (1980) and Friedman (1980) suggests that morphological adaptations exist among the copepods which would permit a high degree of food selection based on the active detection of mechanical and chemical stimuli.

Most enlightening have been the cinematic evidence and physical arguments of Koehl and Strickler (1981) that copepods used the feeding appendages as paddles to move water to the second maxillae, rather than as strainers to filter it. This being the case, the selection of large particles, observed by Frost (1972), Gifford et al. (1981), and many others, would seem due to an active preference for these particles under certain conditions rather than the passive collection of material in the appendages. This is not to imply that copepods never ingest nanoplankton or feed passively, as we know they do. Rather, we suggest that active food selection may be quite common, even typical, in *C. pacificus*.

To understand the adaptive significance of selective feeding on large particles, it is necessary to consider the circumstances under which this sort of feeding might be most useful. Landry (1981) suggested that when the abundance of diatoms decreases in the water, adult *C. pacificus* begins to prey on copepod nauplii. An explanation of this behavior would be that when small particles (diatoms) become scarce and nauplii relatively abundant, it is energetically efficient to capture the larger biomass units (nauplii).

The low phytoplankton density observed during the present study is characteristic of Santa Monica Bay in the fall (Kleppel and Manzanilla 1981). We can extend Landry's (1981) argument somewhat by suggesting that the waning of diatom-sized particles might cause a shift in feeding to large biomass units represented by the cysts of *Halosphaera*. To get a feeling for the advantage of feeding on these cysts in relation to diatoms, we can compare rough estimates of the carbon in a diatom with that of the *Halosphaera* cyst and its rosettes (the individual units of the cyst which will mature into 200-550 motile cells), using equations based on cell volume (Strathmann 1967). We stress that such estimates have wide confidence intervals and should be considered on the basis of scale rather than accuracy.

The diameter of a mature *Halosphaera* cyst ranges from 200 to 800 μm, depending on species (Parke and den Hartog-Adams 1965; Boalch and Mommaerts 1969). The cysts we observed were somewhat smaller, 100-150 μm, indicating that they were not mature. This may explain why no motile cells were detected. Using the smaller measured diameter (100 μm), we calculate a carbon content of 0.031 μg/cyst. Considering only the rosettes (diameter based on literature values = 15-20 μm for the smallest units; Parke and den Hartog-Adams 1965) and assuming them to be round discs, 2 μm thick, we calculate the carbon content of one rosette to be 56-92 pg. If there are 200 rosettes/cyst, then the carbon content of the rosettes in one cyst is 0.011-0.018 μg.

Using the volume of *Skeletonema costatum* (the dominant diatom at station 7B) equal to 1,390 μm^3 (Parsons et al. 1961), the cellular carbon content estimated by the Strathmann equation is 91 pg. Since *S. costatum* typically forms chains 4-10 cells in length, the carbon content of a chain would be 3.7×10^{-4} to 9.1×10^{-4} μg. This is nearly two orders of magnitude lower than the carbon content of one *Halosphaera* cyst or its rosettes.

Although we stress that these estimates are crude and we recognize that numerous factors will affect the actual carbon content of a cell, the magnitude of the difference between the estimated carbon in *Halosphaera* and *Skeletonema* nonetheless seems significant. It would appear that selective feeding on *Halosphaera* would have a distinct advantage for *C. pacificus* by providing a large energy ration with each capture. This would seem of obvious value in ecosystems characterized by patchy food supplies.

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DISTRIBUTION, SIZE RELATIONSHIPS, AND FOOD HABITS OF JUVENILE KING-OF-THE-SALMON, *TRACHIPTERUS ALTIVELIS*, CAUGHT OFF THE OREGON COAST

The king-of-the-salmon is a strikingly colored ribbonfish of the family Trachipteridae that occurs in the oceanic and coastal waters of the eastern Pacific Ocean, from Chile to Alaska. Captures have been recorded from the coastal regions and offshore halfway to the Hawaiian Islands. Specimens have also been taken in coastal waters and estuaries along the United States and Canadian shores on rare occasions (Hart 1943; Walker 1953). Their lower depth limit is not known, but individuals have been taken from the surface down to at least 650 m (Fitch 1964).

Spawning apparently occurs in the open ocean throughout the year, but is probably concentrated in the spring. Plankton surveys off California have recorded the largest catches of larvae during the months of June and July (Fitch 1964). Bongo net and neuston net collections from northern California, Oregon, and Washington frequently contained eggs in April and May 1980, but larvae were rarely taken (Kendall and Clark[1]). August 1980 samples contained relatively few eggs (Kendall and Clark[2]). Egg densities during the spring sampling reached 25 eggs/10 m^2, and the eggs were found from 5 to 320 km offshore (Kendall[3]).

Throughout the early life stages, allometric growth reduces the proportionate size of the fins and alters the body form by increasing the relative size of the posterior portion of the fish (Sette 1923; Hubbs 1926). Fitch (1964) examined the otoliths of five individuals to determine their ages. His fish ranged from a 400 mm juvenile with an estimated age of 1 yr to a 1.5 m adult with an age of 7 yr.

The stomach contents of several adults show that these fish eat whole micronectonic organisms (e.g., small squid, epi- and mesopelagic fishes) as well as macrozooplankton such as euphausiids (Fitch 1964). Roedel (1938) presented a qualitative list of the gut contents of five juveniles (about 100-200 mm long) taken from the stomach of a longnose lancetfish, *Alepisaurus ferox*, caught off Santa Monica, Calif. Copepods were found in three of the stomachs, while polychaetes and fish larvae were each found in one stomach.

During 1980 and 1981, 44 juvenile king-of-the-salmon were collected with a purse seine during a study of the ecology and migration of juvenile salmonids off the Oregon coast. This paper presents an analysis of the spatial distribution, size relationships, and the feeding habits of these unusual fish.

[1]Kendall, A. W., Jr., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and Northern California April-May 1980. Northwest and Alaska Fish. Cent. Process. Rep. 82-11, 44 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[2]Kendall, A. W., Jr., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and Northern California August 1980. Northwest and Alaska Fish. Cent. Process. Rep. 82-12, 43 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[3]Arthur W. Kendall, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112, pers. commun. January 1983.