DISTRIBUTION OF ICHTHYOPLANKTON IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Larval fish were sampled by oblique 1-meter net and neuston net tows in the Southern California Bight quarterly from 1974 through 1976. The northern anchovy, Engraulis mordax, was much more abundant in both types of collections than were all other kinds of larvae combined, but some other fairly common species were found in only one type of tow. Subjective evaluation and analysis of recurrent groups established larval groupings that were distinguished primarily by nearshore versus offshore distribution and summer-fall versus winter-spring occurrence.

RESUMEN

Larvas de peces muestreadas trimestralmente entre 1974 y 1976 en arrastres oblicuos de redes neuston y de 1 metro en la Bahía del Sur de California. En ambos tipos de recoleciones, la anchoveta Engraulis mordax era mucho más abundante que todas las otras clases de larvas combinadas, pero otras especies bastante comunes fueron encontradas en sólo un tipo de arrastre. A través de la evaluación subjetiva y el análisis de groups recurrentes se establecieron agrupaciones de larvas que se distinguieron principalmente por su distribución, cerca de la costa o mar afuera, y aperecer durante los periodos de verano-otoño o en invierno-primavera.

INTRODUCTION

In studies of ichthyoplankton off California over the last three decades, the California Cooperative Oceanic Fisheries Investigation (CalCOFI) has emphasized the sampling of eggs and larvae of California Current pelagic species such as the sardine, which declined dramatically in the late 1940s. Recently, importance of recreational fisheries and increased human modification of California's nearshore zone have prompted concern for the fish populations residing there.

The distributions and abundances of some demersal species with pelagic eggs and larvae have been studied in samples from the CalCOFI surveys (Ahlstrom 1965), and many groups of inshore fishes are represented as larvae in CalCOFI collections, but the early surveys did not adequately sample areas close to shore. Depth increases rapidly with distance from shore off southern California, and the spawning of some neritic species is presumably restricted to a narrow band along the coastline and around the channel islands, banks, and seamounts. Pelagic larvae of such species are subject to dispersal by currents and must somehow remain in or return to the coastal zone in sufficient numbers to maintain adult populations (cf. Leis and Miller 1976 for larvae in Hawaiian waters). The larvae of some inshore spawners may develop rapidly enough to maintain their position in the nearshore zone, even though affected by longshore currents; such species would not be well represented in offshore surveys. Many larvae of species with longer larval life must be carried offshore by currents, especially by Ekman drift during periods of upwelling. Shoreward transport of such larvae by subsurface currents generated during upwelling is also possible (Peterson, Miller, and Hutchinson 1979).

The Southern California Bight lies inshore of the southward-flowing California Current. The bight's surface circulation is generally a cyclonic gyre; nearshore currents alternate between flowing south-southwest or north-northwest, though the latter flow dominates (Tsuchiya 1980). This study was carried out to refine the knowledge of seasonal and areal distributions of pelagic larval fish within the Southern California Bight, emphasizing the nearshore zone not sampled by CalCOFI.

METHODS

Southern California Bight Study (SCBS) station positions were chosen to represent quasi-logarithmic distances from the mainland shore (Table 1); SCBS lines 300, 200, and 100 correspond to CalCOFI lines 87, 90, and 93, respectively (for a map, see Eppley et al. 1977, or Eppley, Sapienza, and Renger 1978). SCBS cruises 1 through 9 cover more than two years—from September 1974 through January 1977.

TABLE 1

**Depths and Locations of Stations Sampled for Ichthyoplankton
in the Southern California Bight Study (SCBS), 1974–77**

Station number	Depth (m)	Distance offshore (km)	Position	
301	16	0.9	33°54.3'N	118°25.5'W
302	18	1.9	33°55.1'N	118°27.2'W
303	42	5.6	33°53.8'N	118°28.8'W
304	320	19	33°50.4'N	118°36.2'W
305	920	46	33°45.5'N	118°47.6'W
306	1650	98	33°30.1'N	119°20.0'W
201	36	0.9	33°29.4'N	117°44.9'W
202	54	1.9	33°29.0'N	117°45.5'W
203	90*	5.6	33°28.0'N	117°47.5'W
205	730	52	33°17.3'N	118°10.4'W
206	1240	96	33°07.0'N	118°31.3'W
San Onofre	5	0.5	33°20.1'N	117°30.4'W
101	20	0.9	32°57.4'N	117°16.5'W
102	38	1.9	32°57.3'N	117°17.3'W
103	230*	5.6	32°56.8'N	117°18.9'W
105	1000	41	32°52.2'N	117°37.8'W
106	1850	107	32°31.6'N	118°07.0'W

*Station position and depths of #103 and 203 varied.

Stations were sampled quarterly with the exception of December 1974, when no cruise was undertaken.

Ichthyoplankton was collected with oblique plankton net hauls and surface or neuston net hauls made simultaneously at each station, except at some very shallow stations where only the neuston net was used. Oblique hauls were made with the standard CalCOFI-type net constructed of 505-μm nylon netting with a mouth diameter of one meter and a straining surface-(pore area)-to-mouth-area ratio of approximately five to one. A digital flow meter was centered in the circular mouth opening, attached to the tubular metal frame.

Oblique samples were collected, preserved, and processed following CalCOFI guidelines as described by Kramer et al. (1972). During cruise SCBS 4, the maximum amount of towing wire let out was reduced from 300 to 200 m. In shallow water on all cruises, the depth of tow was adjusted to avoid hitting the bottom.

The neuston frame carried an identical net to that used for oblique hauls, but the mouth of the net was modified from a circle to a rectangle, and for buoyancy, styrofoam floats were placed inside the frame ends (Ahlstrom and Stevens 1976). No flow meter was attached; the neuston net was towed for a minimum of 10 minutes. Neuston collections were preserved and processed similarly to the oblique collections.

All net tows were done during daylight hours, leading to two potential sources of bias. The abundances of those juveniles and late larval stages that are able to see and avoid the net are underestimated. Also,

a few species (e.g., *Tarletonbeania crenularis*) would be caught in greater numbers in night hauls because they migrate to the surface waters then.

Most samples were completely sorted for all fish eggs and larvae; for stations 303, 305, 306, 205, and 105 on cruise SCBS-2, only 25 percent of the anchovy larvae were removed and counted, but all other fish larvae were removed from these samples.

Identification of larvae was to species level when possible, but taxonomic difficulties exist in several important groups. The most notable is the rockfish genus *Sebastes*, which includes 48 species known to spawn in the Southern California Bight (Miller and Lea 1972). The genera *Citharichthys* (sand dabs), *Hypsoblennius* (blennies), and *Paralabrax* (basses) each include three local species.

We directly compared the distributional records of different taxa to obtain subjective patterns, at least for the relatively common species. Because the number of samples was fairly large, we also applied a statistical grouping technique—the analysis of recurrent groups—that has previously been applied to communities of adult fish (e.g. Fager and Longhurst 1968), benthos (e.g. Lie and Kelley 1970), and zooplankton (e.g. Fager and McGowan 1963). We chose this approach because of the infrequent occurrence of most species (Table 2), and analyzed data from oblique and neuston tows separately. We tested several levels of affinity at which to form groups, since the level of affinity determines how two species can differ in frequency of occurrence and still be placed in the same group. We also analyzed both the entire set of data and the subset of species occurring at least 5 times; this had relatively little effect on major groupings, though analysis of the complete set resulted in some groups of rare species that were not found in the subset analysis.

The species in the resulting groups are frequent components of each other's biotic environments (or, in the extreme case, the very common species in a group are usual components of the environment of the group's very rare species), both seasonally and geographically, though our method of sampling precludes detecting differences in vertical distributions of species in the same group (see below). Although the members of a group necessarily have similar patterns of occurrence, they need not have similar patterns of abundance. The latter relation was tested for the major groups defined from oblique hauls by calculating a coefficient of rank correlation (Tate and Clelland 1957) between the abundances of species in each possible pairing for those samples in which the entire group occurred, and establishing a matrix of correlation coefficients for all pairs within the group.

TABLE 2

Taxa That Occurred in at Least 5 Oblique or Neuston Tows in the Southern California Bight, Ranked in Order of Decreasing Numerical Abundance in Oblique Tows

	Zone	Spawning type	Mean larvae/10 m²	% of total larvae for oblique hauls	Mean larvae/10 m² in positive hauls	No. of occurrences	% of occurrences in 112 oblique hauls	Rank by occurrence in oblique hauls	% of occurrences in 127 neuston hauls
1. *Engraulis mordax*	C	P	733.2	82.83	774.8	106	94.6	1.0	57.4
2. *Sebastes* spp.	C	O	36.5	4.12	52.4	78	69.6	2.0	19.7
3. *Leuroglossus stilbius*	O	P	33.0	3.72	82.0	45	40.2	5.0	
4. *Stenobrachius leucopsarus*	O	P	19.5	2.20	42.0	52	46.4	4.0	
5. *Genyonemus lineatus*	C	P	15.0	1.70	44.3	38	33.9	7.0	14.2
6. *Merluccius productus*	O	P	14.4	1.63	59.7	27	24.1	12.0	
7. *Citharichthys* spp.	C	P	5.0	0.68	22.0	60	53.5	3.0	3.9
8. *Bathylagus ochotensis*	O	P	3.9	0.44	15.6	28	25.0	10.0	
9. *Paralichthys californicus*	I	P	3.0	0.34	8.6	39	34.8	6.0	
10. *Hypsoblennius* spp.	I	D	2.2	0.25	12.8	19	17.0	15.5	18.1
11. *Pleuronichthys verticalis*	I	P	2.1	0.24	8.4	28	25.0	10.0	
12. *Seriphus politus*	I	P	1.9	0.22	12.0	18	16.1	17.5	5.5
13. *Paralabrax* spp.	I	P	1.8	0.20	7.7	26	23.2	13.0	
14. *Peprilus simillimus*	C	P	1.6	0.18	9.7	18	16.1	17.5	
15. *Triphoturus mexicanus*	O	P	1.3	0.15	6.3	23	20.5	14.0	
16. Gobiidae	C	D	1.2	0.14	4.8	29	25.9	8.0	
17. *Argyropelecus* spp.	O	P	1.1	0.12	4.4	28	25.0	10.0	
18. *Sardinops caeruleus*	C	P	1.0	0.11	15.6	7	6.3	29.0	
19. *Pleuronichthys ritteri*	I	P	0.5	0.06	9.8	6	5.4	32.0	
20. *Parophrys vetulus*	I	P	0.5	0.05	5.4	10	8.9	24.0	
21. *Hypsopsetta guttulata*	I	P	0.5	0.05	4.8	11	9.8	22.0	
22. *Tarletonbeania crenularis*	O	P	0.5	0.06	3.2	19	17.0	15.5	
23. *Argentina sialis*	O	P	0.4	0.05	9.2	5	4.5	36.5	
24. *Oxyjulis californica*	I	P	0.4	0.05	4.9	10	8.9	24.0	
25. *Trachurus symmetricus*	O	P	0.4	0.05	4.2	12	10.7	20.5	6.3
26. *Lampanyctus* spp.	O	P	0.4	0.05	2.8	16	14.3	19.0	
27. *Lyopsetta exilis*	C	P	0.3	0.04	7.2	5	4.5	36.5	
28. *Bathylagus pacificus*	O	P	0.3	0.04	5.3	7	6.3	29.0	
29. Blennioidei	C	D	0.3	0.03	4.2	7	6.3	29.0	
30. *Hippoglossina stomata*	I	P	0.3	0.03	3.8	8	7.1	26.5	
31. *Danaphos oculatus*	O	P	0.3	0.03	3.6	8	7.1	26.5	
32. *Protomyctophom crockeri*	O	P	0.3	0.03	2.7	12	10.7	20.5	
33. *Diogenichthys laternatus*	O	P	0.2	0.03	5.5	5	4.5	36.5	
34. *Bathylagus wesethi*	O	P	0.2	0.02	4.0	6	5.4	32.0	
35. *Stomias atriventer*	O	P	0.2	0.02	3.5	5	4.5	36.5	
36. Clinidae	I	D	0.2	0.02	2.5	10	8.9	24.0	
37. *Tetragonurus cuvieri*	O	P	0.1	0.01	2.8	5	4.5	36.5	
38. *Diaphus theta*	O	P	0.1	0.01	2.0	5	4.5	36.5	
39. *Chromis punctipinnis*	C	D	0.1	0.01	1.9	6	5.4	32.0	
Atherinidae	I	S							24.4
Cololabis saira	C	S							22.8
Exocotidae	C	S							5.5
Medialuna californiensis	C	P							4.7
Girella nigricans	I	P							4.7
Scorpaenichthys marmoratus	C	D							3.9
Hexagrammos decagrammus	C	D							3.9

In cases of ties, the taxon with the greatest abundance in those samples in which it occurred (positive hauls) is ranked first. Unranked taxa occurred at least 5 times only in neuston tows. For "zone", I is inshore, O is offshore, C is inshore and offshore. For "spawning type", P is pelagic oviparous, D is demersal oviparous, O is ovoviviparous, S is a special case. S for Atherinidae indicates demersal in beach sand or floating attached egg mass; S for *Cololabis* and Exocoetidae indicates floating attached egg mass.

RESULTS

Abundances of Taxonomic Categories

Thirty-nine families of larval fish were found in oblique and neuston collections; of these, En-graulidae, Scorpaenidae, Bathylagidae, Myctophidae, Sciaenidae, Bothidae, Merlucciidae, and Pleuronectidae were responsible for over 98 percent of all larvae enumerated in the oblique hauls.

The abundances and/or frequencies of all taxa of larvae that occurred in at least five oblique or five neuston hauls are given in Table 2.

The northern anchovy, *Engraulis mordax*, (the only engraulid sampled) occurred in 95 percent of all oblique hauls (Table 2) and accounted for 83 percent of all larvae enumerated. It also was the most frequent (73 occurrences in 127 hauls) in neuston tows, where anchovy eggs were 15 times more abundant than all other fish eggs.

As expected, the neuston tows gave a somewhat different picture of the relative importance of taxa, though comparisons of absolute abundances are not possible since the volume filtered was not measured. Only 34 kinds of larvae were caught compared to 71 kinds in oblique tows. Atherinids (predominantly the grunion *Leuresthes tenuis*) occurred only twice in oblique tows but were found in almost 25 percent of the neuston tows and were particularly abundant in June 1975 at the shallowest station (San Onofre). The saury, *Cololabis saira*, occurred in 23 percent of the neuston tows and not at all in the oblique tows. The other groups occurring in over 10 percent of the neuston tows were *Genyonemus lineatus* (white croaker), *Sebastes* spp., and *Hypsoblennius* spp., all of which were also frequent in oblique tows. Flying fish (Exocoetidae) and *Hexagrammos decagrammus* (kelp greenling) were never taken in oblique tows, but occurred 7 and 5 times, respectively, in neuston tows.

Conversely, several types of larvae encountered frequently in the oblique tows were found in fewer than 5 neuston tows (*Leuroglossus stilbius, Stenobrachius leucopsarus, Merluccius productus, Paralichthys californicus, Pleuronichthys verticalis, Paralabrax* spp., *Peprilus simillimus, Bathylagus ochotensis, Triphoturus mexicanus, Argyropelecus* spp., and Gobiidae).

Geographical and Seasonal Patterns of Taxa and of Recurrent Groups

General zones of occurrence for larvae, based on cumulative records from both CalCOFI and SCBS cruises, are included in Table 2; Table 3 shows seasonal and inshore/offshore distributional patterns for some important larvae on SCBS cruises. Stations were arbitrarily categorized (see Table 3) with regard to depth and distance from the mainland as "nearshore," "intermediate," or "offshore."

Several kinds of larvae, especially from taxa whose adults are mesopelagic, were found primarily at offshore stations (Table 3A). Larvae of *Leuroglossus stilbius, Bathylagus ochotensis, Argyropelecus* spp. (hatchetfish), and *Merluccius productus* (Pacific hake) occur in greatest abundance below the upper mixed

layer (Ahlstrom 1959), and adults of the myctophids *Stenobrachius leucopsarus, Triphoturus mexicanus, Protomyctophum crockeri,* and *Tarletonbeania crenularis* are known to inhabit fairly deep water. Larvae of *Trachurus symmetricus* (jack mackerel) are known to be most abundant in offshore waters (Ahlstrom and Ball 1954; Ahlstrom 1969). Most of the larvae in Table 3A were rarely taken in the inshore zone (except *S. leucopsarus*), but most were well represented in the intermediate zone, and *S. leucopsarus* was most abundant there.

Some larval taxa occurred primarily inshore, though most were also represented in the intermediate zone (Table 3B). The bothid flatfish *Paralichthys californicus* (California halibut) and the pleuronectid flatfish *Pleuronichthys verticalis* (hornyhead turbot) occurred at very few offshore stations, and both early and late larval stages were collected at inshore stations. CalCOFI data from 1955 through 1960 also establish these larvae as being most abundant inshore (Ahlstrom and Moser 1975). Adults of *Hypsoblennius* spp. are restricted to shallow water and spawn demersal eggs, and greatest abundances of larvae on SCBS cruises were in the inshore and intermediate zones. The sardine *Sardinops caeruleus* is included in the inshore group even though earlier CalCOFI data show it occurring both inshore and offshore (Ahlstrom 1959a). Based on the neuston tows, the Atherinidae (grunion) also belong to the inshore group.

Cosmopolitan taxa occurred regularly in all three zones (Table 3C), as did the anchovy (below). *Sebastes* spp. and the bothid flatfishes *Citharichthys* spp. generally exhibited higher concentrations of larvae at offshore and intermediate stations than at inshore stations. Gobies and the Pacific pompano, *Peprilus simillimus*, also occurred in all zones, but numbers of larvae represented were moderate. Larval saury occurred in both nearshore and offshore neuston tows, though they were somewhat more frequent in the latter.

Engraulis mordax exhibits the widest areal and temporal distribution of any larvae sampled, occurring not only on every cruise but at most stations as well. Greatest abundances of larvae appeared in March and June. CalCOFI data show abundance of larvae to be greatest from January through June (Kramer and Ahlstrom 1968). Other kinds of larvae occurring throughout the year in SCBS samples include *Sebastes* spp., *Citharichthys* spp., *Argyropelecus* spp., *Paralichthys californicus*, Atherinidae, and the gobies.

Larvae that occurred most often in June and September were *Hypsoblennius* spp., *Paralabrax* spp., *Sphyraenna argentea* (Pacific barracuda), *Oxyjulis californica* (señorita), *Peprilus simillimus, Trachurus*

TABLE 3
Geographical and Seasonal Distributions of Selected Taxa, Given as Numbers of Larvae per 10m² Sea Surface in Oblique Tows

A. Taxa with offshore larvae

Season	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore
	Stenobrachius leucopsarus			*Leuroglossus stilbius*			*Bathylagus ochotensis*		
Sept.-Oct.	0	0	0.3	0	0	0	0	0	0.1
Dec.-Jan.	4.5	4.8	18.3	0.1	65.3	125.7	0	5.2	24.7
Feb.-Mar.	20.3	161.5	70.3	0.3	43.8	133.2	0.4	5.4	6.1
June	0	3.6	3.3	0	3.1	2.0	0	0.8	0.9
	Merluccius productus			*Trachurus symmetricus*			*Triphoturus mexicanus*		
Sept.-Oct.	0	0	0.2	0	1.7	2.3	0.6	5.7	6.0
Dec.-Jan.	0.7	4.6	74.2	0	0	0	0	0	0
Feb.-Mar.	0	13.8	51.6	0	0	0	0	0	0
June	0	0	0	0.5	0	0.6	0.6	0.8	1.5
	Argyropelecus spp.			*Protomyctophom crockeri*			*Tarletonbeania crenularis*		
Sept.-Oct.	0	0.5	1.9	0	0.5	1.0	0	0.2	1.2
Dec.-Jan.	0	1.0	2.7	0	0	0.5	0.2	0.7	1.8
Feb.-Mar.	0	1.5	3.3	0	0	1.3	0	0.9	0.5
June	0	1.6	0.3	0	0	0.5	0	0	0.5

B. Taxa with nearshore larvae

Season	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore
	Genyonemus lineatus			*Paralichthys californicus*			*Sardinops caeruleus*		
Sept.-Oct.	0.6	0	0	8.7	2.1	0.5	6.9	0.5	0
Dec.-Jan.	25.6	36.7	0.5	4.1	1.4	0	0.1	0	0
Feb.-Mar.	102.5	62.7	10.8	5.5	5.2	0.5	0.2	0	0
June	0	0.8	0	2.1	1.6	0.3	0	0	0
	Hypsoblennius spp.			*Paralabrax* spp.			*Seriphus politus*		
Sept.-Oct.	13.1	1.2	0.3	2.9	12.5	2.1	6.5	1.2	0
Dec.-Jan.	0.2	0	0	0	0	0	0.2	0	0
Feb.-Mar.	0	0	0	0.2	0	0	0	0	0
June	2.5	3.0	0.3	4.4	2.4	0.1	11.6	3.5	0
	Pleuronichthys ritteri			*Pleuronichthys verticalis*					
Sept.-Oct.	2.6	0	0	2.1	1.9	0			
Dec.-Jan.	0.7	0	0	1.3	0	0			
Feb.-Mar.	0.3	1.9	0	7.2	7.6	1.9			
June	0	0	0	4.9	3.2	0			

C. Taxa with cosmopolitan larvae

Season	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore
	Engraulis mordax			*Sebastes* spp.			*Citharichthys* spp.		
Sept.-Oct.	41.0	118.5	73.0	1.6	11.7	2.9	3.0	17.9	5.9
Dec.-Jan.	840.0	214.1	238.4	21.3	29.3	104.6	2.9	3.7	13.8
Feb.-Mar.	490.0	1,567.8	3,074.4	7.0	196.4	94.8	0.6	8.7	3.7
June	1,191.1	1,343.7	167.5	0.4	7.5	7.7	1.4	2.8	1.2
	Gobiidae			*Peprilus simillimus*					
Sept.-Oct.	1.0	1.3	0.5	1.0	2.5	1.1			
Dec.-Jan.	4.7	0.4	0.5	0	0	0			
Feb.-Mar.	0.7	0.5	1.2	0	0	0			
June	0.8	1.2	1.0	8.1	4.6	4.3			

Each seasonal grouping is based on two or three different cruises. The geographical grouping "nearshore" includes the 44 samples from all X01 and X02 stations, 303, and San Onofre (see Table 1); "intermediate" includes the 20 samples from stations 103, 203, and 304; and "offshore" includes the 48 samples from all X05 and X06 stations.

symmetricus, and *Triphoturus mexicanus*. Larval saury were found in every season except winter.

Some of the larvae could be placed into recurrent groups. For the data from neuston tows, we chose an affinity level of ≥ 0.3 as the criteron for grouping. Group N1 (Figure 1) occurred, as a group, in winter and spring primarily at nearshore stations, in spite of the fact that *Engraulis* and the *Sebastes* spp. category were cosmopolitan in distribution (Table 3). Somewhat surprisingly, the three affiliated categories, though themselves of nearshore origin, had higher affinities with the cosmopolites than with *Genyonemus*. Group N2 occurred only six times, in summer and fall,

most often at offshore stations; larval saury *(Cololabis)* were found in spring as well.

Taxa from the oblique tows were grouped using an affinity level of ≥ 0.5. Group O1 (Figure 2) included two offshore larvae (Table 3) and two cosmopolites, and the 34 occurrences as a group were mainly at offshore stations in winter, spring, and summer (Figure 3). Within these 34 occurrences, all of the six possible correlations in abundance were positive, and five were significantly so ($p < 0.05$), which means that the populations constituting the group were cohesive; the times and places that were "best" or "worst" (in terms of abundance) for one population
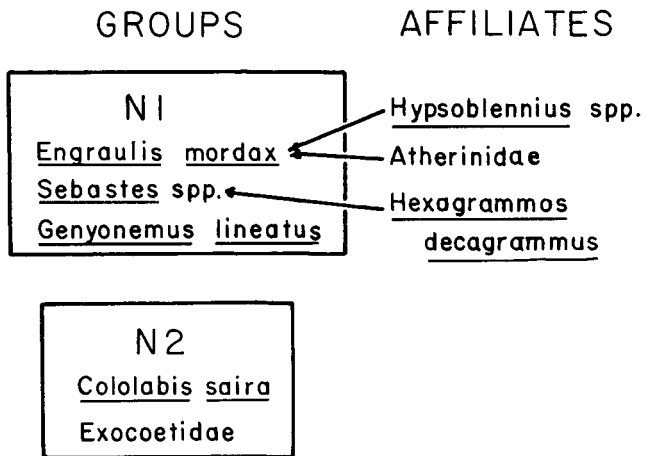
GROUPS

AFFILIATES

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┌─────────────────────┐
│        N I          │
│                     │──→ Hypsoblennius spp.
│  Engraulis  mordax ◄├──
│                     │   ── Atherinidae
│  Sebastes spp. ◄────┤
│                     │   ── Hexagrammos
│  Genyonemus lineatus│        decagrammus
└─────────────────────┘
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┌─────────────────────┐
│        N 2          │
│                     │
│  Cololabis saira    │
│                     │
│  Exocoetidae        │
└─────────────────────┘
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Figure 1. Recurrent groups of larval fish in neuston tows in the Southern California Bight. An affinity index of ≥0.3 is the criterion for grouping. "Affiliates" are those categories having significant affinity with some but not all members of a group, as indicated by arrows.

tended also to be best or worst for all other members of the group. The cosmopolitan flatfish *Citharichthys* was affiliated with the cosmopolitan members of the group, as was the offshore *Bathylagus* with the offshore members.

Group O2 was found exclusively at nearshore stations, and occurred as a group only in summer and fall (Figure 3); this group seems superficially similar to Group O3 in geographic distribution, and the two complete groups occurred together in four of ten pos-
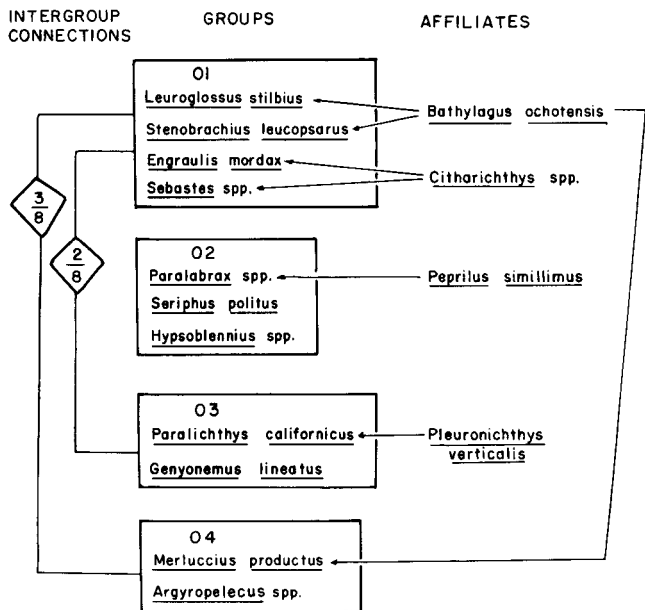
sible cases. The members of Group O2 were not particularly coherent in abundance, since there were a positive, a negative, and a zero correlation between the pairs at the ten stations where the group occurred.

The principal difference between Group O2 and Group O3 was seasonal: the latter group was found in winter and spring as well as fall (Figure 3), and occurred only once (out of 27 times) in summer. The abundances of its two members were positively correlated in the 27 occurrences, but not significantly so.

Group O4 was found offshore, and in fact was combined with Group O1 when an affinity level of 0.4 was used for grouping. It was even more strictly offshore than was Group O1, and only one of 17 occurrences as a group was outside the period between January and March. Its two members had significant, positive correlations in abundances in the 17 occurrences of the group.

When recurrent groups were established with an affinity level of 0.4 as the criterion, an additional

INTERGROUP CONNECTIONS | GROUPS | AFFILIATES

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┌──────────────────────────────┐
│            O I               │
│  Leuroglossus stilbius ──────┤
│                              │── Bathylagus ochotensis
│  Stenobrachius leucopsarus ◄─┤
│                              │
│  Engraulis mordax ◄──────────┤
│                              │── Citharichthys spp.
│  Sebastes spp. ◄─────────────┤
└──────────────────────────────┘

┌──────────────────────────────┐
│            O 2               │
│  Paralabrax spp. ◄───────────┼── Peprilus simillimus
│                              │
│  Seriphus politus            │
│                              │
│  Hypsoblennius spp.          │
└──────────────────────────────┘

┌──────────────────────────────┐
│            O 3               │
│  Paralichthys californicus ◄─┼── Pleuronichthys
│                              │      verticalis
│  Genyonemus lineatus         │
└──────────────────────────────┘

┌──────────────────────────────┐
│            O 4               │
│  Merluccius productus ◄──────┤
│                              │
│  Argyropelecus spp.          │
└──────────────────────────────┘
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Figure 2. Recurrent groups of larval fish in oblique tows in the Southern California Bight. An affinity index of ≥0.5 is the criterion for grouping. "Intergroup connections" indicates the proportion of all possible affinities (the denominator) that were actually realized (the numerator) between pairs of categories whose members were in different groups. "Affiliates" are those categories having significant affinity with some but not all members of a group, as indicated by arrows.
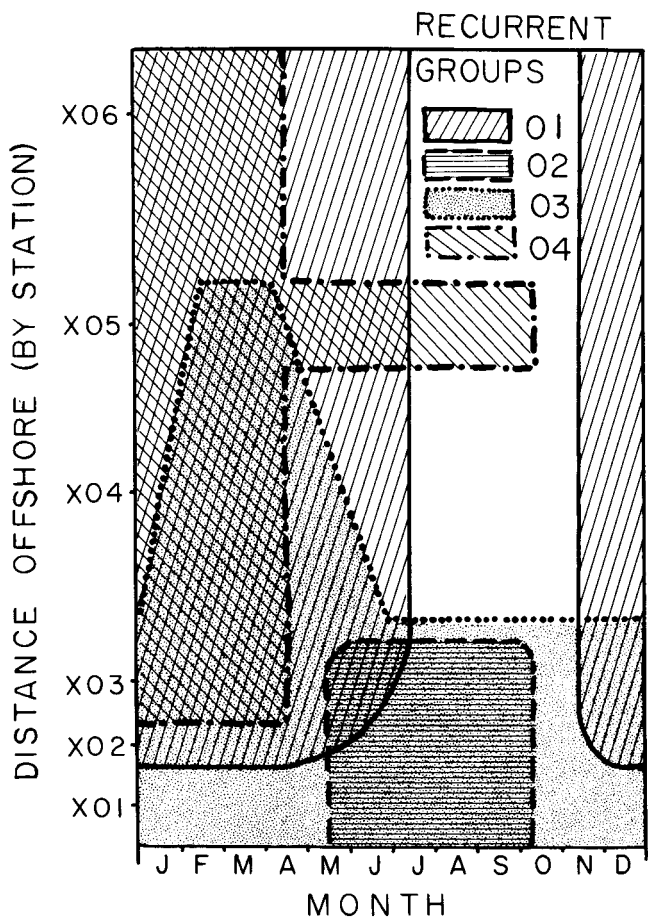

Figure 3. Areal and seasonal distributions of the recurrent groups in oblique tows (see Figure 2). Contour lines enclose all stations at which the entire group occurred. "X" on the ordinate equals 1, 2, or 3; see Table 1 for locations and depths of stations. The 300-m contour and 10-km distance offshore both occur between X03 and X04.

offshore, summer-fall group consisting of *Trachurus symmetricus* and *Triphoturus mexicanus* was found. A second group—*Lyopsetta exilis* (slender sole) and *Parophrys vetulus* (English sole)—was found only in March and at stations an intermediate distance from shore.

DISCUSSION

We have expressed results of oblique tows as catch per 10 m² sea surface; this rests on the assumption that the full depth range for fish eggs and larvae was sampled. Studies in the California Current region indicate that most fish eggs and larvae are distributed within the upper mixed layer or in the upper portion of the thermocline, between the surface and approximately 125 m, even in daytime (Ahlstrom 1959). Since most deep hauls averaged 210 m deep, the depth range for most eggs and larvae offshore was sampled. However, the interpretation of results from shallow stations is less sure, since the depth range for larvae and eggs has not been established and since the area on and just above the bottom was not sampled by our oblique hauls. It is likely (Brewer, Lavenberg, and McGowen, unpublished) that we would have found greater abundances of several nearshore larvae had we used an epibenthic net.

The question of vertical distribution also affects the interpretation of the recurrent groups. As mentioned earlier, a recurrent group consists of organisms that are frequently found in the same samples. Since our net tows integrated from the surface to 210 m at the offshore stations, it is possible that members of the same recurrent group have only minor ecological interactions, because they live at different depths. For example, larval *Engraulis, Sebastes* spp., *Citharichthys* spp., and *Stenobrachius* (formerly *Lampanyctus leucopsarus*) occur primarily in the mixed layer near the surface, while *Bathylagus, Leuroglossus,* and *Merluccius* occur below the thermocline (Ahlstrom 1959). Hence a recurrent grouping based on vertical distributions probably would separate *Leuroglossus* from the other members of Group O1.

Brewer, Lavenberg, and McGowen (unpublished) sampled the inshore waters of the Southern California Bight in spring and fall of 1978. The most significant faunal difference between their results and those reported here was the occurrence of large numbers of larval chub mackerel *(Scomber japonicus),* rivaling *Engraulis* for dominance, in June of 1978.

The analysis of the recurrent groups in the oblique tows amplified the tabulation of geographic distributions (Table 3) by indicating subgroups within the basic distinction between nearshore and offshore oc-

currences. Differences in season of occurrence separated groups that seemed geographically similar, and there was no specifically cosmopolitan group.

A recent study off the coast of Oregon (Richardson and Pearcy 1977) demonstrated clear division of larval fish into an inshore group (the shoreward 28 km, water 100 m deep or less) and an offshore group (37-111 km, water >100 m), with a transition zone where larval fish were rare. Very few species were cosmopolites, and this is perhaps not surprising in view of the relatively simple bathymetry and predominantly longshore transport along the Oregon coast. In the Southern California Bight a complex gyral circulation and a series of deep basins between the coast and the chain of offshore islands and banks make patterns of distribution less clear.

The anchovy *Engraulis* occurred in the offshore assemblage of Oregon and was not as abundant as *Sebastes* spp. and the myctophids *Stenobrachius leucopsarus* and *Tarletonbeania crenularis.* Also, larval anchovy were very seasonal in occurrence off Oregon (June-August), unlike the situation in the Southern California Bight. As in the SCBS collections, *Sebastes* and *Stenobrachius* were found off Oregon in most months, but the season of greatest abundance was the late spring rather than winter and early spring.

A further study off the Oregon coast, based on many transects in the springs of four years, revealed a persistent pattern of two or three coastal assemblages, a transitional assemblage, and one or two offshore assemblages, with the coastal/offshore separation generally paralleling the shelf/slope break (Richardson, Laroche, and Richardson 1980). Minor variations from year to year in the locations of these assemblages may have been related to variations in the strength and direction of coastal winds. An important finding was that the geographical pattern of assemblages was relatively constant in spite of month-to-month and year-to-year variations in the abundances of the species dominating each assemblage, especially near the coast. These variations were not well correlated between species, so that a particular geographically defined assemblage might be dominated by different species in different months or years.

There are some ecological advantages for larvae that develop in the inshore zone. Recently, it has been demonstrated that first-feeding larval *Engraulis mordax* must occur with high concentrations of particles in the size range of large dinoflagellates in order to feed adequately (Lasker 1975). Characteristically, these regions exist close to shore off southern California, and relatively steep inshore-offshore gradients in planktonic stocks (as chlorophyll, primarily produc-

tion, particulate organic carbon, etc.) have already been reported (Eppley, Sapienza, and Renger 1978).

Sardinops caeruleus, the Pacific sardine, occurred only near shore on SCBS cruises. Eggs and larvae of this species used to be taken over wide areas both inshore and offshore (Ahlstrom 1959a), but occurrence has changed primarily to inshore zones. It is likely that when breeding stocks were reduced, the remaining population tended to spawn selectively in areas of high productivity, where survival of larvae is enhanced. Thus, the inshore zone could be important for the recovery of certain overfished or otherwise depleted stocks, including the anchovy if its population were ever drastically reduced. It is important to verify the relation between depleted stocks and the productive inshore zone, since this zone is the most likely to be affected by anthropogenic perturbations.

ACKNOWLEDGMENTS

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