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Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California

Gary D. Brewer & G. S. Kleppel

Fish Harbor Marine Laboratory, Institute for Marine and Coastal Studies, University of Southern California, 820 South Seaside Avenue, Terminal Island, California 90731, USA

ABSTRACT: Ichthyoplankton was sampled with bongos and microplankton was sampled with a pump at 3 to 5 discrete depths over isobaths of 8, 22 and 30 m, during a winter cruise in Santa Monica Bay, California. Although no thermocline was present, fish larvae were significantly stratified ($p < 0.05$) by sampling depth during daylight hours and were relatively more dispersed at night. Larvae of northern anchovy *Engraulis mordax* and white croaker *Genyonemus lineatus* showed length-specific vertical distributions. Many large northern anchovy (≥12 mm in length) apparently migrated to the sea surface at night, but large white croaker (>6 mm in length) did not. Only 9% of northern anchovy larvae contained at least 1 food particle (i.e. 9% feeding incidence), compared to 76% for white croaker larvae. Early life stages of copepods were important foods for both fish species. Bivalve veligers and tintinids occurred relatively frequently in the guts of white croaker but not northern anchovy. There was little relation between daytime feeding distribution of fish larvae and esculent microzooplankton, except that distributions of white croaker and bivalve veligers were significantly correlated ($p < 0.05$). The low densities of bivalve veligers in samples ($\bar{x} = 3\ l^{-1}$), and paradoxically, their frequent occurrence in the guts of white croaker, are discussed in relation to their availability as food for fish larvae. The diel vertical positions of neritic fish larvae may, in part, be an expedient strategy for their retention in shallow waters.

INTRODUCTION

The belief that the early life history stages of fishes are highly susceptible to starvation, that starvation may enhance predation, and that together, starvation and predation may be the overwhelming causes of mortality (Hunter 1981) are important reasons for studying the foods and feeding ecology of larval fishes. Yet, knowledge of the small-scale, spatial distribution of ichthyoplankton and their co-occurring foods is virtually absent for neritic waters of the eastern North Pacific.

Information on the vertical distribution of ichthyoplankton, the food habits of fish larvae, and the distribution of microplankton within the California Current region have been reported independently. Previous work in offshore waters of the region have indicated that (1) most kinds of fish larvae occur predominantly in the upper mixed layer, generally at depths < 50 m (Ahlstrom 1959), (2) the eggs, nauplii and copepodite stages of copepods are the most important foods of fish larvae (Arthur 1976, Sumida & Moser 1980, 1984), although other microplankton is sometimes important (Gadomski & Boehlert 1984), (3) the apparent densities of naturally occurring foods of larval fishes are often too low for fish larvae to feed successfully (Hunter 1981), but high density patches of microplankton may occur in variable spatial and temporal dimensions, and young larvae must locate and remain in such patches in order to obtain an adequate diet (Lasker 1981, Owen 1981, Blaxter 1984), and (4) fish larvae collected with nets may show morphological signs of starvation (O'Connell 1980).

Our interest in the interaction of small-scale biological and physical features on the distribution on young fishes in shallow, nearshore waters (i.e. <40 m isobath) of southern California has been stimulated by reports that show (1) moderate to high densities of fish larvae relative to offshore waters, (2) an ichthyoplankton fauna that is different from that of offshore waters (Brewer & Brewer unpubl.), and (3) increasing microplankton densities onshore (Beers & Stewart 1967, 1970, Lasker 1978), which may indicate a region where the feeding success of fish larvae is enhanced.

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This report is the second of a series on ichthyoplankton, emerging from a winter cruise off southern California. Brewer et al. (1984) described the apparent predation on ichthyoplankton by zooplankton and fishes as identified from samples collected by bongo net and trawl. This previous paper assessed the daytime and nighttime vertical distribution of ichthyoplankton in relation to co-occurring densities of apparent predators. Fish eggs were distributed predominately in near-surface depths, but larvae of both white croaker *Genyonemus lineatus* and northern anchovy *Engraulis mordax* became strongly epibenthic during daylight hours. Both species were relatively more dispersed at night. Brewer et al. (1984) speculated that in addition to predation, the observed depth distributions of the young fishes might also be related to (1) distributions of prey, (2) an energy sparing mechanism associated with diel swim bladder inflation (Hunter & Sanchez 1976), and (3) a behavior that enables coastal fishes to maintain a nearshore distribution by avoiding unfavorable currents directed offshore. In this paper, we provide additional details on the distribution of the fish larvae, and we evaluate the hypothesis that the observed vertical gradient in densities of the larvae was a response to available microplankton foods. As in our previous report (Brewer et al. 1984), we have restricted our analysis to larvae of northern anchovy and white croaker, which are the 2 numerically dominant species in water ≤36 m in the southern California bight (Brewer & Brewer unpubl.).

METHODS AND MATERIALS

We sampled ichthyoplankton with bongo nets and microplankton with a pump during a 6 d cruise aboard the RV *Sea Watch* in Santa Monica Bay, California during January 1982. Station locations and techniques for sampling discrete surface, mid-depth and bottom strata with the bongos were described previously, as were laboratory techniques for sorting the bongo samples (Brewer et al. 1984). Our methods included both continuous and discrete measurements of temperature (CTD) and *in vivo* fluorescence at stations over isobaths of 8, 22 and 30 m along 7 transects.

Selected stations were sampled day and night with bongos (0.7 m mouth diameter with 0.335 mm mesh Nitex) fitted with an opening-closing device (McGowan & Brown 1966) and depth transducer We towed bongos horizontally (1 m s^{-1}) along surface (0 to 1 m), mid-depth (4, 11 and 15 m over bottom depths of 8, 22 and 30 m, respectively) and bottom (within 1 m of the substrate) strata. About 100 m^3 of water were filtered for each sample. We collected surface samples clear of disturbances from the ship's wake by deploying the bongos off a 4 m long horizontal boom located on the ship's port side. All running and cabin lights were turned off during nighttime surface sampling. Mid-depth and bottom samples were collected off the ship's stern.

We used a pump with a flow rate of 100 l min^{-1} to sample microzooplankton and phytoplankton at 3 to 5 depths (from 0.5 m deep to 1 m above the bottom) at selected stations that were sampled with bongos or along adjacent transects over the same isobaths (see Brewer et al. 1984). Water samples (100 l) from each depth were collected quickly and held in separate reservoirs. Water from each reservoir was then siphoned through successive Nitex screens of 0.335 mm and 0.032 mm mesh. Particles retained on the 0.032 mm screen were preserved in 4 % formalin-seawater. A 1 l subsample of water collected at each depth was preserved in Lugol's iodine for phytoplankton analysis.

In the laboratory, we identified and enumerated preserved microzooplankton and phytoplankton using a Sedgwick-Rafter cell under a compound microscope. We made aliquots of the bongo samples with a Folsom splitter (McEwen et al. 1954) to obtain representative fish larvae for measurement and gut analysis. Over 13,000 northern anchovy and white croaker were measured. Samples of larvae were placed in glycerin, and the guts of 970 northern anchovy and 967 white croaker from 21 representative bongo samples were examined for the presence or absence of food particles (i.e. feeding incidence) (Arthur 1976). We dissected randomly selected specimens from those larvae that contained at least 1 food particle, including 61 northern anchovy and 83 white croaker. The digestive tracts of the larvae were opened with insect pins, and the gut contents of each larva were broadly classified, enumerated and measured. Standard errors were computed for densities and sizes of larvae as a measure of statistical significance among sampling depths, isobaths and times.

Note that a thorough analysis of larval feeding habits is beyond the scope of this paper; such a report is planned as data from subsequent seasonal cruises becomes available.

RESULTS

As reported previously (Brewer et al. 1984), no thermocline was present over the shallow depths that were sampled; surface to bottom temperatures varied between 14.0° and 13.3 °C. Chlorophyll fluorescence was highest between the surface and 10 m depth. Total fish eggs were highly stratified, with large numbers occurring in the surface samples and low numbers

occurring in the bottom samples during both day and night. Conversely, highest densities of total fish larvae during hours of daylight occurred in the bottom samples. At night, total fish larvae were not vertically stratified. Larvae of northern anchovy and white croaker predominated the ichthyoplankton taxa, representing 24 and 63 %, respectively, of all fish larvae collected.

most abundant in bottom strata (Table 1). For example, note that the mean size of larvae in the bottom strata at the 8 m depth was greater than the mean size of larvae collected in mid-depth strata at 4, 11 and 15 m depths. While many more individuals were collected at night, (night:day catch ratio 4), the mean lengths of northern anchovy were not significantly different between samples from all depths collected during the day (length

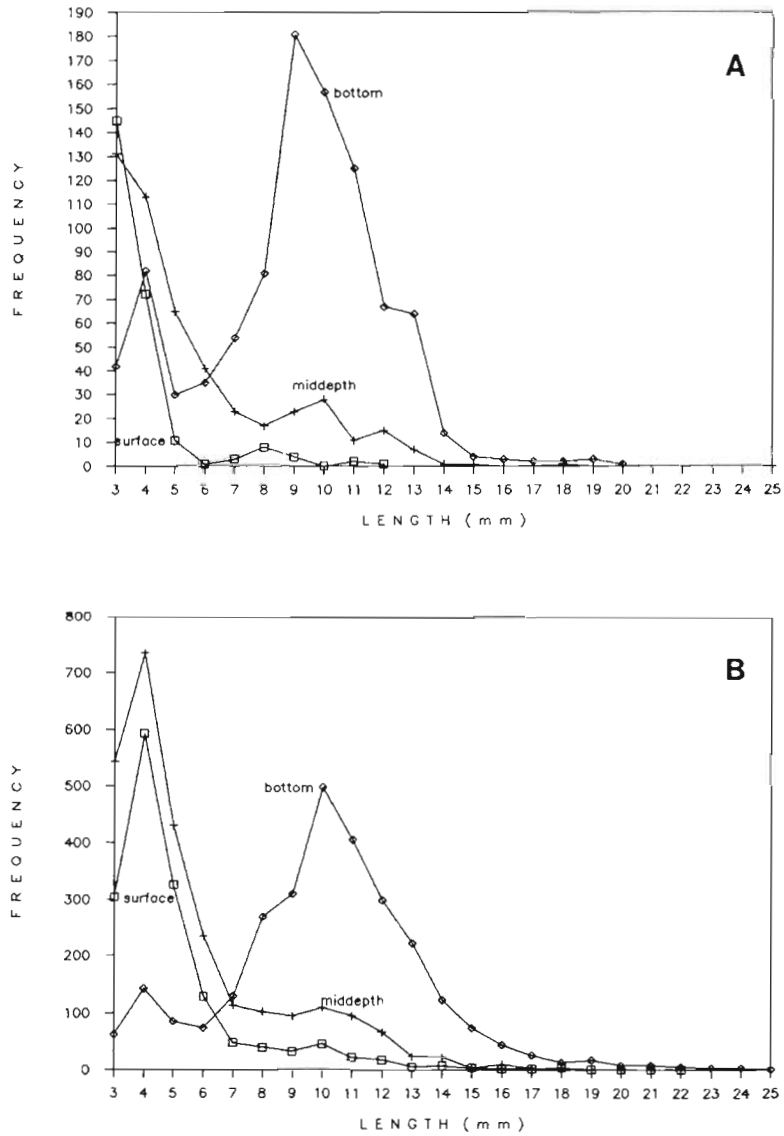


Fig. 1. *Engraulis mordax*. Length frequency data for northern anchovy larvae in 54 bongo samples collected from surface, mid-depth and bottom strata over isobaths of 8, 22, and 30 m during (A) daytime and (B) nighttime sampling

Vertical and size distribution of fish

Perhaps the salient feature of the distribution of northern anchovy larvae was the high number of large individuals in the bottom samples compared to surface and mid-depth samples (Fig. 1). Recently hatched (length 3 to 4 mm) larvae were prevalent in surface and mid-depth strata, while larvae >6 mm in length were

7.2 mm, standard error 0.1 mm) and night (length 7.3 mm, standard error <0.1 mm).

Vertical migration of northern anchovy larvae during hours of darkness was indicated because (1) individuals >12 mm in length were collected in surface samples only at night, and (2) the ratio of night:day catches was higher for surface samples (7.0) than for mid-depth (4.3) or bottom (2.8) samples.

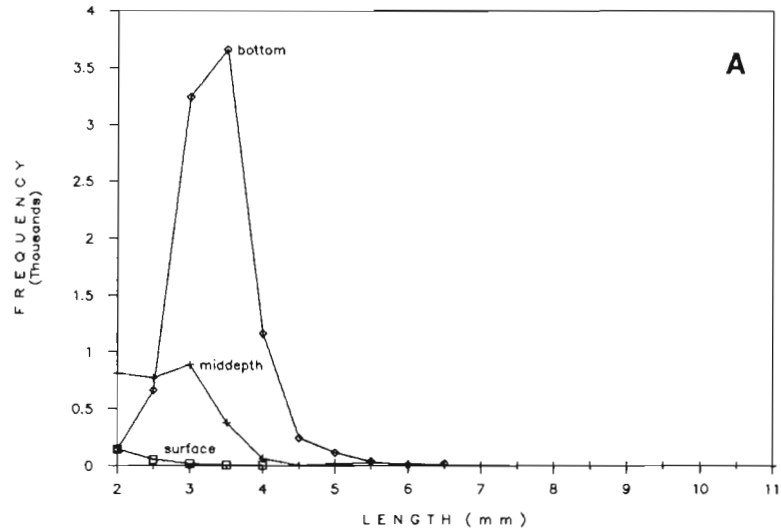
The smallest white croaker larvae (length 2 mm) were found in moderate numbers in surface and mid-depth strata, whereas larvae >3 mm in length occurred most frequently in bottom strata (Fig. 2). White croaker >6.5 mm in length were uncommon in the samples, and they were collected exclusively in bottom samples. White croaker averaged 3.2 mm in length (standard error <0.1 mm) in both daytime and nighttime bongo samples. Mean densities of white croaker by depth indicated marked vertical stratification during daylight hours (Table 1) and a more dispersed distribution at night. The ratios of night:day catches of white croaker were 10.3, 0.7 and 0.5 for surface, mid-depth and bottom samples, respectively. Although high densities of white croaker were collected in the surface strata at night compared to low densities in surface strata during the day, the absence of larvae >6.5 mm in length in nighttime surface samples suggests that large white croaker were not migrating to the sea surface.

Fish larvae feeding

Plots of feeding incidence at time of sampling show a striking contrast between the 2 species (Fig. 3). Overall, only 9 % of the northern anchovy contained at least 1 food particle, while 76 % of the white croaker contained food. Except for the period between 0400 and 0800 h PST, most white croaker contained food during both day and night, and in at least 6 samples, 100 % of the white croaker contained food. The incidence of feeding in northern anchovy was virtually 0 % between 2000 h PST and sunrise (0710 h) and never exceeded 31 % during daylight hours.

Table 1. *Engraulis mordax* and *Genyonemus lineatus*. Daytime and nighttime mean densities ($\bar{x}$ m^{-3}) and mean lengths (mm) of northern anchovy and white croaker larvae by sampling depth and isobath from 54 bongo samples (SE = standard error)

Sampling depth	Isobath (m)	Day		Night	
		$\bar{x}$ m^{-3} (SE)	$\bar{x}$ length (SE)	$\bar{x}$ m^{-3} (SE)	$\bar{x}$ length (SE)
Northern anchovy					
Surface	8	0.2 (0.1)	3.5 (<0.1)	2.5 (1.2)	6.0 (0.2)
	22	0.8 (0.6)	3.6 (<0.1)	5.1 (1.3)	4.8 (<0.1)
	30	0.6 (0.4)	4.2 (0.3)	2.0 (0.4)	4.4 (<0.1)
	Surface total	0.5 (0.2)	3.7 (<0.1)	3.5 (0.8)	5.0 (<0.1)
Mid-depth	8	0.6 (0.2)	5.6 (0.3)	2.4 (0.8)	7.7 (0.2)
	22	1.8 (0.5)	5.1 (0.1)	4.4 (1.0)	4.9 (<0.1)
	30	0.7 (0.0)	6.8 (0.4)	7.8 (2.7)	5.1 (<0.1)
	Mid-depth total	1.0 (0.3)	5.5 (0.1)	4.3 (0.9)	5.6 (<0.1)
Bottom	8	2.4 (1.1)	8.5 (0.1)	5.0 (2.5)	11.2 (0.1)
	22	1.5 (1.5)	9.5 (0.1)	5.4 (1.7)	9.5 (<0.1)
	30	0.8 (0.4)	10.2 (0.2)	3.4 (2.8)	9.8 (0.1)
	Bottom total	1.7 (0.6)	9.0 (<0.1)	4.8 (1.1)	10.1 (<0.1)
Total	8	1.0 (0.4)	7.8 (0.1)	3.3 (0.9)	9.1 (<0.1)
	22	1.3 (0.4)	6.5 (0.1)	5.0 (0.7)	6.8 (<0.1)
	30	0.7 (0.1)	7.5 (0.2)	4.4 (1.5)	6.1 (<0.1)
White croaker					
Surface	8	0.1 (0.4)	2.4 (<0.1)	2.0 (0.4)	3.8 (<0.1)
	22	1.0 (0.6)	2.1 (<0.1)	8.3 (4.3)	3.0 (<0.1)
	30	0.1 (0.1)	3.1 (0.1)	0.2 (0.1)	3.2 (0.1)
	Surface total	0.4 (0.2)	2.2 (<0.1)	4.1 (2.4)	3.1 (<0.1)
Mid-depth	8	0.7 (0.2)	2.2 (<0.1)	4.5 (2.1)	2.4 (<0.1)
	22	16.4 (3.1)	2.8 (<0.1)	6.0 (3.1)	2.9 (<0.1)
	30	4.5 (2.3)	2.8 (<0.1)	4.4 (2.7)	2.9 (<0.1)
	Mid-depth total	7.5 (2.9)	2.8 (<0.1)	5.1 (1.4)	2.8 (<0.1)
Bottom	8	5.7 (2.9)	2.8 (<0.1)	7.0 (3.9)	4.6 (<0.1)
	22	36.5 (9.7)	3.4 (<0.1)	9.4 (1.1)	3.3 (<0.1)
	30	6.1 (5.2)	3.4 (<0.1)	7.7 (7.5)	3.1 (<0.1)
	Bottom total	16.1 (6.0)	3.6 (<0.1)	8.2 (1.8)	3.6 (<0.1)
Total	8	2.1 (1.2)	2.7 (<0.1)	4.8 (1.6)	3.7 (<0.1)
	22	16.3 (5.6)	3.2 (<0.1)	7.9 (1.6)	3.1 (<0.1)
	30	3.6 (1.9)	3.1 (<0.1)	4.1 (2.5)	3.0 (<0.1)



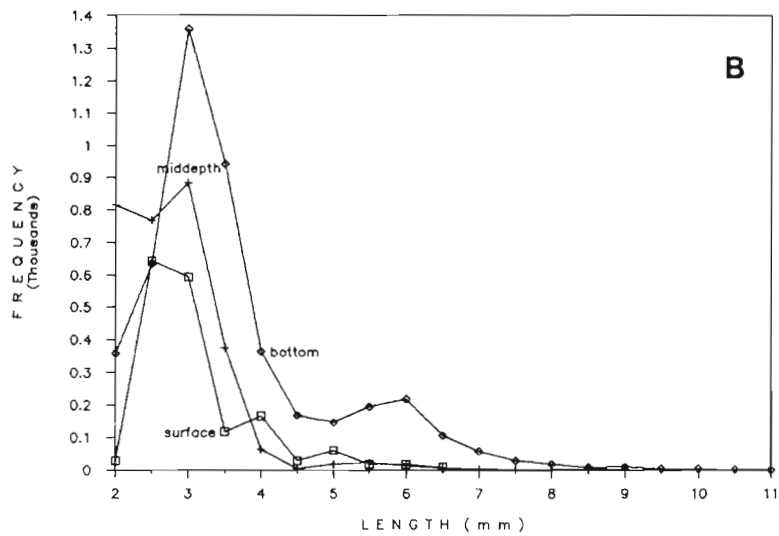


Fig. 2. *Genyonemus lineatus*. Length frequency data for white croaker larvae in 54 bongo samples from surface, mid-depth and bottom strata over isobaths of 8, 22, and 30 m during (A) daytime and (B) nighttime sampling

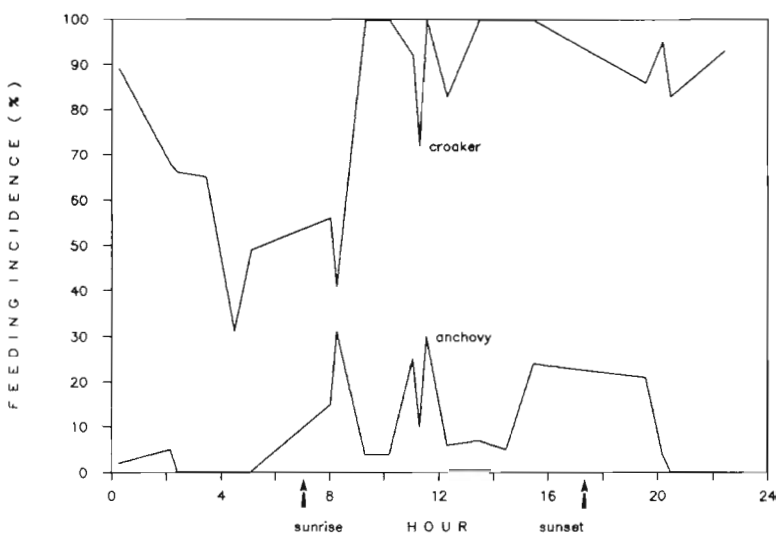


Fig. 3. *Engraulis mordax* and *Genyonemus lineatus*. Feeding incidence of northern anchovy and white croaker larvae at time of capture

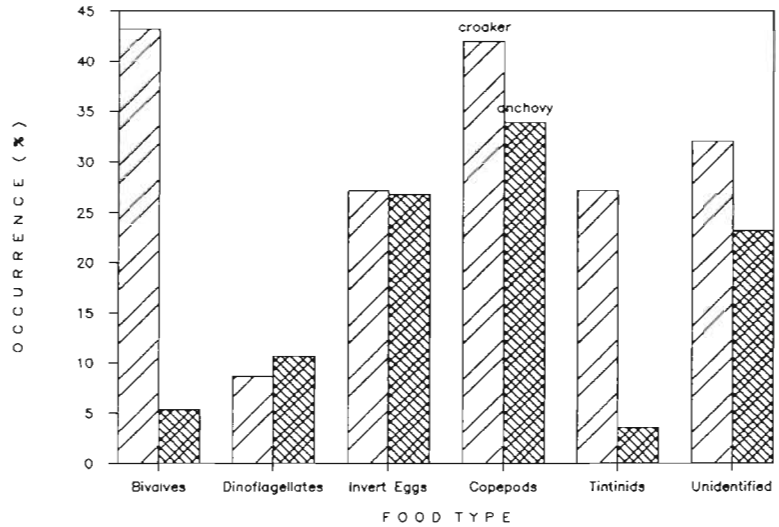


Fig. 4. *Engraulis mordax* and *Genyonemus lineatus*. Occurrence of major food types in northern anchovy and white croaker larvae. Percentages are based upon only those larvae which contained food particles

Copepods (nauplii and copepodites) occurred in 34 % of the northern anchovy and 43 % of the white croaker that contained foods (Fig. 4). Invertebrate eggs (primarily copepods) occurred commonly in northern anchovy and white croaker, while the percentage of larvae containing dinoflagellates was low for both species. Bivalve veligers and tintinids were present more frequently in white croaker (43 and 27 %, respectively) than in northern anchovy (5 and 4 %, respectively). Small white croaker, 2 to 3 mm in length, were often gorged with bivalve veligers. Bivalves that were ingested by white croaker ranged in size from 0.05 to 0.33 mm (i.e. the smallest dimension across the shell). One larva, 3.2 mm in length and with a much dis-

Table 2. Mean densities and range of densities (in parentheses) of microzooplankton taxa ($\bar{x}$ l^{-1}) from 44 samples, and phytoplankton taxa ($\bar{x}$ ml^{-1}) from 25 samples by sampling depth and isobath (SE = standard error)

Sampling depth	Isobath (m)	Copepods (nauplii & copepodites)	Invertebrate eggs	Tintinids	Bivalves	Total microzooplankton	Dinoflagellates		Diatoms	Total phytoplankton
							Armored	Unarmored		
Surface	8	37.0 (36–38)	5.5 (1–10)	39.5 (10–69)	2.0 (1–3)	132.0 (88–176)	3.6 (3–5)	6.4 (5–7)	80.4 (50–111)	110.5 (76–145)
	22	22.0 (14–24)	7.6 (3–30)	10.4 (3–31)	3.0 (0–4)	71.0 (39–142)	4.1 (3–6)	4.8 (4–6)	107.5 (49–166)	129.4 (68–191)
	30	22.8 (12–35)	10.0 (4–17)	10.7 (4–30)	3.0 (1–8)	72.0 (44–128)	2.1 (2)	1.6 (1–2)	86.0 (32–140)	97.7 (44–152)
Mid-depth	8	28.3 (12–45)	9.0 (2–14)	21.0 (4–54)	1.3 (1–2)	90.7 (58–145)	2.8 (1–5)	7.0 (7)	77.3 (38–117)	100.7 (58–143)
	22	26.7 (12–36)	10.2 (2–33)	14.1 (2–36)	2.0 (1–6)	90.8 (46–133)	1.6 (1–2)	3.7 (3–6)	74.6 (16–136)	92.9 (37–153)
	30	24.1 (6–41)	14.4 (1–26)	14.4 (2–57)	2.6 (1–8)	80.8 (43–151)	1.7 (1–2)	3.4 (1–5)	53.9 (7–102)	69.8 (14–122)
Bottom	8	43.0 (30–56)	23.5 (18–29)	29.5 (7–52)	4.0 (4)	177.5 (151–204)	– –	– –	– –	– –
	22	38.8 (27–66)	19.3 (2–38)	49.3 (3–127)	5.0 (2–14)	160.5 (57–318)	1.4 (1–2)	2.8 (3)	68.2 (26–110)	81.6 (41–122)
	30	18.8 (6–32)	4.6 (0–12)	38.2 (17–68)	1.6 (1–2)	105.2 (51–178)	2.4 (2–3)	3.4 (2–4)	60.5 (34–87)	74.7 (44–105)
Overall $\bar{x}$ (SE)		26.4 (1.9)	10.8 (1.3)	20.5 (3.7)	2.7 (0.4)	96.6 (8.2)	2.2 (0.2)	4.0 (0.3)	74.0 (8.8)	92.5 (9.3)

tended gut, contained 13 bivalves ranging in size from 0.08 to 0.12 mm. When present, an average of 3.3 bivalves occurred within the stomachs of white croaker. Besides bivalves, small white croaker contained roughly equal proportions of invertebrate eggs, tintinids, and copepod nauplii. Bivalves and copepodites were numerically dominant in larvae up to 6 mm in length and copepodites predominated in the largest larvae that we examined (8 mm in length). Invertebrate eggs, dinoflagellates, and unidentified spherical particles were numerically dominant in the smallest northern anchovy larvae (3 to 4 mm in length). Copepod nauplii and copepodites were relatively abundant in larvae of intermediate size. Unlike the large white croaker larvae, few of the large northern anchovy larvae (>10 mm in length) contained food (see Arthur 1976). The largest northern anchovy that we dissected (up to 13 mm in length) contained only copepods.

Densities and distribution of microplankton

Microzooplankton and phytoplankton were typically patchy, showing wide variability by sampling depth and isobath (Table 2). Densities of tintinids and total microzooplankton differed significantly among surface, mid-depth and bottom samples (Table 3), with highest concentrations found in bottom samples. Armored dinoflagellates varied significantly among 8, 22 and 30 m isobaths, with highest concentrations collected over the 8 m bottom depth. It is noteworthy that the single highest concentration of total fish larvae (56.8 m^{-3}) was collected in a bottom sample over the 22 m isobath, as were the highest densities of copepod nauplii and copepodites (66 l^{-1}), invertebrate eggs (38 l^{-1}), tintinids (127 l^{-1}), bivalve veligers (14 l^{-1}) and total microzooplankton (318 l^{-1}). Hence, densities of microzooplankton in the one sample were 2 to 6 times average concentrations.

DISCUSSION

We found marked vertical gradients during daylight hours in the densities of fish eggs (Brewer et al. 1984) and in the densities and length frequencies of fish larvae. It is striking that such density and size gradients of fish larvae existed in these shallow waters in the absence of gradients in prey abundance and in the absence of significant thermal structure. Both day and night samples showed fish eggs most concentrated in surface strata, young larvae (northern anchovy <6 mm in length and white croaker <3 mm in length) occurring most frequently in mid-depth strata and large larvae most abundant in bottom strata. Also of particular interest to us were the differences in the incidence of feeding and gut contents between northern anchovy and white croaker larvae collected in the same samples.

Diel vertical distribution

Ahlstrom's (1959) analysis of the vertical distribution of northern anchovy larvae, which encompassed sampling depths from the surface to 285 m, emphasized the relation of the thermocline with the vertical position of the larvae. Larvae were collected as deep as 105 m but over 87% occurred in the upper 41 m; virtually all larvae occurred in the upper mixed layer. Ahlstrom's (1959) data were re-examined by Hunter & Sanchez (1976), and these latter authors

Table 3. Probability of significant variability (Kruskal-Wallis analysis of variance, Siegel 1956) of ichthyoplankton, microzooplankton and phytoplankton by diel period (day and night), sampling depth (surface, mid depth and bottom) and isobath (8, 22 and 30 m)

	Total fish eggs	Total fish larvae	Northern anchovy	White croaker	Copepods (nauplii & copepodites)	Invertebrate Eggs	Tintinids	Bivalves	Total microzooplankton	Dinoflagellates		Diatoms	Total phytoplankton
										Armored	Unarmored		
Diel	ns	0.05	0.001	ns	ns	ns	ns	ns	ns	ns	ns	0.001	0.001
Sampling depth	0.001	0.001	ns	0.001	ns	ns	0.05	ns	0.05	ns	ns	ns	ns
by day only	0.001	0.001	0.05	0.001	ns	ns	ns	ns	ns	0.05	ns	ns	ns
by night only	0.01	ns	ns	ns	ns	ns	0.01	ns	0.05	ns	ns	ns	ns
Isobath	ns	0.001	ns	0.01	ns	ns	ns	ns	ns	ns	0.01	ns	ns

ns: Not significant ($p > 0.05$)

indicated that only larvae >11.75 mm in length showed evidence of vertical migration to the surface. Similarly, our nearshore data showed northern anchovy >12 mm in length occurring in surface samples only at night. Schlotterbeck & Connolly (1982) captured large anchovy (to a length of 30 mm) relatively frequently in neuston samples at night. Hunter & Sanchez (1976) suggest that northern anchovy fill their swim bladders at the sea surface in order to conserve energy during nighttime hours when the larvae do not feed. Many clupeoids apparently exhibit similar behavior (Blaxter & Hunter 1982).

Previous nighttime collections in neuston, mid-depth and bottom strata over isobaths between 8 and 15 m corroborate our data on the vertical distribution of white croaker larvae. Schlotterbeck & Connolly (1982) found that the smallest white croaker larvae (<3 mm in length) often predominated in the mid-depth and neuston strata, while larger larvae were most abundant in bottom strata; white croaker >6 mm in length were almost never collected in the neuston.

Hence, our data suggest that both northern anchovy and white croaker larvae were vertically stratifed during daylight hours and both species were relatively more dispersed at night. Many large northern anchovy migrated to the sea surface at night but apparently large white croaker did not.

We recognize that the results may be influenced by the ability of larger larvae to avoid capture, especially during daylight hours. Smith (1981) showed that the night:day capture ratio increased with the length of northern anchovy larvae when sampling was conducted with bridled, 1 m diameter plankton nets. Net avoidance is markedly reduced by using bongos or other bridle-free nets (Smith & Richardson 1977), and our results suggest that net avoidance did not significantly confound the diel patterns in vertical distribution. Large northern anchovy larvae were more prevalent in our nighttime samples, and the overall night:day capture ratio was 4. However, the average size of northern anchovy did not vary significantly between night and day because small larvae were also captured more frequently at night. More white croaker larvae were captured during the day (night:day ratio, 0.7), and the average size of the larvae was not significantly different between night and day. The differences in the night:day capture ratios may be attributable, in part, to diel changes in (1) migration of larvae to strata not sampled by our nets, and (2) the advection of larvae from offshore waters.

Our results might be biased if the susceptibility of larvae to capture varies among nets towed along surface, mid-depth and bottom strata. For example, escapement might be reduced along the surface and bottom relative to mid-depths, because in the surface and bottom strata, options for escape are, perhaps, restricted by physical barriers.

Incidence of feeding

There has been considerable interest in the spatial and temporal co-occurrence of larval fishes and microplankton, and in the prey densities that are required for successful feeding by fish larvae (Blaxter 1984). Previous work has shown that the eggs, nauplii and copepodite stages of copepods are the primary foods of northern anchovy larvae (Arthur 1976) and most marine fish larvae (Hunter 1981, Turner 1984), and our nearshore work substantiates the important role of copepods in the diet of northern anchovy and also white croaker. The densities of copepod early life history stages that we found in Santa Monica Bay (Table 2) were typical of other regions that have been studied (Theilacker & Dorsey 1980). However, microplankton were probably in low to moderate densities during January compared to late winter and spring months, when spawning by northern anchovy and white croaker peak (Brewer & Brewer unpubl.). There was little evidence of significant vertical stratification of microzooplankton from our samples collected by pump that would complement the daytime (feeding) distribution of the larval fishes (Table 3). Correlations among the distributions of fish larvae, microzooplankton and phytoplankton taxa were significant ($p < 0.05$) only between total fish larvae and bivalve veligers and between white croaker and bivalve veligers (Spearman's rank correlation coefficient, Siegel 1956). However, we have already noted ('Results' section) the spatial correspondence between the highest sample density of microzooplankton and the highest sample density of total fish larvae. The low incidence of feeding that we found for northern anchovy was similar to the incidence of feeding that Arthur (1976) found for northern anchovy and is typical of fish larvae with straight digestive tracts, i.e. larvae with straight guts often void their gut contents upon capture (Hay 1981, Blaxter & Hunter 1982). White croaker larvae have a coiled gut and were apparently not susceptible to gut clearance when collected. Voiding of gut contents by fish larvae is an artifact of sampling that may have important effects on the interpretation of feeding incidence. Partial gut clearance and differential gut clearance of certain sizes or taxa of food particles are possible. Nevertheless, we are confident that our data reveal general patterns of feeding incidence and foods eaten that reflect real conditions.

The percentage of northern anchovy and white croaker that contained food often varied considerably in the same sample. For example, within the bongo

sample collected at 0825 h PST (Fig. 4) occurred both the highest percentage of northern anchovy containing food (31 %) and the lowest percentage of white croaker containing food (41 %) during daylight hours. Similarly, within the sample collected at 0930 h PST, we observed 100 % feeding incidence for white croaker and only 4 % feeding incidence for northern anchovy. Besides the probable artifacts of sampling associated with the voiding of gut contents by northern anchovy, differences in food habits might account for some of the variability in feeding incidence between the 2 species.

While the incidence of food in the gut of northern anchovy fell to zero within 2.5 h of sunset, the incidence of food in the guts of white croaker remained high until midnight and then declined rapidly, reaching the lowest level at about 0400 h PST (Fig. 3). The apparent slower rate of digestion for white croaker may be related to the shape of their gut and perhaps the frequent occurrence of bivalve veligers in their gut contents.

Kinds of food

Mollusc veligers have been reported as an infrequent food for other species of fish larvae (Hunter 1981), and Arthur (1976) reported the occurrence (2 individuals) of bivalve veligers in northern anchovy larvae. Checkley's (1982) laboratory experiments showed that herring *Clupea harengus* larvae, 3.0 mm in length and with a straight gut similar to northern anchovy, ingested bivalve veligers but did not digest them. Larger herring larvae refused bivalves as food. Our samples from Santa Monica Bay showed that only northern anchovy < 3.5 mm had ingested bivalves. By comparison, we have observed bivalves in the guts of white croaker larvae (throughout the size range captured with bongos), not only during the winter cruise in Santa Monica Bay, but during previous and subsequent cruises in nearshore areas throughout southern California (unpubl.). We have also noted the occurrence of bivalve veligers in the guts of the larvae of other croakers (family Sciaenidae) including queenfish *Seriphus politus,* California corbina *Menticirrhus undulatus,* black croaker *Cheilotrema saturnum,* and white sea bass *Atractoscion nobilis* during spring and summer cruises and in several species of gobies (family Gobiidae) and other taxa collected throughout the year.

Mean densities of bivalve veligers in our microplankton samples were well below the mean densities of other larval fish foods, including copepod nauplii and copepodites, invertebrate eggs and tintinids (Table 2). None of the 44 microzooplankton samples had extraordinary concentrations of bivalves, with $14\ l^{-1}$ the highest concentration recorded. The low densities of bivalves, and paradoxically, their frequent occurrence in the guts of white croaker, are inconsistent with our current understanding of larval fish searching behavior and feeding success (Hunter 1981). High densities of bivalves may have occurred either in patches that were too small to be discriminated by our sampling techniques or in strata not sampled. Owen (1981) demonstrated that microplankton patches occur at scales of < 1 m, which is well below the spatial resolution of our pump and net samples. Perhaps the high density of white croaker larvae in the bottom samples during the day is a clue to the distribution of the bivalves, i.e. bivalves may have occurred in an epibenthic layer just below our near-bottom samples of microplankton.

In nearshore waters, white croaker and certain other larvae may exploit bivalve veligers as a relatively rich source of food that are not suitable as food for the numerically dominant clupeoids. We need to test this supposition with both laboratory feeding experiments on assimilation efficiency and with finescale sampling in the field to learn more about the nature and extent of these distributional enigmas and feeding relations.

Finally, while fish larvae may seek favorable environments in both horizontal and vertical planes by responding to gradients in foods (Lasker 1981), other cues including, light, turbulence, oxygen, currents, conspecifics (i.e. schooling) and predators may also be important (Theilacker & Dorsey 1980, Sameoto 1984). The environmental factors that are most advantageous at any given time probably vary by species and life stage (Sameoto 1984). For neritic fishes such as white croaker that as adults feed and spawn exclusively over shallow depths, mechanisms that help retain their early life history stages in nearshore waters would be expedient (see Parrish et al. 1981, Bakun & Parrish 1982). For example, Smith et al. (1978) proposed that diel vertical positions of yellowtail flounder *Limanda ferruginea* would result in their localized settlement because at night the larvae were caught in the wind-driven surface layer, while during the day the larvae moved in the opposite direction at mid-depths. A similar behavioral strategy may be used by coastal fishes off southern California where surface transport is generally shoreward (Schwartzlose & Reid 1972, Dewees & Strange 1984). The largest mean lengths of northern anchovy and white croaker larvae (Table 1) were found at night at the most shoreward (8 m isobath) stations, possibly indicating a cycle of onshore transport associated with nighttime, upward migrations. Larvae might also help maintain their position nearshore by residing in a stable boundary layer, just above the sediments (Brewer et al. 1984).

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