THE SPATIAL STRUCTURE OF COASTAL ICHTHYOPLANKTON ASSEMBLAGES OFF CENTRAL AND SOUTHERN CALIFORNIA

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ABSTRACT

We examined the assemblage structure of the coastal ichthyoplankton off central and southern California in relation to depth and region, based on data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI), the Los Angeles County Museum, monitoring of coastal power plants, and other sources. Point Conception was a transition region for ichthyoplankton from San Francisco to San Diego, with distinct depth-related ichthyoplankton assemblages north and south of Point Conception. Northern and southern shallow assemblages were dominated by larval gobies (Gobiidae), with *Acanthogobius flavimanus* and *Lepidogobius lepidus* more important in the north and *Gillichthys mirabilis* in the south. The more offshore assemblage north of Point Conception was dominated by a variety of larval sculpins (Cottidae), while there was greater influence from several croaker species (Sciaenidae) in the Southern California Bight (SCB). There was a faunal transition zone at 15–22 m depth in the SCB. The shallow larval assemblages were primarily characterized by demersally spawning species, while species with planktonic eggs were generally found more offshore. Analysis of several coastal data sets suggested that ichthyoplankton programs may target distinct larval assemblages even within the relatively narrow coastal zone and that such differences may be more pronounced during certain seasons. Our results have important implications for marine spatial planning and for monitoring coastal marine protected areas.

INTRODUCTION

A growing interest in ecosystem management based on marine spatial planning—in particular the design, establishment, and monitoring of representative systems of marine protected areas (MPAs)—has led to the need to better understand biogeographic patterns and their underlying physical and biological processes. California initiated a process of marine spatial planning based on the Marine Life Protection Act (MLPA) of 1999, which directed the state to re-evaluate and redesign its system of MPAs using the best available science. Fundamental to this process is an understanding of the spatial structure of marine ecological communities along the California coast, as well as historical baselines for the composition of these communities.

One of the oldest and richest data sets for California's coastal communities is for the ichthyoplankton. Ichthyoplankton data have been systematically collected off California since 1949 as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. CalCOFI sampling has been carried out mostly seaward of about 35–50 m depth, with most studies centering primarily on the offshore larval fish assemblages (Loeb et al. 1983; Moser and Smith 1993; Hsieh et al. 2005). However, sampling within California's coastal zone has also been carried out by government and academic institutions, most notably the National Marine Fisheries Service (NMFS) and the Los Angeles County Museum (LACM). Further ichthyoplankton sampling has been carried out by industry as part of environmental impact assessment and monitoring studies of power generating stations situated along California's coast.

Synthesis of these various data sets is hindered by the varied temporal and spatial scales of the studies. However, these studies mostly adopted a common sampling gear: the CalCOFI bongo net towed obliquely through the upper water column. In addition, the taxonomic knowledge of the ichthyoplankton has improved considerably since the inception of CalCOFI and the taxonomic expertise developed largely at NMFS through the CalCOFI program is well disseminated (e.g., Moser 1996) and adopted by all agencies.

Since the mid-1970s, many studies have examined the coastal ichthyoplankton within the Southern California Bight (SCB), focusing on their horizontal (Gruber et al. 1982; Barnett et al. 1984; Lavenberg et al. 1986; Walker et al. 1987; McGowen 1993; Watson et al. 2002) and vertical distributions (Barnett et al. 1984; Schlotterbeck and Connally 1982; Brewer and Kleppel 1986; Moser and Pommeranz 1999) as well as some rarely sampled habitats (Jahn and Lavenberg 1986). Although most of these works displayed very different temporal and spatial coverage, they often reported similar patterns of cross-shelf change in species composition as well as pronounced seasonal differences in the abundance of dominant taxa.

Several studies have adopted a community approach, using multivariate techniques to assess the ichthyoplankton assemblages within various regions of the SCB (McGowen 1993; Walker et al. 1987; Watson et al. 2002). These community-based studies identified "season" as an important factor structuring larval fish assemblages in the area. In addition, McGowen (1993) indicated distinct cross-shelf assemblage structure for different icthyoplankton groups but no significant alongshore variation in assemblage composition within the SCB. In contrast, Watson et al. (2002) found little evidence for cross-shelf zonation, but noted certain assemblage differences alongshore, primarily because they covered the transitional region off Point Conception—a well-known zoogeographical boundary (Horn and Allen 1978).

Ichthyoplankton studies off the central California coast (from Point Conception to Monterey Bay) have mostly centered on a few selected taxa, such as larval rockfishes (*Sebastes* spp.) (Larson et al. 1994; Sakuma and Ralston 1995; Yocklavich et al. 1996; Bjorkstedt et al. 2002; Wilson et al. 2008), sanddabs (Paralichthyidae) (Sakuma and Larson 1995; Sakuma and Ralston 1995; Sakuma et al. 1999) or Pacific hake (*Merluccius productus*) (Sakuma and Ralston 1995; Sakuma et al. 2007). The only study to assess the entire nearshore ichthyoplankton assemblage in central Californian waters was the 15 month study off Diablo Canyon, which documented the species composition and seasonal abundances of eggs and larvae at two stations at 20 and 60 m depth (Icanberry et al. 1978).

The objectives of this paper are: 1) conduct a community-based analysis of the composition and variability of coastal ichthyoplankton assemblages over the region from San Francisco to San Diego; 2) examine cross-shelf changes in the coastal ichthyoplankton on different spatial and temporal scales in several hydrologically different regions off central and southern California; and 3) compare larval fish assemblages sampled by different ichthyoplankton programs in the area.

MATERIALS AND METHODS

Data sources

Several coastal ichthyoplankton data sets from government, academic, and private industry sources were used in our analysis (table 1). The Tenera Environmental Inc. (further referred to as Tenera) data set is based on biological monitoring of twelve power plants/generating stations

TABLE 1
Coastal ichthyoplankton data sets used in this study.

Coastal ichthyoplankton data set	Coverage (year, month)	Depth range (m)	Stations	Samples	Taxa recorded	Type of bottom	Coastline
Los Angeles County Museum	1978–85	8–75	73	1450	172	sand	open coast
LACM 1978	6–7, 9–12	8–36	39	231	91	sand	open coast
LACM 1979	1–5, 8–12	8–36	65	409	107	sand	open coast
LACM 1980	1–7	8–36	47	322	86	sand	open coast
LACM 1981	8	8–36	12	12	42	sand	open coast
LACM 1982	1–6, 8–10,12	8–75	20	116	97	sand	open coast
LACM 1983	2,4,6,8,10,12	8–75	20	115	95	sand	open coast
LACM 1984	1–4, 6,8,10,12	8–75	20	125	84	sand	open coast
LACM 1985	2,4,6,8,10,12	8–75	20	120	69	sand	open coast
Tenera Environmental Inc.							
Alamitos Bay Generating Station	2006	2–14	6	72	69	sand, mud	embayment
Diablo Canyon Power Plant	1997–99	4–72	64	1535	114	rocks	open coast
Encina Power Plant	06.2004–05.2005	4–35	5	65	81	sand	open coast
Harbor Generating Station	2006	10–29	2	24	55	sand, mud	embayment
Huntington Beach Generating Station	09.2003–08.2004	8–24	7	116	58	sand	open coast
Morro Bay Power Plant	06.1999–12.2000	2–4	5	121	72	sand, mud	embayment
Moss Landing Power Plant	03.1999–05.2000	2–5	1	45	43	sand, silt	open coast embayment
Potrero (San Francisco Bay) Power Plant	01.2001–02.2002	1–14	9	224	81	soft mud	Bay
Redondo Beach Generating Station	2006	5–26	7	84	100	sand, silt, clay	open coast embayment
San Onofre Nuclear Generating Station	04.2006–01.2007	8–10	1	10	41	sand, cobble, rocks	open coast embayment
Santa Monica Bay Power Plant	2006	7–31	10	120	108	sand, silt, clay	open coast embayment
South Bay (San Diego Bay) Power Plant	01.2001–10.2003	1–9	5	95	40	sand, silt, clay	Bay
MERRP (Big Sycamore Canyon)	1998–99	12–370	60	240	88	Sand	open coast
MERRP (Vandenberg Ecological Reserve)	1998–99	12–210	60	232	79	Sand, rocky headlands & outcrops	open coast
SCCOOS	2004–07	6–25	9	107	61	sand	open coast
CalCOFI (innermost stations)	1978–85	40–151	23	23	59	sand	open coast

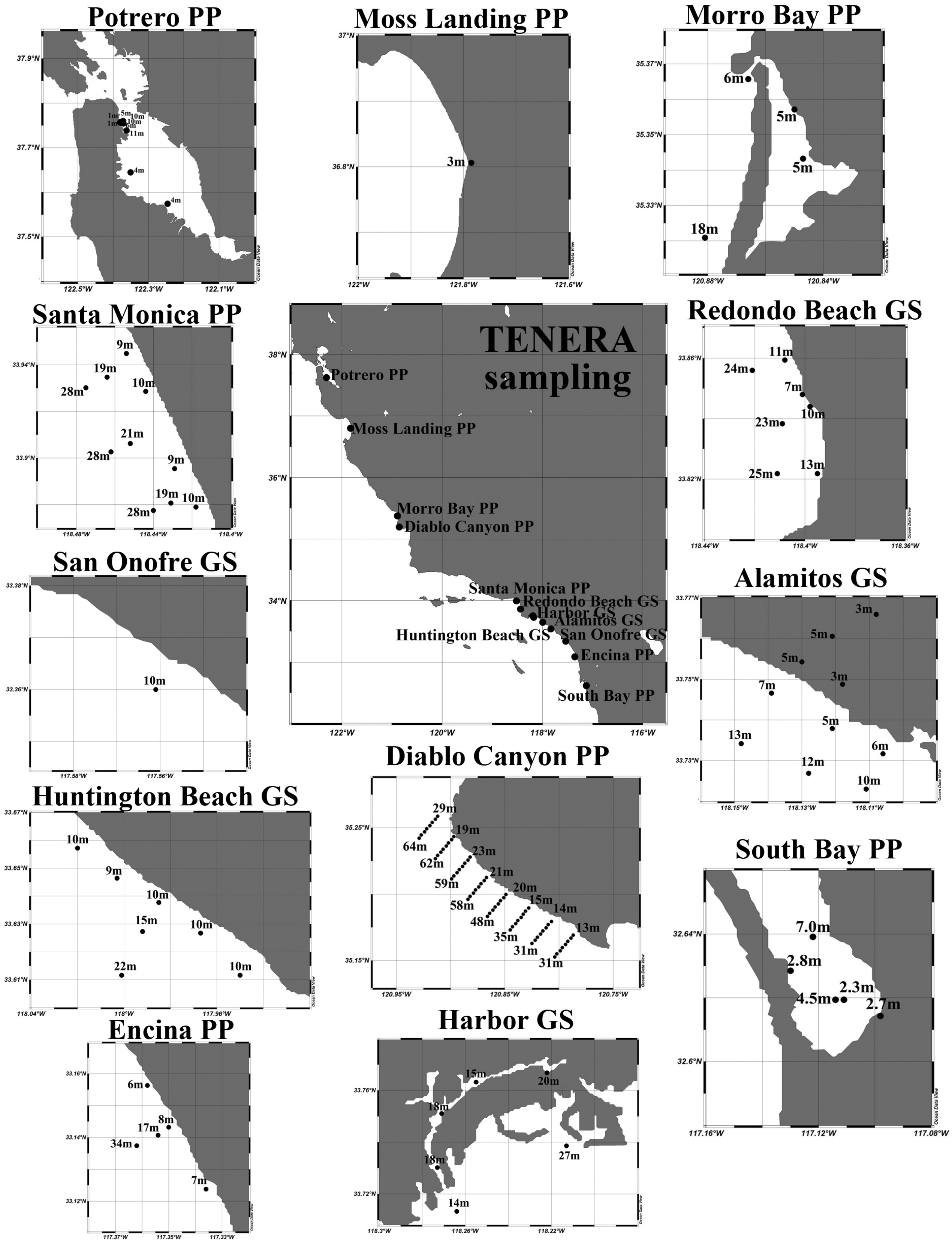

Figure 1a. Ichthyoplankton sampling locations from Tenera Environmental Inc., PP/GS – power plant/generating station.

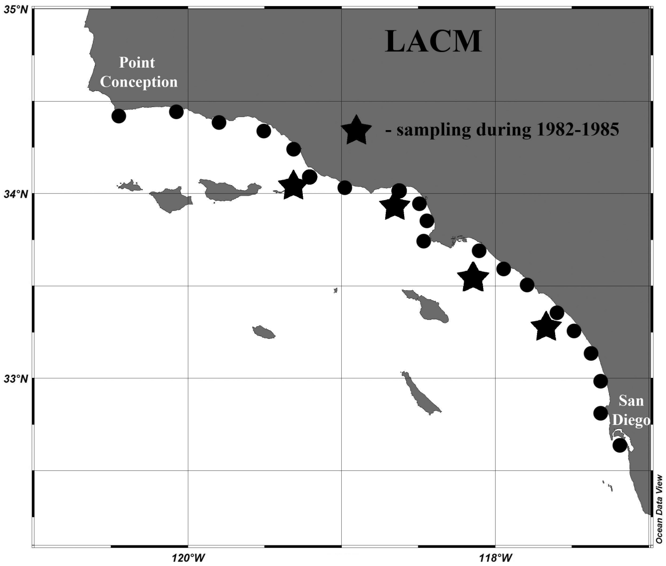

Figure 1b. Ichthyoplankton sampling locations of the Los Angeles County Museum.

located along the coast of central and southern California (fig. 1a), extending from San Francisco Bay to San Diego Bay and covering a variety of habitats from large bays to small coastal enclosures and from nearshore to ~50 m depth. Sampling effort varied considerably between these sites, from one station off Moss Landing and San Onofre Generating Station to 64 stations along eight transects off Diablo Canyon. These locations were sampled throughout the year, thus covering the entire spawning season of the various species. Sampling was carried out over somewhat varying years from 1997 to 2007 (table 1).

The Los Angeles County Museum (LACM) data are from ichthyoplankton sampling carried out during 1978–85 (fig. 1b). Collections from 1978–80 covered 20 transects along the entire SCB with typically four stations on the 8, 15, 22, and 36 m isobaths. Ichthyoplankton data for 1981 was omitted from the analysis because it was confined to only three transects in the central portion of the SCB and was conducted during a single month. Sampling during 1982–85 was confined to four lines spanning the area from Ormond Beach to San Onofre. At the same time, sampling lines during this period were extended offshore to include additional stations along the 75 m isobath (Lavenberg et al. 1986; McGowen 1993).

Among smaller areas within and just outside the SCB, we examined larval fish and egg data from the two coastal areas surveyed as part of the National Marine Fisheries Service Marine Ecological Reserves Research Program (MERRP) off Big Sycamore Canyon Ecological Reserve and Vandenberg Ecological Reserve (fig. 1c). These data were collected during four cruises in late winter-summer 1998–99 (Watson et al. 2002) (table 1). However, we only present data for Big Sycamore Canyon, since no meaningful patterns were found for ichthyoplankton collected off Vandenberg Ecological Reserve.

In recent years, nine nearshore stations were added to the CalCOFI grid as part of the SCCOOS (Southern California Coastal Ocean Observing System) program (fig. 1d). We used data from three years of sampling (2004–07) to compare the ichthyoplankton assemblage from the SCCOOS stations with that found at other coastal CalCOFI stations and from nearby Tenera sampling sites (Alamitos, Encina, Harbor, Santa Monica, and San Onofre).

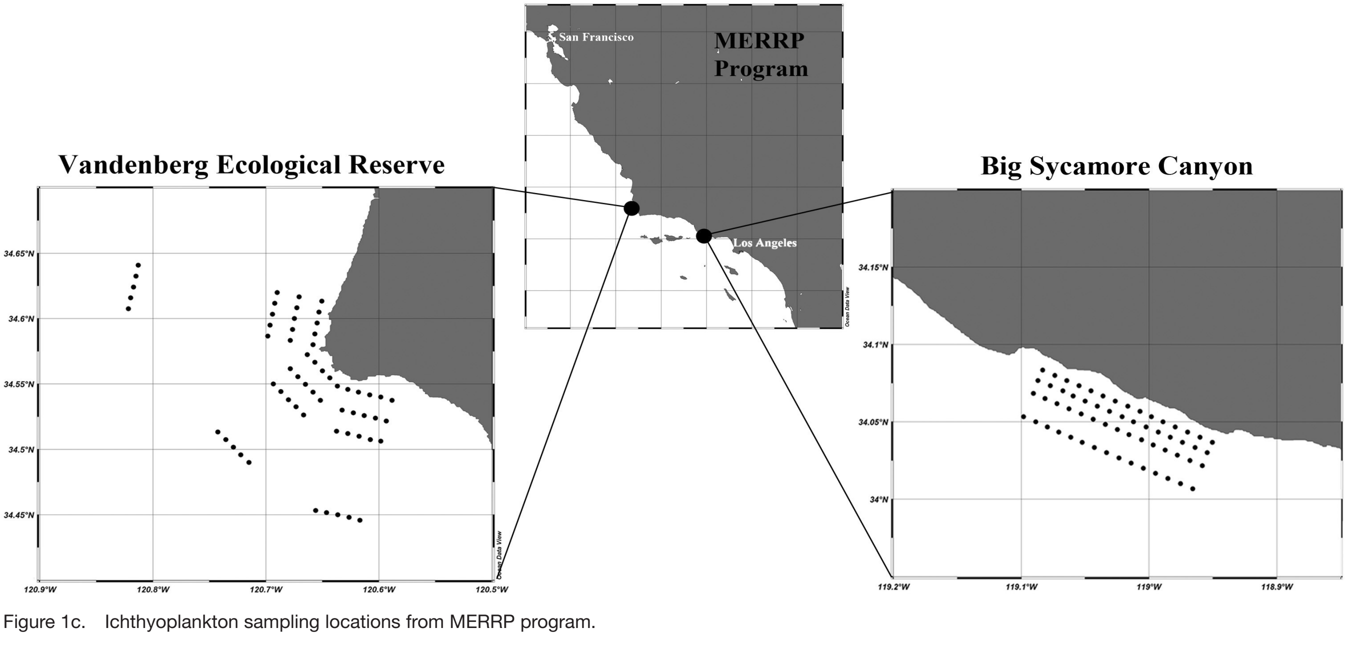

Figure 1c. Ichthyoplankton sampling locations from MERRP program.

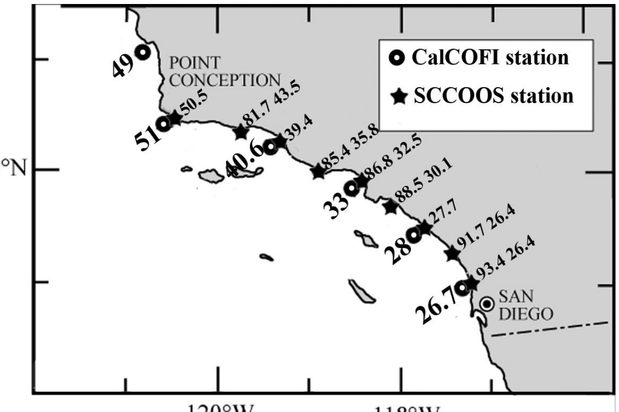

Figure 1d. Ichthyoplankton sampling locations from CalCOFI (inshore stations) and SCCOOS programs.

Due to temporal and spatial overlap between some of these data sets, it was possible to combine several (or components of them) to obtain a broader view of ichthyoplankton community structure and cross-shelf variability in the region. Thus, we compared larval fish assemblages present in the SCB during the late 1970s–early 1980s based on the LACM and CalCOFI data sets (innermost stations of the sampling grid), and during the most recent decade using data from the innermost CalCOFI, Tenera, and SCCOOS stations (sampling during 2004–07). For this purpose, we averaged ichthyoplankton data over monthly sampling periods (LACM + innermost CalCOFI stations) or over the entire period of sampling (5 Tenera locations + innermost CalCOFI + SCCOOS stations).

The coastal data sets were collected during different periods, often characterized by different oceanographic regimes, and generally in different locations, depths and distances offshore. We therefore analyzed them separately or in particular combinations in order to avoid artifacts due to differences in sampling period or location. However, the distinct characteristics of these data sets also enabled us to examine distinct biogeographic issues related to alongshore and onshore-offshore variability in the ichthyoplankton assemblages along the southern and central California coasts.

Ichthyoplankton samples in these data sets were collected using similar sampling procedures and gear. CalCOFI and Tenera used bongo nets with 0.505 mm mesh, while LACM and MERRP used bongos with 0.333 mesh. All programs carried out oblique tows to sample the water column to 200 m maximum depth. However, the LACM study was conducted with a wheeled bongo net, designed to sample the epibenthic layer as well as the water column (Lavenberg et al. 1986), because several nearshore fishes have a preferentially epibenthic distribution (Barnett et al. 1984). The MERRP study used a vertically towed bongo that covered the same depth range but with a smaller sampling volume (Watson et al. 2002). Detailed information on sampling procedures, sample sorting, processing, and preservation for the CalCOFI program is available (Kramer et al. 1972; Ohman and Smith 1995). Procedures for the other sampling programs were generally similar; technical information can be found in references describing the original studies and listed above. In our description of ichthyoplankton assemblages and cross-shelf changes, "depth" always refers to bottom depth. Prior to the analysis, larval abundances were standardized to numbers/10 m^2.

Data analysis

To examine spatial variation in ichthyoplankton assemblages off central and southern California, we first normalized larval abundance within the Tenera data sets over the seasonal cycle by averaging larval fish abundances (numbers/10 m^2) over the sampling period at each station. For Diablo Canyon, which had more extensive sampling (64 stations on eight transects, fig. 1a), larval abundances at each transect were averaged, reducing the number of samples to eight.

To investigate cross-shelf changes in ichthyoplankton assemblages, we averaged larval abundances from each depth stratum over each year for the 1978–85 LACM data set, which provided 33 stations for analysis. For the MERRP sampling off Vandenberg and Big Sycamore Ecological Reserves, we used larval abundances without further normalization. For the 64 Tenera Diablo Canyon stations, we averaged monthly larval abundances over the two-year sampling period.

We used Primer-5 (Clarke and Gorley 2001) to examine ichthyoplankton assemblage structure. Agglomerative hierarchical cluster analysis was carried out using the Bray-Curtis similarity coefficient on fourth-root transformed data. Nonmetric multidimensional scaling (MDS) analysis was carried out as well, based on the same Bray-Curtis similarity matrices, to examine the robustness of groups defined by classification and to observe possible further structure within the ichthyoplankton assemblages not revealed in a one-dimensional classification. Univariate indices such as Shannon-Weaver diversity (H') and Pielou evenness (J') were calculated for ichthyoplankton groups, as well as mean larval abundances and number of taxa at particular locations, using the Primer-5 routine, DIVERSE.

The statistical significance of the groups delineated by our classification procedure was tested using a series of "similarity profile" (SIMPROF) permutation tests (significant at $p < 0.01$, indicated by dotted branches on dendrograms). Groups were examined with the Similarity Percentage (SIMPER) procedure to identify within-group sample similarity and the spe-

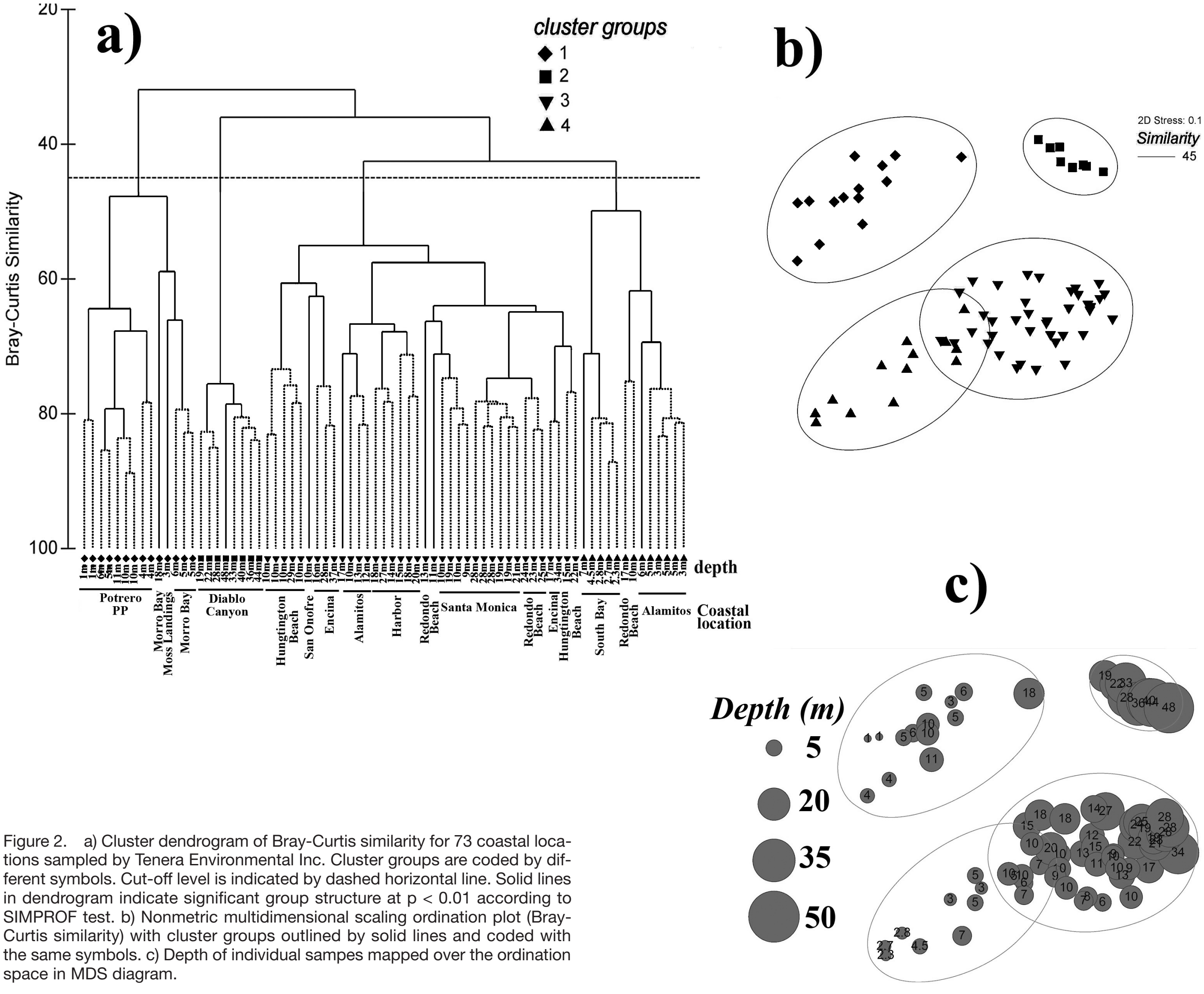

Figure 2. a) Cluster dendrogram of Bray-Curtis similarity for 73 coastal locations sampled by Tenera Environmental Inc. Cluster groups are coded by different symbols. Cut-off level is indicated by dashed horizontal line. Solid lines in dendrogram indicate significant group structure at $p < 0.01$ according to SIMPROF test. b) Nonmetric multidimensional scaling ordination plot (Bray-Curtis similarity) with cluster groups outlined by solid lines and coded with the same symbols. c) Depth of individual sampes mapped over the ordination space in MDS diagram.

cies numerically responsible for group identity. Dominating species defined by SIMPER are those with the highest contribution to the average similarity within particular groups.

We also used Indicator Species Analysis (ISA; Dufrêne and Legendre 1997) to identify taxa indicative for each group outlined in cluster analysis (PC-ORD software, McCune and Mefford 1999). ISA is helpful in examining the fidelity of occurrence of a particular taxon within a certain group. The calculations in ISA are based on the abundance of particular taxa in a group relative to their abundance in all groups and the percent frequency of that taxon in each group. Indicator values range from 0 (no indication) to 100 (perfect indication). Monte-Carlo procedures were used to evaluate the statistical significance of the maximum indicator value recorded for particular species (Dufrêne and Legendre 1997).

RESULTS

Biogeography

The Tenera data set was characterized by the broadest geographic ambit, with 73 stations from 12 coastal locations ranging from San Francisco Bay to San Diego Bay (table 1). Classification revealed four large groups at the level of 45% similarity (fig. 2a). The two most distinct groups (I) and (II) are from the area north of Point Conception, while two others (III) and (IV) were within the SCB. The larval fish assemblages can be further separated based on depth, with shallow (I, IV) and deep assemblages (II, III) forming distinct clusters.

The northernmost assemblage (group I) includes nine stations within San Francisco Bay, four stations within or just outside Morro Bay, and one shallow station at the entrance to Moss Landing Harbor. All of these shallow

TABLE 2

Results of SIMPER and Indicator Species Analysis (ISA) for Tenera coastal ichthyoplankton data. Only top 8–9 taxa in each analysis are shown for each group. Taxa are arranged in descending order of indicator value. Av. Abund. – average abundance of species in the group, Av. Sim. – average similarity of species in the group, S(i) – average contribution (%) of species to overall similarity within the group, IndVal – indicator value, N, H', J' – mean number of species, Shannon-Weaver diversity and Pielou evenness indices for a particular group. NS – non significant

Group	Species	Av. Abund	Av. Sim	S(i)	Ind Val	N	H'	J'
I central California shallow waters, embayments	*Clupea pallasii*	1.47	4.53	7.66	93	41	3.42	0.92
	Leptocottus armatus	0.86	3.18	5.39	80			
	Lepidogobius lepidus	1.39	4.52	7.65	79			
	Acanthogobius flavimanus	1.23	2.99	5.05	58			
	Ammodytes hexapterus	0.37	0.70	1.19	57			
	Gobiidae spp.	2.15	7.63	12.91	24 (NS)			
	Engraulis mordax	1.43	4.29	7.26	22 (NS)			
	Genyonemus lineatus	0.96	3.24	5.48	3 (NS)			
II central California offshore	*Rathbunella* spp.	0.71	1.01	1.29	100	95	4.43	0.97
	Gadidae spp.	0.49	0.68	0.88	98			
	Cebidichthys violaceus	1.10	1.46	1.87	97			
	Sebastes spp.	2.09	3.18	4.07	97			
	Scorpaenichthys marmoratus	1.12	1.66	2.12	97			
	Sardinops sagax	1.77	2.53	3.24	96			
	Bathymasteridae spp.	1.36	2.03	2.60	92			
	Stenobrachius leucopsarus	1.68	2.47	3.16	89			
III southern California offshore	*Seriphus politus*	1.31	2.43	4.02	96	53	3.84	0.97
	Pleuronichthys ritteri	0.82	1.38	2.29	95			
	Paralabrax spp.	1.08	1.76	2.92	90			
	Sciaenidae spp.	1.44	2.85	4.73	90			
	Paralichthys californicus	1.27	2.32	3.85	85			
	Genyonemus lineatus	2.16	3.92	6.49	81			
	Engraulis mordax	1.96	3.69	6.12	46 (NS)			
	Hypsoblennius spp.	1.70	1.14	5.21	38 (NS)			
	Gobiidae spp.	1.57	2.86	4.75	10 (NS)			
IV southern California shallow waters, embayments	Gobiidae spp.	2.94	11.24	18.55	66	33	3.26	0.93
	Labrisomidae spp.	0.78	2.21	3.65	65			
	Syngnathus spp.	0.61	2.03	3.36	62			
	Atherinops affinis	0.55	1.70	2.81	59			
	Hypsoblennius spp.	1.91	6.36	10.49	52			
	Atherinopsis californiensis	0.74	2.88	4.75	34 (NS)			
	Engraulidae spp.	1.15	3.92	6.48	21 (NS)			
	Genyonemus lineatus	1.00	2.70	4.46	7 (NS)			

central California locations are within coastal enclosures/bays or near the entrances to such features.

SIMPER analysis indicated that group I was dominated by typical inshore and embayment species, such as Bay goby (*Lepidogobius lepidus*), yellowfin goby (*Acanthogobius flavimanus*), and some unidentified gobies (most likely species of genera *Clevelandia*, *Ilypnus*, and *Quietula*) (McGowen 1993; Moser and Watson 2006), common coastal pelagics such as Pacific herring (*Clupea pallasii*) and northern anchovy (*Engraulis mordax*), as well as white croaker (*Genyonemus lineatus*) and Pacific staghorn sculpin (*Leptocottus armatus*), together contributing to 51% of the average similarity of 59.1 for this group. However, some of those dominant taxa had less than significant ($p > 0.05$) Indicator Values (IndVal). Species with the highest IndVal included: Pacific herring, Pacific staghorn sculpin, Bay goby, yellowfin goby, and Pacific sand lance (*Ammodytes hexapterus*) (table 2).

The deeper-water assemblage north of Point Conception (group II) included all samples collected off Diablo Canyon. Larval rockfishes, northern anchovy, Pacific sardine (*Sardinops sagax*) and northern lampfish (*Stenobrachius leucopsarus*) were the key species here, contributing 15% to the average similarity of 78.1 within this group. Group II showed the least dominance by individual species, with 65 species making up 90% of the average similarity between samples, and it had highest values for the mean number of species and diversity and evenness indices. Indicator species analysis identified 78 species with significant IndVal, with deeper-water and rocky bottom taxa including larval ronquils (*Rathbunella* spp.), unidentified codfishes (Gadidae), monkeyface prickleback (*Cebidichthys violaceus*), rockfishes and cabezon (*Scorpaenichthys marmoratus*) having the highest IndVal (table 2).

The deeper-water assemblage south of Point Conception (group III) included 38 samples taken at vari-

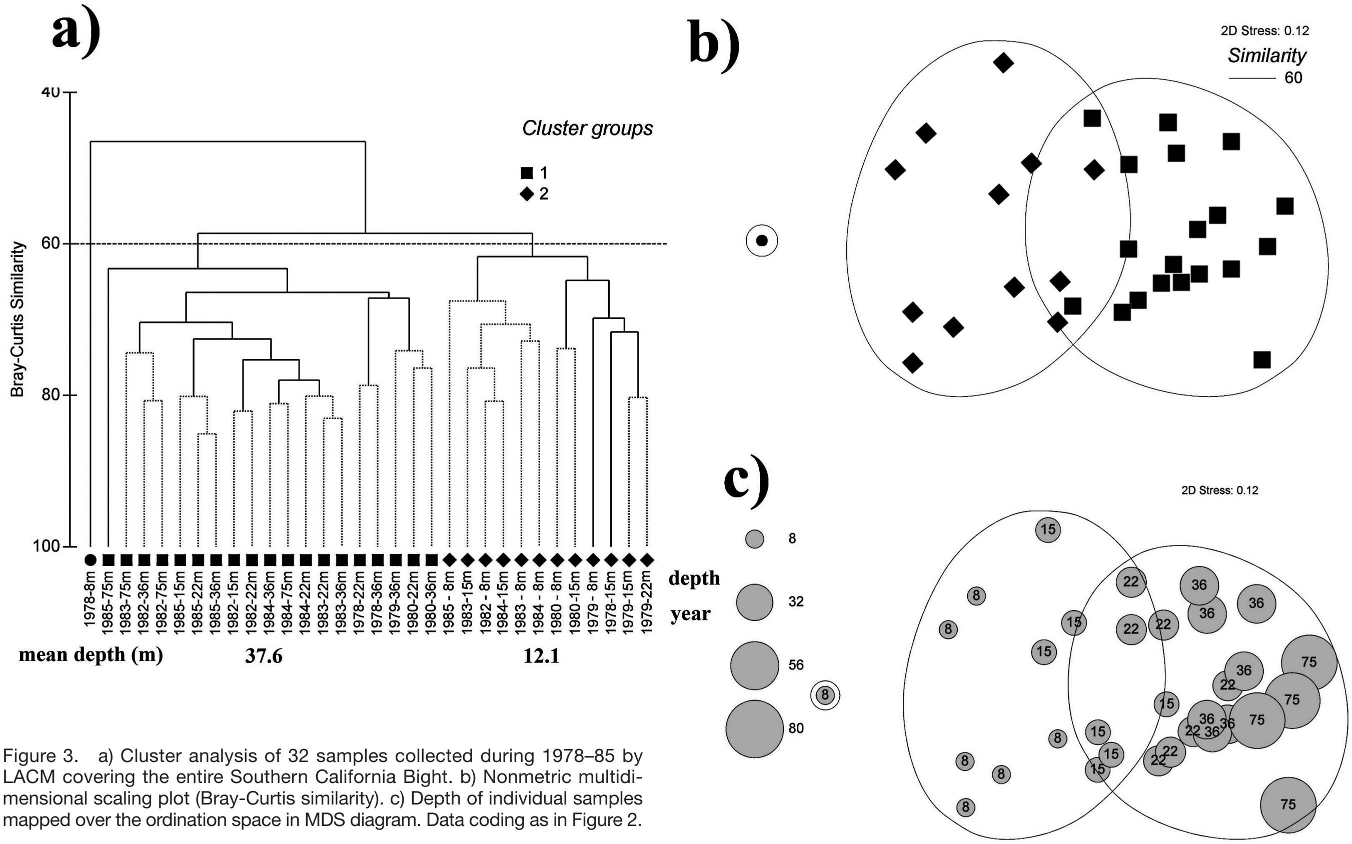

Figure 3. a) Cluster analysis of 32 samples collected during 1978–85 by LACM covering the entire Southern California Bight. b) Nonmetric multidimensional scaling plot (Bray-Curtis similarity). c) Depth of individual samples mapped over the ordination space in MDS diagram. Data coding as in Figure 2.

ous locations within the SCB (with the exception of the shallowest stations inside the enclosed channels leading to the Redondo Beach and Alamitos generating stations). Overall, this group can be described as a primarily croaker-flatfish assemblage, with queenfish (*Seriphus politus*), unidentified croakers (Sciaenidae), seabass (*Paralabrax* sp.), white croaker, and several flatfish species displaying highest group fidelity (table 2). Species contributing the most to the average similarity of 60.3 were white croaker, northern anchovy, unidentified combtooth blennies (*Hypsoblennius* sp.), and unidentified gobies and croakers.

The shallow-water assemblage from the SCB (group IV) is composed of fish larvae collected from stations within San Diego Bay, and the shallow channels leading to Redondo Beach and Alamitos generating stations. Compared to other groups, this assemblage displayed the highest abundances of unidentified larval gobies and combtooth blennies, together contributing to 30% of the average similarity of 60.6 between samples, and both identified as significant indicator species for this group. In addition, larval labrisomid kelpfishes (Labrisomidae), pipefishes (Syngnathidae) and topsmelt (*Atherinops affinis*) were also top indicator species for this assemblage (table 2). Overall, this group displayed the lowest mean number of species, as well as low diversity and evenness values.

Distinct assemblages based on geographic location (north and south of Point Conception) and depth also form clear groups on the MDS plot. The first axis represents a depth gradient, separating embayment/shallow and coastal/deep coastal assemblages in two biogeographically different regions (group I and IV), while the second axis separates assemblages north and south of Point Conception (II and III) (figs. 2b,c).

Onshore-offshore variation and depth-related gradients

To further analyze potential faunistic boundaries related to depth in the coastal zone of southern California, we first assessed broad patterns of cross-shelf variation based on the extensive sampling of the LACM ichthyoplankton program which spanned the entire SCB. We further refined this analysis by centering on larval assemblages sampled on smaller spatial and temporal scales, based on sampling within the SCB (Big Sycamore Canyon), near Point Conception (Vandenberg), and off central California (Diablo Canyon).

Southern California Bight. Classification and ordination of 33 samples representing averaged depth strata of the LACM sampling resulted in two large groups, based on depth (figs. 3a–c).

The deeper-water assemblage (I) was comprised of 19

TABLE 3
Results of SIMPER and ISA for LACM (Los Angeles County Museum) ichthyoplankton data. Sim/SD – Similarity/Standard deviation, other abbreviations and data structure as in Table 2.

Group	Species	Av. Abund	Av. Sim	Sim/SD	S(i)	Ind Val	N	H'	J'
I deep	*Stenobrachius leucopsarus*	1.7	1.98	3.75	2.84	95	61	1.7	0.4
	Citharichthys spp.	1.68	2.02	6.61	2.91	93			
	Engraulidae sp.	3.37	4.04	5.94	5.8	88			
	Oxyjulis californica	1.07	1.29	4.9	1.86	87			
	Icelinus quadriseriatus	0.98	1.01	1.79	1.45	86			
	Engraulis mordax	5.13	6.46	9.46	9.29	84			
	Clupeiformes spp.	2.79	3.4	6.01	4.89	70			
	Sardinops sagax	2.27	2.55	2.71	3.67	76			
	Genyonemus lineatus	3.05	3.68	3.94	5.28	57 (NS)			
II shallow	*Gobiesox rhessodon*	0.89	1.39	4.75	2.13	93	58	2.1	0.5
	Heterostichus rostratus	0.76	1.06	1.82	1.63	91			
	Paraclinus integripinnis	0.52	0.71	1.3	1.08	80			
	Hypsypops rubicundus	0.65	0.76	1.26	1.17	79			
	Leuresthes tenuis	0.92	1.55	3.97	2.37	77			
	Gobiidae spp.	2.09	3.7	5.95	5.66	67			
	Genyonemus lineatus	2.79	4.52	5.53	6.92	43 (NS)			
	Seriphus politus	2	3.27	5.6	5	42 (NS)			
	Engraulis mordax	3.3	5.48	6.65	8.38	16 (NS)			
	Engraulidae sp.	2.01	3.22	5.02	4.92	12 (NS)			

TABLE 4
Results of SIMPER and ISA analysis for ichthyoplankton data collected off Big Sycamore Canyon by MERRP (Marine Ecological Reserves Research Program). Abbreviations and data structure as in Table 2, 3. Groups I and III are shallower assemblages from 1998 and 1999, respectively; groups II and IV are deeper assemblages from those years.

Year	Group	Species	Av. Abund	Av. Sim	Sim/SD	S(i)	Ind Val	N	H'	J'
1998	I	*Engraulis mordax* (larvae)	1.89	16.85	2.16	25.07	67	5	1.18	0.78
		Paralichthys californicus (eggs)	2.55	25.53	5.93	37.97	29 (NS)			
		Engraulis mordax (eggs)	0.80	3.52	0.58	94.54	8 (NS)			
		Genyonemus lineatus (eggs)	1.89	17.66	2.24	64.23	6 (NS)			
	II	*Argentina sialis* (eggs)	1.35	9.47	5.30	14.00	59	11	2.00	0.85
		Argentina sialis (larvae)	0.88	4.24	1.06	6.27	58			
		Engraulis mordax (eggs)	1.58	10.88	6.15	16.08	35			
		Merluccius productus (eggs)	1.41	10.04	6.05	45.94	21 (NS)			
		Engraulis mordax (larvae)	1.25	8.49	5.76	72.48	12 (NS)			
		Paralichthys californicus (eggs)	1.55	10.17	4.48	31.10	5 (NS)			
1999	III	*Genyonemus lineatus* (eggs)	3.55	16.9	5.57	26.02	63	10	1.41	0.63
		Citharichthys stigmaeus (eggs)	2.19	9.62	5.30	14.81	61			
		Pleuronichthys verticalis (eggs)	1.45	5.00	1.32	7.69	57			
		Atherinopsis californensis (larvae)	0.47	0.40	0.24	0.62	27			
		Genyonemus lineatus (larvae)	3.07	13.43	10.99	46.70	36 (NS)			
		Paralichthys californicus (eggs)	2.10	9.67	6.34	61.59	13 (NS			
	IV	*Parophrys vetulus* (eggs)	1.54	5.77	2.30	8.71	67	14	1.90	0.73
		Merluccius productus (eggs)	1.76	6.70	2.86	10.12	62			
		Leuroglossus stilbius (larvae)	1.42	3.94	1.23	5.95	62			
		Merluccius productus (larvae)	1.38	4.96	2.23	7.49	44			
		Leuroglossus stilbius (eggs)	1.04	2.36	0.76	3.56	60			
		Citharichthys stigmaeus (eggs)	1.87	7.26	4.15	25.63	34 (NS)			
		Paralichthys californicus (eggs)	1.93	6.83	2.78	35.94	24 (NS)			
		Genyonemus lineatus (eggs)	2.56	9.71	3.64	14.66	1 (NS)			

samples, mostly from the 22, 36, and 75 m depth strata (average station depth 37.6 m). Twelve shallow samples (8 and 15 m depth, with one sample from 22 m, average depth: 12.1 m) formed the shallow assemblage (II). Overall, both assemblages displayed similar dominant species, such as the common coastal pelagics, northern anchovy, and Pacific sardine, and the croakers, white croaker and queenfish, with higher abundances more

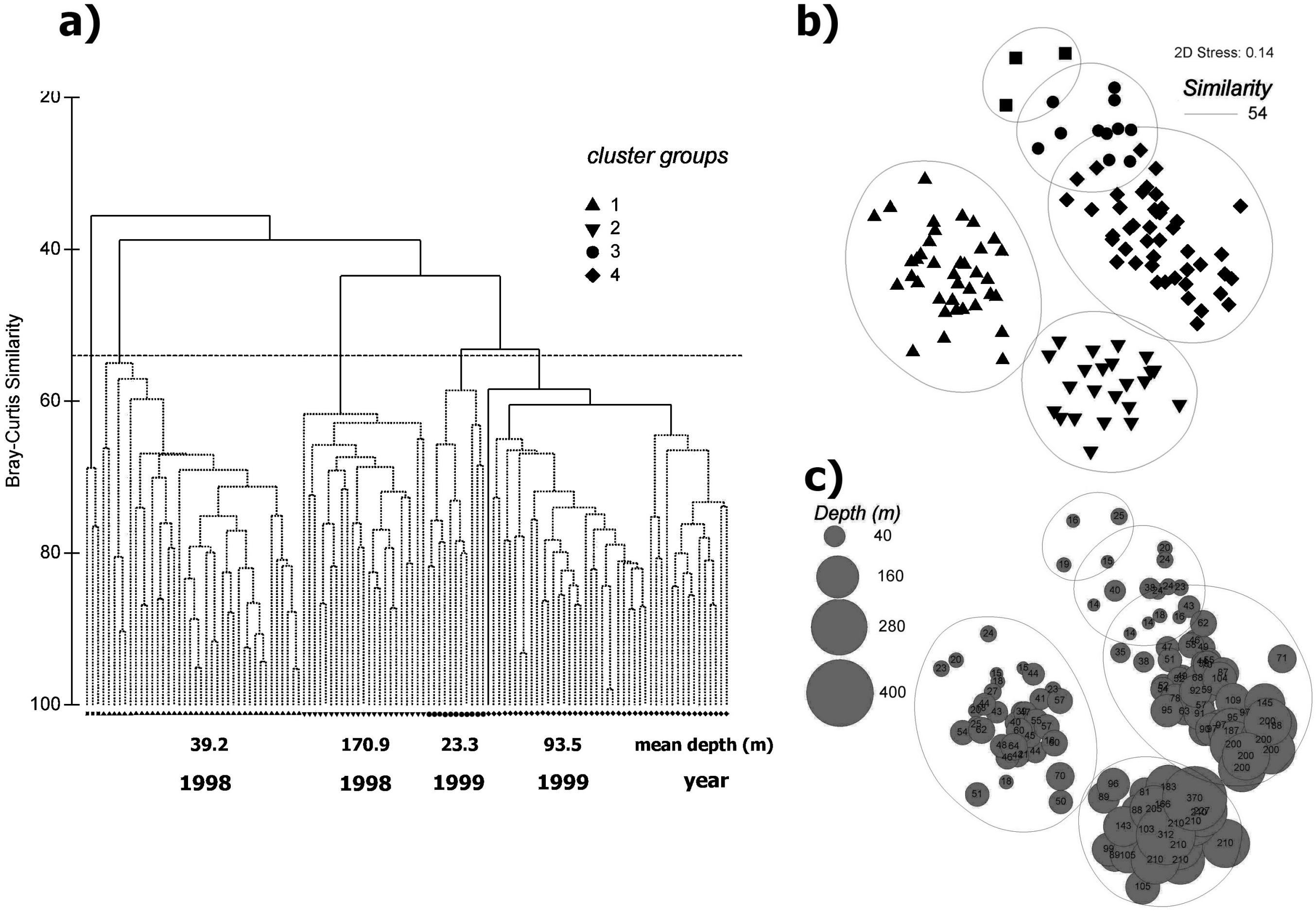

Figure 4. a) Classification of 119 samples obtained during 1998–99 sampling off Big Sycamore Canyon Ecological Reserve. b) Nonmetric multidimensional scaling plot (Bray-Curtis similarity) with cluster groups outlined by solid lines and coded with the same symbols. c) Depth of individual samples mapped over the ordination space in MDS diagram. Data coding as in Figure 2.

offshore. However, ISA suggested distinct sets of indicator species—northern lampfish, sanddabs (Paralichthyidae), señorita (*Oxyjulis californica*), and northern anchovy for the deeper assemblage and larval clingfishes (Gobiesocidae), clinid kelpfishes (Clinidae), labrisomids, garibaldi (*Hypsypops rubicundus*), and grunion (*Leuresthes tenuis*) for more inshore waters (table 3). Both groups had similar average species richness and evenness, but the shallow group was characterized by higher Shannon-Weaver diversity values (table 3).

Big Sycamore Canyon Ecological Reserve. Classification of 119 samples collected during winter in 1998–99 off Big Sycamore Canyon revealed one small and four large groups (I–IV) at a similarity level of 54% (fig. 4a). The four principal groups displayed very close Bray-Curtis similarities ranging from 64.9 to 67.6 and can be described as shallow and deep larval fish assemblages of 1998 (El Niño year) and 1999 (La Niña year).

The shallow assemblage of 1998 (group I) is composed of 37 samples collected over depths of 15–70 m (mean depth: 39 m), while the deep group (II) included 23 samples from depths of between 81 and 370 m (mean depth: 171 m). These assemblages were mainly discriminated by the relative abundance of eggs of offshore and inshore spawning species. Thus, eggs and larvae of mesopelagic, e.g., North-Pacific argentine (*Argentina sialis*), California smoothtongue (*Leuroglossus stilbius*), and northern lampfish and offshore species such as Pacific hake (*Merluccius productus*), showed much higher abundances at deeper stations, while shallow samples had higher contributions from eggs and larvae of typical coastal benthic species, such as croakers and flatfishes (fig. 5). Larval northern anchovy was a significant indicator species for the shallow group, while eggs and larvae of North-Pacific argentine and eggs of northern anchovy were significant indicators for the deep assemblage.

Depth was also important in structuring the ichthyoplankton assemblages in 1999, although these differences were less distinct compared with the previous year. Similar to 1998, the shallow larval assemblage (III) of 1999 displayed somewhat higher abundances of eggs and larvae of croakers and flatfishes, while the deeper group

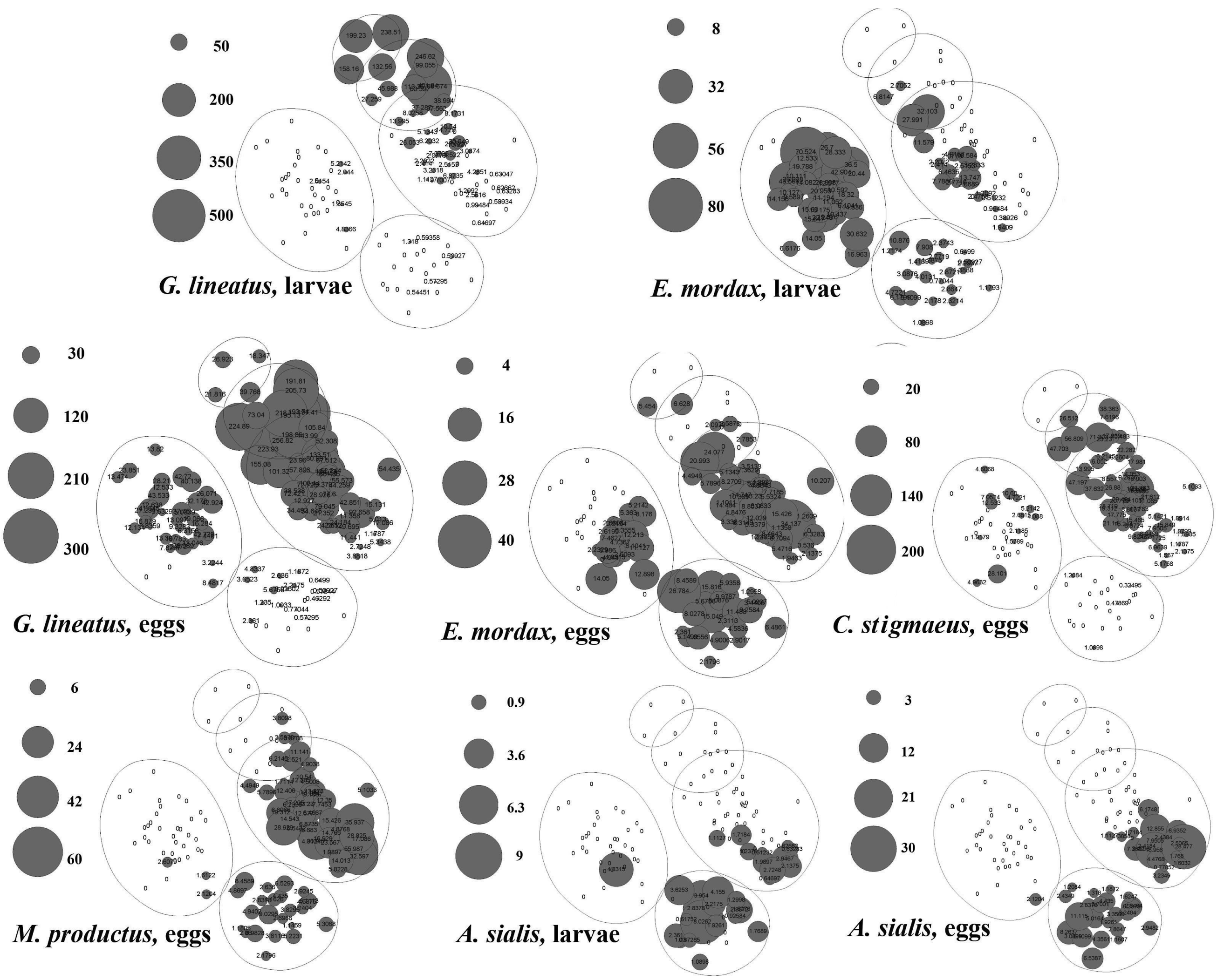

Figure 5. a) Abundances (spec./10 m^2) of most significant species according to SIMPER results and Indicator Species Analysis mapped in ordination space of two first axes on MDS plot.

(IV) was influenced by oceanic species such as deep-sea smelts and Pacific hake (table 4, fig. 5). Eggs of white croaker, speckled sanddab (*Citharichthys stigmaeus*), and hornyhead turbot (*Pleuronichthys verticalis*) and larvae of jack silverside (*Atherinopsis californensis*) were significant indicators for the shallow La Niña assemblage, while eggs and larvae of California smoothtongue and Pacific hake and eggs of English sole (*Parophrys vetulus*) were characteristic of the deeper assemblage.

North-Pacific argentine, a species with southerly affinities, was more abundant during the El Niño. Several species, however, were more abundant in 1999: white croaker, Pacific hake, and speckled sanddab.

Ordination analysis revealed similar groupings based on the first two MDS axes (fig. 4b). The first horizontal axis primarily separates the El Niño from La Niña assemblages, while the second axis separates the shallow and deep assemblages. Mapping the depths of the individual samples clearly shows the dominant depths associated with these assemblages (fig. 4c).

We did not find clear assemblages related to depth off Big Sycamore Canyon during summer. There was also no significant effect of depth on assemblage structure off Vandenberg Ecological Reserve, just north of Point Conception, which was sampled during the same MERRP ichthyoplankton surveys. Strong currents and intense sand transport apparently create poor fish habitat at this site, possibly eliminating potential faunistic boundaries in the pelagic environment.

Diablo Canyon. Classification of 64 samples from Diablo Canyon based on averaged larval abundances over a two year sampling period revealed three groups of samples at a 64.7% similarity level (fig. 6a). The MDS plot indicates a depth gradient in the ichthyoplankton assemblages (figs. 6b, c).

The more offshore assemblages (groups I and III in

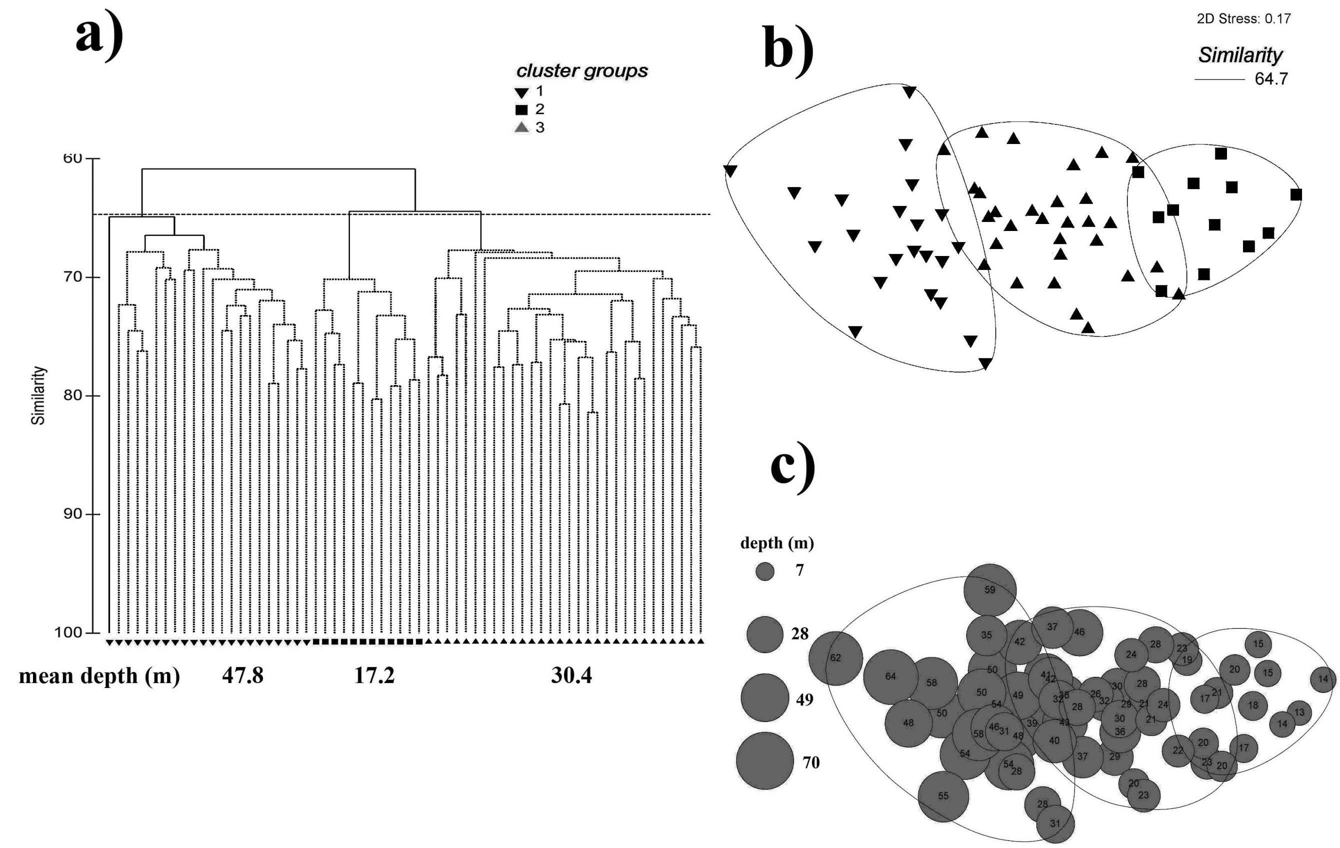

Figure 6. a) Cluster dendrogram of 64 coastal stations performed in the vicinity of Diablo Canyon Power Plant. b) Non-metric multidimensional scaling plot (Bray-Curtis similarity) with cluster groups outlined by solid lines and coded with the same symbols. c) Depth of individual samples mapped over the ordination space in MDS diagram. Data coding as in Figure 2.

the dendrogram), were characterized by similar dominant species (northern anchovy, Pacific sardine, various rockfishes, and northern lampfish), with higher abundances more offshore. Most important indicator species for the deepest assemblage (I) were Pacific hake, mesopelagic blue lanternfish (*Tarletonbeania crenularis*), and *Nannobrachium* spp., and also Pacific sanddab (*Citharichthys sordidus*) and slender sole (*Lyopsetta exilis*). The top indicator species for the intermediate-depth assemblage (III) were the ronquils (Bathymasteridae), sculpins (smoothhead sculpin *Artedius lateralis*, and unidentified sculpin species), gadids, and sand sole (*Psettichthys melanostictus*) (table 5). The shallowest assemblage (group II) was primarily characterized by several typical nearshore groups: clinids (*Gibbonsia* spp.), sculpins (tidepool sculpin *Oligocottus maculosus*, *Oligocottus* spp.), monkeyface prickleback, and blind goby (*Typhlogobius californiensis*). This group had the lowest species richness and abundances (table 5).

Larval fish assemblages as revealed by different studies

Inshore CalCOFI stations and LACM data set, 1978–85. Because of the infrequent sampling in late 1970s-early 1980s by the CalCOFI program, we limited the analysis to geographic locations and months sampled by both LACM and CalCOFI. Classification of larval fish data from these samples resulted in three large groups, revealing patterns of seasonality and distance from shore (fig. 7). The first group (I) was comprised of 16 LACM samples obtained primarily during spring (but with two winter and two fall samples as well) from 20–30 m station depth. The top five indicator species were white croaker, jack silverside, unidentified clinids, turbot (*Pleuronichthys* sp.) and English sole. The second group (II) represented a mixture of LACM (n=7) and CalCOFI (n=6) locations sampled during the summer (plus one fall sample) mainly at depths of 45 m or less with important indicator species: chub mackerel (*Scomber japonicus*), seabasses, Pacific barracuda (*Sphyraena argentea*), Mexican lampfish (*Triphoturus mexicanus*), and reef finspot (*Paraclinus integripinnis*). The final group (III) comprised 13 CalCOFI winter-spring samples from approximately 40–100 m (fig. 7a). The deeper CalCOFI winter-spring assemblage (group III) was strongly dominated by northern anchovy and was characterized by low species richness and larval abundances (fig. 7, table 6). No statistically significant indicator species were found

TABLE 5
Results of SIMPER and ISA analyses (top 8–10 indicator species) for ichthyoplankton data collected off Diablo Canyon by Tenera. Abbreviations and data structure as in Tables 2, 3.

Group	Species	Av. Abund	Av. Sim	Sim/SD	S(i)	Ind Val	N	H'	J'
I deep	*Citharichthys sordidus*	0.76	1.29	1.93	1.89	70	113	2.4	0.62
	Tarletonbeania crenularis	0.93	1.84	6.58	2.7	68			
	Merluccius productus	0.84	1.49	2.59	2.19	68			
	Nannobrachium spp.	0.92	1.75	2.86	2.57	66			
	Sardinops sagax	2.06	4.25	12.36	6.24	66			
	Engraulis mordax	2.23	4.63	14.48	6.8	52			
	Stenobrachius leucopsarus	1.92	3.93	9.65	5.76	63			
	Rhinogobiops nicholsii	1.41	2.89	9.51	4.24	57			
	Lyopsetta exilis	0.7	1.12	1.35	1.64	64			
	Sebastes spp.	2.14	4.54	12.95	6.65	39 (NS)			
II shallow	*Gibbonsia* sp.	1.33	3.64	8.25	5.06	80	56	2.74	0.77
	Oligocottus maculosus	0.5	1.02	1.08	1.42	70			
	Oligocottus sp.	0.57	1.09	1.06	1.52	66			
	Cebidichthys violaceus	1.44	4.02	6.46	5.58	66			
	Typhlogobius californensis	1.06	2.81	4.11	3.9	53			
	Genyonemus lineatus	1.22	3.28	5.79	27.31	27 (NS)			
	Sebastes spp.	1.8	4.72	7.72	6.56	24 (NS)			
	Engraulis mordax	1.54	3.99	5.35	17.69	14 (NS)			
III intermediate	Bathymasteridae spp.	1.45	2.97	6.04	4.24	59	89	2.63	0.68
	Cottidae spp.	0.98	1.93	2.87	2.76	51			
	Gadidae spp.	0.41	0.54	0.8	0.77	40			
	Psettichthys melanostictus	0.37	0.45	0.67	0.64	33			
	Artedius lateralis	1.15	2.35	7.17	3.35	46			
	Engraulis mordax	1.98	4.23	9.74	6.04	33 (NS)			
	Sebastes spp.	2.03	4.19	7.06	5.98	37 (NS)			
	Sardinops sagax	1.63	3.33	6.46	4.75	28 (NS)			
	Stenobrachius leucopsarus	1.53	3.2	8.13	4.57	27 (NS)			

for this group. Northern anchovy was the dominant species in all three assemblages, which differed from one another due to input from other taxa (table 6). A number of nearshore taxa contributed to the primarily spring LACM group (I): croakers, flatfishes (Pleuronectidae and Paralichthyidae), gobies, sculpins, lanternfishes, rockfishes, and clinids (fig. 7b). The summer assemblage (II) was strongly influenced by chub mackerel and seven species of right-eyed flounders (Pleuronectidae), with smaller contributions from croakers, seabasses, lanternfishes, and blennies (fig. 7b).

Inshore CalCOFI stations, SCCOOS stations, and Tenera data sets, 2004–07. Classification of 38 samples collected by SCCOOS, Tenera, and CalCOFI programs produced two principal groups (fig. 8a). The first assemblage included all the nearshore Tenera locations (mostly shallower than 25 m), with the second group comprising the six coastal CalCOFI stations and seven SCCOOS stations (mostly offshore of 25 m). The first, more inshore group had 20 significant indicator species, with unidentified larval gobies, diamond turbot (*P. guttulatus*), unidentified croakers, queenfish, and combtooth blennies being most important, while the second group had only two significant indicator species: unidentified rockfishes and mussel blenny (*Hypsoblennius jenkinsi*). Croakers were the dominant taxon in the first group, while northern anchovy was dominant in the second (table 7). In general, however, similar taxa were found in the two groups, although their contribution to average similarity differed somewhat: pleuronectid and paralichthyid flatfishes, blennies, and myctophids (fig. 8b). The stations in the Tenera group on average contained twice as many species and had greater larval abundances.

DISCUSSION

It has been hypothesized that ichthyoplankton assemblages represent an adaptive feature, resulting from similar responses of different species to selective pressures in the pelagic environment (Frank and Leggett 1983). Understanding spatio-temporal patterns of such multispecies associations is important to gaining insight into specific niches during early ontogeny, resource utilization, and optimal environmental conditions for growth and survival.

Our study examined the biogeography of coastal ichthyoplankton in the region from San Francisco Bay to San Diego Bay. Alongshore within this region, the major breakpoint was Point Conception, with distinct assemblages north and south. This is in agreement with many previous studies, which emphasized the importance of Point Conception as a major zoogeographical

TABLE 6
The results of SIMPER and ISA analyses for classification of inshore CalCOFI stations and LACM dataset. Abbreviations and data structure as in Tables 2, 3.

Group	Species	Av. Abund	Av. Sim	Sim/SD	S(i)	Ind Val	N	H'	J'
I	*Genyonemus lineatus*	2.91	6.24	2.92	11.76	76			
LACM	Clinidae spp.	0.89	1.55	1.28	2.92	56			
spring	*Atherinopsis californiensis*	0.68	1.00	0.87	1.88	55			
	Pleuronichthys sp.	0.8	1.57	1.24	2.95	54	31	3.2	0.9
	Parophrys vetulus	0.73	0.83	0.71	1.57	54			
	Gobiidae spp.	1.58	3.06	1.66	5.76	52			
	Paralichthys californicus	1.34	2.49	1.51	4.69	48			
	Sebastes spp.	1.53	2.56	1.41	4.82	39 (NS)			
	Engraulis mordax	5.01	11.08	4.13	20.88	37 (NS)			
II	*Scomber japonicus*	2.26	4.75	3.17	10.41	94			
LACM + CalCOFI	*Paralabrax* spp.	1.69	3.46	2.48	7.58	91			
summer	*Sphyraena argentea*	1.10	1.67	1.07	3.66	74	31	3.2	1
	Triphoturus mexicanus	1.45	2.98	1.93	6.54	67			
	Hypsoblennius spp.	1.62	2.79	1.36	6.11	58			
	Paraclinus integripinnis	0.37	0.30	0.58	0.67	54			
	Engraulis mordax	3.41	8.06	3.24	17.67	25 (NS)			
III	*Engraulis mordax*	5.12	47.28	2.66	87.02	38 (NS)			
CalCOFI	*Merluccius productus*	0.72	3.17	0.46	5.84	28 (NS)			
winter-spring	*Sebastes* spp.	0.84	1.58	0.38	2.90	9 (NS)	4.1	1	0.9
	Stenobrachius leucopsarus	0.52	0.64	0.27	1.18	7 (NS)			
	Genyonemus lineatus	0.62	1.20	0.37	2.20	6 (NS)			

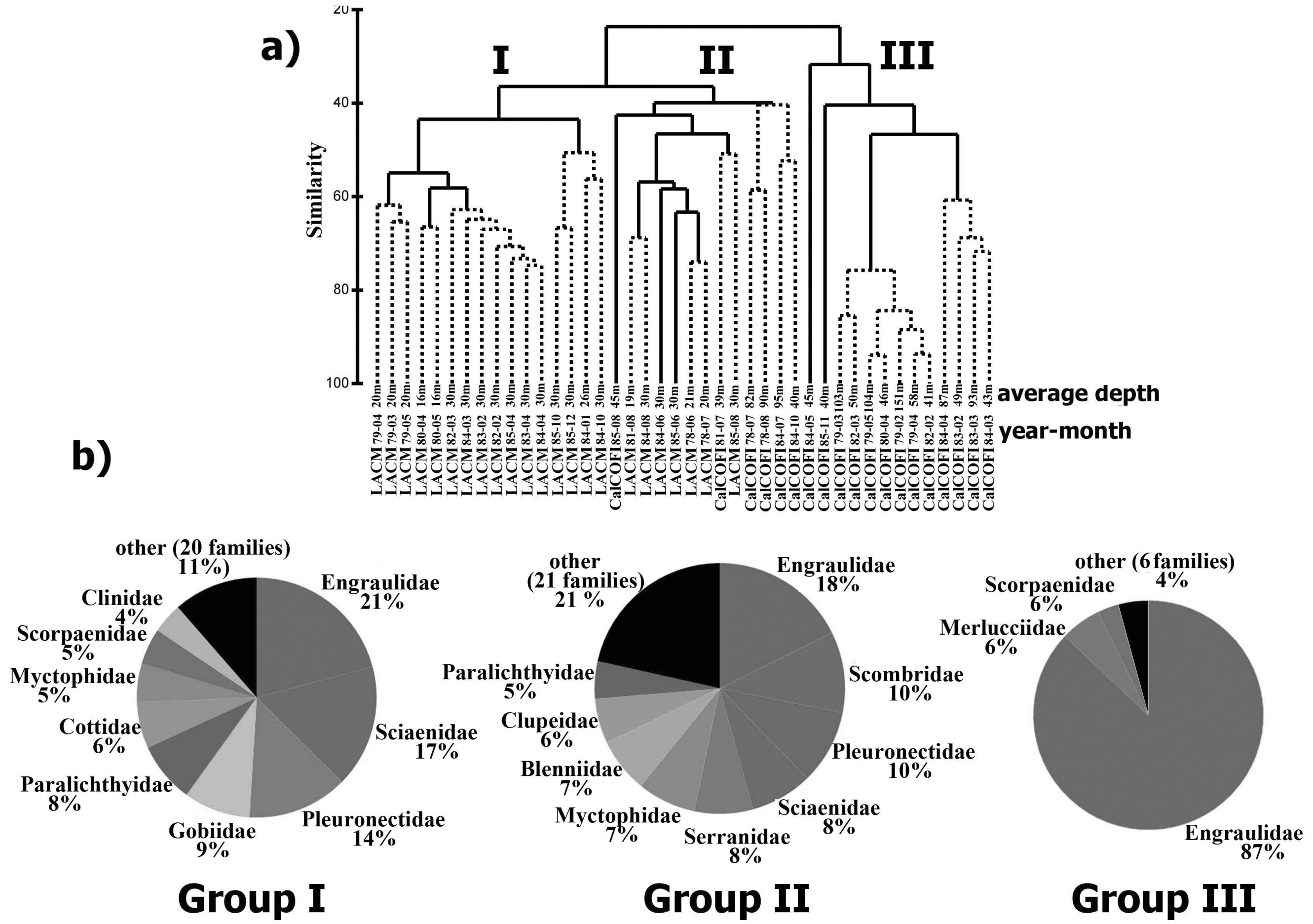

Figure 7. a) Cluster dendrogram of larval assemblages observed at five inshore CalCOFI stations and from the LACM data set, based on similar months and areas sampled during 1978–85. b) Contribution of different fish families (based on pooled species contributions) to the average similarity between cluster groups.

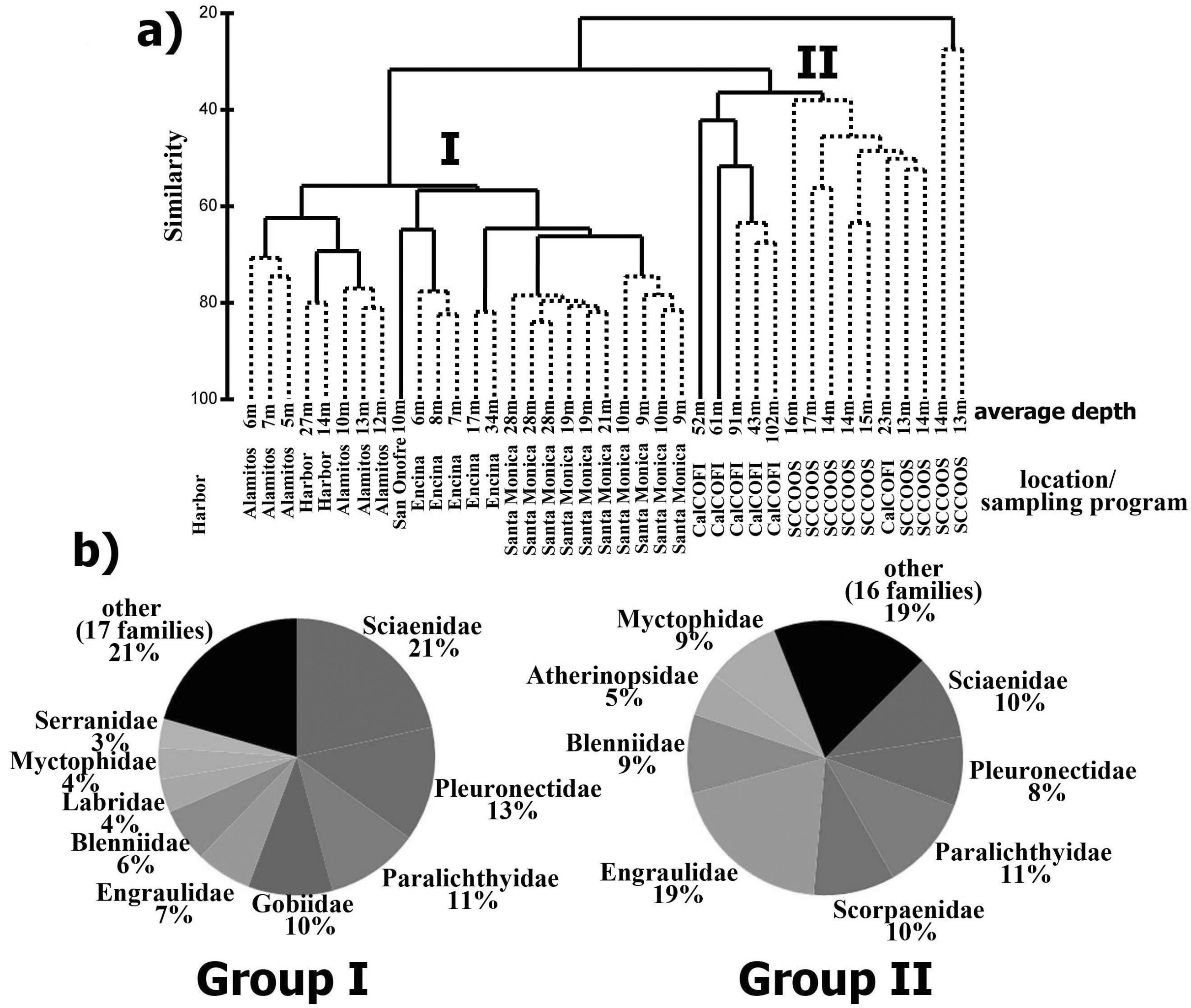

Figure 8. a) Cluster dendrogram of larval assemblages observed at inshore CalCOFI station, coastal SCCOOS stations and power plant locations sampled by Tenera during 2004–07. b) Contribution of different fish families (based on pooled species contributions) to the average similarity between cluster groups.

boundary in the region, separating the Oregonian faunal province from the San Diegan or Californian (Briggs 1974; Horn et al. 2006). This faunal break was found for assemblages in nearshore and embayment habitats and for those found more offshore on the continental shelf.

We also observed a strong nearshore gradient in ichthyoplankton assemblages off both central and southern California. Northern and southern shallow coastal/embayment larval assemblages were dominated by larval gobies, a typical demersally spawning coastal family. However, different gobiid species were more important north of Point Conception (*A. flavimanus*, *L. lepidus*) and south of it (*G. mirabilis*) within the SCB. The northern and southern shallow assemblages displayed pronounced differences in the dominance of other families as well, consistent with the distribution of adult fishes (Horn and Allen 1978; Horn et al. 2006). Thus, when SIMPER values of particular species are combined into family contributions, bays and shallow open coastal habitats off central California appeared more influenced by larval sculpins, clupeids (mainly Pacific herring), flatfishes (left and right flounders combined), stichaeids, rockfishes, sand lances, and ronquils; while southern shallow assemblages in the SCB were structured by larval silversides, combtooth blennies, clinids, labrisomids, and clingfishes (*Gobiesox* spp.). However, a number of taxa, such as the jack silverside, northern anchovy, croakers, combtooth blennies, and pipefishes, were important in both northern and southern shallow assemblages.

Estuarine fish assemblages in California have relatively low species diversity, a pattern observed in other temperate zones worldwide (Allen et al. 2006). We found

TABLE 7
Results of SIMPER and ISA for classification of inshore CalCOFI (California Cooperative Fisheries Investigations) stations, SCCOOS (Southern California Coastal Ocean Observing System) stations and power plant locations sampled by Tenera during 2004–07. Abbreviations and data structure as in Table 2.

Group	Species	Av. Abund	Av. Sim	S(i)	Ind Val	N	H'	J'
I	Gobiidae spp.	1.55	2.92	4.79	100			
Tenera	*Pleuronichthys guttulatus*	0.89	1.84	3.03	100			
	Sciaenidae spp.	1.48	3.08	5.07	100			
	Seriphus politus	1.25	2.17	3.56	96			
	Hypsoblennius spp.	1.79	3.64	5.97	96	50	3.8	0.97
	Genyonemus lineatus	2.26	4.38	7.19	81			
	Engraulis mordax	2.08	4.00	6.57	37 (NS)			
	Gobiidae spp.	1.55	2.92	4.79	30 (NS)			
	Sciaenidae spp.	1.48	3.08	5.07	25 (NS)			
	Hypsoblennius spp.	1.79	3.64	5.97	20 (NS)			
II	*Sebastes* spp.	1.09	3.25	7.76	87			
CalCOFI	*Hypsoblennius jenkinsi*	1.16	3.35	8.01	81			
SCCOOS	*Engraulis mordax*	2.40	8.17	19.52	61	24	3.06	0.97
	Paralichthys californicus	0.99	3.48	8.31	21 (NS)			
	Genyonemus lineatus	1.34	3.79	9.04	15 (NS)			

a similar pattern in the ichthyoplankton, with embayment/estuarine assemblages north and south of Point Conception having lower species richness and diversity values compared with more offshore larval assemblages.

Pronounced differences were also evident in the open coastal assemblages north and south of Point Conception. The northern open coast assemblage was dominated by a variety of larval sculpins in comparison with the SCB, which was dominated by larval croakers. Typical offshore families, such as myctophids, bathylagids, and argentinids all had higher influence in structuring northern open coast larval assemblages. Oceanic larval fishes are more easily advected into shallow coastal habitats off the central California coast than within the SCB, where the coast is further from the main axis of the California Current. In addition, engraulids, gobiids, blenniids, labrids, and silversides were more important groups in the SCB, while larval greenlings, ronquils, and clupeids were more important for offshore assemblages in the north.

The lack of significant alongshore variation in the larval assemblages within the SCB based on our analysis of the LACM data is consistent with the gyral circulation in this region, with poleward flow nearshore dominating in fall and winter and equatorward flow in spring and summer (Lynn and Simpson 1987). The region has generally been recognized as forming a single biogeographic province, and previous studies of coastal ichthyoplankton in the area have reached similar conclusions (Lavenberg et al. 1986; McGowen 1993).

Several earlier studies of the shallow habitats in the region reported cross-shelf patterns in larval distribution, although without specifying the precise boundaries (Gruber et al. 1982; Barnett et al. 1984; Lavenberg et al. 1986; McGowen 1993). Our data for the SCB based on averaged annual ichthyoplankton abundances suggested a faunal transition zone between 15–22 m, separating inshore and more offshore assemblages. Due to the fluid nature of the pelagic environment and rather small spatial scale of this boundary, there was considerable overlap in the species that dominate these assemblages, such that they are characterized primarily by differences in relative abundance. Interestingly, a more localized study off San Onofre reported a very similar transitional zone (or ecotone) located between the 12 and 22 m isobaths (Marine Review Committee 1977). A similar pattern was noted for the coastal zooplankton community in the region, with the inshore-offshore boundary in the vicinity of the 30 m isobath (Barnett and Jahn 1987).

We found that our assemblages were often characterized by distinct sets of indicator species, which indicate there are micro-faunal zones in coastal waters. Thus, larval silversides, clinids, gobiesocids, labrisomids, and stichaeids were indicators for the shallow assemblages, while clupeids, engraulids, hexagrammids, labrids, merlucciids, myctophids, paralichthyids, pleuronectids, and sphyraenids characterized more offshore habitats. Some families spanned these faunal zones, such as the sculpins and gobies, with Pacific staghorn sculpin and longjaw mudsucker (*Gillichthys mirabilis*) characteristic of the shallow assemblage and yellowchin sculpin (*Icelinus quadriseriatus*) and Bay goby of deeper water. Notably, indicator species of the shallow assemblage are characterized by demersal spawning, either depositing small numbers of eggs in the substratum or attaching them to seaweeds or rocks, thus reducing planktonic dispersal, a pattern observed in temperate (Marliave 1986; Suthers and Frank 1991), as well as tropical regions (Leis and Miller 1976). Larvae of demersal spawners are also relatively more developed and have greater sensory and swimming capability and thus are more capable of choosing a particular habitat (Suthers and Frank 1991). On the other hand, indicator species for more offshore assemblages spawn large quantities of planktonic eggs with a long larval duration and often have multiple spawnings through the year (Moser 1996). Distinct onshore-offshore gradients in larval distribution have been described for coastal regions worldwide, including upwelling areas, such as the Benguela (Olivar 1990) and Humboldt Currents (Suntsov 2000; Hernandez-Miranda et al. 2003), and northern California Current (Richardson et al. 1980; Doyle et al. 1993).

The importance of depth in structuring the coastal assemblages was also evident on a more restricted temporal and spatial scale off Big Sycamore Canyon (SCB) and Diablo Canyon (central California). In addition, these two areas provided information on the persistence and structure of the assemblages throughout the year, in different habitats as well as during large environmental disturbances such as El Niño/La Niña. We found distinct ichthyoplankton assemblages off Big Sycamore only during winter months; there were no clear depth-related assemblages during summer. Many coastal species off the U.S. West Coast spawn during winter-spring, when coastal upwelling is minimal, thereby maximizing larval retention nearshore; offshore Ekman transport apparently precludes the formation of persistent larval assemblages during summer months.

The strong El Niño of 1998 and ensuing La Niña in 1999 significantly affected the structure of the coastal assemblages sampled off Big Sycamore Canyon. Although distinct inshore/offshore groups were present both years, they were characterized by different indicator species, with certain sciaenids, pleuronectids, and paralichthyids more abundant in 1999, and engraulids and argentinids more prevalent during the El Niño. In addition, the coastal assemblage observed in 1999 had more offshore affinities and was also restricted to nearshore stations centering around the 20 m isobath, whereas during the warmer conditions of 1998 the inshore assemblage expanded offshore. Our data for differential cross-shelf distributions of larvae and eggs of northern anchovy is in good agreement with some previous studies, where the shallow water zone was hypothesized as a larval nursery area for this species (Barnett et al. 1984).

Compared to the Big Sycamore Canyon area, the ichthyoplankton assemblages off Diablo Canyon were less distinct, although these two regions were sampled over a similar depth range. Big Sycamore Canyon is characterized by soft bottom substrates and relatively quiet hydrological conditions (Watson et al. 2002), while Diablo Canyon is a turbulent rocky habitat, characterized by dense kelp beds and is well exposed to northeasterly winds and large ocean swells (Icanberry et al. 1978), which likely contribute to greater mixing of assemblages. However, onshore-offshore structure was also evident here. Again, the more offshore assemblage was characterized by oceanic species or families with planktonic eggs (e.g., Myctophidae, Merlucciidae, Pleuronectidae, Paralichthyidae), whereas the more inshore assemblage was characterized by species with demersal eggs (e.g., Cottidae, Clinidae, Stichaeidae, Gobiesocidae). However, the numerically dominant species in both of these assemblages were northern anchovy and rockfishes, consistent with observations in Monterey Bay (Yoklavich et al. 1996).

Significant cross-shelf structure in the ichthyoplankton assemblages implies that different coastal ichthyoplankton programs target distinct larval communities. In the SCB, there were few differences between the ichthyoplankton at the innermost CalCOFI and SCCOOS stations, although the SCCOOS stations are somewhat further inshore because the large vessels conducting the CalCOFI and SCCOOS programs cannot work within the 10–12 m isobaths where the nearshore ichthyoplankton assemblage is found. The distinct nearshore and embayment assemblages were sampled by Tenera in its monitoring of coastal power plants. The Tenera stations had higher contributions from coastal families such as croakers, right-eyed flounders, gobies, wrasses, and sea basses, and lesser input from anchovies or lanternfishes. These differences may be less distinct during certain seasons. For example, the assemblages at the innermost CalCOFI stations and LACM data differed most in winter-fall (due to the dominance of northern anchovy), while forming a mixed group later in the year.

In conclusion, the results of this study suggest that nearshore habitats off central and southern California host distinct and diverse ichthyoplankton assemblages, with differences related to local geomorphology, hydrology and season. This information has important implications for future ichthyoplankton monitoring of nearshore coastal habitats as a means to assess the impact of establishing a network of marine protected areas along the California coast.

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