ON THE ROLE OF FOOD-SEEKING IN THE SUPRABENTHIC HABIT OF LARVAL WHITE CROAKER, *GENYONEMUS LINEATUS* (PISCES: SCIAENIDAE)

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ABSTRACT

Fish larvae and their prey were sampled from discrete depths within the bottom meter and at middepth near the 15 m depth contour off southern California. The smallest white croaker larvae (<2.7 mm NL) occurred mostly at middepth. Mid-sized larvae (2.7 mm to the beginning of flexion) were almost all collected at the two depths nearest the bottom. All preflexion-stage larvae ate small (50–300 μm in length) prey, chiefly rotifers, copepod nauplii, tintinnids, and invertebrate eggs. Although small and mid-size larvae ate these items in different proportions, this difference could not be ascribed to vertical distribution. Diet of the largest larvae, flexion and postflexion (roughly 5–15 mm), consisted mainly of copepods and differed by >90% from diets of smaller larvae. Though largest larvae were only captured 50 cm above the bottom, their prey, with one exception (amphipods), were more abundant at or above 1 m. It was concluded that the observed suprabenthic concentration of older white croaker larvae was probably not motivated by food-seeking.

Disparity between concentrations of food required for survival and growth of laboratory-reared fish larvae and observations of average concentrations of food organisms in the ocean has led to the widely accepted idea that aggregations of fish larvae and their food must frequently overlap in nature (see reviews by Theilacker and Dorsey [1980] and Hunter [1981]). Direct and indirect evidence for the importance of overlapping concentrations of larvae and their prey (Lasker 1975, 1978; Govoni et al. 1985; Buckley and Lough 1987) comes from sampling at fronts and discontinuities in the pelagic environment. One interface that attracts many zooplankters is the seabed itself (Hamner and Carleton 1979; Wishner 1980; Sainte-Marie and Brunel 1985). On the southern California continental shelf, the seabed serves as a surface of aggregation for larvae of numerous fish species (Brewer et al. 1981; Schlotterbeck and Connally 1982; Barnett et al. 1984; Jahn and Lavenberg 1986) and other zooplankton (Clutter 1969; Barnett and Jahn 1987) and of large-zooplankton biomass (Jahn and Lavenberg 1986). While it is tempting to suggest a trophic advantage to the suprabenthic habit of the fish larvae, near-bottom concentrations of organisms actually eaten by larval fishes have yet to be demonstrated along the open coast.

In all cases reported, concentration in the near-bottom zone was greater in older larvae and, when observations permitted, greater during the day than at night (Brewer and Kleppel 1986; Jahn and Lavenberg 1986). The phenomenon is therefore thought to be behavioral. Possible advantages of such behavior, including avoidance of midwater predators, maintenance of position on the shelf, and increased encounters with high concentrations of food, have been discussed elsewhere (Barnett et al. 1984; Brewer et al. 1984; Brewer and Kleppel 1986; Jahn and Lavenberg 1986). In discussing the near-bottom schooling behavior of a larval clupeoid in Japan, Leis (1986) stated, "knowledge of the biology of epibenthic fish larvae is too rudimentary to allow a clear assessment of the advantages and disadvantages. . . ." Whatever the advantages, a seemingly more answerable question about the near-bottom habit is what causes the larvae to behave as they do? In another study from Japan, Tanaka (1985) showed that juvenile red sea bream, *Pagrus major*, exploited suprabenthic copepod populations, and he speculated that the distribution of prey was a template for the descent of the fish from midwaters and its subsequent migration into estuaries. The question addressed in the present study was whether the fine-scale layering of larval fishes was a direct response to that of their prey field.

Because of the immediate behavioral aspect of

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the question posed, a 1-d study was thought appropriate. Though environmental conditions on this day might differ from "average", fish larvae were assumed to be capable of a constant array of behaviors. In other words, response (if any) of the larvae to the vertical distribution of their prey was assumed to be a deterministic rather than a statistical phenomenon. If their vertical distribution resembled that of their prey, then food-seeking would remain a plausible explanation for the near-bottom habit; if not, then other stimuli must be considered important in shaping these near-bottom concentrations of fish larvae.

The sampling was planned for daylight hours, when most feeding by larvae was expected to occur (Hunter 1981; Govoni et al. 1983). Late winter was chosen because in this season peak larval abundances of several species of interest to us (northern anchovy, *Engraulis mordax*; white croaker, *Genyonemus lineatus*; California halibut, *Paralichthys californicus*; and sometimes queenfish, *Seriphus politus*, often overlap (Lavenberg et al. 1986). A survey cruise in late February found moderate-to-high abundance of the first three species plus California sardine, *Sardinops sagax*, (all >0.2 m^{-3}, Lavenberg unpubl. data), and so this study was scheduled for 19 March 1985 off Seal Beach, CA (lat. 33°41'N, long. 118°05'W; for a map, see Jahn and Lavenberg 1986).

As it happened, we chanced to encounter conditions that were less typical than those found on the February cruise. Only one fish species, white croaker, was abundant enough to merit analysis, and an uncommonly reported prey item, rotifera, was important for small larvae. The diet of various-sized larvae with respect to the abundance of prey organisms at an array of heights above the seabed was nevertheless useful in questioning whether food-seeking shaped the observed larval distribution.

METHODS

Field

At the hour of 0750 PST, an array of Interocean model S4[2] electromagnetic current meters was set out over the 15 m isobath, with current meters 1, 4, and 8 m above the seabed. These meters were set to record average current vectors and temperature at 5-min intervals. The vessel (RV *Westwind*) was then anchored some 200 m seaward of the current meter array. A Nielson model NCH fish pump, rated at 227 m^3 h^{-1} at a 2 m head, was used to sample fish larvae and zooplankton. The end of the hose was tethered between a 200 kg flat steel weight and several subsurface floats, with a pulley arrangement such that divers could adjust the distance between hose mouth and seabed. A similar setup was previously found to give repeatable, fine-scale resolution at vertical separations of 25 cm (Jahn and Lavenberg 1986). Sampling heights above the bottom were 50 cm, 1 m, and 6.7 m. The 15.2 cm diameter hose was nearly horizontal at the tether point, so that nominal sampling strata were $z \pm 7.6$ cm. Vessel surge, transmitted through the stiff hose, caused occasional downward excursions of some 10 cm.

Accompanying each pump sample was a cast of water bottles for phytoplankton and microplankton analysis. Rigid arrays of horizontally held 4 L Niskin bottles (cf. Owen 1981) were used to take water samples simultaneously from 25, 50, and 100 cm above the bottom. The bottle array was designed to be tripped by messenger, but poor performance led to diver-implemented use after the second cast. A midwater sample, 7.5 m below the surface, was obtained via a single Niskin bottle for each sample set.

The sampling plan thus consisted of duplicate pump samples from each of three strata, each pump sample to be accompanied by a set of bottle samples from four standard heights, three within 1 m of the seabed and one at midwater column. One-liter samples from the bottles were fixed in Lugol's solution for later identification of phytoplankton and microplankton. Pump samples of 15-min duration (approximately 35 m^3) were mainly directed into an overboard, 330 μm mesh plankton net for retention of large zooplankton and ichthyoplankton. Unexpected problems in reading an inline flowmeter required that volumes be estimated as 2.4 m^3 min^{-1}, based on previous experience with the pump under similar conditions aboard the same vessel. To collect smaller zooplankton, a 5 cm diameter hose led from the intake side of the fish pump to a 100 μm mesh plankton net. This small-meshed net was suspended over a watertight box, which was marked such that exactly 0.5 m^3 could be subsampled for animals too small to be quantitatively retained by the large net. This subsample, which

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

was first seived through 330 μm mesh, took about 10 minutes to obtain; the portion retained on the 330 μm mesh was added to the contents of the large plankton net. All pump samples were preserved in 5% formalin.

Laboratory

All fish larvae and eggs were sorted from the large zooplankton samples and identified. All specimens of white croaker, the only species abundant in all six collections, were measured with an eyepiece micrometer in units of 0.024, 0.062, or 0.159 mm, depending on magnification. Length was measured from tip of snout to end of straight (NL) or flexed (FL) notochord or to the end of the hypural plate when this margin was vertical (SL). A further designation of developmental stage indicated the amount of yolk present: "free embryos" (Balon 1975) had a relatively massive yolk sac and may or may not have had functional eyes and mouths; more advanced individuals with a much-reduced or totally resorbed yolk sac, fully pigmented eyes, and an apparently functional mouth were designated "feeding-stage" larvae, or simply "larvae".

All larvae, plus a maximum of 20 free embryos with apparently functional mouths from each collection, were dissected for gut contents analysis by methods described in Arthur (1976) and Gadomski and Boehlert (1984). Length, rather than width, of prey items was measured, because it was considered a more conservative property of often crushed specimens and because our concern was not so much with what the larvae *could* eat (Hunter 1981) as with what they *did* eat. Lengths of prey items (of copepods, cephalothorax length) were recorded in 50 μm classes up to 200 μm, by 100 μm classes from 200 μm to 1 mm, and by 0.5 mm classes at larger sizes. In a few cases, these size categories were inconvenient, and more inclusive ranges were used.

Water bottle samples of phytoplankton and microzooplankton were prepared following procedures in Utermöhl (1931). From a thoroughly agitated sample, a 50 mL subsample for net phytoplankton was taken and placed in a settling chamber overnight (about 14–18 hours). Cells were identified and counted in 10 ocular fields, and mean density (cells per liter) calculated as the number counted scaled by the proportion of the area of the 10 fields (20.6 mm^2 total) to the area of the slide (510.7 mm^2).

Microzooplankton was filtered from a 500 mL subsample onto a 35 μm mesh screen, washed from the screen into a 50 mL settling tube and allowed to settle overnight. All organisms >50 μm were counted and identified to taxon and size category, using the same system as for larval fish gut contents. Densities were scaled to number per liter.

The 100 μm zooplankton samples were concentrated to 200 mL, then subsampled twice using a 10 mL Stempel pipette. Organisms were identified and classified to size categories as described above for larval fish prey. Counts from two subsamples were averaged and expressed as number per m^3.

Data Analysis

The microzooplankton (from water bottles) data set consisted of six vertical profiles of four sampling heights each. Principal components analysis was used to look for vertical layering and time-correlated changes in the makeup of these assemblages. A list of taxa present in three or more samples from at least one sampling height was chosen. Abundances were log-transformed $[\log_{10}(x + 1)]$, and principal components computed from the covariance matrix. Component scores for each of the 24 samples were used to make plots in which two- and three-dimensional groupings were sought that could be clearly related to sampling height or to the sequence in which the samples were taken. The taxa having high loadings on axes (components) identified with time and vertical trends were subsequently scrutinized individually. A similar analysis was done for phytoplankton, but omitted here in the interest of brevity.

Gut contents were conveniently analyzed by lumping taxa into the 10 categories: dinoflagellate, tintinnid, rotifer, polychaete larva, lamellibranch larva, crustacean nauplius, copepodite and adult copepod, amphipod, invertebrate egg, and "other". Unidentifiable matter was ignored in all comparisons. To test for differences in diet between subsets of larvae, we used an adaptation of the "bootstrap" (Efron 1982). The test criterion was the percentage of prey comprised by a major item in one of the two groups of guts. The null hypothesis that two sets were not different was simulated by combining the two data sets and then, through repeated sampling, determining the probability of observing the criterion percentage from such a mixture.

RESULTS

General Observations

The water column was very weakly stratified, with temperatures of 12.9 ± 0.1°C at 1 m, 13.0 ± 0.2°C at 4 m and 14.1 ± 0.1°C 8 m above the bottom during the time of biological sampling. Near the bottom, a turbid suspension limited visibility to arm's length; the surface of the sediment was never clearly seen on any of the seven descents during the hours of 0930–1630. The midwaters below about 3 m from the surface were densely populated with larvaceans (visually estimated and later confirmed to be about 10 L^{-1}). Total diatom cell counts (principally *Nitzschia* spp.) were of order 10^5 L^{-1} in all samples, bloom quantities suggestive of recent upwelling (cf. Tont 1981).

Currents and Plankton

During the hours of biological sampling, currents ran steadily alongshore to the southeast, being deflected counterclockwise near the bottom and ranging from about 14 cm s^{-1} at 8 m to 6 m s^{-1} at 1 m above the seabed. At these current speeds, one may expect that the approximately 5-h period from beginning to end of biological sampling should correspond to a minimum spatial spread of 1–2.5 km. Distances of this order were previously found to be an important length scale of variation in larval fish abundance (Jahn and Lavenberg 1986). Because the spatial dimension of interest regarding distribution of larval fish prey was the vertical, we needed to quantify, at least partially, the effects of time (vertical migration?) and distance (advection) on the composition and vertical dispostion of the plankton.

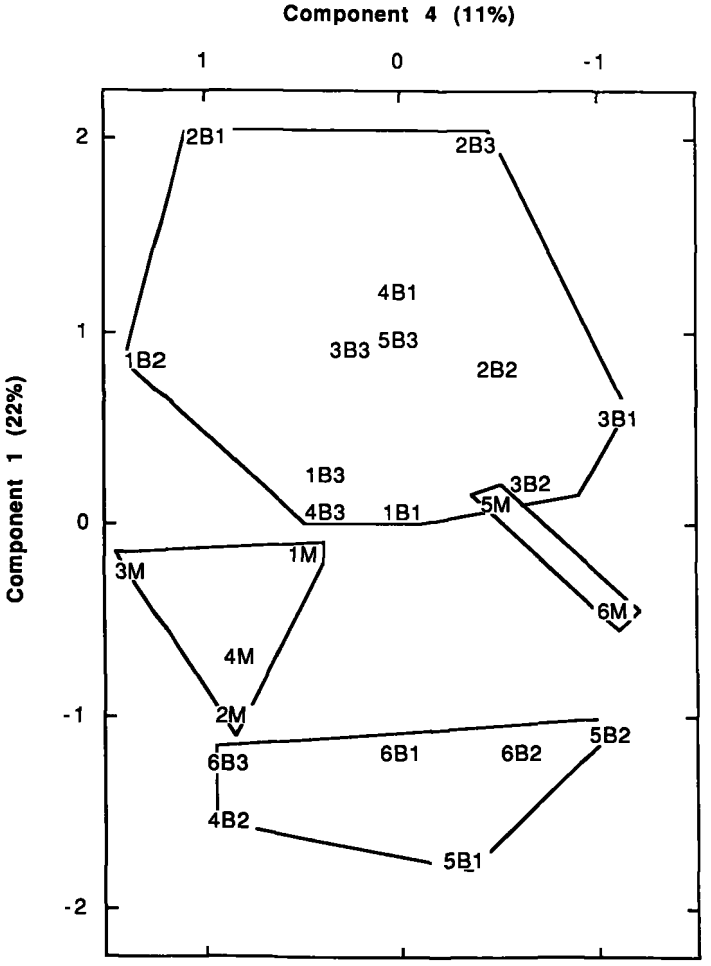

FIGURE 1.—Projections of microzooplankton samples onto the first and fourth principal component axes. The initial digit represents profile number, M = midwater, B = near-bottom, final digit is proximity to bottom (1 = 25 cm, 2 = 50 cm, 3 = 100 cm), see Figure 3.

Accordingly, the microplankton data set, representing six vertical profiles separated in time, was reduced to principal components for examination of possible time effects.

Twenty-four taxonomic/size categories of microzooplankton were used to compute principal component scores for the 24 samples. The first four principal components accounted for 60% of the variance. No clear separation of midwater from near-bottom samples was seen. The first component, which accounted for 22% of the variance, separated the near-bottom samples into two groups, morning to midday and afternoon (Fig. 1), leaving the midwater samples at intermediate projections. The midwater samples were in turn separated by the fourth component (11% of the variance) into time groups corresponding to those of the near-bottom set. No stratification by sampling height was seen within the near-bottom samples, and none of the other axes provided separation by time. The highest loading variables on components 1 and 4 (Table 1) were various sizes of rotifer and, for component 1, three genera of tintinnids (*Favella*, *Acanthocystis*, and *Dadayella*). Much of the time-correlated variance structure depicted in Figure 1 thus appears to be due to change in the size composition of rotifers, described in a later section, and a decrease in these three tintinnids near the bottom in late afternoon (Table 2). An identical analysis of the phytoplankton data found no trends in time or depth.

TABLE 1.—Loadings of important variables on the first and fourth principal components of microplankton data.

Component 1		Component 4	
Variable	Loading	Variable	Loading
Rotifer		Rotifer, 100–150 μm	0.388
150–200 μm	0.572		
200–300 μm	−0.380	Egg, 50–100 μm	0.349
Tintinnids		Copepod nauplii,	
Favella sp.	0.365	150–200 μm	−0.252
Acanthocyctis sp.	0.331		
Dadayella sp.	0.314		

Larval Fish Abundance

Of 1,125 total fish larvae taken in the six pump samples, 666 (59%) were white croaker, a deep-bodied, robust larva (Watson 1982). More than half (338) of these had absorbed the yolk sac and were thus of feeding size. The second most abundant feeding-stage larva was an unidentified gobiid type (84 specimens), but this taxon was not taken above 100 cm of the seabed and so was excluded from the gut analysis. Feeding-stage California sardine, northern anchovy, and California halibut—all relatively abundant (>0.2 m^{-3}) in the area three weeks earlier—each represented <1% of the catch. Although the earlier survey employed oblique bongo net tows, past comparison of the Nielsen pump with bongo tows found no significant differences in diversity or abundance estimates based on similar-volume samples (R. Schlotterbeck[3]). We therefore think the differences between the February survey and our March samples were due mainly to a real change in the ichthyoplankton, from a typical late winter assemblage (McGowen 1987; Walker et al. 1987) to a more depauperate one.

Vertical Distribution and Feeding Incidence of Larval White Croaker

White croaker free embryos ranged in abundance from <0.1 m^{-3} at 0.5 m to ≈1 m^{-3} at 1 m to >2 m^{-3} at 6.7 m above the bottom. Of 61 free embryos dissected, none had gut contents.

Feeding-stage larvae of white croaker were only slightly more abundant at 6.7 m (1.9–2.2 m^{-3}) than at 1 m and 0.5 m (1.1–1.6 m^{-3}), but

[3]R. Schlotterbeck, Robert Schlotterbeck, Inc., 18842 Ridgeview Cr., Villa Park, CA 92667, pers. commun. April 1986.

TABLE 2.—Density (cells per liter) of three tintinnids as a function of time and sampling height. Each set of three numbers gives the density of *Favella* spp. (F), *Acanthocystis* spp. (A), and *Dadayella* spp. (D).

Height	Time (PST)																	
	1030			1130			1220			1313			1425			1454		
(cm)	F	A	D	F	A	D	F	A	D	F	A	D	F	A	D	F	A	D
750	6	4	20	0	4	22	0	4	12	2	0	12	46	12	14	42	6	18
100	2	4	24	30	18	24	6	18	48	0	2	26	8	4	24	0	0	26
50	0	6	18	26	12	44	0	2	24	0	0	4	0	0	4	0	6	12
25	2	6	4	14	12	44	0	22	54	10	2	26	0	0	0	0	0	0

there was a marked gradient in development with proximity to the seabed (Fig. 2). All the larvae at 6.7 m had unflexed notochords, and most were <2.5 mm NL. Feeding incidence (proportion of larvae with nonempty guts) was 78% at this height. At 1 m, modal larval length was 2.65 mm, with a single postflexion specimen (Fig. 2); feeding incidence was 74%. At 0.5 m there were still some preflexion larvae, but a second length mode at 6.8 mm represented postflexion-stage larvae. Feeding incidence was 90% at 0.5 m above the bottom, being somewhat greater among flexion

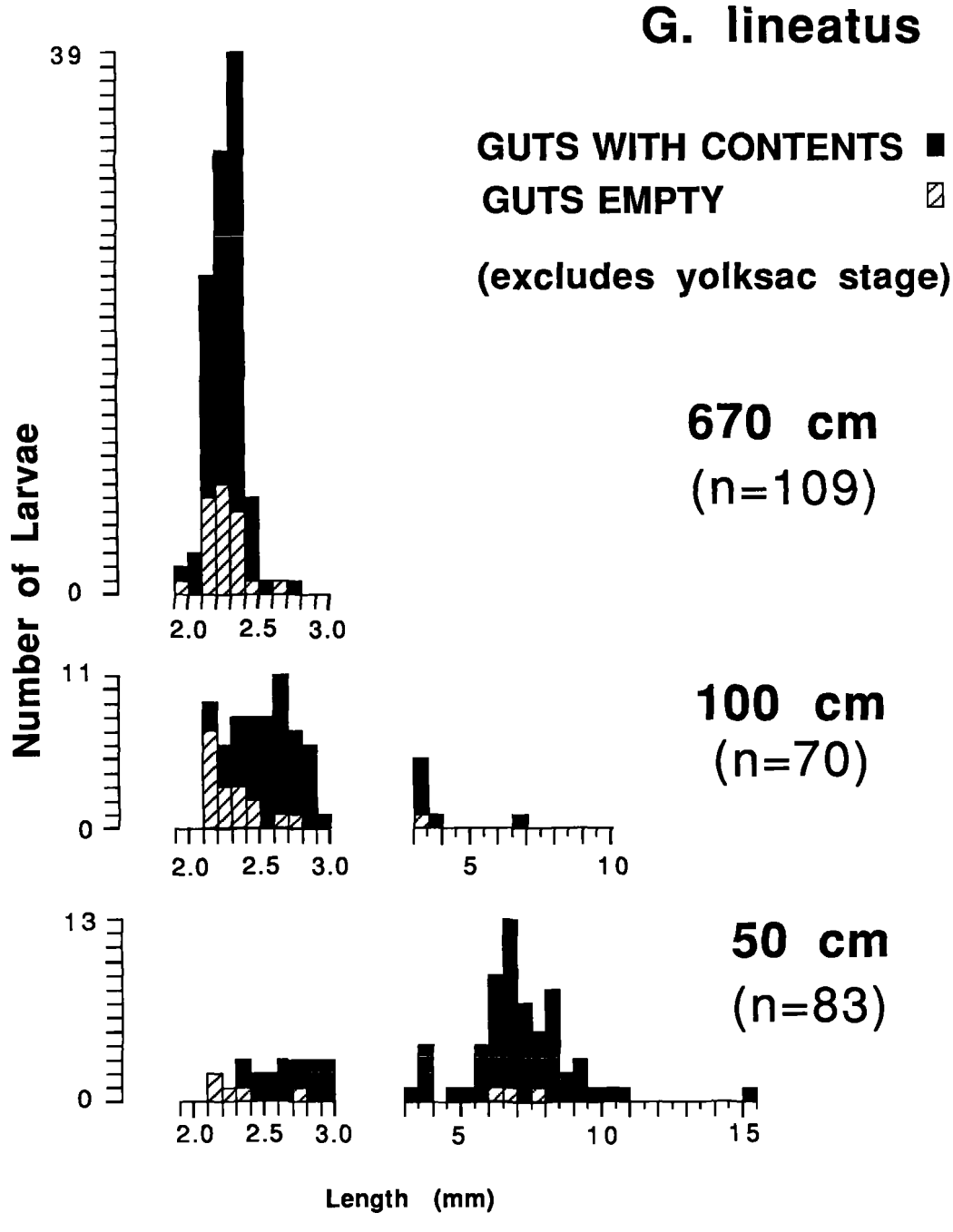

FIGURE 2.—Length frequencies of feeding-stage larvae of *Genyonemus lineatus* at three sampling heights.

and postflexion larvae (95%) than among preflexion larvae (82%).

Gut Contents

The white croaker larvae were divided into three size classes for analysis of gut contents with regard to height above the bottom: preflexion larvae <2.7 mm (size 1), preflexion larvae >2.7 mm (size 2), and flexion and postflexion larvae (size 3). The largest preflexion larva was 4.6 mm NL, and the smallest flexion stage larva was 5.5 mm FL. The division of preflexion larvae at 2.7 mm retained all but one specimen at 6.7 m in size 1 while partitioning the preflexion larvae at 1 m and 0.5 m about equally into sizes 1 and 2 (Figs. 2, 3). Besides the 2.75 mm specimen at 6.7 m, a single flexion stage larva at 1 m was excluded by these criteria from the comparisons.

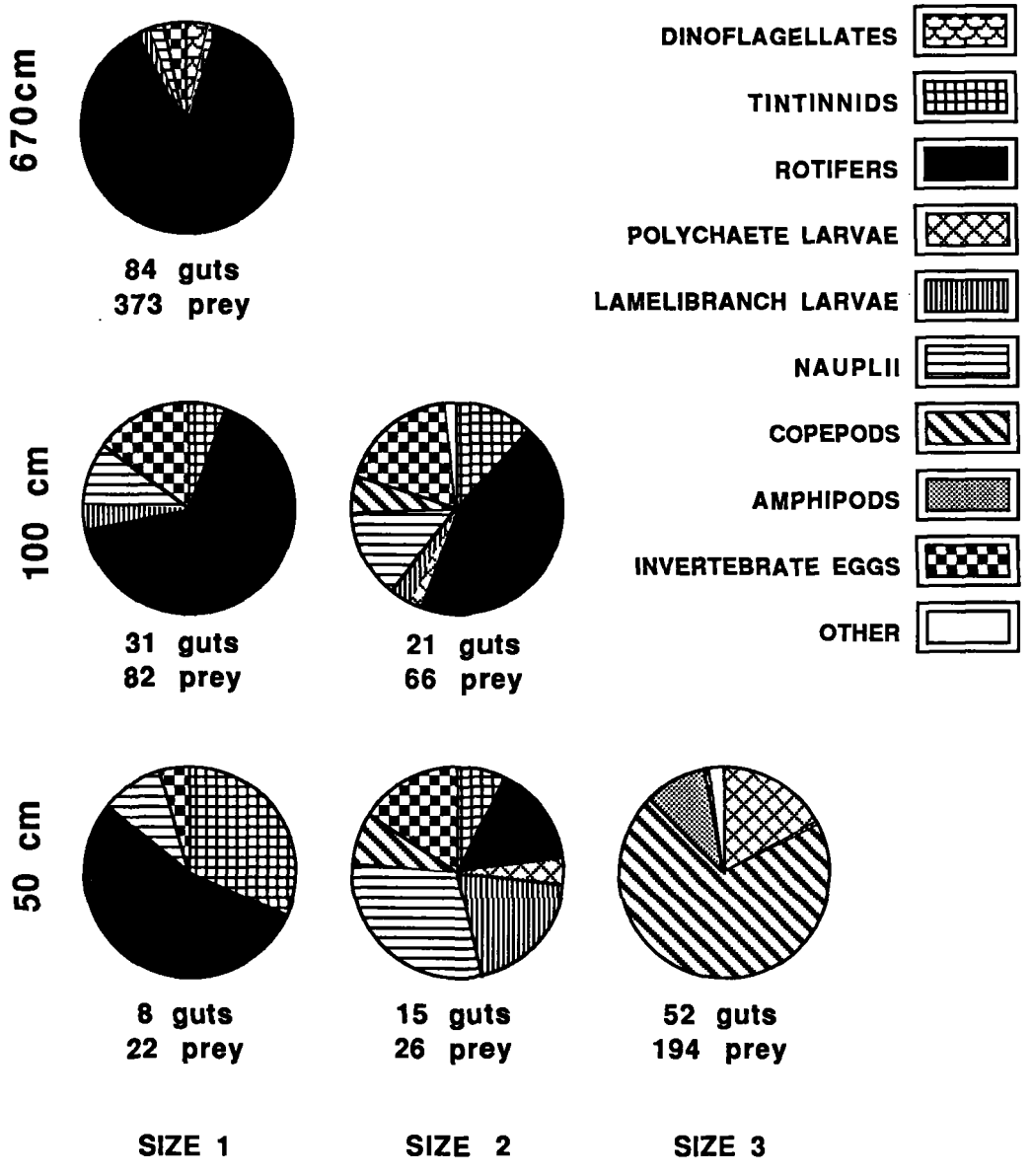

FIGURE 3.—Percentage contribution of 10 food categories to the diet of larval white croaker at three heights above the bottom. Size 1 = preflexion larvae <2.7 mm NL; size 2 = preflexion larvae >2.7 mm NL; size 3 = flexion and postflexion-stage larvae.

Most identifiable prey items fit into the nine categories: dinoflagellate, tintinnid, rotifer, polychaete larva, lamellibranch larva, crustacean nauplius, copepodite and adult copepod, amphipod, and invertebrate egg (Fig. 3). The "other" category applied only to size-2 larvae at 1 m (1 *Globigerina* sp.) and to size-3 larvae (1 zoea, 3 larvaceans, and two large [1 mm] unidentified spheres).

Guts of preflexion (sizes 1 and 2) larvae from the three sampling heights contained an array of small (<300 μm) organisms that varied mainly in proportions from mostly rotifers (88%) in size-1 larvae at 6.7 m to a diverse mix of prey numerically dominated by nauplii in size-2 larvae at 0.5 m (Fig. 3). Percent similarity (overlap) among the 5 groups of preflexion larvae ranged from 24 to 75%. The gut of the single size-2 larva at 6.7 m, not included in Figure 3, contained two tintinnids.

Size-3 larvae had a diet consisting chiefly of copepodite and adult copepods that overlapped only 8–9% with size-2 larvae and 1% or less with the three groups of size-1 larvae. The copepods eaten by size-3 larvae were mostly *Corycaeus anglicus* (62% of all copepods), unidentified copepodites (cyclopoid and calanoid, 25%), and *Paracalanus parvus* (9%). Polychaete larvae were identified only from the presence of setae in the guts, so the proportion (nominally 16% of all prey items) of this taxon in the diet is more an indication of incidence than of numerical importance. Amphipods, mostly in the length range 1–1.5 mm, were found in white croaker larvae ranging from 6.5 mm FL to 10.3 mm SL. The gut of the flexion-stage larva at 1 m, not included in Figure 3, contained three *C. anglicus* and traces of polychaete setae.

While there can be no doubt that flexion and postflexion larvae had a different diet than preflexion larvae, the pattern of decreasing proportion of rotifers with increasing size and proximity to the bottom among preflexion larvae was of questionable statistical significance. The first question asked was whether the very high percentage of rotifers in the diet of size-1 larvae at 6.7 m was likely to have arisen by chance from a random sampling of size-1 larvae. Formally stated, H_0 = "all size-1 larvae had the same percentage of rotifers". The 123 nonempty guts were pooled, and random samples of 84 each were drawn. In 1,000 iterations, <4% of the samples had ≥88% rotifers, so it was concluded that larvae at 6.7 m ate significantly more rotifers than similar-sized larvae near the bottom. The remaining 75 preflexion larvae (sizes 1 and 2) are divided into 4 small groups at 0.5 and 1 m, so we next tested for a size effect by pooling across sampling height, such that the guts of the 39 near-bottom size-1 larvae contained 64% rotifers, and the 36 size-2 larvae had 36% rotifers. Bootstrapping as before, <2% of samples of 36 had ≤36% rotifers, so it was concluded that size-1 and size-2 larvae differed in this regard. Further testing (e.g., of a height effect within sizes) was not done because of small sample sizes and multiple testing considerations.

Abundance and Vertical Distribution of Prey

Rotifers, all identified as the brachionoid *Trichocerca* sp., figured importantly both in the diet of preflexion larvae and in the time-related variance structure of the microplankton. As shown in Table 3, there was a change in the size spectrum of these animals that coincided approximately with the time of changing from near-bottom sampling to midwater sampling with the fish pump. It was only the largest category of rotifer (200–300 μm, including the "toe") that was found in the guts of the larvae. The relative abundance of total rotifers in the plankton at the times and heights of pump sampling differed very little (25–33% of all organisms in the 100–300 μm size class), but the percentage of rotifers in the 200–300 μm class increased from 21% (near-bottom, morning) to 86% of all rotifers (midwater, afternoon). The dominance of rotifers in the diet of size-1 larvae in midwaters is thus likely related to the larger size of rotifer resident in the water column when that height was sampled.

The most notable dietary difference among the larval size groups analyzed was the switch from small (50–300 μm) to larger (0.5–2.5 mm) prey, principally the copepod *Corycaeus anglicus* (0.5–0.8 mm), upon flexion of the notochord. The abundance of *Corycaeus* from the 100 μm mesh pump samples (Table 4) shows that this prey item was equally or more abundant in midwater than near the bottom, where all the flexion and postflexion larvae were captured. (Within the bottom meter, the similar-sized but more transparent *Paracalanus parvus* outnumbered *C. anglicus* by a factor of 5–20.) The only prey found in numbers in these larvae that was restricted to the 0.5 m samples was gammarid amphipods. Larger crustaceans—cumaceans, crab and shrimp zoea,

TABLE 3.—Density (rotifers per liter) of *Trichocerca* sp. as a function of time and sampling height. Each set of three numbers gives the density of 100–150 μm, 150–200 μm, and 200–300 μm rotifers. Height of simultaneous pump sample is given.

Time (PST):	1030			1130			1220		
Pump height:	0.5 m			0.5 m			1 m		
Sampling height (cm)	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm
750	8	0	4	4	0	10	0	0	20
100	8	14	0	0	66	0	14	22	10
50	24	18	0	0	8	40	0	34	0
25	0	2	12	16	46	0	0	30	0
Time (PST):	1313			1425			1454		
Pump height:	1 m			6.7 m			6.7 m		
Sampling height (cm)	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm
750	20	0	0	0	12	14	0	0	60
100	0	4	0	12	24	0	46	0	102
50	6	0	34	0	4	16	0	0	42
25	0	26	0	0	0	6	0	2	0

TABLE 4.—Abundance (animals m^{-3}) of copepodite and adult *Corycaeus* spp. in 100 μm mesh samples from the fish pump.

Height (m)	First sample	Second sample
6.7	1,080	460
1	120	500
0.5	180	140

mysids, and euphausid furcilia larvae—were all abundant (>10 m^{-3}) in the 0.5 m, 330 μm mesh samples but with the exception of the *callianassa* zoea mentioned above (from the gut of an 11 mm larva) were not found in these white croaker larvae.

DISCUSSION

The chief drawback of the pumping system used was its inability to obtain a simultaneous vertical profile. The sampling sequence left the possibility that differences among heights might be confounded by trends in time, as discussed by Jahn and Lavenberg (1986). Slight time effects were found among the vertical profiles of microplankton, increasing the suspicion that the apparent vertical distributions of fish larvae and macrozooplanktonic prey might have horizontal components. To contradict the argument that food-seeking did not bring postflexion larvae near the bottom, one would need to invoke either an afternoon increase of some two orders of magnitude in copepod abundance (Table 4) or else the presence of flexion and postflexion larvae throughout the water column in morning and midday followed by their sudden disappearance in the afternoon.

A two-order-of-magnitude change in copepod species abundance over a distance of roughly 1 km (2 hours at 14 cm s^{-1}) is certainly possible; though zooplankton structures reported from the southern California continental shelf are generally larger than this (Star and Mullin 1981; Barnett and Jahn 1987), there is always the possibility of sampling the edge of a patch. Since no such edge was evident in the abundance or overall composition of microplankton or of phytoplankton, it seems unlikely that a macrozooplankton change of this order occurred. Moreover, the main copepod eaten, *Corycaeus anglicus*, is generally more abundant in midwater than near the bottom over the shallow shelf (A. Barnett[4]), in accord with its apparent distribution in this study. As to a possible midwater abundance of postflexion white croaker larvae, no such concentration has ever been reported. In some nine vertical profiles taken in daylight over a 6-d period, Brewer and Kleppel (1986) took virtually all specimens >3.5 mm in their near-bottom sampler. White croaker appears similar to another abundant sciaenid, queenfish, in this regard (cf. Jahn and Lavenberg 1986).

[4]A. Barnett, Marine Ecological Consultants, 531 Encinitas Blvd., Encinitas, CA 92024, pers. commun. July 1987.

The only unequivocal instance in which a prey item of larval white croaker was vertically distributed similarly to the larvae was the trace of amphipods found in the guts of competent (flexion and postflexion) larvae. At the lengths of larvae sampled (<12 mm) the prey were all planktonic and nearly all about equally abundant in midwaters as near the bottom. The small numbers of amphipods eaten may indicate an incipient transition to larger, suprabenthic crustacean prey. The size gap between the large prey of these competent larvae and the smaller prey of preflexion larvae is probably an artifact of the bimodal size distribution of sampled larvae. Though all of the prey eaten by size-1 (<2.7 mm) larvae were <300 μm in length, the more varied diet of larger preflexion larvae contained some copepods as big as 500 μm. There is therefore nothing in these data to suggest that the switch from microplanktonic to macroplanktonic prey is anything but a gradual transition as the larvae grow.

Brewer and Kleppel (1986) also reported a change to copepod prey in white croaker larvae >6 mm. Our findings are further similar to those of Brewer and Kleppel in that there was no indication that food-seeking had anything to do with the descent of larval white croaker from midwaters to the near-bottom zone. The other definable dietary trend in this study (besides ontogenetic change) was the high percentage of rotifers eaten by midwater preflexion larvae. This was apparently related to subtle but important differences in the available planktonic prey—significantly, to a greater abundance of suitable-size rotifers—at the time the midwater stratum was sampled.

It seems safest to conclude that white croaker larvae descend toward the bottom for reasons quite apart from seeking food (see discussions in Barnett et al. [1984], Brewer and Kleppel [1986], Jahn and Lavenberg [1986]) and simply eat whatever they find there that suits them. Many potential macroplanktonic prey also favor the near-bottom layer (Jahn and Lavenberg 1986; Barnett and Jahn 1987). Older larvae and their prey may occupy the near-bottom layer for different reasons, or it may be that a single advantage, or set of pressures, underlies the behavior of these diverse planktonic and semi-planktonic taxa. Some species need to remain near shore, and living in the bottom boundary layer helps assure this. The boundary layer also tends to be more turbid than overlying waters and so may lessen an animal's jeopardy to visual (biting) planktivores. (The generality of the latter explanation only holds if suprabenthic fish larvae are less important planktivores than other water-column inhabitants—see Cushing 1983.)

Rotifers have never to our knowledge been reported as an important food of ocean-caught fish larvae, even though the genus *Brachionus* is commonly cultured for feeding larval fish in the laboratory. Schmitt (1986) reported that small, laboratory-reared larval northern anchovy readily fed upon (unidentified) wild-caught rotifers. Rotifers are only occasionally abundant in neritic waters, and never in oceanic waters (J. Beers[5]). Their rarity notwithstanding, rotifers have the ability very rapidly to dominate marine microplanktonic assemblages (Hernroth 1983), and their good food quality (Theilacker 1987) and high secondary productivity for a period of weeks might constitute a significant enhancement to growth and survival of a larval fish cohort.

Our previous experience in handling larval white croaker specimens agrees with the findings of Brewer and Kleppel (1986) in that lamellibranch larvae, easily seen through the body wall, are a common food for small white croaker larvae. In our study, this taxon was a minor constituent of the plankton and of the larval fish diet. We cannot say how unusual were the circumstances we encountered, but we know that in terms of diatom numbers and larval fish diversity these conditions were not typical of March on the southern California continental shelf. That white croaker larvae appeared to find these conditions salubrious may be one reason this species is so successful in southern California (Love et al. 1984).

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[5]J. Beers, Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. November 1986.

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LITERATURE CITED

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517–530.

BALON, E. K.
1975. Terminology of intervals in fish development. J. Fish. Res. Board Can. 32:1633–1670.

BARNETT, A. M., AND A. E. JAHN.
1987. Pattern and persistence of a nearshore planktonic ecosystem off southern California. Cont. Shelf Res. 7:1–25.

BARNETT, A. M., A. E. JAHN, P. D. SERTIC, AND W. WATSON.
1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish. Bull., U.S. 82:97–111.

BREWER, G. D., AND G. S. KLEPPEL.
1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser. 27:217–226.

BREWER, G. D., G. S. KLEPPEL, AND M. DEMPSEY.
1984. Apparent predation on ichthyoplankton by zooplankton and fishes in nearshore waters on southern California. Mar. Biol. (Berl.) 80:17–28.

BREWER, G. D., R. L. LAVENBERG, AND G. E. MCGOWEN.
1981. Abundance and vertical distribution of fish eggs and larvae in the Southern California Bight: June and October 1978. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:165–167.

BUCKLEY, L. J., AND R. G. LOUGH.
1987. Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44:14–25.

CLUTTER, R. I.
1969. The microdistribution and social behavior of some pelagic mysid shrimps. J. Exp. Mar. Biol. Ecol. 3:125–155.

CUSHING, D. H.
1983. Are fish larvae too dilute to affect the density of their food organisms? J. Plankton Res. 5:847–854.

EFRON, B.
1982. The jackknife, the bootstrap and other resampling plans. Soc. Ind. Appl. Math., Philadelphia, PA, 92 p.

GADOMSKI, D. M., AND G. W. BOEHLERT.
1984. Feeding ecology of pelagic larvae of English sole, *Parophrys vetulus*, and butter sole, *Isopsetta isolepis*, off the Oregon coast. Mar. Ecol. Prog. Ser. 20:1–12.

GOVONI, J. J., D. E. HOSS, AND A. J. CHESTER.
1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*. Mar. Ecol. Prog. Ser. 13:189–199.

GOVONI, J. J., A. J. CHESTER, D. E. HOSS, AND P. B. ORTNER.
1985. An observation of episodic feeding and growth of larval *Leiostomus xanthurus* in the northern Gulf of Mexico. J. Plankton Res. 7:137–146.

HAMNER, W. M., AND J. H. CARLETON.
1979. Copepod swarms: attributes and role in coral reef ecosystems. Limnol. Oceanogr. 24:1–14.

HERNROTH, L.
1983. Marine pelagic rotifers and tintinnids—important trophic links in the spring plankton community of the Gullmar Fjord, Sweden. J. Plankton Res. 5:835–846.

HUNTER, J. R.
1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae: morphology, ecology, and relation to fisheries, p. 34–77. Washington Sea Grant Program, Seattle.

JAHN, A. E., AND R. J. LAVENBERG.
1986. Fine-scale distribution of nearshore, suprabenthic fish larvae. Mar. Ecol. Prog. Ser. 31:223–231.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453–462.
1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212–330.

LAVENBERG, R. J., G. E. MCGOWEN, A. E. JAHN, J. H. PETERSEN, AND T. C. SCIARROTTA.
1986. Southern California nearshore ichthyoplankton: a study of abundance patterns. CalCOFI Rep. 27:53–64.

LEIS, J. M.
1986. Epibenthic schooling by larvae of the clupeid fish *Spratelloides gracilis*. Jpn. J. Ichthyol. 33:67–69.

LOVE, M. S., G. E. MCGOWEN, W. WESTPHAL, R. J. LAVENBERG, AND L. MARTIN.
1984. Aspects of the life history and fishery of the white croaker, *Genyonemus lineatus* (Sciaenidae), off California. Fish. Bull., U.S. 82:179–198.

MCGOWEN, G. E.
1987. Coastal zone ichthyoplankton assemblages off Southern California. Ph.D. Thesis, Univ. Southern California, Los Angeles, 304 p.

OWEN, R. W.
1981. Microscale plankton patchiness in the larval anchovy environment. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:364–368.

SAINTE-MARIE, B., AND P. BRUNEL.
1985. Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod crustacea over a muddy shelf in the Gulf of Saint Lawrence. Mar. Ecol. Prog. Ser. 23:57–69.

SCHLOTTERBECK, R. E., AND D. W. CONNALLY.
1982. Vertical stratification of three nearshore southern California larval fishes (*Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*). Fish. Bull., U.S. 80:895–902.

SCHMITT, P. D.
1986. Prey size selectivity and feeding rate of larvae of the northern anchovy, *Engraulis mordax* Girard. CalCOFI Rep. 27:153–161.

STAR, J. L., AND M. M. MULLIN.
1981. Zooplanktonic assemblages in three areas of the North Pacific Ocean as revealed by continuous horizontal transects. Deep-Sea Res. 28A:1303–1322.

TANAKA, M.
1985. Factors affecting the inshore migration of pelagic larval and demersal juvenile red sea bream, *Pagrus major*, to a nursery ground. Trans. Am. Fish. Soc. 114:471–477.

THEILACKER, G.
1987. Feeding ecology and growth energetics of larval northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 85:213–228.

THEILACKER, G., AND K. DORSEY.
1980. Larval fish diversity, a summary of laboratory and field research. FAO Intergov. Oceanogr. Comm. Workshop Rep. No. 28, p. 105–142.

TONT, S. A.
1981. Historical changes of diatom abundance off southern California as reflected in sea surface temperature, air temperature, and sea level. J. Mar. Res. 39:191–201.

UTERMÖHL, N.
1931. Neue Wege in der quantitativen Erfassung des Planktons. Verh. Int. Ver. Limnol. 5:567–597.

WALKER, H. J., JR., W. WATSON, AND A. M. BARNETT.
1987. Seasonal occurrence of larval fishes in the nearshore Southern California Bight off San Onofre, California. Estuarine Coastal Shelf Sci. 25:91–109.

WATSON, W.
1982. Development of eggs and larvae of the white croaker, *Genyonemus lineatus* Ayres (Pisces:Sciaenidae), off the southern California coast. Fish. Bull., U.S. 80:403–417.

WISHNER, K. F.
1980. The biomass of the deep-sea benthopelagic plankton. Deep-Sea Res. 27:203–216.