Vertical distribution of eggs and larvae of northern anchovy, *Engraulis mordax*, and of the larvae of associated fishes at two sites in the Southern California Bight

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Abstract.–We studied fine-scale vertical distribution of northern anchovy, *Engraulis mordax*, eggs and larvae and larvae of associated species at two stations off southern California in March–April 1980 using a Manta (neuston) net and a MESSHAI (multiple opening-closing net) sampler. A pump and fluorometry system was used to obtain chlorophyll profiles. A storm with associated heavy seas interrupted sampling for two days at the inshore station and provided an opportunity to compare pre- and poststorm egg and larval distribution and abundance. A total of 95,552 fish larvae were taken in the MESSHAI (63 tows) and Manta nets (41 tows), representing 49 taxa (genera or species) in 27 families. *Engraulis mordax* was the most abundant fish (95% of the total), followed by *Leuroglossus stilbius*, *Genyonemus lineatus*, *Stenobrachius leucopsarus*, *Sebastes* spp., *Seriphus politus*, *Peprilus simillimus*, *Paralichthys californicus*, *Citharichthys* spp., and *Merluccius productus*. Anchovy eggs and larvae had a shallow distribution: 90% of larvae and 95% of eggs were found in the upper 30 m. Peak egg density was found in the neuston; peak larval density, in the 10–20 m stratum. Larvae of shallow-living shelf species (*G. lineatus*, *P. simillimus*, *P. californicus*) typically occurred in the upper 20–30 m, whereas larvae of predominantly deeper-living demersal species (*Sebastes* spp., *M. productus*) were found in the upper 80 m. Midwater species (*L. stilbius*, *S. leucopsarus*) occurred at least to 200 m. Anchovy eggs decreased in number after the storm. Anchovy larvae declined even more sharply, despite an increase in zooplankton and potential larval fish prey, suggesting that starvation may have resulted from disturbance of microscale food patches. Alternatively, larvae may have been advected away from the site. Shallow-water shelf species were rare at the inshore station before the storm but appeared suddenly afterwards as a result of seaward advection of shelf water by Ekman transport.

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The use of ichthyoplankton techniques for estimating the biomass of fish stocks has increased markedly over the past two decades (Hunter and Lo, 1993). Information on the horizontal and vertical distribution of eggs or larvae of a target species is a requirement for quantitative sampling of these stages and for interpreting data from integrated net tows and from recently developed samplers such as the continuous underway egg pump (Checkley et al., 1997). The daily egg production method (DEPM) was developed at the Southwest Fisheries Science Center to provide annual biomass estimates needed to manage northern anchovy, *Engraulis mordax*, an important coastal pelagic species inhabiting the California Current region (Lasker, 1985). During the development of this method a cruise was conducted off southern California that employed a MESSHAI, a sampler with opening-closing nets and environmental sensors, to determine fine-scale vertical distribution of eggs and larvae of *E. mordax* (see preliminary data in Pommeranz and Moser, 1987). This information was needed to supplement Ahlstrom's (1959) vertical distribution study based on 22 Leavett net tows taken on 9 cruises over a 14-year period off southern California and Baja California. The MESSHAI study supplied information on depth, ambient temperature, and diurnal periodicity of *E. mordax* eggs needed to develop the DEPM (Lasker, 1985). To compare distributions at different bottom depths, sampling was conducted at two localities: an offshore site over the Santa Catalina Basin and an inshore site over the upper continental slope off Dana Point, California. Anchovy larvae, the dominant species in the MESSHAI samples, were counted and measured for subsequent growth and mortality studies. A storm interrupted sampling at the inshore station and provided an opportunity to study the influence of water column disturbance on the abundance and depth distribution of eggs and larvae of anchovy and associated species. Mullin et al. (1985) described the effects of this storm on the abundance and vertical structure of phytoplankton, zooplankton, and total fish larvae on the basis of pump samples taken at the same time as the MESSAI sampling at a locality just shoreward of the inshore MESSHAI site.

This paper presents a preliminary analysis of the fine-scale vertical distribution of anchovy eggs and larvae and the larvae of other taxa, with comparisons of the offshore and inshore sites and of the prestorm and poststorm periods at the inshore site. A separate paper addressing age-specific vertical distribution and mortality of anchovy eggs and larvae is in preparation.

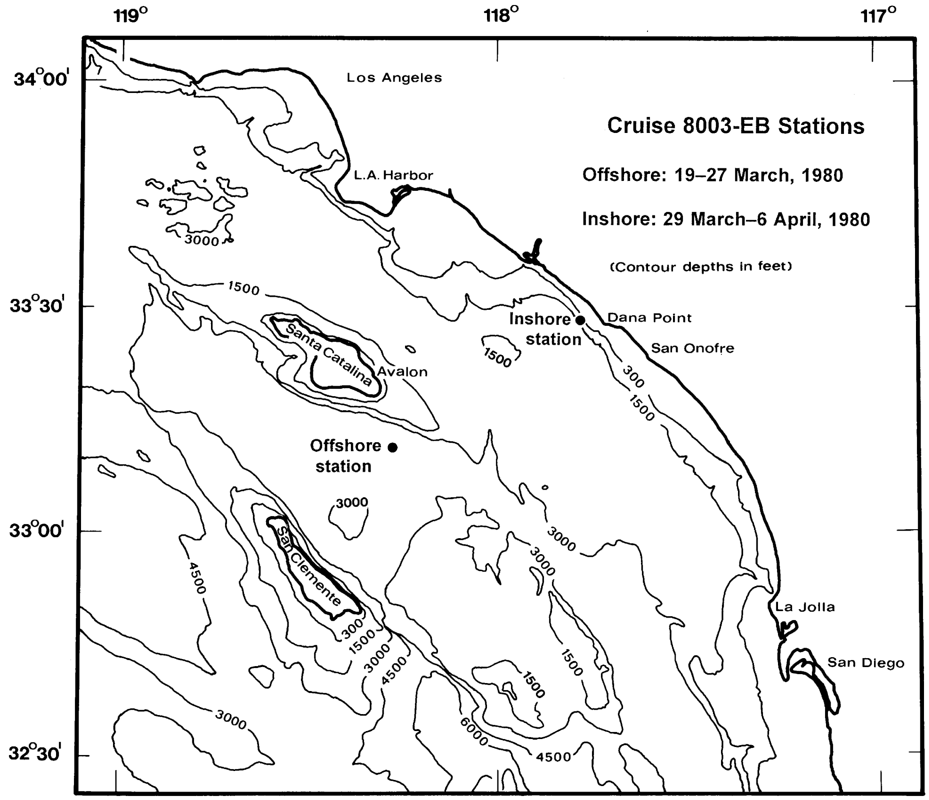

Figure 1

The Southern California Bight, showing stations occupied on Cruise 8003-EB (modified from Shepard and Emery, 1941).

Methods and materials

Cruise 8003-EB was conducted aboard RV *Ellen B. Scripps* at two sampling sites in the Southern California Bight (SCB; Fig. 1). The first site (33°11.1'N, 118°16.5'W), occupied 19–27 March 1980, was located 13 km south of the east end of Santa Catalina Island, over an ~1150 m bottom depth. This site lies over the Santa Catalina Basin, one of 13 deep basins that characterize the offshore region of southern California (Ebeling et al., 1970; Eppley, 1986). The midwater fish fauna of these basins is a mix of subarctic, transitional species of the California Current and species from the eastern tropical Pacific and central water masses whose distributions extend into the region. The site is close enough to Santa Catalina Island to have larvae of shelf species (Hobson and Chess, 1976) in addition to larvae of slope and basin floor species (Cross, 1987). The second site (33°28.5'N, 117°47.0'W), occupied 29 March–6 April 1980, was ~4.5 km off Dana Point, over the upper continental slope at approximately 430 m bottom depth. Here the adjacent shelf narrows to a minimum of about 3 km but supports rich fish communities associated with rocky reefs and kelp forests (Feder et al., 1974; Cross and Allen, 1993) and soft-bottom habitats (Mearns, 1979; Love et al., 1986; Allen and Herbinson, 1991; Cross and Allen, 1993). The continental slope, also relatively narrow here, supports a fish assemblage typical of other southern California slope regions (Cross, 1987). The first site corresponds to California Cooperative Oceanic Fisheries Investigations (CalCOFI) station 90.2, 35.8 and the second to station 90.0, 28.2. Sampling at the offshore station was interrupted twice by heavy seas (0055, 21 March to 0908, 23 March; and 1730, 26 March to 0836, 27 March). A storm with associated heavy seas curtailed sampling at the inshore site at 0315, 1 April; the station was reoccupied at 0655, 3 April.

The principal samplers used were the Manta net (Brown and Cheng, 1981) for sampling the surface layer (0–15.5 cm) and the MESSHAI for sampling discrete depth strata in the upper 200 m. The MESSHAI sampler was a modified Gulf-V sampler (Arnold, 1959; Nellen and Hempel, 1969) with a 25×25 cm mouth opening, six opening and closing nets operated from a computer deck unit, and an environmental sensing package (Pommeranz and Moser, 1987). All nets were fitted with 300-μm mesh. A sampling sequence for a day or night station consisted of a five-minute Manta tow, followed by an oblique MESSHAI tow that sampled 10-m strata from 50 m to the surface, an oblique MESSHAI tow which sampled 40-m strata from 200 m to the surface, a second MESSHAI tow which sampled 10-m strata from 50 m to the surface, and a second Manta tow. A total of 17 Manta tows (10 day, 7 night) were taken at the offshore station, 24 (13 day, 11 night) at the inshore station (Figs. 2 and 3). All MESSHAI tows were stepped oblique hauls. In the shallow tows the sampler was lowered to 50 m and retrieved through five 10-m strata, each in 2.5-m steps lasting two minutes, with a total of five horizontal phases per stratum. Depth, temperature, and flowmeter profiles were recorded by the deck unit throughout each tow. Bucket surface temperatures were taken periodically to calibrate the MESSHAI temperature sensor. In the deep tows the sampler was lowered to 200 m and retrieved through five 40-m strata, each in five steps lasting two minutes. The total number of successful MESSHAI tows was 24 (shallow: 9 day and 8 night; deep: 4 day and 3 night) at the offshore station and 36 (shallow: 12 day and 12 night; deep: 6 day and 6 night) at the inshore station. Improper preservation or breakage resulted in the loss of anchovy eggs in net 4 (20–30 m stratum) of tow 42 and the entire sample from net 3 (30–40 m stratum) of tow 61. Three MESSHAI tows were unsuccessful owing to technical difficulties, and the samples were subsequently discarded. All tows were made at a ship speed of ~1.5 knots. Before each net tow series at the inshore station, a pump and fluorometry system (Lasker, 1978) was used to obtain a chlorophyll profile down to 40 m depth. Water samples were taken at the surface and at the chlorophyll maximum for chlorophyll-*a* and phaeophytin extraction and fluorometry, and for identification and counts of major phytoplankton taxa (analyses not included in this paper). Oblique bongo net samples were taken at each station at a ship speed of about 1.5 knots; except for length-frequency information, data from these tows are not addressed in this paper.

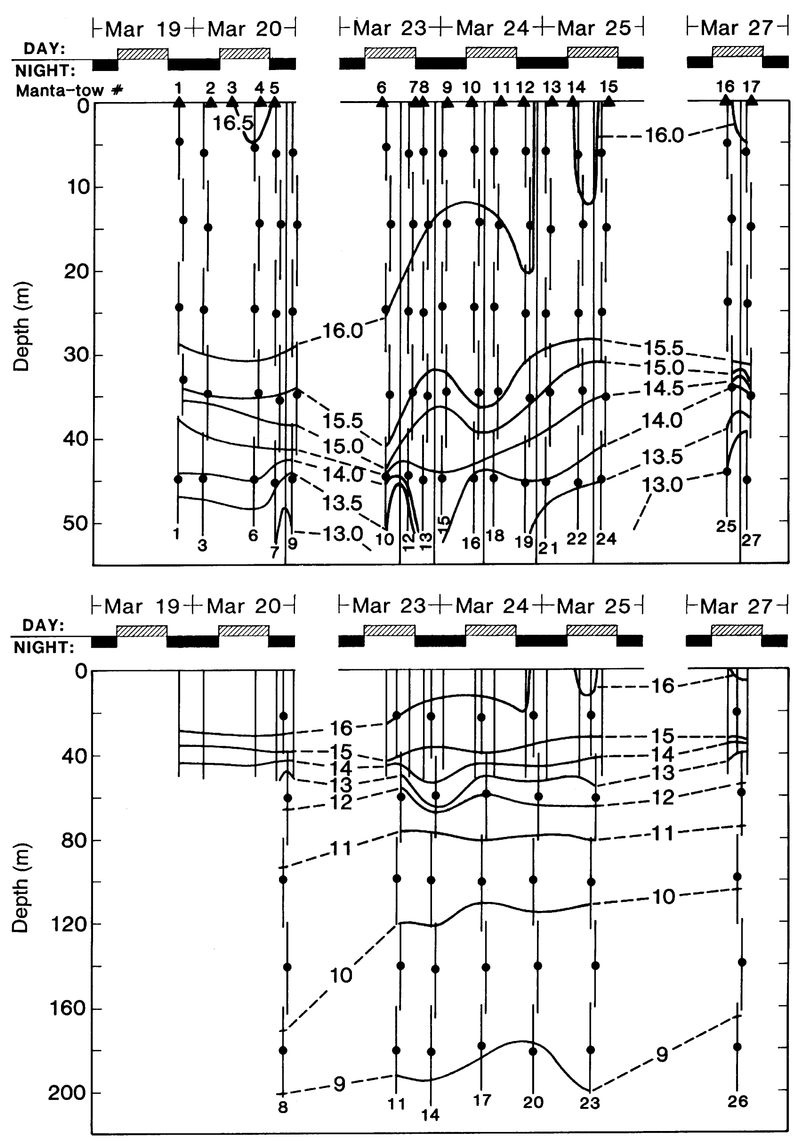

Figure 2

Diagram showing chronology of MESSHAI tows, depth strata sampled, and isotherms for the offshore station (from Pommeranz and Moser, 1987). (**Above**) Shallow (50 m) and Manta tows; the dots represent average depths for each net; the seven complete vertical lines show when deep (200 m) tows were taken. Tow numbers for Manta tows are given above solid triangles and tow numbers for MESSHAI tows are given at the bottom of each series of vertical lines. Isotherms are shown in 0.5°C intervals. (**Below**) Deep tows; the 17 lines extending down to 50 m indicate when shallow tows were taken. Isotherms are shown in 1°C intervals.

Most samples were preserved in 5% buffered formalin; selected samples were preserved in 80% ethyl alcohol for analysis of otolith daily growth rings in anchovy larvae. Prior to sorting, wet zooplankton displacement volume of each sample was measured using standard techniques (Kramer et al., 1972). Anchovy larvae and eggs were identified and removed during the plankton sorting process; eggs were classified by stage according to the criteria of Moser and Ahlstrom (1985) and length measurements of larvae were taken to the nearest 0.5 mm. Larvae of other fish were identified to the lowest taxon possible and body lengths were measured to 0.1 mm.

We used analysis of variance (ANOVA) to compare the pre- and poststorm densities of anchovy eggs and larvae for shallow strata and also for deep strata at the inshore and offshore stations. Day and night data were pooled for each of these categories because the data did not indicate a diurnal shift in vertical distribution of eggs or larvae. All data were log-transformed for statistical analyses because the original data were highly skewed. Data from the shallow strata included the Manta tows, the MESSHAI shallow tows (0–50 m), and the upper 40 m from the MESSHAI deep tows. Data for the deep strata were from below 40 m from the deep MESSHAI tows. A two-way ANOVA was performed for the shallow strata, the two factors being station (inshore and offshore) and tow type (Manta, MESSHAI shallow, and MESSHAI deep). Interaction terms were included in the analysis. One-way ANOVA was performed for data from the deep strata to compare anchovy larval density at inshore and offshore stations.

In the analysis of prestorm and poststorm conditions two separate ANOVAs were performed because an initial ANOVA of anchovy eggs from the shallow strata indicated a strong interaction between tow type and pre- or poststorm period; one analysis was based on data from shallow and deep MESSHAI tows and the other was based on Manta tows only. A single two-way ANOVA test was performed for anchovy larvae because the density of anchovy larvae in Manta tows was low and the analysis adequately described the effect of the storm on larval density based on both shallow and deep MESSHAI tows.

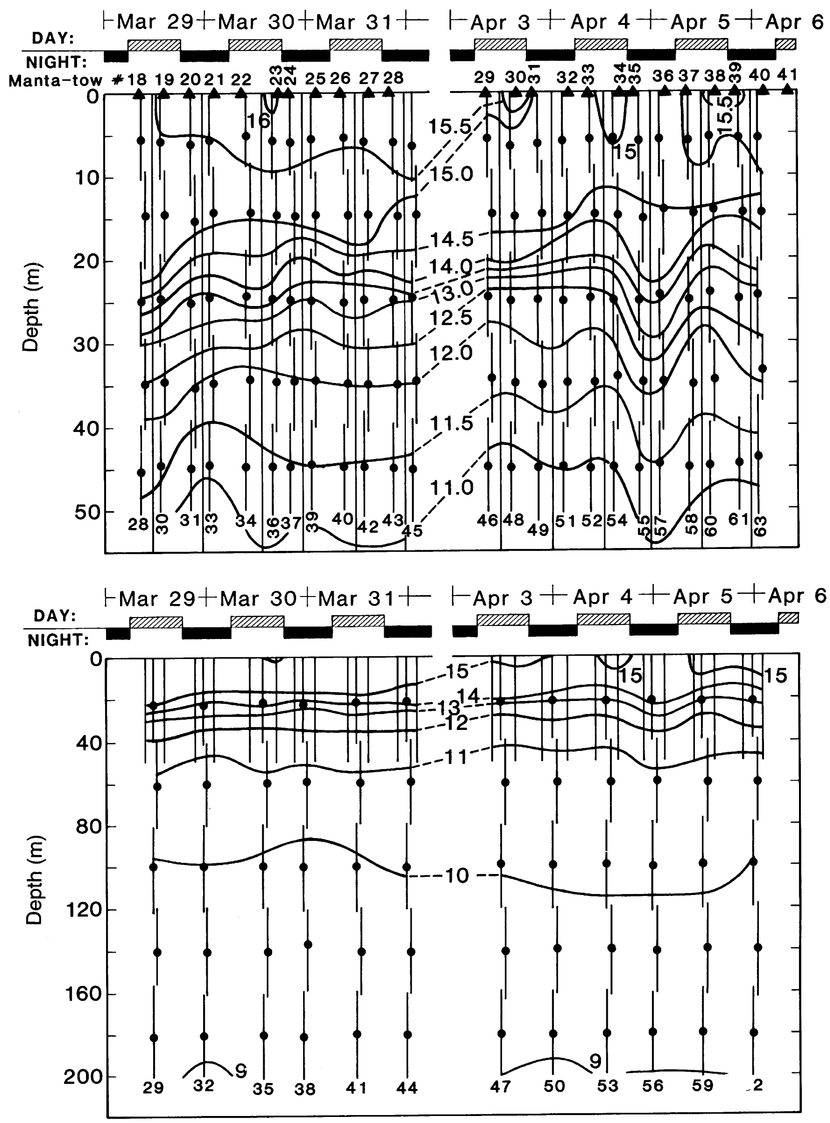

Figure 3

Diagram showing the chronology of MESSHAI tows, depth strata sampled, and isotherms at the inshore station. Symbols and labels are the same as those in Figure 2 (from Pommeranz and Moser, 1987).

Results

Environmental features

The thermal structure of the study area was typical for March–April in that region of the SCB, with a pool of relatively warm water subject to intrusions of advected upwelling plumes from the Point Conception area (Lasker et al., 1981; Lynn et al., 1982). The mixed layer was about 30–40 m deep at the offshore station (Fig. 2) and only about 10–30 m deep at the inshore station (Fig. 3). Overall, the water was colder at the inshore station, which lacked the prominent 16.0° isotherm present offshore. Average temperature was higher at the offshore station in all depth strata except 160–200 m (Fig. 4, A and B). At the inshore station after the storm the thermocline shoaled to 15–20 m and water temperature was lower than before the storm at all depths below 80 m (Figs. 2; 3; 4, C and D).

Wind and sea-state observations taken during the cruise and supplemented by data from the Naval Air Station at San Clemente Island, southwest of the offshore station, and the San Onofre Nuclear Generating Station, just southeast of the inshore study area (Fig. 1), indicated an oscillating land-sea system which was more evident at San Onofre than at San Clemente (Fig. 5). During the night and morning, winds typically were from the NNE, after which they shifted through the south to the NW until late afternoon or evening. Average wind speed was about 10 knots at the offshore station and about 6 knots at the inshore station; average swell height was about 1.7 m and about 1 m at the two sites, respectively (Fig. 6). At the inshore station wind speed was more than 24 knots during the storm.

Prior to the storm at the inshore station there was a moderate to strong chlorophyll maximum at 18–29 m (Fig. 7). Following the storm, the chlorophyll peak became shallower and generally broader. The peak was at 15 m on the morning of 3 April; by the evening of 4 April, the maximum was near the surface. On the following two days the peak reappeared and began to deepen and strengthen. Average plankton volumes of Manta and MESSHAI samples from the upper 40 m were distinctly higher at the inshore station than at the offshore station (Fig. 8, A and B). Average volumes were generally higher in strata within the upper 40 m in poststorm samples compared with those taken prior to the storm (Fig. 8, C and E). Average plankton volume increased markedly in the 40–80 m stratum, whereas there was little change in deeper strata (Fig. 8E).

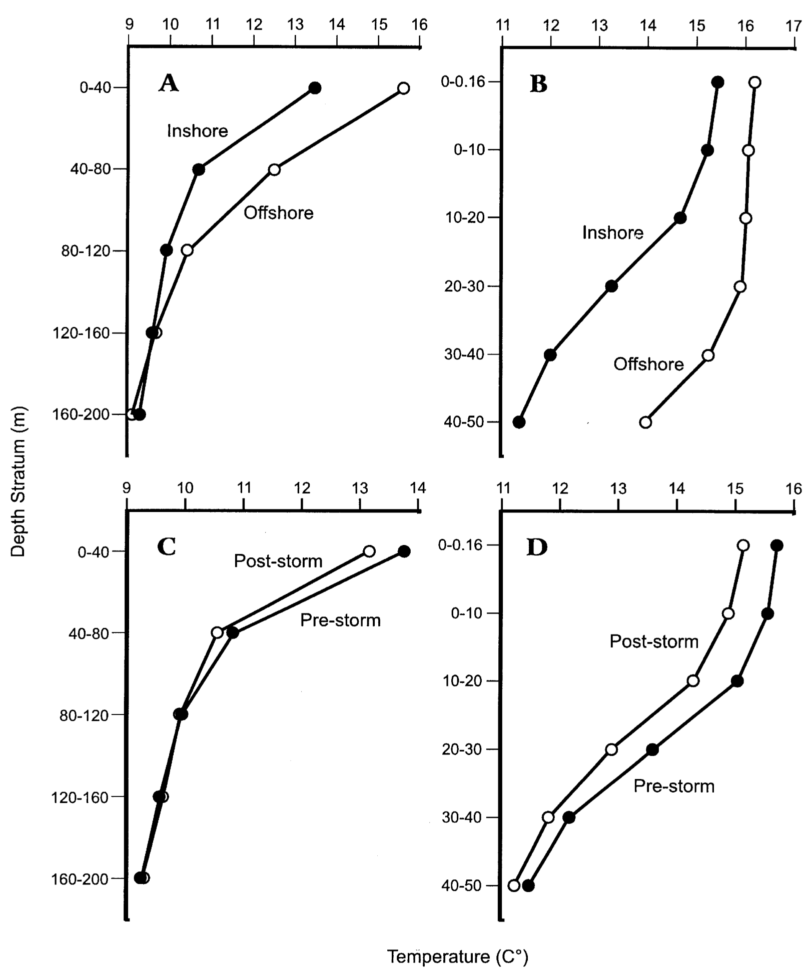

Figure 4

Average temperatures for strata sampled with the MESSHAI, based on data from the MESSHAI temperature sensor. (**A**) Deep tows at inshore (dots) and offshore (circles) stations; (**B**) shallow tows at inshore (dots) and offshore (circles) stations; (**C**) deep tows at inshore station before the storm (dots) and after the storm (circles); (**D**) shallow tows at inshore station before the storm (dots) and after the storm (circles).

Engraulis mordax eggs

A total of 67,157 *E. mordax* eggs were collected in the MESSHAI and Manta nets. Anchovy eggs had a slightly shallower distribution than larvae, with approximately 95% of eggs in the upper 30 m (Fig. 9, A and B). In shallow strata (including Manta, shallow MESSHAI, and the 0–40 m stratum of the deep MESSHAI tows), average density was greater at the offshore station than at the inshore station ($F_{1,95}$=4.72, P=0.003). Yet egg density in the deep strata was similar at the two stations. Average egg density in the surface layer was more than double that in the 0–10 m stratum (Fig. 9B). In the shallow strata at the inshore station, egg densities in MESSHAI tows were reduced after the storm ($F_{1,32}$=12.73, P=0.001), whereas egg densities did not change much in Manta tows ($F_{1,22}$=1.58, P=0.048) and in deep (>40 m) MESSHAI tows ($F_{1,10}$=2.67, P= 0.132) (Fig. 9, C and F).

Fish larvae

A total of 95,552 fish larvae were taken in the MESSHAI and Manta nets,

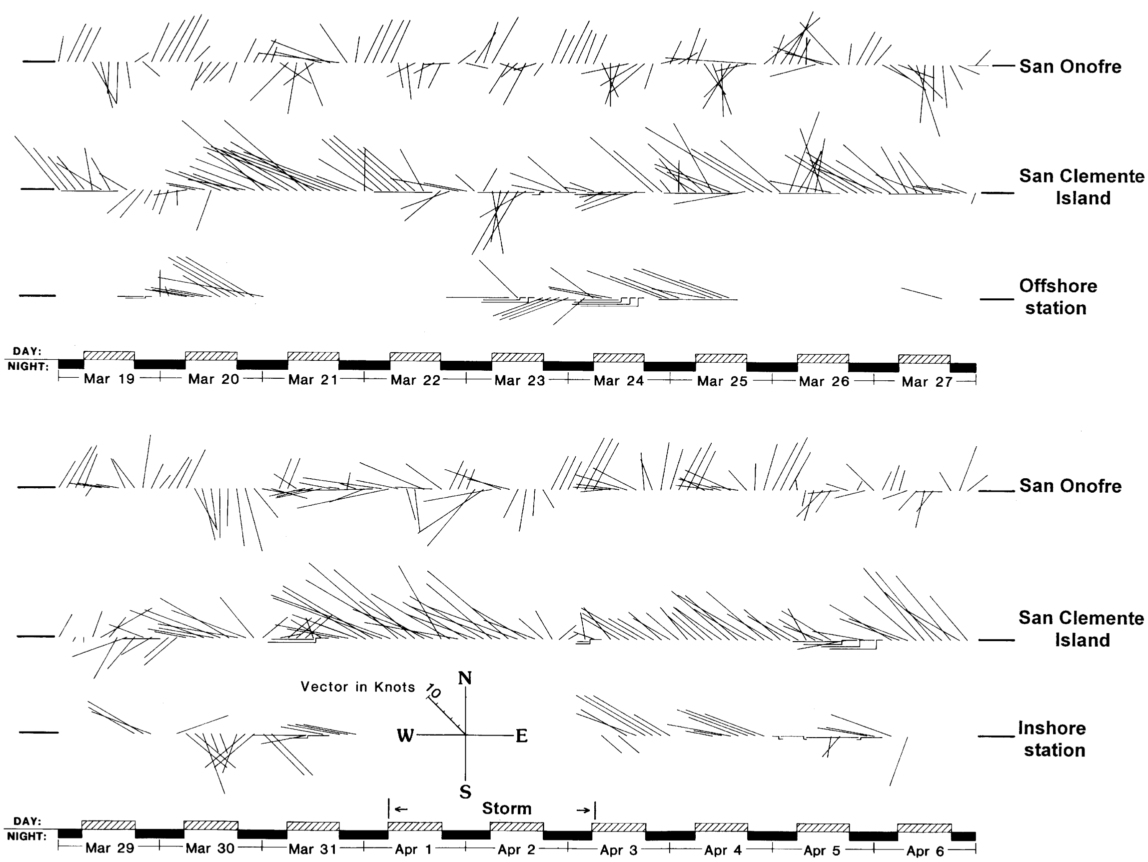

Figure 5

Wind direction and speed during Cruise 8003-EB based on data from San Onofre Nuclear Generating Station, the Naval Air Station on San Clemente Island, and observations made aboard RV *E. B. Scripps* (from Pommeranz and Moser, 1987).

representing 49 taxa (genera or species) in 27 families; 90,402 (95% of the total) were northern anchovy, *Engraulis mordax* (Table 1). Anchovy larvae were more than 40 times as abundant as the next most abundant species, California smoothtongue (*Leuroglossus stilbius*). White croaker (*Genyonemus lineatus)* ranked third, and the northern lampfish (*Stenobrachius leucopsarus*) ranked fourth, followed by the rockfish genus *Sebastes*. These five taxa constituted 99% of the total larvae. Following in abundance were queenfish (*Seriphus politus*), Pacific pompano (*Peprilus simillimus*), California halibut (*Paralichthys californicus*), the sanddab genus *Citharichthys*, and Pacific hake (*Merluccius productus*) (Table 1).

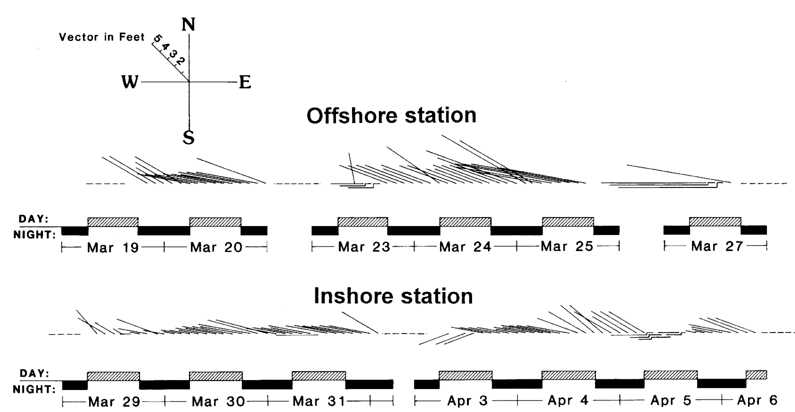

Figure 6

Swell direction and height during Cruise 8003-EB from observations made aboard RV *E. B. Scripps* (from Pommeranz and Moser, 1986).

Most of the larvae captured in the MESSHAI nets were at yolksac and preflexion stages. Relatively fewer anchovy larvae <3.0 mm and relatively more anchovy larvae >3.0 mm were taken by the bongo

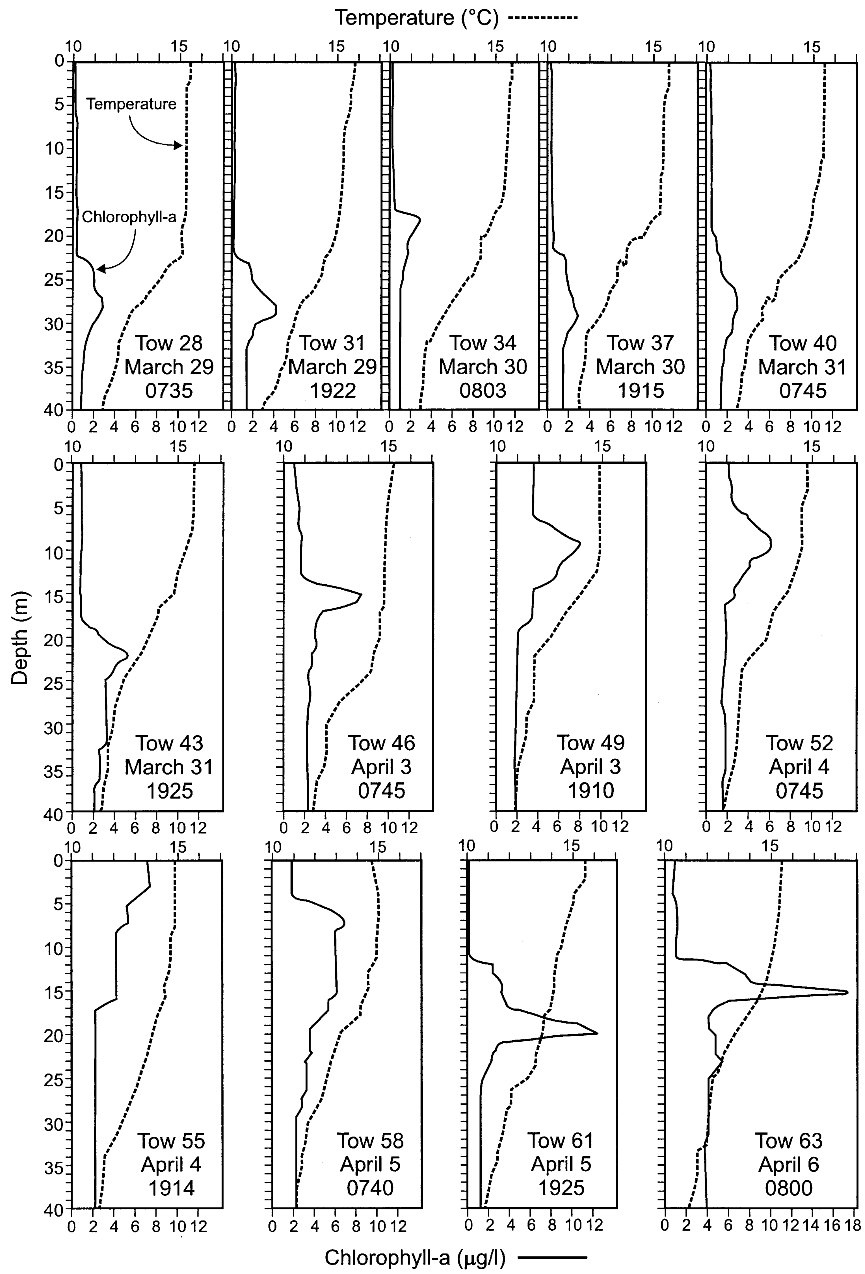

Figure 7

Chlorophyll-*a* (μg/l) and temperature (°C) profiles at the inshore station on Cruise 8003-EB. Tow numbers are given for shallow MESSHAI tows from which temperature profiles were derived.

net than in the MESSHAI tows (Fig. 10, A and B). The length-frequency distribution of larvae captured by the Manta net was bimodal, with peaks at 3.0 and 7.0 mm (Fig. 10C). For species other than northern anchovy, length distributions generally were similar for larvae caught in Manta and MESSHAI nets. Exceptions were a sample of 38 *Sebastes* spp. larvae captured in Manta net tow 18 (length range 5.0–9.4 mm, average length 7.2 mm) and an 8.0 mm presettlement *Paralichthys californicus* larva captured in Manta tow 31.

***Engraulis mordax* larvae** Anchovy larvae had a shallow distribution, with approximately 90% of the larvae in the upper 30 m (Fig. 11, A and B). In shallow strata, average larval density was greater at the

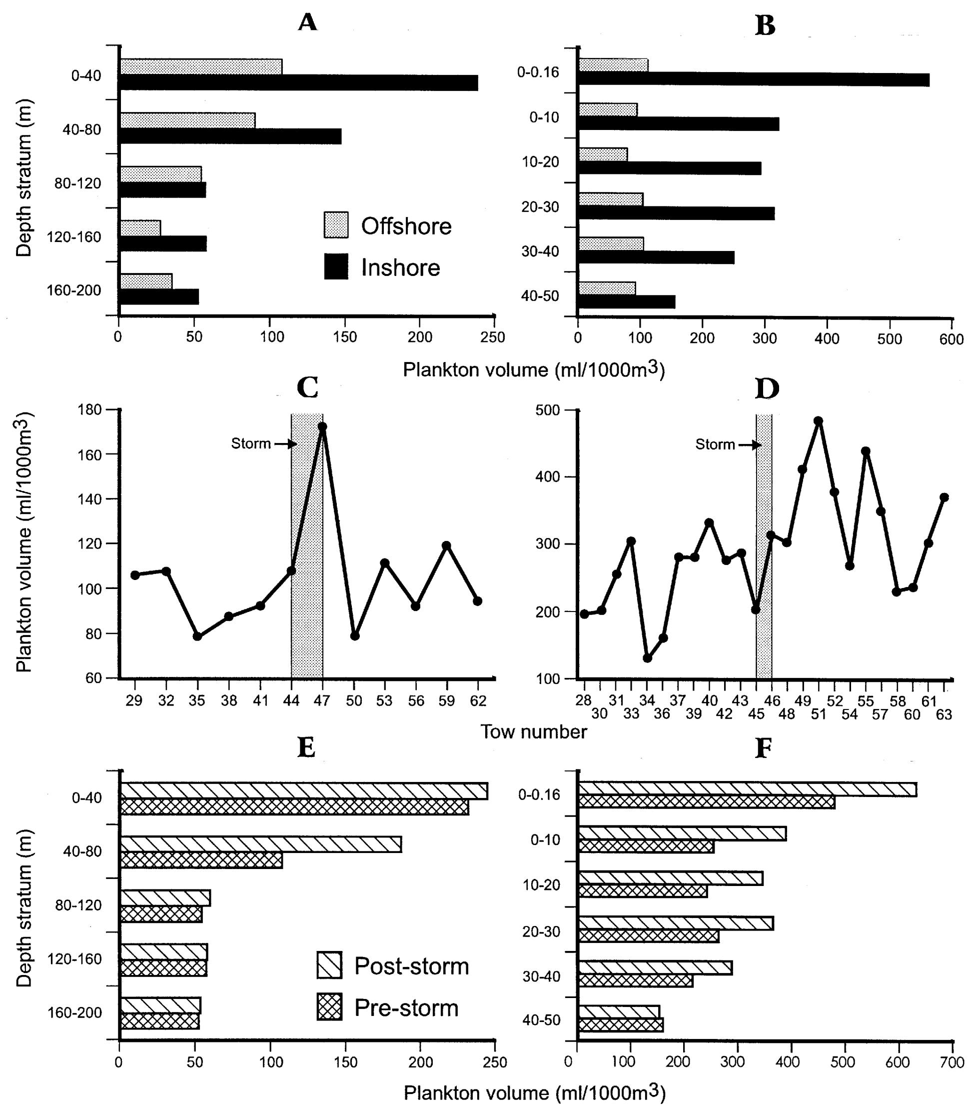

Figure 8

Plankton volumes (mL/1000 m^3) in MESSHAI tows. Average volumes from (**A**) deep tows and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) volumes in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) volumes in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep tows and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

inshore station than at the offshore station (Fig. 11A; ANOVA of shallow strata, $F_{1,95}$=31.78, P=0.003). Within the upper 50 m at the inshore station, average density was highest in the 10–20 m stratum, accounting for approximately 40% of larvae. Density in the surface layer was comparatively low. In deep strata no significant difference in larval density was found between inshore and offshore stations ($F_{1,17}$=0.53, P=0.47). At the inshore station, average larval densities were lower in poststorm samples than in prestorm samples (shallow strata: $F_{1,54}$= 11.21, P=0.001; deep strata: $F_{1,10}$=10.05, P=0.001). Overall, larval distribution was somewhat shallower after the storm (Fig. 11, E and F).

***Leuroglossus stilbius* larvae** In deep MESSHAI tows, larvae of *L. stilbius* occurred in relatively high densities in most strata down to 200 m (Fig. 12A). The lower limit of their distribution was not determined by the MESSHAI samples, but another study

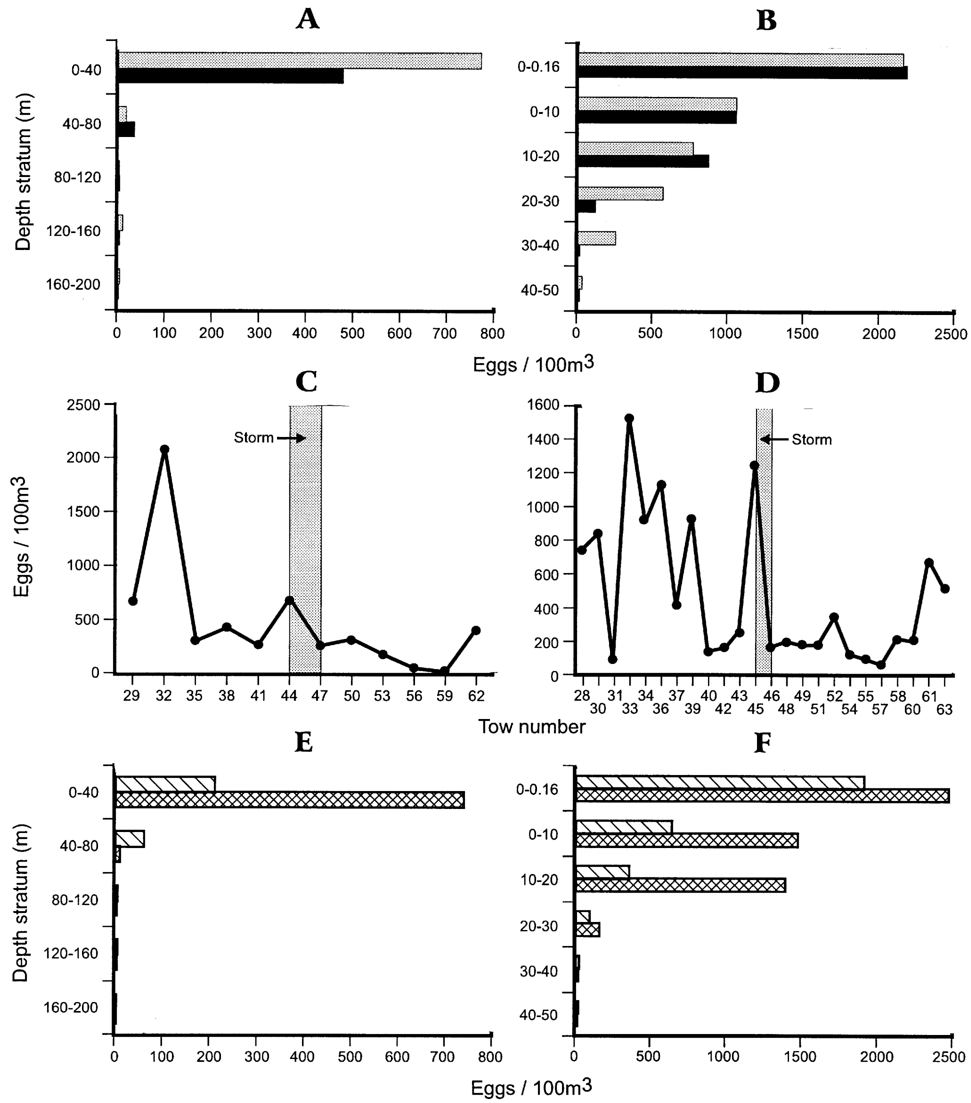

Figure 9

Anchovy eggs (no./100 m^3) in MESSHAI tows. Average from (**A**) deep tows and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep tows and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

(Moser and Smith, 1993) showed that they may occur down to 300 m. Average densities were generally higher at the inshore station than at the offshore station. Larvae were absent from the 0–40 m stratum offshore and were nearly absent from this stratum in prestorm inshore samples (Fig. 12, A and E). In samples at the inshore station, average densities following the storm increased markedly at 0–80 m, decreased at 80–160 m, and increased slightly in the 160–200 m stratum (Fig. 12E). Larvae were not taken in Manta tows nor in the upper 40 m of shallow MESSHAI tows at the offshore station (Fig. 12B). At the inshore station the distribution was shifted upward in poststorm samples and average larval densities were relatively high in strata as shallow as 30–40 m (Fig. 12F).

***Genyonemus lineatus* larvae** White croaker larvae were absent from offshore samples and were abundant only in the upper 30 m at the inshore station (Fig. 13, A and B). Average densities were extremely low in prestorm samples but were relatively high in

Table 1

Taxa captured by Manta and MESSHAI nets on Cruise 8003-EB. Numbers of larvae are unadjusted counts; occurrences are listed in parentheses with onshore occurrences to the left of the slash and offshore occurrences to the right. Only taxa identified to genus or species are included.

		Number of larvae and occurrences			
Taxon	Family	Manta	Shallow MESSHAI	Deep MESSHAI	Total
Engraulis mordax	Engraulidae	3,066 (24/15)	67,640 (24/17)	19,696 (12/7)	90,402 (99)
Leuroglossus stilbius	Bathylagidae	0	785 (22/2)	1,401 (12/7)	2,186 (43)
Genyonemus lineatus	Sciaenidae	49 (7/0)	740 (19/0)	173 (8/0)	962 (34)
Stenobrachius leucopsarus	Myctophidae	1 (0/1)	349 (24/9)	193 (12/7)	542 (53)
Sebastes spp.	Sebastidae	53 (3/0)	264 (22/12)	134 (10/7)	441 (54)
Seriphus politus	Sciaenidae	17 (6/0)	164 (12/0)	106 (5/0)	287 (23)
Peprilus simillimus	Stromateidae	6 (4/0)	180 (21/2)	35 (10/0)	221 (37)
Paralichthys californicus	Paralichthyidae	9 (3/0)	82 (16/0)	23 (6/0)	114 (25)
Citharichthys spp.	Paralichthyidae	0	63 (17/1)	14 (7/1)	77 (26)
Merluccius productus	Merlucciidae	0	36 (15/0)	12 (5/4)	48 (24)
Atherinopsis californiensis	Atherinidae	44 (9/0)	0	0	44 (9)
Pleuronichthys verticalis	Pleuronectidae	1 (1/0)	25 (9/0)	8 (3/0)	34 (13)
Lyopsetta exilis	Pleuronectidae	0	27 (16/0)	5 (4/0)	32 (20)
Bathylagus ochotensis	Bathylagidae	0	21 (13/0)	10 (4/4)	31 (21)
Parophrys vetulus	Pleuronectidae	0	19 (9/0)	7 (5/0)	26 (14)
Cataetyx rubrirostris	Bythitidae	0	20 (12/0)	4 (3/0)	24 (15/0)
Argentina sialis	Argentinidae	0	9 (8/0)	8 (6/0)	17 (14)
Protomyctophum crockeri	Myctophidae	0	1 (1/0)	10 (4/4)	11 (9)
Argyropelecus spp.	Sternoptychidae	0	0	9 (4/0)	9 (4)
Pleuronichthys spp.	Pleuronectidae	0	6 (3/0)	3 (3/0)	9 (6)
Ophidion scrippsae	Ophidiidae	0	1 (1/0)	6 (3/0)	7 (4)
Atractoscion nobilis	Sciaenidae	0	6 (2/0)	0	6 (2)
Neoclinus stephensae	Chaenopsidae	6 (2/0)	0	0	6 (2)
Hypsoblennius spp.	Blenniidae	3 (2/0)	2 (2/0)	0	5 (4)
Pleuronichthys coenosus	Pleuronectidae	4 (3/1)	1 (1/0)	0	5 (5)
Coryphopterus nicholsii	Gobiidae	0	4 (3/0)	0	4 (3)
Scorpaenichthys marmoratus	Cottidae	4 (2/0)	0	0	4 (2)
Triphoturus mexicanus	Myctophidae	0	1 (1/0)	3 (2/0)	4 (3)
Bathylagus wesethi	Bathylagidae	0	3 (2/0)	0	3 (2)
Chauliodus macouni	Chauliodontidae	0	0	3 (2/1)	3 (3)
Hypsopsetta guttulata	Pleuronectidae	0	3 (3/0)	0	3 (3)
Lampanyctus spp.	Myctophidae	0	1 (1/0)	2 (1/1)	3 (3)
Oxyjulis californica	Labridae	0	3 (2/0)	0	3 (2)
Tarletonbeania crenularis	Myctophidae	0	2 (2/0)	1 (1/0)	3 (3)
Zaniolepis frenata	Hexagrammidae	0	2 (2/0)	1 (1/0)	3 (3)
Girella nigricans	Kyphosidae	0	2 (2/0)	0	2 (2)
Pleuronichthys ritteri	Pleuronectidae	0	2 (1/1)	0	2 (2)
Tactostoma macropus	Melanostomiidae	0	0	2 (1/0)	2 (1)
Bathylagus milleri	Bathylagidae	0	1 (1/0)	0	1 (1)
Brosmophysis marginata	Bythitidae	0	1 (1/0)	0	1 (1)
Chilara taylori	Ophidiidae	0	1 (0/1)	0	1 (1)
Cololabis saira	Scomberesocidae	1 (0/1)	0	0	1 (1)
Hypsoblennius gentilis	Blenniidae	1 (1/0)	0	0	1 (1)
Hypsoblennius jenkinsi	Blenniidae	1 (1/0)	0	0	1 (1)
Lampanyctus ritteri	Myctophidae	0	1 (0/1)	0	1 (1)
Melamphaes sp.	Melamphaidae	0	1 (1/0)	0	1 (1)
Scomber japonicus	Scombridae	0	1 (1/0)	0	1 (1)
Trachipterus altivelis	Trachipteridae	0	1 (1/0)	0	1 (1)
Typhlogobius californiensis	Gobiidae	1 (1/0)	0	0	1 (1)

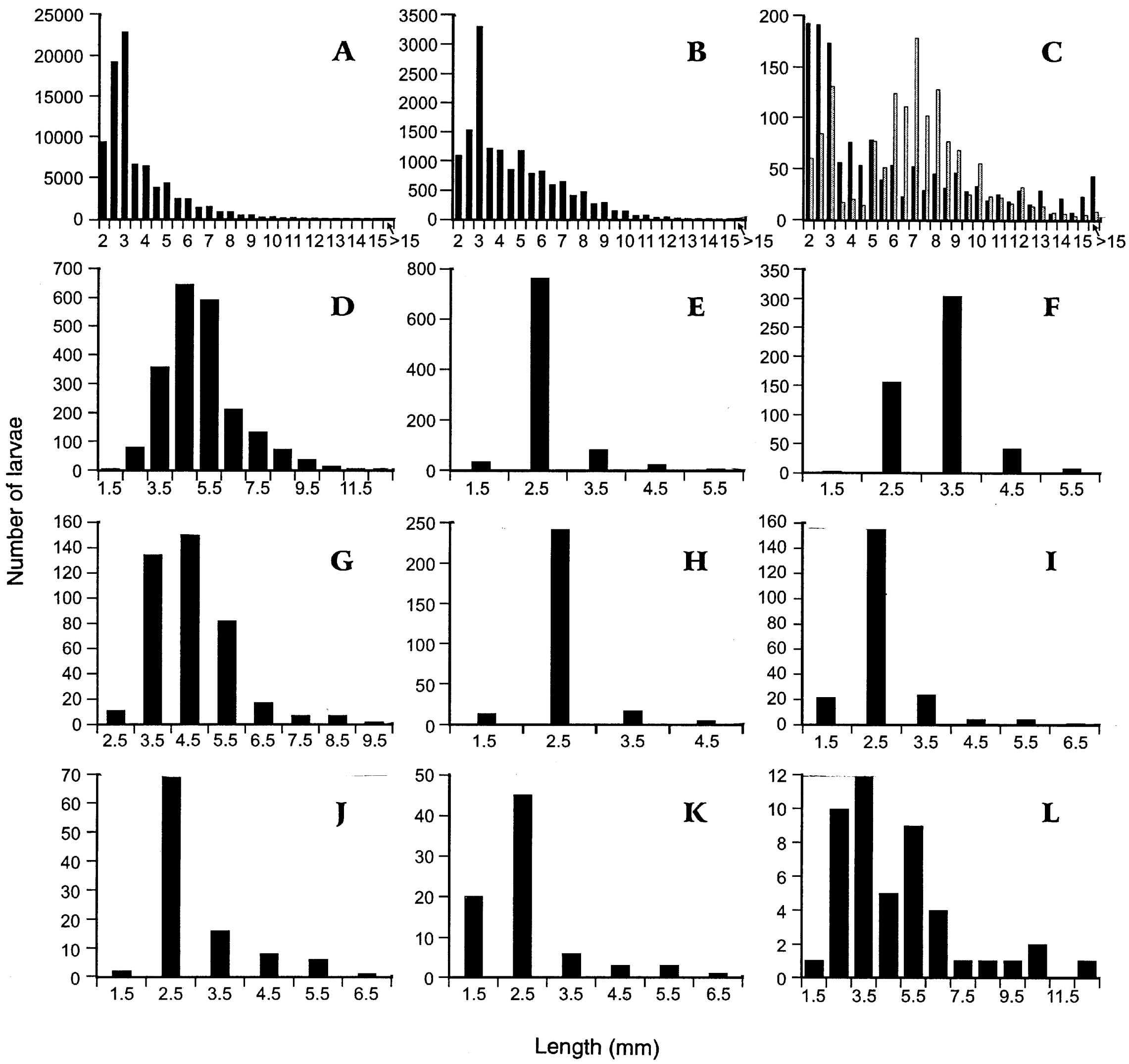

Figure 10

Length frequencies of larvae of the 10 most abundant taxa taken in MESSHAI (**A** and **D–L**), (**B**) oblique bongo, and (**C**) Manta tows on Cruise 8003-EB. (**A–C**) *Engraulis mordax*; day (shaded) and night (solid) are shown for Manta tows; (**D**) *Leuroglossus stilbius*; (**E**) *Genyonemus lineatus*; (**F**) *Stenobrachius leucopsarus*; (**G**) *Sebastes* spp.; (**H**) *Seriphus politus*; (**I**) *Peprilus simillimus*; (**J**) *Paralichthys californicus*; (**K**) *Citharichthys* spp.; (**L**) *Merluccius productus*. In A–C, bars represent 0.5-mm size classes; in D–L, bars represent the midpoints of 1.0-mm size classes.

poststorm samples from the surface to 30 m (Fig. 13, E and F). Individual tows showed a sharp increase in larval density immediately following the storm, peaking 2 days after the storm and declining to prestorm levels 3 days after the storm (Fig. 13, C and D).

***Stenobrachius leucopsarus* larvae** Larvae of northern lampfish occurred throughout the water column to 200 m depth at the inshore station, with highest average densities in the 20–30 m and 30–40 m strata (Fig. 14, A and B). Average densities were greater at the inshore station than at the offshore station. In deep MESSHAI tows taken at the offshore station, average density was greatest in the 40–80 m stratum; larvae were absent between 80 and 160 m. At the inshore station, maximum prestorm larval densities were in the 0–40 m and 40–80 m strata; in poststorm samples, densities were highest at 0–40 m (Fig. 14E). The center of distribution of larval densities from shallow MESSHAI tows shifted upward from 30–40 m in prestorm samples to 20–30 m in poststorm samples (Fig. 14F). Individual deep

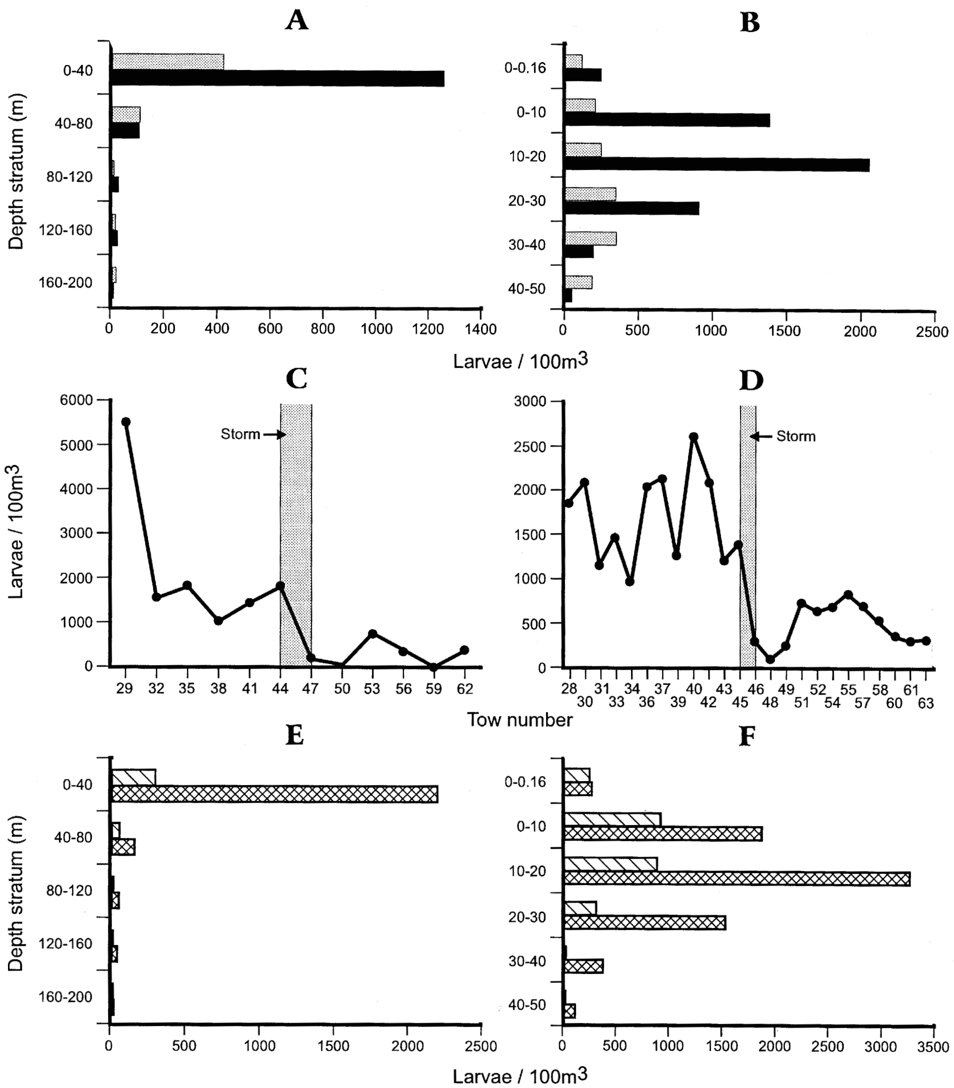

Figure 11

Anchovy larvae (no./100 m³) in MESSHAI tows. Average from (**A**) deep tows and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

MESSHAI tows in the upper 200 m showed a trend of increasing density just before the storm and a sharp decrease in poststorm tows (Fig. 14C). In shallow MESSHAI tows, densities peaked in two tows taken one day before the storm but were not appreciably different in pre- and poststorm samples (Fig. 14D).

***Sebastes* spp. larvae** Rockfish larvae were concentrated in the upper 80 m of the water column, with low average densities between 80 and 200 m (Fig. 15A). In deep MESSHAI tows the highest average density was in the 40–80 m stratum at the offshore station but in the 0–40 m stratum at the inshore station (Fig. 15A). In shallow MESSHAI tows at the inshore station, average density was highest in the 20–30 m stratum, relatively low in the 0–10 m and 10–20 m strata, and nearly as high at the surface as in the 20–30 m stratum. Offshore, shallow MESSHAI tows showed extremely low average densities in the upper 30 m of the water column; larvae were not taken in surface net tows. At the inshore station, average larval densities were higher in samples

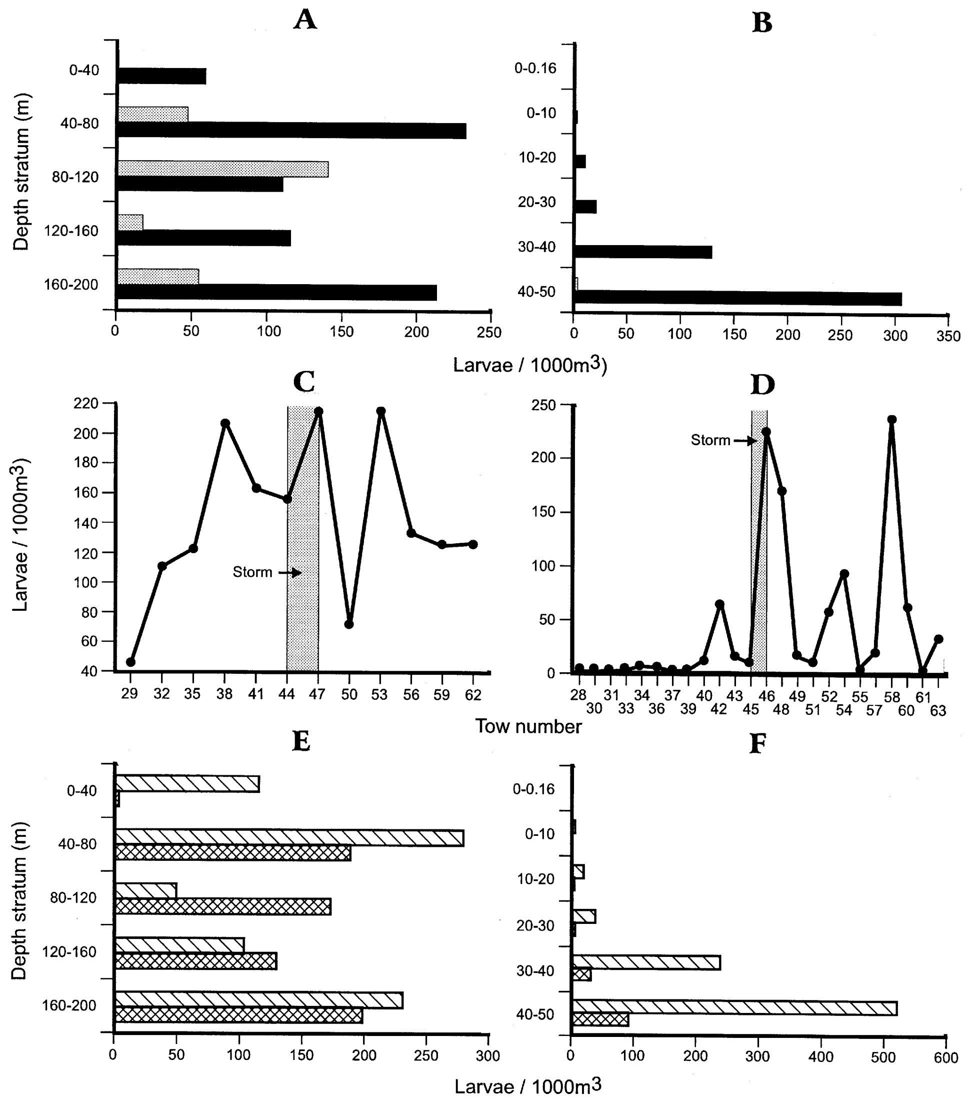

Figure 12

Leuroglossus stilbius larvae (no./1000 m3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

taken before the storm than those taken afterwards; however, the disparity between average densities before and after the storm was due largely to several prestorm tows with unusually high larval counts (Fig. 15, C–F).

***Seriphus politus* larvae** Queenfish larvae occurred only at the inshore station, primarily in the upper 10 m of the water column (Fig. 16, A and B). At the inshore station, larvae were virtually absent from tows taken before the storm; larval density increased abruptly immediately following the storm, then subsided to prestorm level within about two days after the storm (Fig. 16, C–F).

***Peprilus simillimus* larvae** Larval Pacific pompano occurred primarily in the upper 40 m, with highest average densities in the upper 20 m of the water column (Fig. 17, A and B). Except for two tows at the 30–40 m stratum, larvae did not occur in offshore

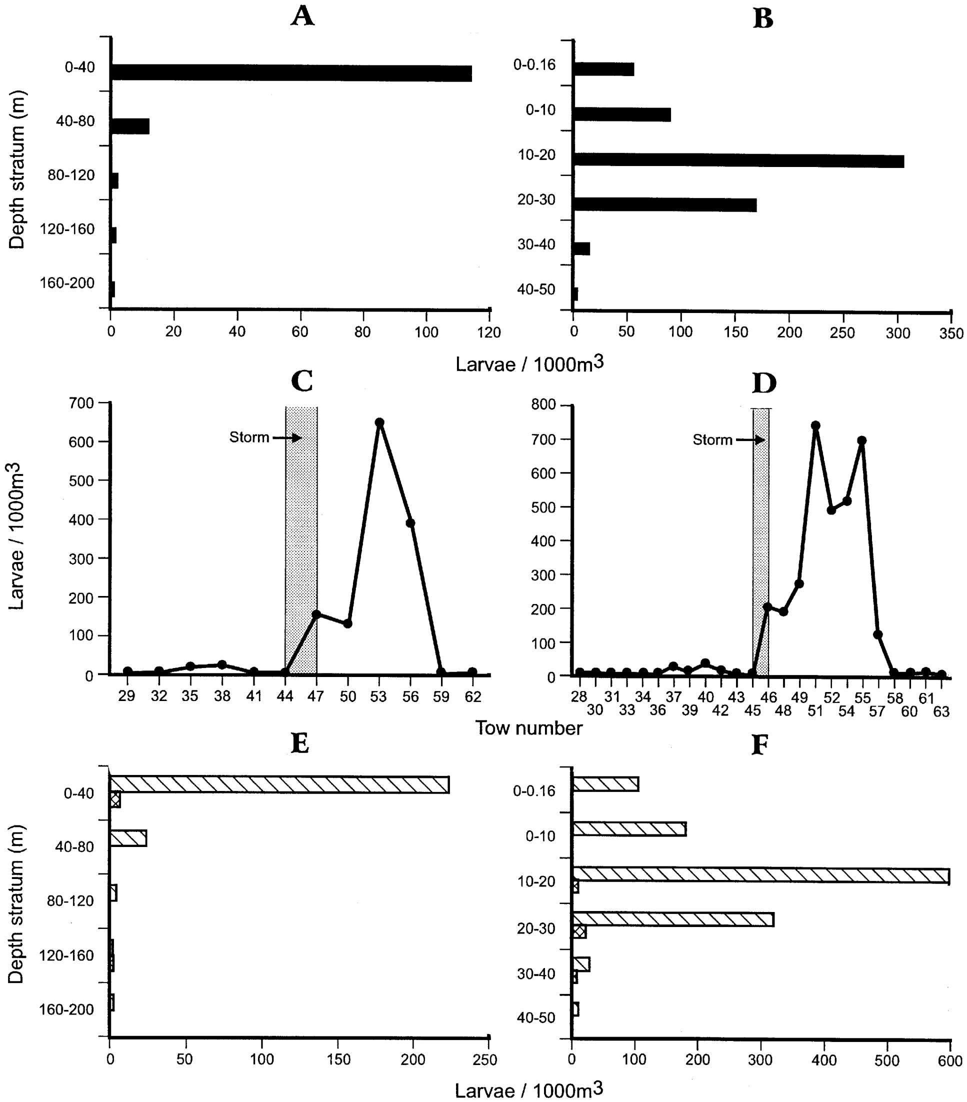

Figure 13

Genyonemus lineatus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

samples. At the inshore station, larval densities were comparatively low in prestorm samples but increased markedly after the storm (Fig. 17, C–F).

***Paralichthys californicus* larvae** California halibut larvae occurred only at the inshore station and were restricted to the upper 30 m of the water column (Fig. 18, A and B). Average larval density was highest in the 0–10 m stratum, where it was four times higher than in the 20–30 m stratum or at the surface (Fig. 18B). Larvae appeared in several of the shallow MESSHAI tows prior to the storm at densities as high as approximately 20 per 1000 m^3; after the storm, densities increased steadily to more than 60 per 1000 m^3, then decreased to prestorm levels within 2 days following the storm (Fig. 18D). Average poststorm larval density for the 10-m stratum was more than 7 times higher than prestorm density, and overall vertical distribution was slightly shallower in poststorm samples (Fig. 18F). Larvae occurred in Manta net samples only in poststorm tows.

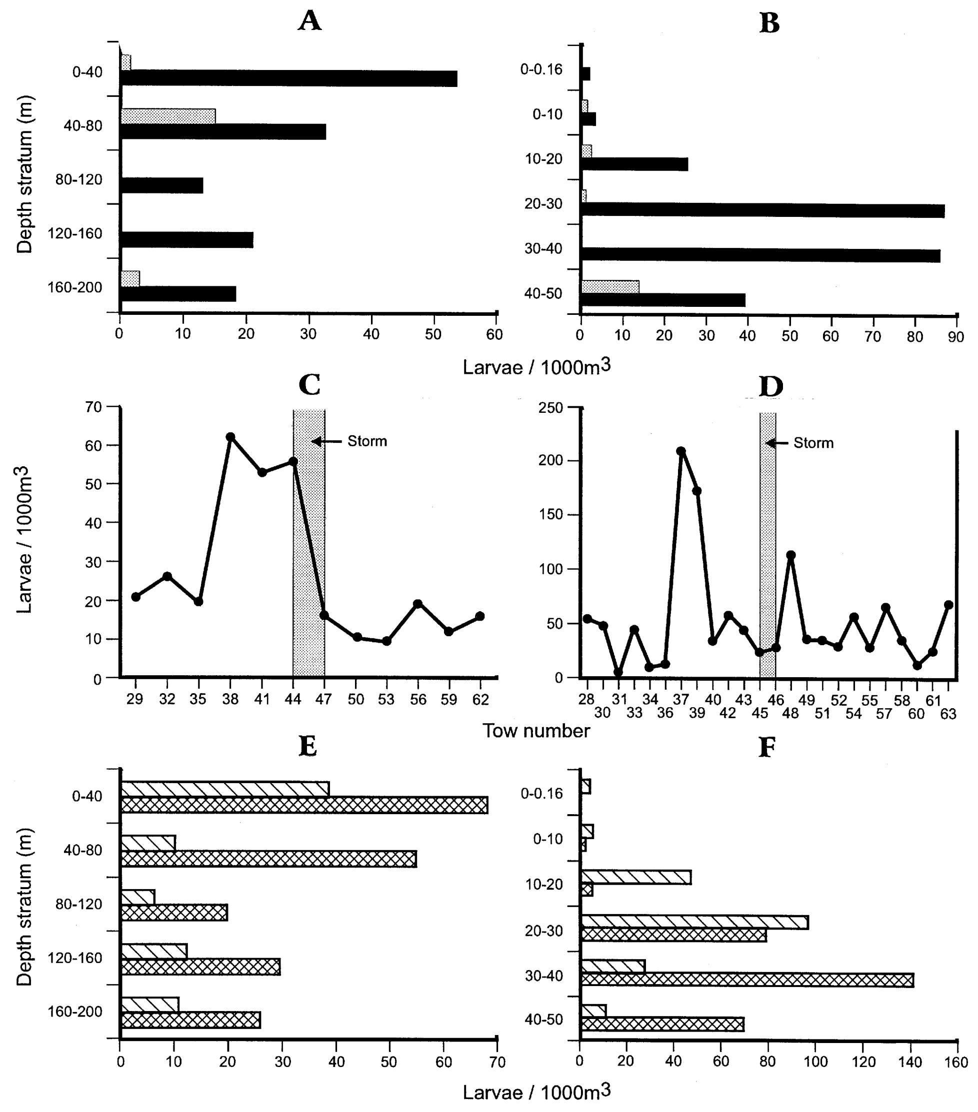

Figure 14

Stenobrachius leucopsarus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

***Citharichthys* spp. larvae** Sanddab larvae were taken primarily in the upper 50 m of the water column at the inshore station (Fig. 19, A and B). In shallow MESSHAI tows, peak average density was in the upper 10 m. Poststorm samples contributed most of the larvae (Fig. 19, C–F). A few larvae appeared sporadically in tows taken before the storm; following the storm there was a steady increase in larval density and then a sharp decline by the second day after the storm (Fig. 19, C and D). The distribution was shifted upward by approximately 20 m in poststorm samples (Fig. 19F).

***Merluccius productus* larvae** Hake larvae were taken in deep MESSHAI tows in the 40–80 and 80–120 m strata; average densities were similar in inshore and offshore samples (Fig. 20A). Larvae occurred in shallow MESSHAI tows only at the inshore station and were taken as shallow as 10–20 m (Fig. 20B). After the storm only one deep MESSHAI tow was positive, but for shal-

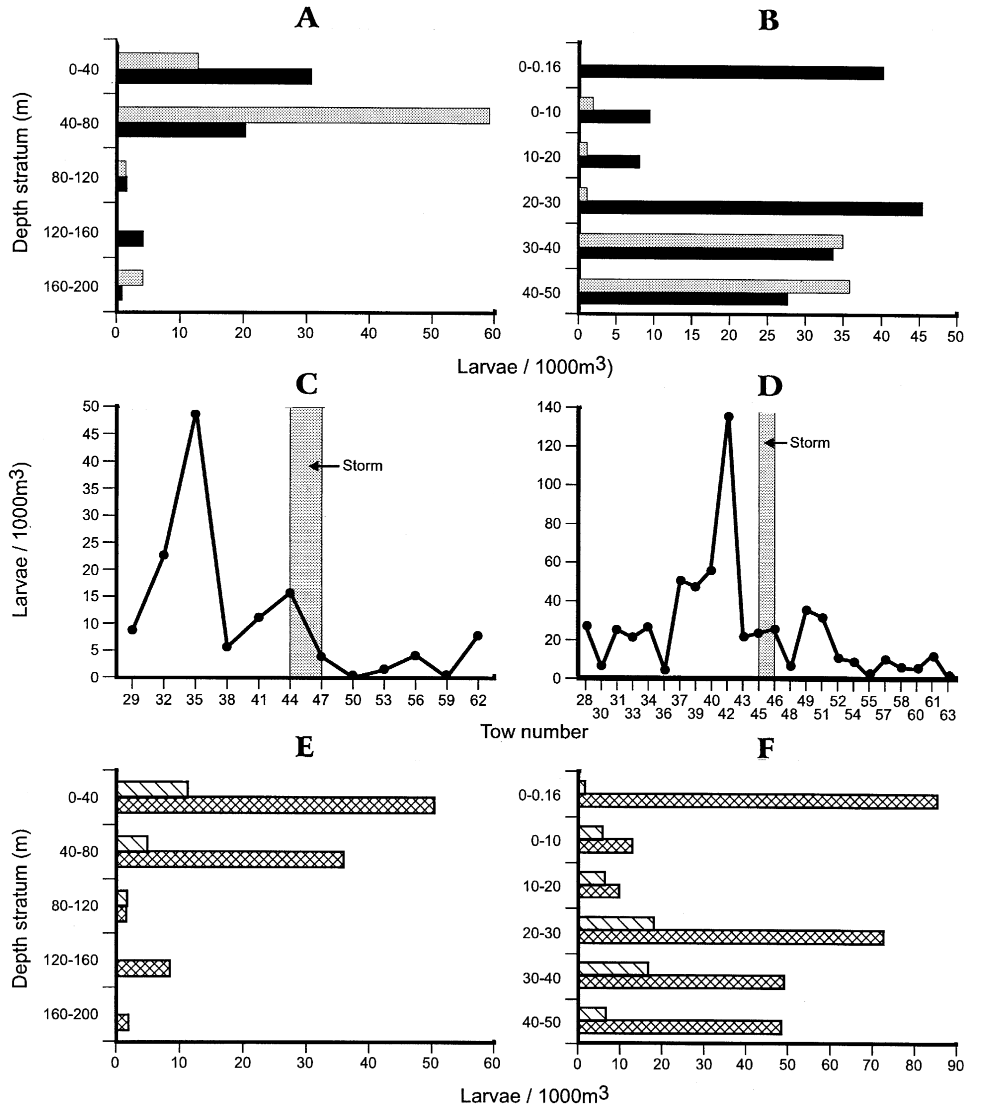

Figure 15

Sebastes spp. larvae (no./1000 m^3) in MESSHAI tows. Average of (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

low MESSHAI tows, the frequency of positive tows increased, along with larval densities (Fig. 20, C and D). The distribution of larvae became somewhat shallower in shallow MESSHAI tows after the storm (Fig. 20F).

Discussion

Northern anchovy larvae dominated samples from both study sites. The midwater species *Leuroglossus stilbius* and *Stenobrachius leucopsarus* and the rockfish genus *Sebastes* were relatively abundant at the two sites. These three taxa, along with *Merluccius productus* (ranked 10th in abundance) and *Bathylagus ochotensis* (ranked 13th), constitute a distinct larval recurrent group in the California Current region (Moser and Smith, 1993). These three taxa were also closely linked in other analyses of larval fish assemblages in the study region (Gruber et al., 1982; McGowen, 1993). *Sebastes* spp. and *Merluccius*

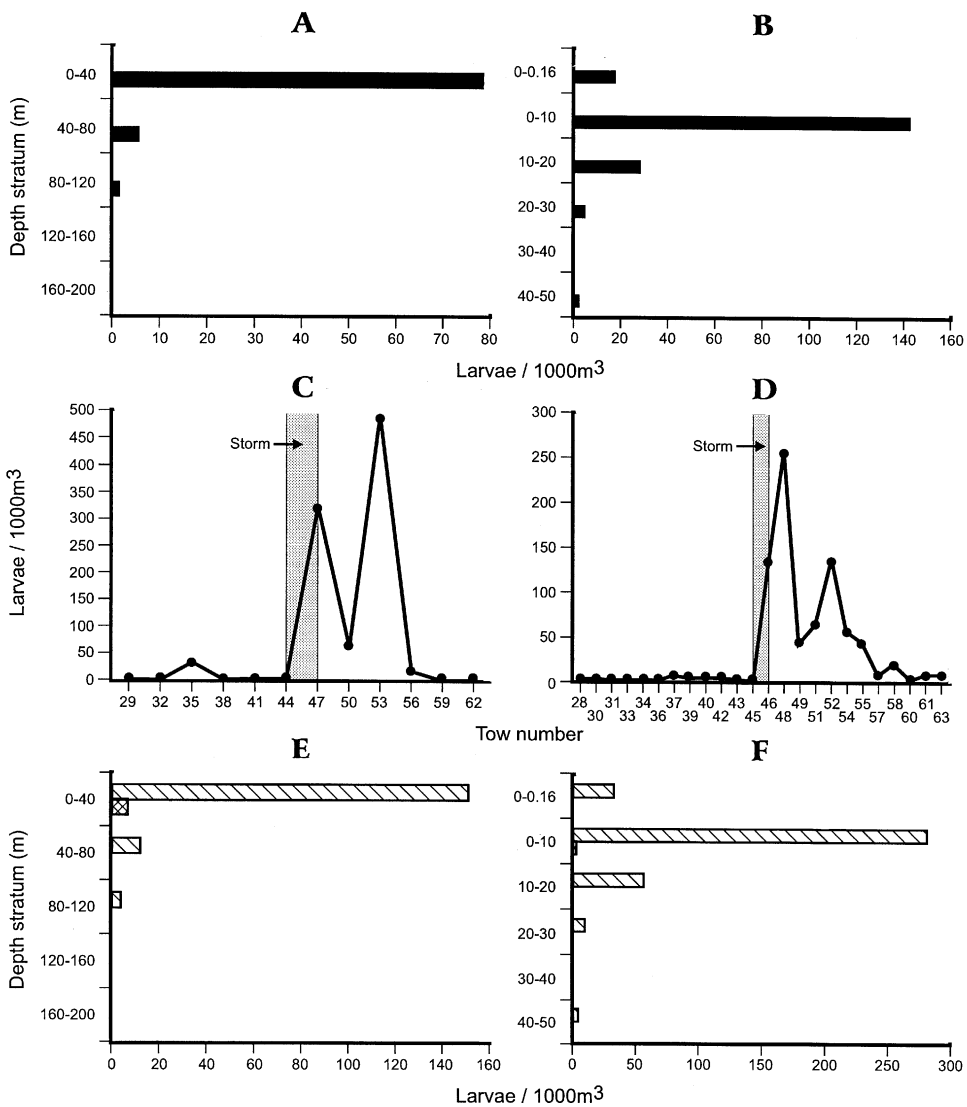

Figure 16

Seriphus politus larvae (no./1000 m³) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

productus are demersal and their larvae are found throughout the SCB at this season (Moser et al., 1993). Other studies (Gruber et al., 1982; McGowen, 1993) have shown that larvae of *Leuroglossus stilbius* and *Stenobrachius leucopsarus* are relatively abundant nearshore and, according to Barnett et al. (1984), *S. leucopsarus* may extend shoreward to midshelf. This can be explained, in part, by the narrowness of the shelf in this region and the proximity to deep-water habitat. These species are unusual in comparison with other bathylagids and myctophids in this region in having relatively high larval abundances near the coast (Moser et al., 1993). Most larvae of other taxa collected in this study were taken at the nearshore station and represent demersal shelf species. The most abundant of these, *Genyonemus lineatus*, spawns during winter and early spring over shelf waters throughout the SCB (Gruber et al., 1982; Schlotterbeck and Connally, 1982; Watson, 1982; Barnett et al., 1984; Brewer and Kleppel, 1986; Lavenberg et al., 1986; Walker et al., 1987; McGowen, 1993; Moser et al., 1993). *Seriphus politus*, the next

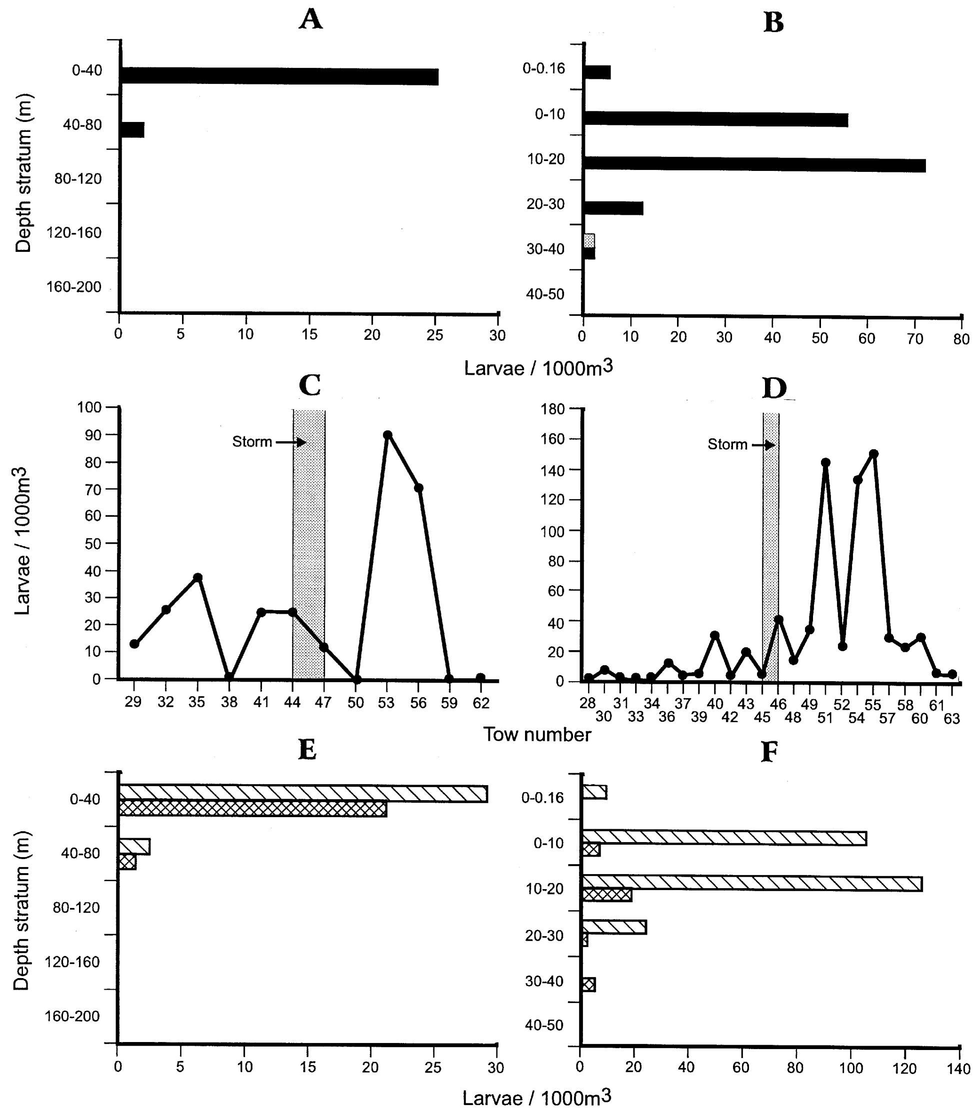

Figure 17

Peprilus simillimus larvae (no./1000 m³) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

most abundant shelf species in the samples, typically spawns from late spring to summer; however, spawning began unusually early in 1980 since larvae were abundant as early as March off San Onofre (Walker et al., 1987). *Peprilus simillimus*, *Paralichthys californicus*, and *Citharichthys* spp. have broad spawning seasons with high larval abundance in late winter to early spring. This was particularly evident in 1980 (Walker et al., 1987; Moser et al., 1993).

The vertical distribution of larval fishes is closely related to the temperature profile of the water column. Ahlstrom (1959) described two general categories: those taxa whose larvae occur almost entirely within the upper mixed layer and in the upper part of the thermocline; and those that occur within or below the thermocline. Larvae of shorefishes, including most clupeoids, typically fall within the first category. Generally, slope and offshore taxa produce deeper-living larvae, although many oceanic taxa also have shallow-living larvae. Northern anchovy had similar vertical profiles at the slope and offshore stations although densities were much higher at the slope station, where the

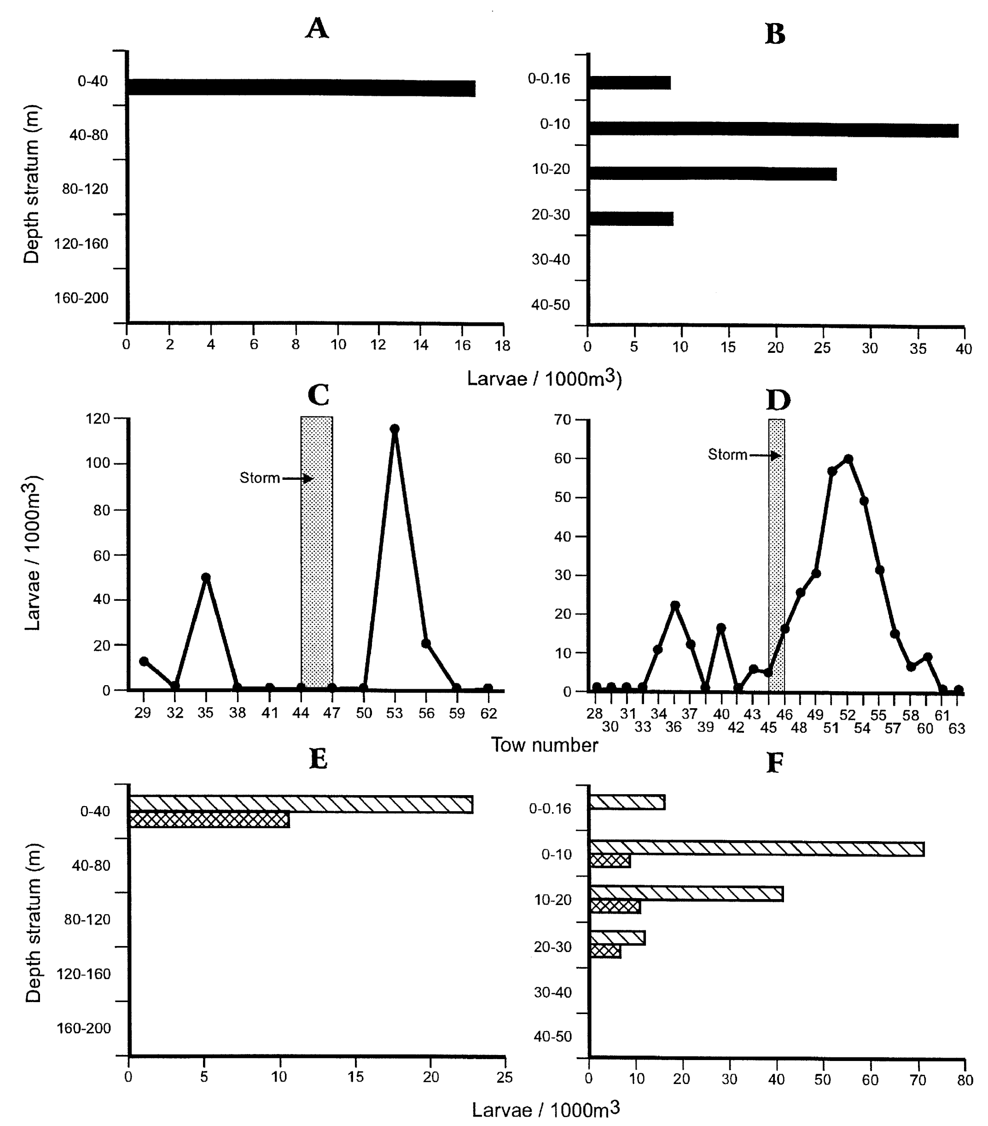

Figure 18

Paralichthys californicus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

density peak was more pronounced and was about 10 m shallower than at the offshore station. Probably this peak was related to the relatively shallow mixed layer at the slope station compared with the offshore station. Eggs of the anchovy had a shallower distribution than the larvae, with an apparent density peak in the neuston. The effect of the different mixed layer depths at the two stations is evident in the slightly deeper lower distribution boundary of eggs at the offshore station.

Like the anchovy, the nearshore shelf species (white croaker, queenfish, California halibut, California pompano, and some sanddab species) had shallow larval distributions essentially limited to the upper 30 m of the water column of the inshore station, with peak densities in either the 0–10 m or 10–20 m strata. Such shallow distributions appear to be typical of nearshore species although previous studies have lacked the fine-scale sampling capability needed to show this. The many *Sebastes* species occupy a wide range of habitats on the shelf and upper slope and produce larvae that are found within and below the thermocline and that generally avoid the upper mixed layer, except for the

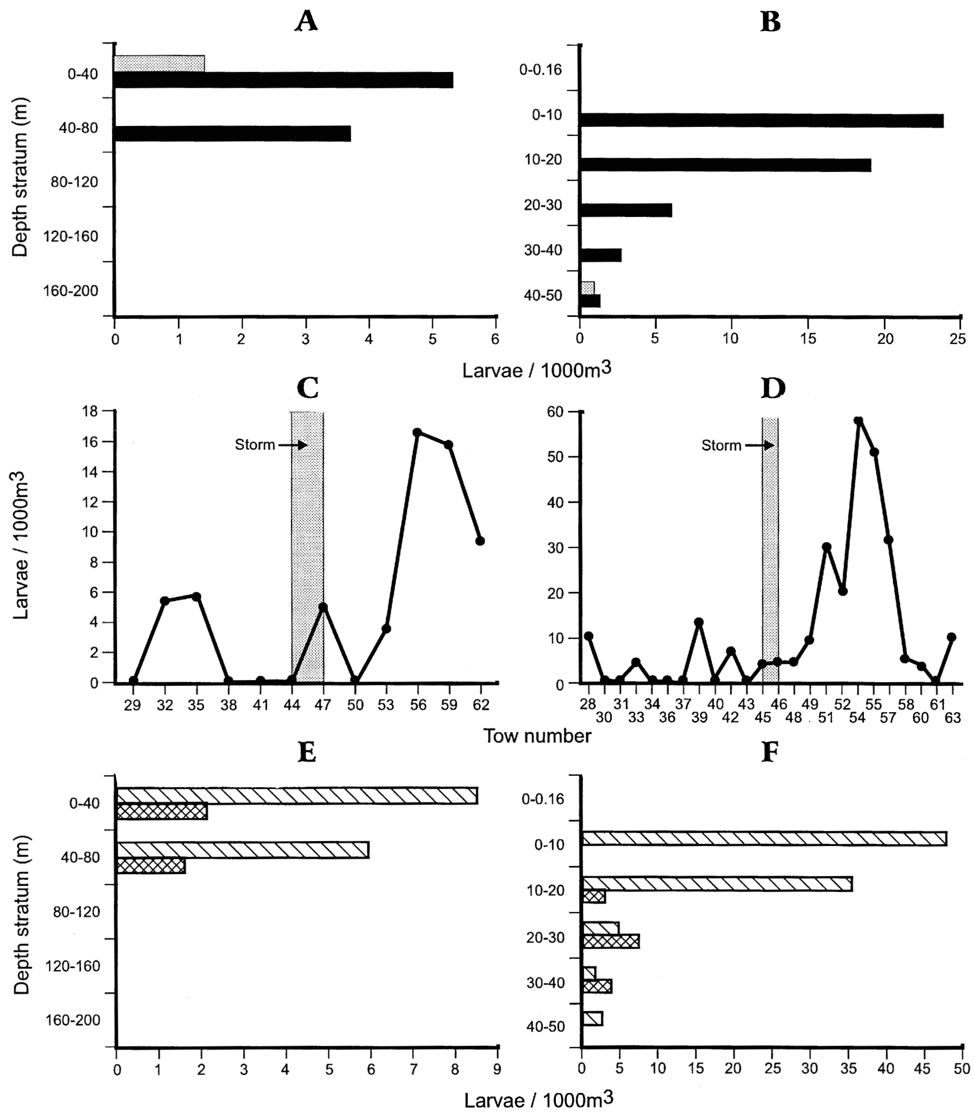

Figure 19

Citharichthys spp. larvae (no./1000 m³) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–80 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m strata (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

neustonic zone (Ahlstrom, 1959; Moser and Boehlert, 1991). This distribution is clearly shown by comparing the stratum of highest density at the inshore and offshore stations. Likewise, Pacific hake are broadly distributed over the shelf and slope and have deep-living larvae (Ahlstrom, 1959; Mullin and Cass-Calay, 1997). In our study, hake larvae were absent from samples above 50 m depth at the offshore station.

A comparison of larval anchovy length distributions from MESSHAI, bongo, and Manta net tows shows that the MESSHAI is less effective in catching larvae over 3 mm than the other two (Fig. 10, A–C). The mouth opening of the MESSHAI net is relatively much smaller (25×25 cm) than that of the bongo net (71 cm diameter). Why the Manta net captures larger larvae is conjectural. It may be related to the absence of an upward escape plane for larvae in the path of the net or it may reflect the size frequency of larvae in the surface layer. The bimodal length distribution for anchovy captured in Manta

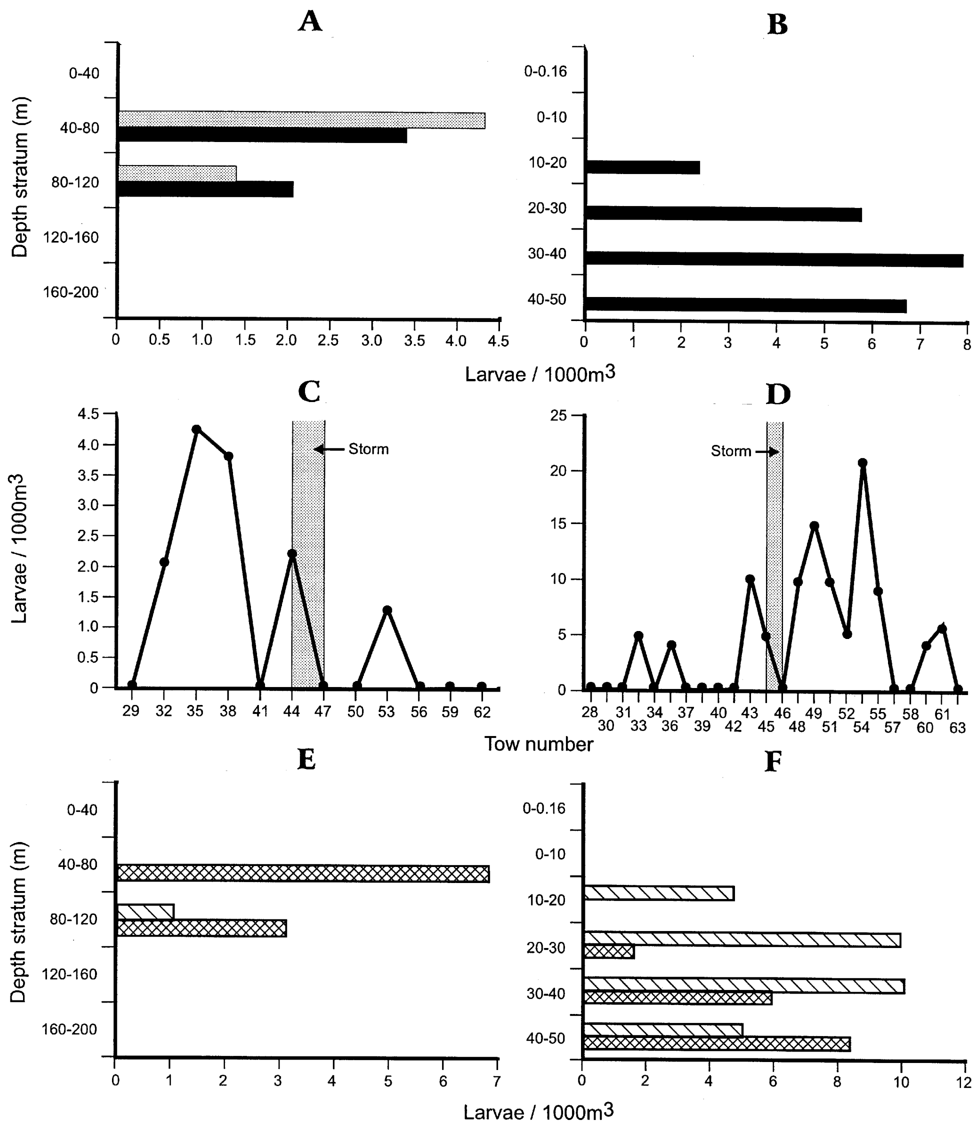

Figure 20

Merluccius productus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

tows results from relatively large numbers of 6.0–10.0 mm larvae caught at the surface during the day (Fig. 10C). This was a consistent feature of Manta catches throughout the cruise, suggesting that anchovy larvae may have been migrating to the surface layer to feed during the day.

The storm that interrupted sampling for two days at the inshore station significantly affected the relative abundance and distribution of fish larvae and their physical and biotic environment. Average densities of anchovy larvae declined markedly in most strata following the storm, possibly as a result of mortality associated with starvation. This argument is contradicted by the results of Mullin et al. (1985) who showed that important larval fish prey, such as copepod nauplii increased in concentration after the storm, were no less stratified than before the storm, and had a 15-m upward shift in peak abundance that mirrored the shoaling of anchovy larval distribution in our study. Moreover, the chlorophyll maximum was below the peak depth zone of anchovy larval abundance before the storm, whereas it coincided with the depth zone of highest larval abundance afterwards. Pre- and poststorm peak concentrations of important fish larva prey coincided with pre- and poststorm peaks in the chlorophyll maximum (Mullin et al., 1985). If starvation was the reason for the decline in anchovy larvae, then it is likely that the cause was disruption of micropatches of food, as suggested by Mullin et al. (1985). In this case, Lasker's (1981) stable ocean hypothesis was operative at the centimeter scale, and reduced survival was a result of disruption of the fine-scale geometry of food patches (Vlymen, 1977; Owen, 1989). Another explanation for the poststorm decline in anchovy larval abundance would be advection of larvae away from the study site (Mullin et al., 1985). The strong northwest winds resulted in offshore movement of surface water (the upper 10 m) by Ekman transport at a rate of about 10 cm per second; thus, virtually all the surface water at this region of the shelf was moved offshore during the storm and was replaced by deeper water (Winant[1]). This could explain the sharp decline in anchovy larval densities at the slope station after the storm, providing, of course, that densities of anchovy larvae were lower over the shelf than at the station before the storm. The latter would not be expected since Barnett et al. (1984) showed high concentrations of anchovy larvae over the shelf at a similar habitat south of our inshore station.

The storm had an opposite effect on densities of shorefish larvae (*Genyonemus lineatus, Seriphus politus, Peprilus simillimus, Paralichthys californicus, Citharichthys* spp.), which occurred in extremely low densities or which were absent in prestorm samples. Larval densities of these species began to increase immediately after the storm, peaked within 1–2 days, and then declined abruptly to prestorm levels. The sudden appearance of these larvae at the nearshore station after the storm was a result of storm-induced advection from shallow regions of the shelf. The narrow shelf in this region of the coast would make nearshore fish larvae particularly vulnerable to transport off the shelf during storms with northwest winds. Such advection may be important in the transport of nearshore fish larvae seaward where they become available to slope or eddy circulation, thus providing the opportunity for dispersion to other regions. The subsequent rapid decline in larval densities could have been caused by mortality associated with disturbance of micropatches of food, by predation, or by active or passive movement of larvae away from the sampling site. Starvation of these inshore larvae over slope waters may be related to the difference in composition and concentration of prey organisms in nearshore and offshore waters (Watson and Davis, 1989). Some portion of the larvae that appeared at the inshore site after the storm may have been transported back to the nearshore region. This return transport may have been enhanced by upward movement of these larvae to the surface where they could be carried by shoreward currents created by internal wave cells (Shanks, 1983, 1986).

Among the species with deeper-living larvae, those of *Sebastes* spp. declined markedly in all strata after the storm, whereas those of *Stenobrachius leucopsarus* showed a decline in deeper strata but increased in strata shallower than 30 m. This probably was caused by upward turbulent advection of larvae from deeper strata. Likewise, larval density of *Leuroglossus stilbius* increased in strata shallower than 50 m following the storm, with sporadic high counts in individual tows, suggesting pulses of upwardly advected larvae.

[1] C. D. Winant. 1998. Center for Coastal Studies, Scripps Institution of Oceanography, La Jolla, CA 92093. Personal commun.

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