p. 81-113. In: The Ecology of Marine Fishes: California and Adjacent Waters. 2006.
L.G. Allen, D.J. Pondella, and M. H. Horn (eds.). University of California Press, Berkeley, 670 pp.

CHAPTER 4

Ecological Classification

LARRY G. ALLEN AND DANIEL J. PONDELLA II

Introduction

The marine environment off the California coastline supports a diverse ichthyofauna consisting of northern, cold water (Oregonian) and southern, warm water (San Diegan) fish species as well as Panamic species primarily from Cortez Province (Horn and Allen, 1978). To a large extent, this high faunal diversity reflects the great variety of marine habitats that are available to fishes within the expansive latitudinal range covered by California proper and Baja California (e.g., bays and estuaries, nearshore soft bottom, shelf, slope, rocky intertidal, kelp beds, shallow and deep rocky reefs, as well as pelagic habitats) (Horn, 1980). Fortunately, the fishes of these various California habitats have been the subject of numerous ichthyofaunal studies (see table 4-1) during the past 40 years. These studies allow us to ask and begin to answer one of the most fundamental questions of all, "Which fishes occur where in California's marine waters?" In the Californias, marine fishes are readily quantifiable by various techniques and, in terms of taxonomy, are relatively well understood compared to other groups of organisms. Data from these ecological and fishery surveys can be applied easily to models of numerical ecology. For these reasons, the descriptions of marine habitats and inferences about them can be made using data obtained from the study of these fishes. In fact, the major biogeographical provinces in the tropical eastern Pacific have been described using information from fish surveys (Hastings, 2000). More specifically, this chapter will seek to answer the following questions:

1. What are the basic types of marine fish habitats that occur off California?
2. Which types of fishes tend to occur in these habitats?
3. Which types of fishes are most abundant or otherwise distinctive to the different habitats?
4. Which physical attributes define these habitats and how might these influence the fishes there?
5. Are all species linked to particular habitats or are there habitat generalists?
6. Which families and orders of fishes are best represented overall in the various habitats and the fish fauna?
7. How many different species occur in the various habitats and in what relative abundance?
8. Why are there more species in some habitats than in others?

The analysis presented here represents the first attempt at a coastwide synthesis of information about all California marine fish species and their habitats. To address these general questions, this chapter will (1) present a quantitative classification of marine habitats off California, based on the affinities of their fish assemblages; (2) present a quantitative classification of fish species according to habitat affinity; and (3) describe the general patterns of diversity within the various habitat types and attempt to explain them.

The Approach

This analysis is an extension of that reported in Allen (1985) for the fishes and habitats of southern California nearshore waters. However, the present analysis greatly extends the latitudinal, depth, and offshore range of the previous study.

Data on species composition and relative abundances of fishes from 168 locales from 77 ichthyofaunal studies (table 4-1) of all marine habitats except those of the meso- and bathypelagic zones were compiled for analysis. These quantitative studies ranged in latitude from Eureka in northern California south to Isla Asuncion on the mid-Pacific coast of Baja California (fig. 4-1). Relative abundances of species in each study were expressed as the percentage that the species represented in the total number of individuals (juveniles and adults could not be distinguished). For a species to be included in the analysis, it must have had a relative abundance of >0.1% in the study. The species abundances were, therefore, standardized to 100% in each study for subsequent numerical classification. This approach to quantifying species within habitats carried two major, but not unreasonable, assumptions. First, we assumed that the

TABLE 4-1

Study Localities Used in the Present Synthesis

Habitat	*Region*	*Locality*	*Sampling Methods*	*Source(s)*
Bay/estuary	NOCAL	San Pablo Bay	MT, OT	Ganssle (1966)
	CENCAL	Elkhorn Slough	OT, BS, SS	Yoklavich et al. (1991)
		Morro Bay	BS	Horn (1980)
	SOCAL	Upper Anaheim Bay	BS, GN, OT	Lane and Hill (1975)
		Carpenteria Slough	BS, TR	Brooks (1999)
		Colorado Lagoon	BS	Allen and Horn (1975)
		Mugu Lagoon	BS	Onuf and Quammen (1983)
		South San Diego Bay (2 regions)	OT, PS, BS, SS	Allen et al. (2002)
		Upper Newport Bay	BS, GN, OT	Horn and Allen (1981)
		Upper Newport Bay	BS, GN, OT	Allen (1988)
	BAJA	Bahia de Ojo Liebre	OT	Galvan et al. (2000)
		Estero de Punta Banda	OT, GN, BT	Beltran-Felix et al. (1986); Rosales-Casian (1997)
		Bahia de San Quintin	BT, OT, BS, GN	Rosales-Casian (1996)
Coastal pelagic	SOCAL	San Onofre-Oceanside	LP	Allen and DeMartini (1983)
Deep bank	SOCAL	San Pedro Channel (2 regions)	LL, OT	Cross (1987)
Deep reef	CENCAL	Soquel Canyon, Monterey Bay	SM	Yoklavich et al. (2000)
	SOCAL	Southern California (9 regions, 3 depths)	SM	Love and Yoklavich (unpubl. data)
		Tanner - Cortez Bank	SM	Love and Yoklavich (unpubl. data)
Harbor	SOCAL	Cabrillo Beach	BS GN OT	Allen et al. (1983)
		Outer Los Angeles–Long Beach Harbor	OT	Stephens et al. (1974)
		Lower Newport Bay	BS GN OT	Allen (1976)
		Outer Anaheim Bay	BS, OT	Lane and Hill (1975)
		Port of Los Angeles	OT, LP, BS	MEC (1988)
		North San Diego Bay	OT, PS, BS, SS	Allen et al. (2002)
Kelp bed rock reef	CENCAL	Diablo Cove, California	DT	Burge and Schultz (1973)
		Monterey Bay	DT	Miller and Geibel (1973)
		Diablo Cove, California	DT	Burge and Schultz (1973)
	SOCAL	Big Fisherman's Cove, Catalina Island	DT, P	Allen et al. (1992)
		King Harbor Redondo Beach	DT, P	Stephens et al. (1986)
		Naples Reef near Santa Barbara	DT	Ebeling et al. (1980)
		Santa Cruz Island	DT	Ebeling et al. (1980)
		Palos Verdes Peninsula	DT	Stephens et al. (1984)
		San Mateo Kelp Bed	DT	DeMartini (unpubl. data)
		San Onofre Kelp Bed	DT	DeMartini (unpubl. data)
		Hermosa Beach	DC	Turner et al. (1969)
		King Harbor Redondo Beach	DT	Stephens and Zerba (1981)
		Malibu Beach	DC	Turner et al. (1969)
		Mission Bay Breakwater	DT	DeMartini and Roberts (1981)
		La Jolla–Pt. Loma	DT	DeMartini (1981)
		Santa Monica Beach	DC	Turner et al. (1969)
	SOCAL/BAJA	Del Mar, La Jolla, and Papalote Bay (Baja Calif.)	DC, P	Quast (1968)
		Santa Barbara to Isla Asuncion, Baja (23 sta)	DT	Love et al. (1999)
Inner shelf	CENCAL	Elkhorn Slough	OT	L.G. Allen (unpubl. data)
		Morro Bay	OT	"
	SOCAL	Southern California Coast, Islands and Bays	GN	Pondella and Allen (2000)
		Southern California Bays (3 regions)	OT	"
Pelagic	CALIF	Pelagic (4 regions)	LL, AR, MT	Hanan et al. (1993), Squire (1983), Mais (1974)
Rocky intertidal	NOCAL	Arena Cove	P	Yoshiyama et al. (1987)
		Dillion Beach	P	Grossman (1982)

TABLE 4-1 (continued)

Habitat	*Region*	*Locality*	*Sampling Methods*	*Source(s)*
	CENCAL	Diablo Cove	DT, P	Burge and Schultz (1973)
		San Simeon, California	B, P	Allen and Horn (unpubl. data)
	SOCAL	Corona del Mar	P	Cross (unpubl. data)
		Pin Rock Catalina Island	P	Allen (1985)
		Resort Point, Palos Verdes Peninsula	B	Crase (1990)
	BAJA	Punta Clara	P	Stepien et al. (1991)
Rocky subtidal	NOCAL	Arena Cove	DT, P	Yoshiyama et al. (1987)
	CENCAL	Diablo Cove, California	DT, P	Burge and Schultz (1973)
	SOCAL	Palos Verdes Peninsula	P	Walker (unpubl. data)
Shelf	CENCAL	Fort Ord, Monterey Bay (3 depths)	OT	Burton et al. (1995)
	SOCAL	Palos Verdes Peninsula (3 depths)	OT	LAUSD (unpubl. data)
		Newport Beach (3 depths)	OT	Allen (1976)
		Southern California Shelf (3 regions; 3 Depths)	OT	M.J. Allen et al. (1999)
		San Onofre–Oceanside	OT	DeMartini and Allen (1984)
Slope	NOCAL	Eureka Region (2 depths)	OT	NOAA (unpubl. data)
	CENCAL	Monterey Region (2 depths)	OT	"
		Pt. Conception Region (2 depths)	OT	"
	SOCAL	Southern California Region (2 depths)	OT	"
Surf zone	CENCAL	Monterey Bay Coast	BT	Allen (unpubl. data)
		Morro Bay Coast	BT	"
	SOCAL	Carpinteria–Coronado	BS	Carlisle et al. (1960)
		Southern California Coast (3 regions)	BT	Allen (unpubl. data)
		Southern California Islands (3 regions)	BT	"
		Aliso Canyon Beach	BS	Tetra Tech (1977)
		Enlisted Man's Beach	BS	Tetra Tech (1977)
		San Onofre Beach	BS	Tetra Tech (1977)
	BAJA	Bahia de San Quintin Coast	BT	Rosales-Casian (1997)
		Bahia de Todos Santos	BT	Rosales-Casian (1997)

NOTE: Habitat designations are post facto. (AR = Aerial survey; B = Bail tidepool; BS = Beach Seine; BT = Beam Trawl; DC = Diver Census; DT = Diver Transect; GN = Gill Net; LL = Long Line; LP = Lampara seine; MT = Midwater Trawl; OT = Otter Trawl; P = Poison quadrats; PS = Purse Seine; SM = Submersible transects; SS = Small Seine; TR = Traps).

methods employed were those most effective for sampling fishes in that particular habitat. Second, the methods sampled the most abundant and common species in the habitat in proportion to their actual abundances. A synthesis such as that presented here is wrought with problems, which must be considered before formulating conclusions. These inherent problems (see table 4-1) include, but are not limited to the following: (1) the major habitats were physically different; (2) the methods employed differed between habitats; (3) the durations of the studies were variable; (4) sample sizes (unit of effort and total effort) were variable; (5) some studies employed multiple methods, whereas others used only one method; and (6) the expanses of the sampling areas were different. The first two problems (1 and 2 above) were addressed by the two major assumptions stated previously. The general importance of items 3–6 to the estimation of habitat diversity was minimized by using Shannon Wiener H' as a diversity index and by taking the mean species proportions of all the samples within a particular habitat in a latitudinal region (essentially collapsing the "replicates").

Both species and habitats were classified by computer-aided cluster analysis using Statistica (Statsoft, Inc). Clustering was carried out using the Pearson correlation coefficient (r) as the similarity measure. Relative abundance data were log-transformed to minimize the impact of highly abundant species. Only those species having a minimum occurrence at two sites or a minimum summed percentage of 0.1% were clustered. These minimum inclusion values resulted in a data matrix that included 244 species of fish within the 168 habitat sites. Complete sorting was used to maximize the separation between groups. Clustering of species based on correlation coefficients emphasized species co-occurrence, thus producing distinct and interpretable groupings.

Because of the large size of the data matrix, the determination of site groupings was a two-stage process. First, the 168 original sites were reduced to 38 site groups based on species associations using cluster analysis. The mean relative abundances of the 244 species within these site groups were then used to cluster the 38 site groups, which formed 15 major types of marine fish habitats found in California waters (table 4-2).

Species groups were also determined from the mean relative abundances within the 38 site groups to minimize variation introduced by individual site samples. The numerical dominance of young-of-year (YOY) rockfishes (genus *Sebastes*) consistently led to habitat groups, particularly in the north, based solely on their presence regardless of other associated species. For high YOY rockfish abundance, the relative abundances were adjusted by reducing them by two orders of magnitude (relative abundance/100) to minimize their impact on species groupings. This adjustment also emphasized the adult associations of the particular species in question.

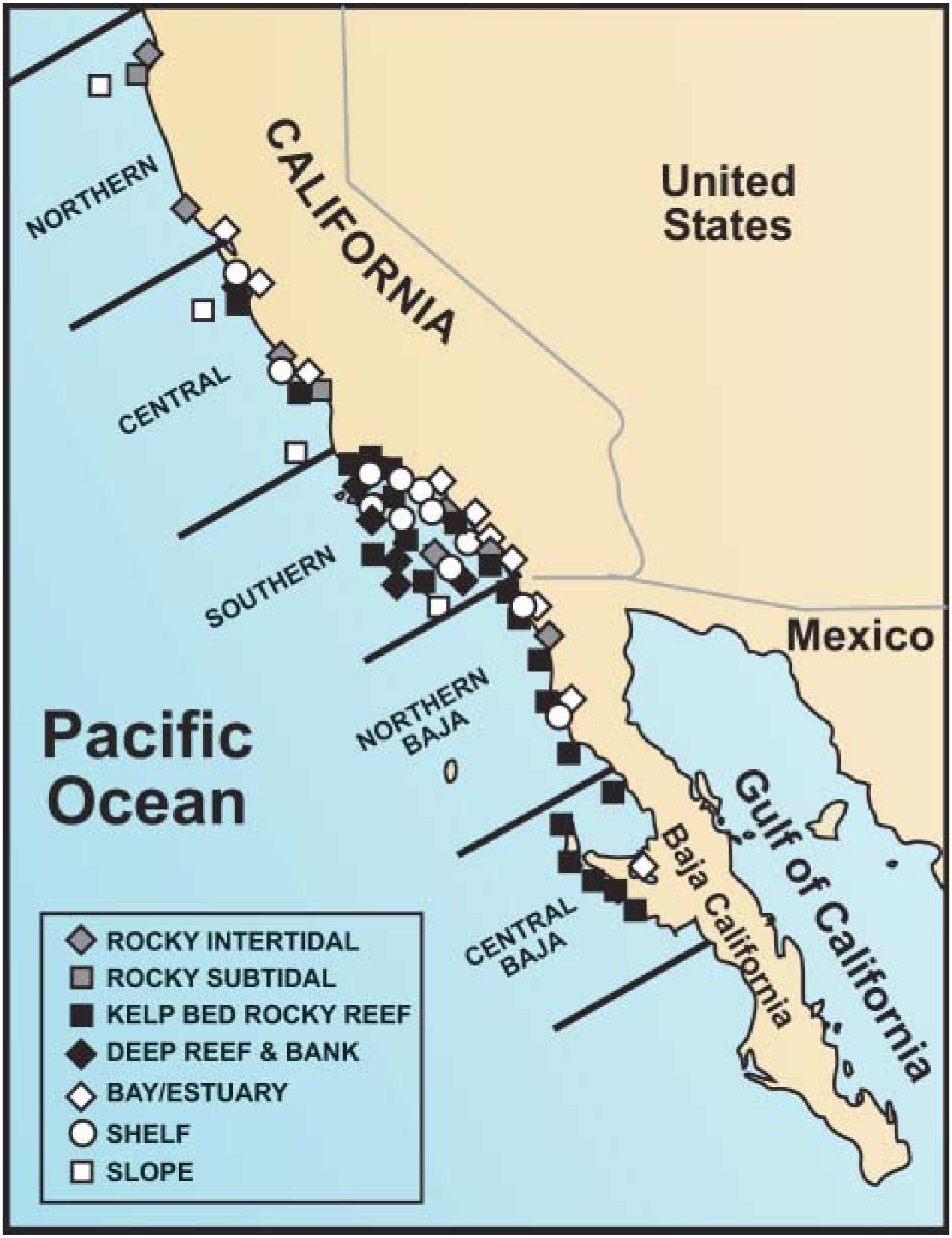

FIGURE 4-1 Locations of the ichthyofaunal studies used in the quantitative assessments of California fish habitats and species groups. Designations of major habitat are from the subsequent analysis. Not all studies in southern California are depicted due to their high concentration. Diagonal lines separate the five major latitudinal regions.

TABLE 4-2

Thirty-Eight Site Groups

Major Habitat	*Designation*	*Site Group*	*Description*
Pelagic	PEL	1	PELAGIC ALL
Rocky intertidal	RIT	2	RIT SOCAL NOBAJA
		3	RIT NOCAL CENCAL
Rocky subtidal	RST	4	RST CENCAL SOCAL
Kelp bed rocky reef	KBRF	5	KBRF CENBAJA
		6	KBRF SOCAL BAJA
		7	KBRF SOCAL
		8	KBRF SOCAL NOBAJA
		9	KBRF SOCAL
		10	CRRF SOCAL
		11	KBRF SOCAL
		12	KBRF SOCAL
		13	KBRF BAJA
		14	KBRF CENCAL NOBAJA
		15	RRF SOCAL
Surf zone	SZ	16	SZ SOCAL
		17	SZ NSB NOBAJA
Bay/estuary	BE	18	BE SOCAL
		19	BE SOCAL
		20	BE BAJA
		21	BE CENCAL
		22	BE NSB SOCAL
Coastal pelagic	CP	23	CP SOCAL
Inner shelf	IS	24	IS SOCAL
		25	IS SOCAL
		26	IS SOCAL
		27	IS CENCAL SOCAL
		28	IS CENCAL SOCAL
Middle shelf	MS	29	MS DSB SOCAL
Outer shelf	OS	30	OS CENCAL SOCAL
Mid-depth rocky reef	MDRF	31	MDRF SOCAL
		32	MDRF SOCAL
Deep rocky reef	DDRF	33	DDRF SOCAL
		34	DDRF SOCAL
		35	DCYN CENCAL SOCAL
Shallow slope	SSLP	36	SSLP NOCAL CENCAL SOCAL
Deep slope	DSLP	37	DSLP NOCAL CENCAL SOCAL
Deep bank	DBNK	38	DBNK SOCAL

NOTE: Derived by primary cluster analysis grouped into major habitats derived by secondary clustering of the original 38 based on mean relative abundances of co-occurring species. Legend: Habitats: BE = bay/estuary; CP = coastal pelagic; CRRF = cryptic reef fish; DBNK = deep bank; DCYN = deep canyon; DDRF = deep rocky reef; DSLP = deep slope; IS = inner shelf; KBRF = kelp bed rocky reef; MDRF = mid-depth deep rocky reef; MS = middle shelf; OS = outer shelf; PEL = pelagic; RRF = rocky reef (no kelp); RIT = rocky intertidal; RST = rocky subtidal; SLP = slope; SSLP = shallow slope; SZ = surf zone; Locations: NOCAL = Northern California; CENCAL = central California; SOCAL = southern California; NOBAJA = northern Baja California; CENBAJA = central Baja California.

Patterns of diversity within the habitat groups defined by cluster analysis were examined in two ways. First, the Shannon-Weiner (H') information function (Shannon and Weaver, 1949) was calculated using all species with >0.1 % of the abundance at each sample site. Second, species richness (*S*) was calculated for each of the 168 sampling sites where *S* equaled the number of species contributing ≥0.1% of the individuals "sampled." Because species richness by individual sampling site was so highly variable, a second measure of richness was calculated. This richness value was the total number of species recorded within major habitats within the five latitudinal regions (northern California, central California, southern California, northern Baja California, and central Baja California). Species that composed >0.1% of the mean relative abundance within the habitat/region were summarized and compared among regions and by major habitat.

Habitat and Species Associations

Biological Basis of Groups

WHAT ARE THE BASIC TYPES OF MARINE FISH HABITATS THAT OCCUR OFF CALIFORNIA?

Quantitative clustering of sites based on species composition yielded 15 major habitats that clustered into three main groups: shallow, deep, and pelagic (fig. 4-2). The major shallow habitats were designated as bay/estuary (BE), surf zone (SZ), nearshore soft

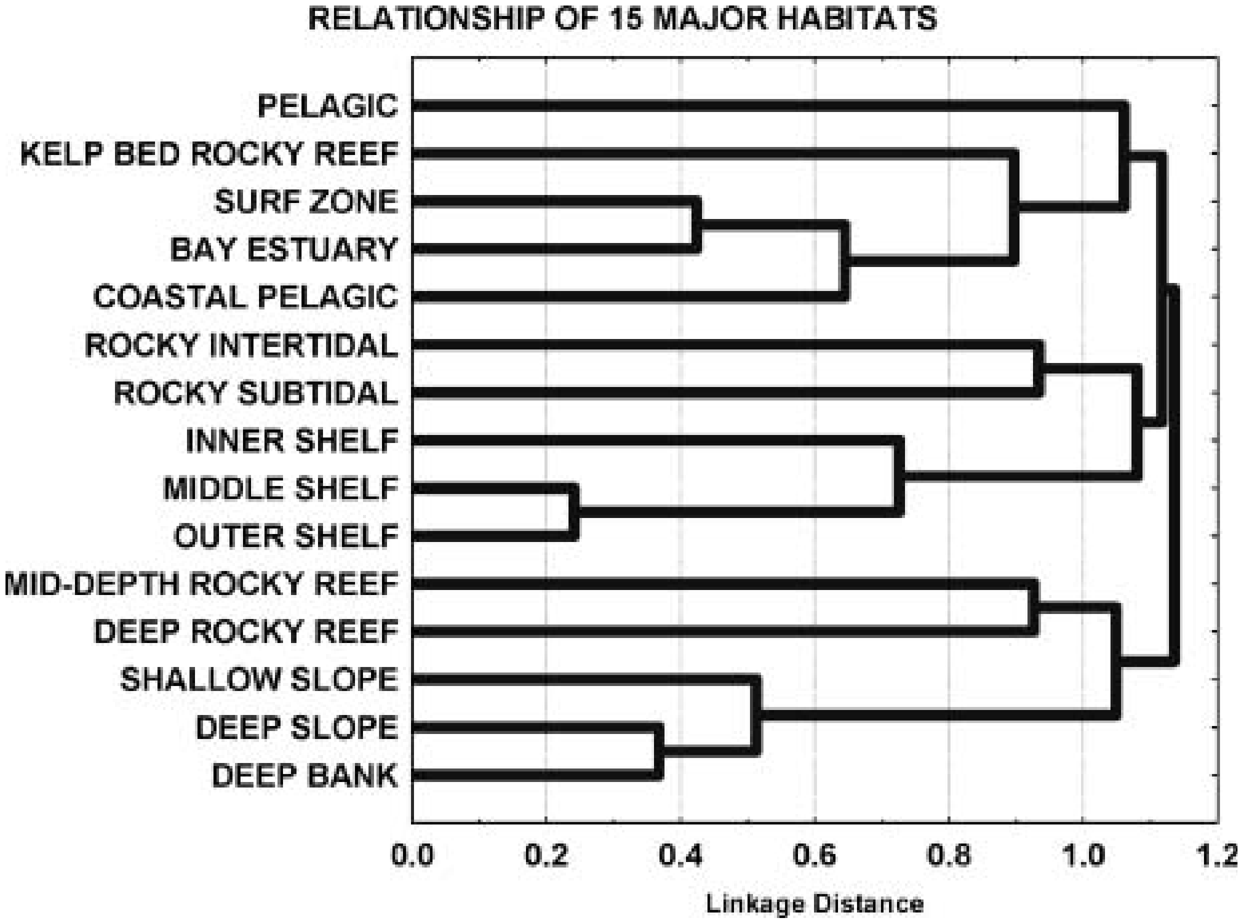

FIGURE 4-2 Dendrogram depicting the relationships among the 15 major habitats derived through cluster analysis of the relative abundances of species within the original 38 defined habitats. Groups and relationships were defined using correlation coefficients and complete linkeage.

bottom (NSB), coastal pelagic (CP), rocky intertidal (RIT), rocky subtidal (RST), and kelp bed rock reef (KBRF). The deeper habitats fell into the following categories: inner shelf (IS), outer shelf (OS), mid-depth rock reef (MDRF), deep rock reef (DRF), deep slope (DSLP), deep bank (DBNK), and continental slope (SLP) (fig. 4-3). These habitats are discussed in detail in the chapters of Unit II.

The seven shallow habitats fell into two major types based on their respective fish assemblages, those associated with soft substrata and those with rock substrata. Of the three major habitats with soft substrata, the bay and estuary (BE) and coastal pelagic (CP) habitats showed the closest affinity. The surf zone (SZ) was next in similarity to the BE-CP group followed by nearshore soft bottom (NSB). The kelp bed (KBRF) habitat had a higher similarity (lower distance) to the shallow, soft-bottom habitat than it did to the other two, shallow rock substratum habitats, the rocky intertidal (RIT) and rocky subtidal (RST). This unanticipated finding resulted from the large number of nearshore, soft-bottom species that are associated with the margins of rocky reefs. Physically, the KBRF sites were segregated according to latitude, substratum (cobble or bench rock), and whether or not they supported kelp beds at the time of sampling. The RIT habitat was restricted to the rocky intertidal zone and adjacent shallow subtidal areas (>2m depth). The RST habitat was located close to shore at depths from (approximately) 2–10 m and contained many cryptic species. KBRF habitats were generally found further offshore at depths between about 8 and 30 m. These depth limits apply only to the sites used in this analysis and should not be interpreted as definite boundaries between all such habitats in California. Harbor breakwaters and jetties were classified as RST habitats with close KBRF affinities.

WHICH TYPES OF FISHES TEND TO OCCUR IN THESE HABITATS?

The 244 species used in the analysis clustered into 42 species groups (table 4-3). The species within these groupings represent the most common or, otherwise conspicuous (i.e., large predators with relatively low abundance) members of the fish assemblages within the major types of habitats. The species groups in numerical order vary from pelagic (species groups 1–2) to primarily rock associated groups (3–14), to groups with more widespread occurrence across the major shallow habitats (15, 18, 19), and to groups (with few exceptions) whose species were primarily restricted to soft substratum habitats (16–17 and 20–33). Species groups 33–42 are associated primarily with deep water, benthic habitats.

WHICH TYPES OF FISHES ARE MOST ABUNDANT OR OTHERWISE DISTINCTIVE TO THE DIFFERENT HABITATS?

In the following characterizations, species groups with widespread distributions among major habitats are referred to as generalized and those with restricted distributions are specialized. Species Group 1 contained 16 species of pelagic fishes,

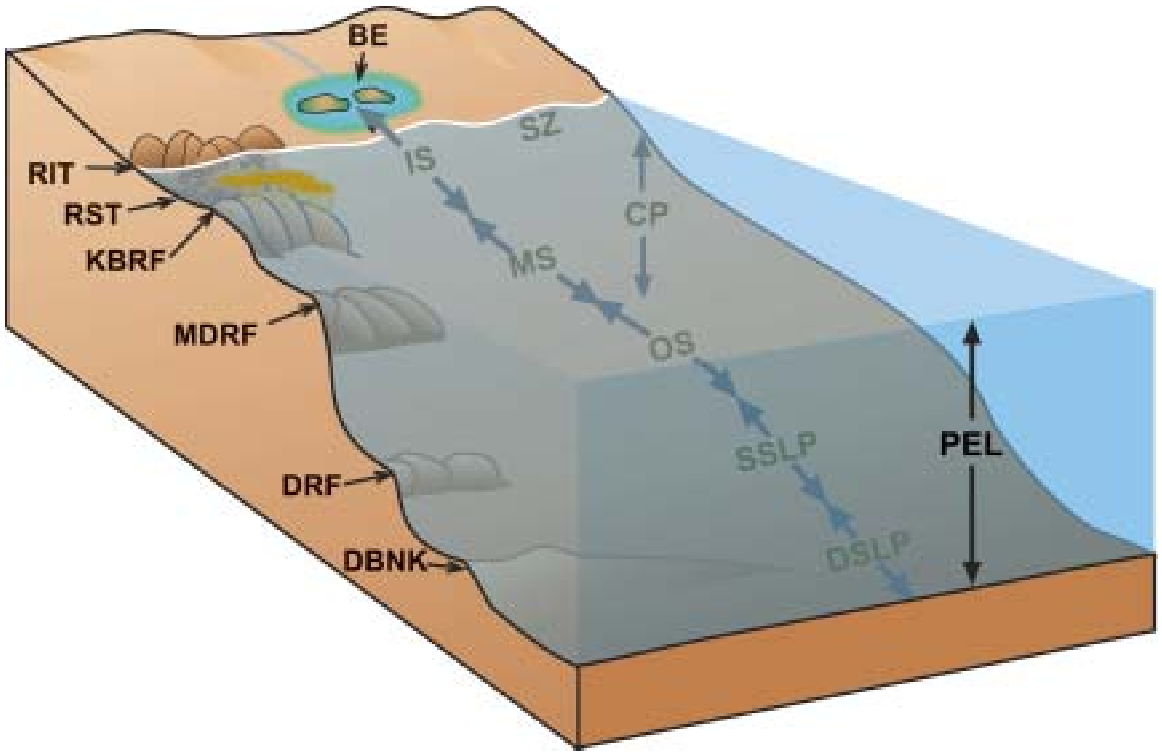

FIGURE 4-3 Diagrammatic representation of the relative positioning of the major habitats derived through cluster analysis.

which only rarely enter the waters over the continental shelf. According to the data analyzed, yellowtail and Pacific bonito (Species Group 2) were allied to both the open ocean species, coastal pelagic, and reef systems. These two species migrate along the coast of the Californias annually moving north in the spring–summer months and south in the late fall and winter (fig. 4-4). Yellowtail are also found in association with kelp patties drifting in pelagic environments.

Species Groups 3–5 included fishes almost exclusively from rocky intertidal and adjacent subtidal areas (RIT). Group 3 contained four species that occur in greatest abundance in the southern rocky intertidal habitat. Group 4 included two species, which were common to the intertidal and shallow subtidal habitats in both northern and southern locations, and Group 5 was made up of 15 distinct species found on the rocky shoreline of central and northern California (fig. 4-5).

Species Group 6 was composed of five species of primarily northern fishes that occurred both in the rocky intertidal (as juveniles) and rocky subtidal habitats (fig. 4-6). Cabezon regularly occur on southern California reefs. Species Groups 7–9 consisted of rock-associated species with northern affinities (fig. 4-6). Group 7 included four species common to northern subtidal and kelp bed habitats, which also occur commonly in the cooler portions of southern California and in the northern Baja upwelling area. Group 8 also contained four species with widespread occurrence in kelp beds and rocky reefs of the north and the northern part of southern California. Species Group 9 was composed of the most abundant, cryptic reef fishes in the northern rocky subtidal and reef habitats.

Species Groups 10–15 contained kelp bed and rocky reef species from a wide latitudinal distribution. Group 10 and 11 were made up of species from rocky reefs and kelp beds of southern California and Baja California (fig. 4-7). Nine cryptic species, which inhabit mainly the cobble substratum and crevices of rocky subtidal and reef areas, formed Species Group 10. Four of these cryptic species also occur in the intertidal zone as adults. Group 11 contained seven abundant or otherwise distinctive southern kelp bed species. One of them, the blacksmith, is often the most abundant fish found in southern kelp beds, and, another, the giant sea bass, is the top carnivore in this system. Group 12 included seven species, which were found primarily in the southernmost reefs of central Baja California, although three of these, rock wrasse, ocean whitefish, and zebraperch, are often abundant as far north as the reefs systems in the southern half of the southern California Bight. Group 13 consisted of five, widespread kelp bed and rocky reef species and included the señorita, which is common to most kelp beds from central California south into northern Baja California. The last group, 14, consisted of two species of rocky subtidal and reef fishes with more northern affinities.

Species Group 15 contained six generalist species, which occur over a wide range of substrata and shallow water habitats (fig. 4-7). Four of these were surfperches, which inhabit both rocky and soft bottom substrata from the shoreline out to depths of about 30 m throughout central, southern, and northern Baja California. The remaining two species were serranids (kelp bass and barred sand bass) that inhabit a variety of shallow water habitats south of Point Conception.

TABLE 4-3

Mean Abundance of Members within Species Groups in Major Habitats

	Shallow Habitats										*Deep Habitats*				
SPP GRP	*PEL*	*RIT*	*RST*	*KBRF*	*SZ*	*BE*	*CP*	*IS*	*MS*	*OS*	*MDRF*	*DRF*	*SSLP*	*DSLP*	*DBNK*
1	0.6														
2	0.4														
3		0.4													
4		0.3													
5		0.3													
6		0.2	0.2												
7			0.6	0.1							0.1				
8			0.1	0.1											
9			0.3												
10		0.1		0.1											
11		0.1		0.3	0.1										
12				0.1											
13				0.2											
14				0.1											
15				0.4	0.1			0.2							
16						0.3									
17						0.2									
18				0.1	0.8	1.0	0.1	0.2							
19				0.1	0.1	0.1	0.1	0.1							
20	0.3				0.1	0.3	0.8	0.2							
21					0.1	0.1	0.2	0.3	0.1						
22					0.6		0.1	0.1							
23					0.1			0.1							
24						0.1		0.1							
25	0.4						0.1	0.1							
26								0.1							
27								0.1							
28			0.2					0.3	0.3	0.2					
29								0.1							
30							0.4	0.3	0.2	0.3					
31								0.1	0.3	0.5					
32									0.5	0.2		0.1			
33									0.6	0.6			0.1		
34										0.1	0.3	0.1			
35											0.5	0.1			
36											0.1	0.5			
37												0.3			
38				0.1						0.1	0.1	0.1			
39									0.1	0.1	0.1	0.3	0.1		
40									0.1	0.1		0.1	0.4	1.2	0.3
41												0.1	0.4	0.5	0.9
42												0.2	0.9	0.1	0.3

NOTE: Only mean abundances >0.1% are shown to emphasize the most important components of the major habitats.

Species Groups 16 and 17 are made up of species common to the bays and estuaries of California (fig. 4-8). Group 16 contained seven species that are indigenous to the BE habitats in Southern and Baja California. Five of them, the longjaw mudsucker, California killifish, shadow goby, barred pipefish, and California halfbeak, are commonly associated with the salt marsh portions of these habitats. The second group, 17, consisted of estuarine and nearshore species of central and northern California. At least three of them, coho salmon, American shad, and striped bass, are anadromous species that pass through estuaries on spawning migrations and use them as nursery areas. The latter two were introduced to California from the eastern seaboard (see chapter 25). The remaining members of Group 17 (Pacific herring, surf smelt, staghorn sculpin, and starry flounder) are euryhaline, marine species that spend all or part of their lives in northern estuaries.

The members of Species Groups 18 and 19 can be characterized as nearshore generalist species (fig. 4-9). Species in both groups are commonly encountered in a wide range of shallow, nearshore habitats. Topsmelt and shiner perch (Group 18) are often very abundant in all nearshore soft bot-

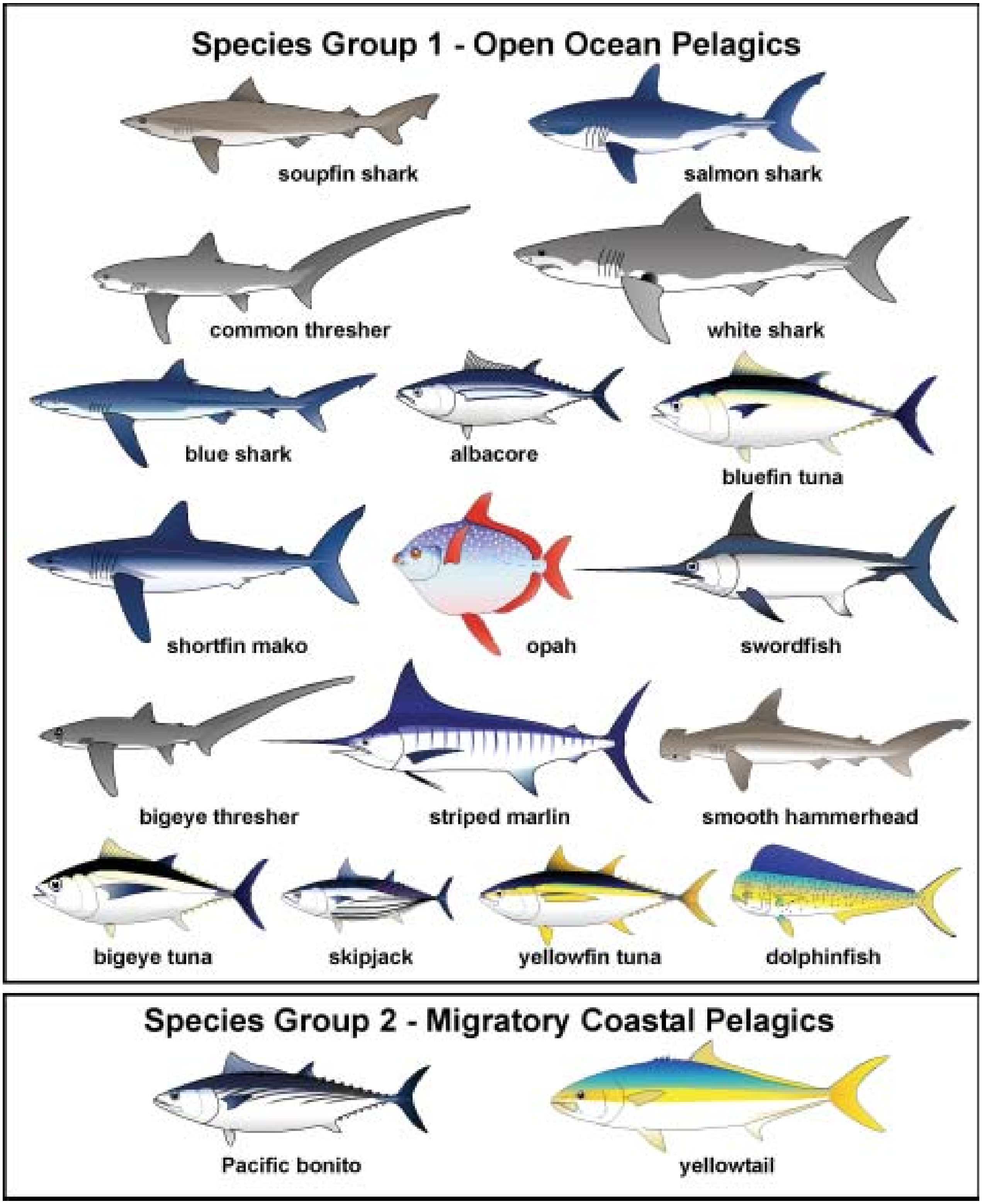

FIGURE 4-4 Pelagic members of Species Groups 1 and 2 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

tom habitats and are also sometimes associated with reefs. Jacksmelt and sargo (Group 19) are schooling species that move among various nearshore habitats. Further, sargo occur in numbers only south of Point Conception, whereas the others occur throughout California coastal waters.

Species Group 20 contained three abundant coastal pelagic species (Fig. 4-9). The northern anchovy has been the most abundant nearshore marine fish off California for most of the last 50 years and can occur up to 1000 km offshore (see chapter 12). The second member, the Pacific sardine, is also an

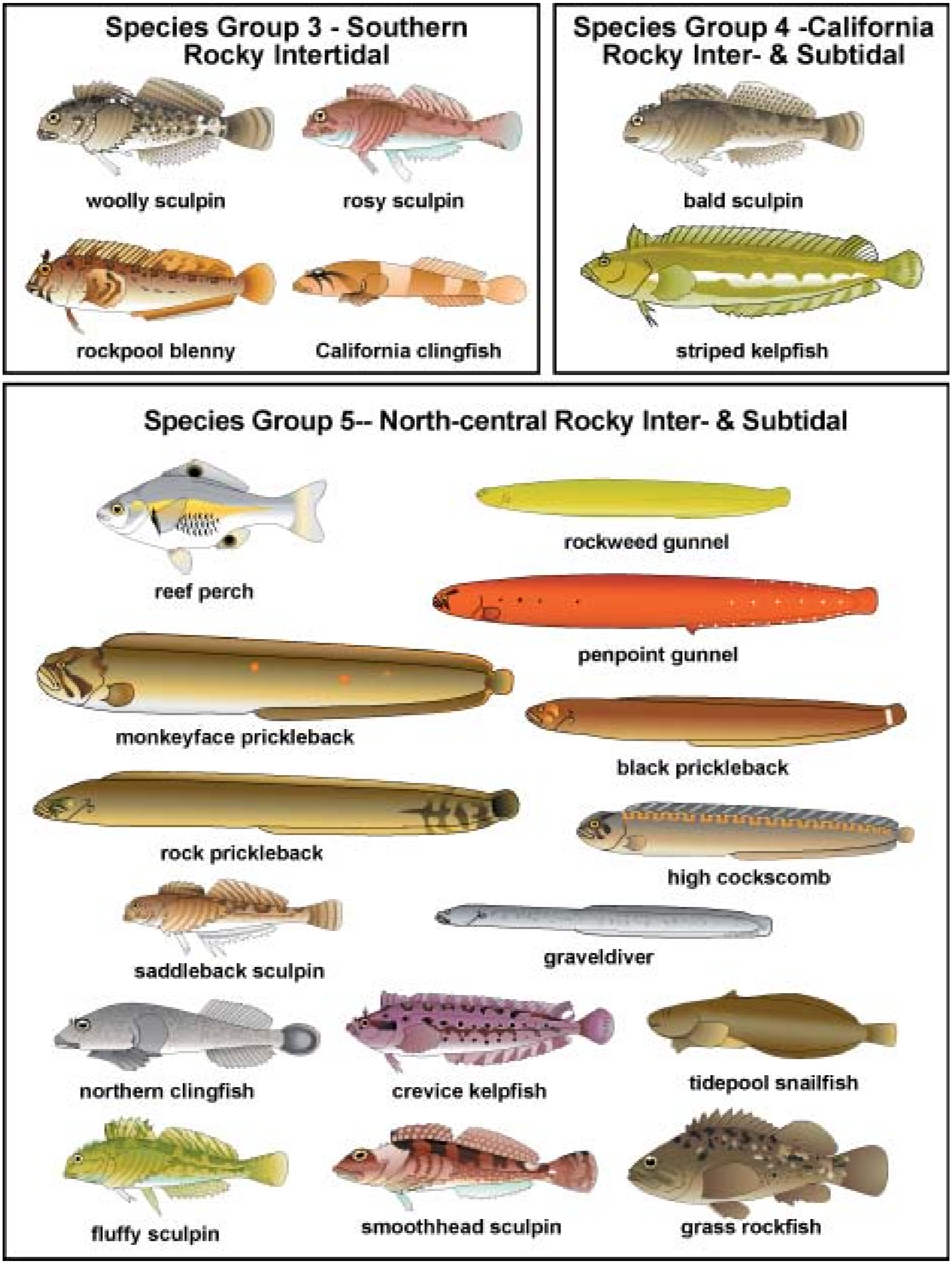

FIGURE 4-5 Benthic members of Species Groups 3, 4 and 5 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

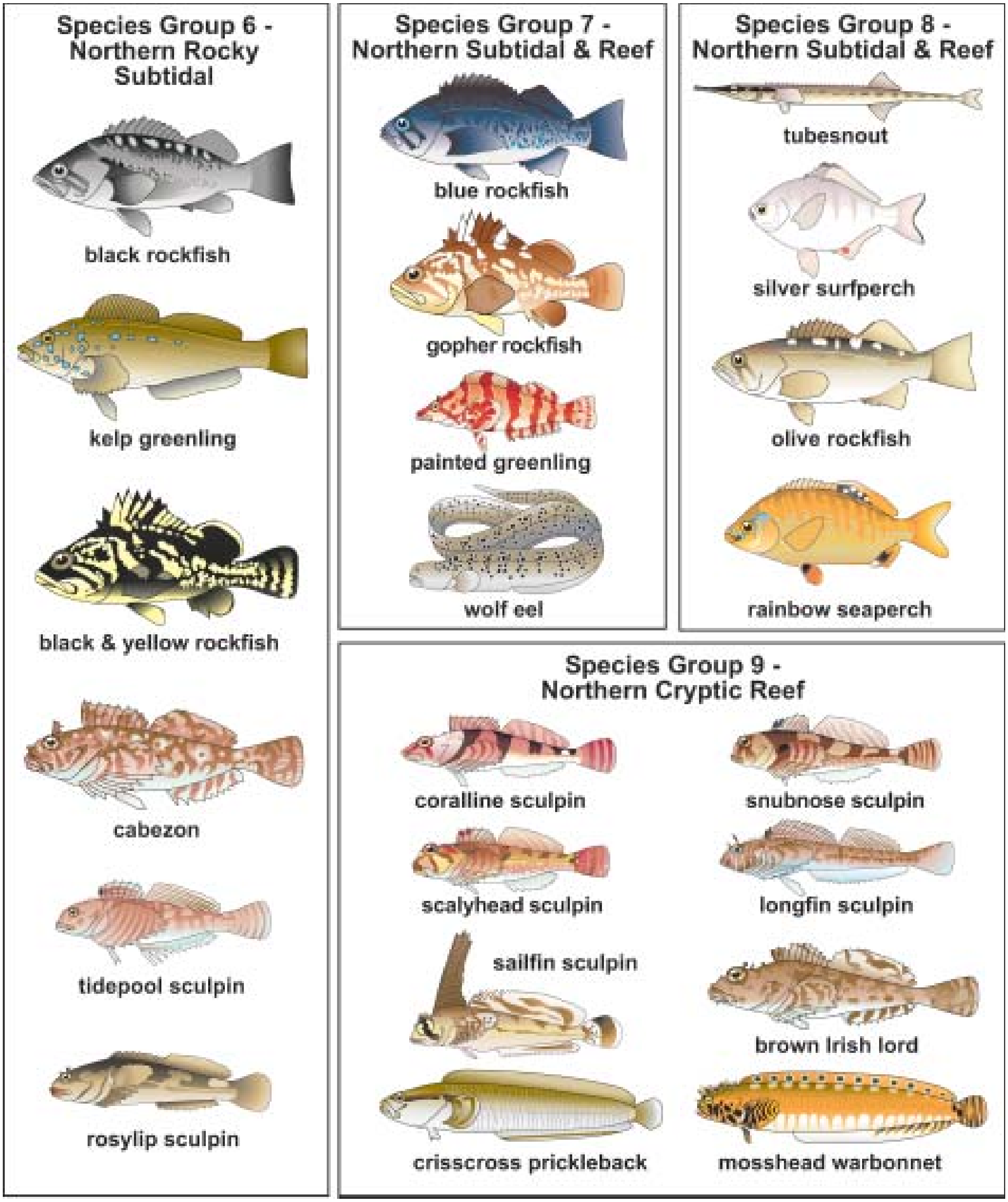

FIGURE 4-6 Members of Species Groups 6–9 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

abundant species that has cyclically replaced the northern anchovy as the most abundant species during the last few centuries (see chapters 12 and 17). Pacific sardine was also one of the most important commercial species in the state (see chapter 23). The third species, the Pacific pompano, is also an abundant and largely underappreciated pelagic fish of coastal waters.

Members of Species Groups 21–24 can be characterized as southern nearshore generalists, although individually the groups exhibit affinities to particular habitats (fig. 4-10). The five members of Group 21 are commonly found in the shallow nearshore waters of the inner shelf, harbors, and deeper parts of bays and estuaries in southern and Baja California. One member, the queenfish, is possibly the second most abundant fish in the nearshore waters off southern California (Allen and DeMartini, 1983). Group 22 contained species that are also found throughout the shallow, nearshore zone of southern

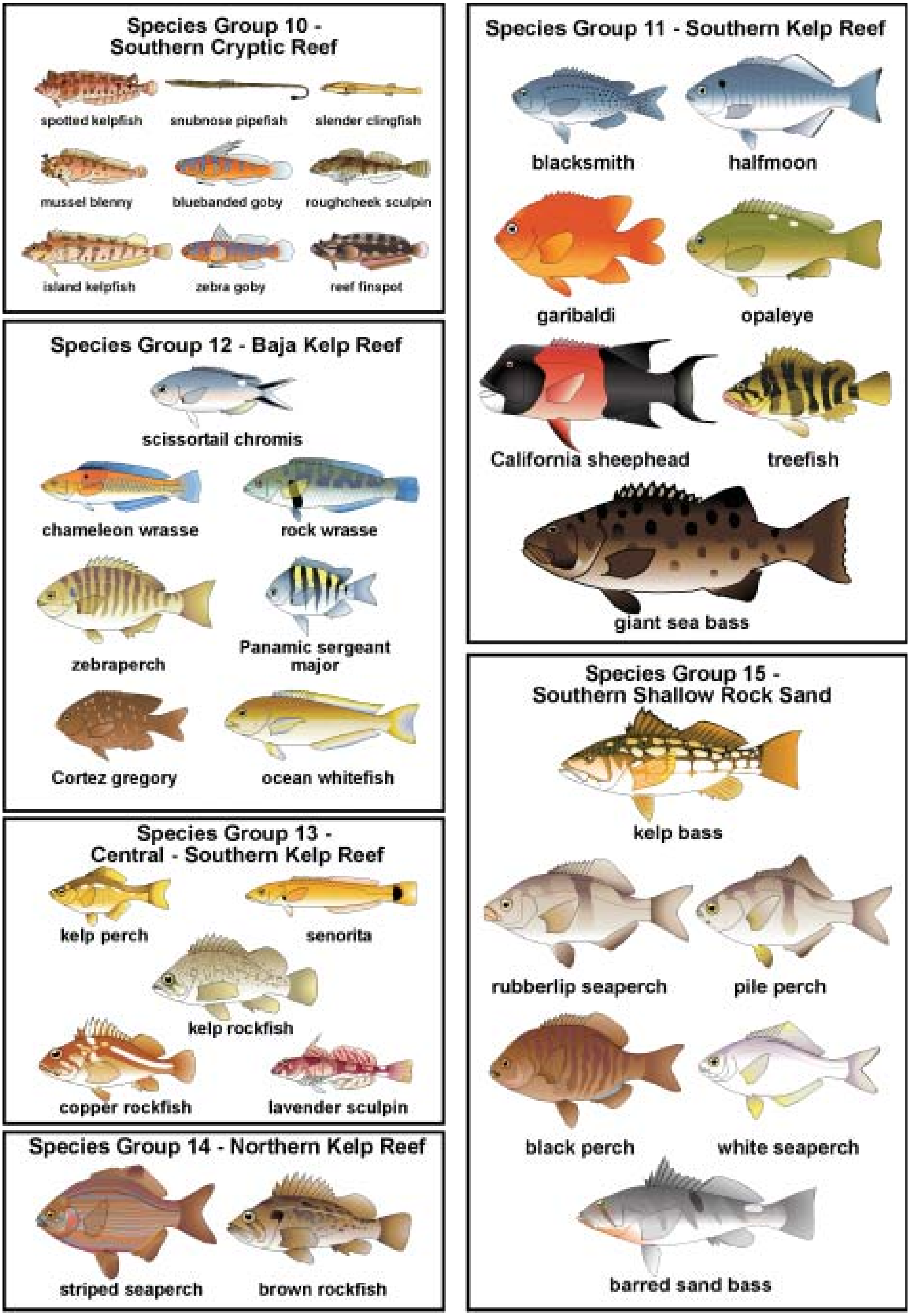

FIGURE 4-7 Reef associated members of Species Groups 10–15 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

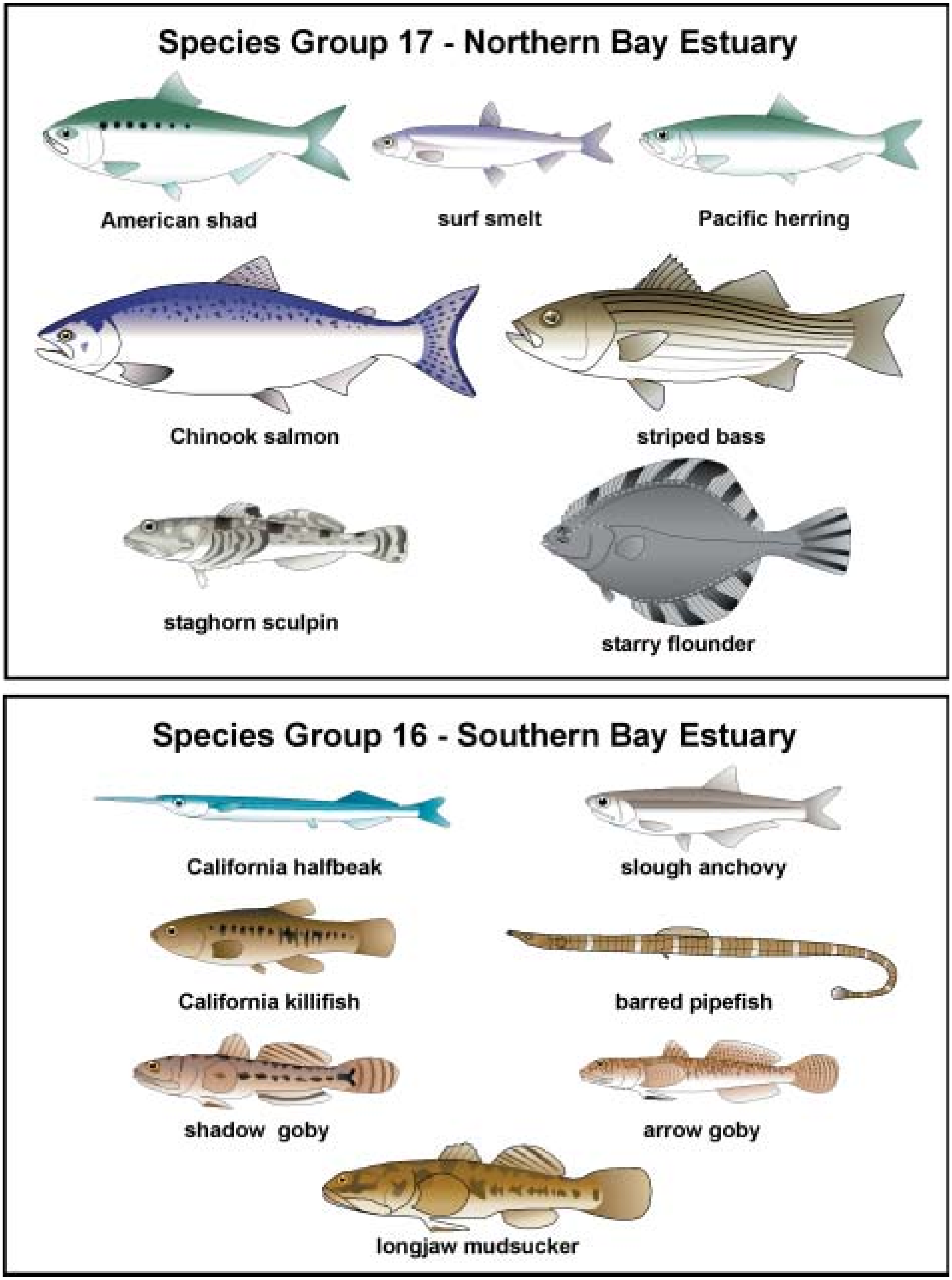

FIGURE 4-8 Bay and estuary associated members of Species Groups 16 and 17 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats. Groups are arranged north to south.

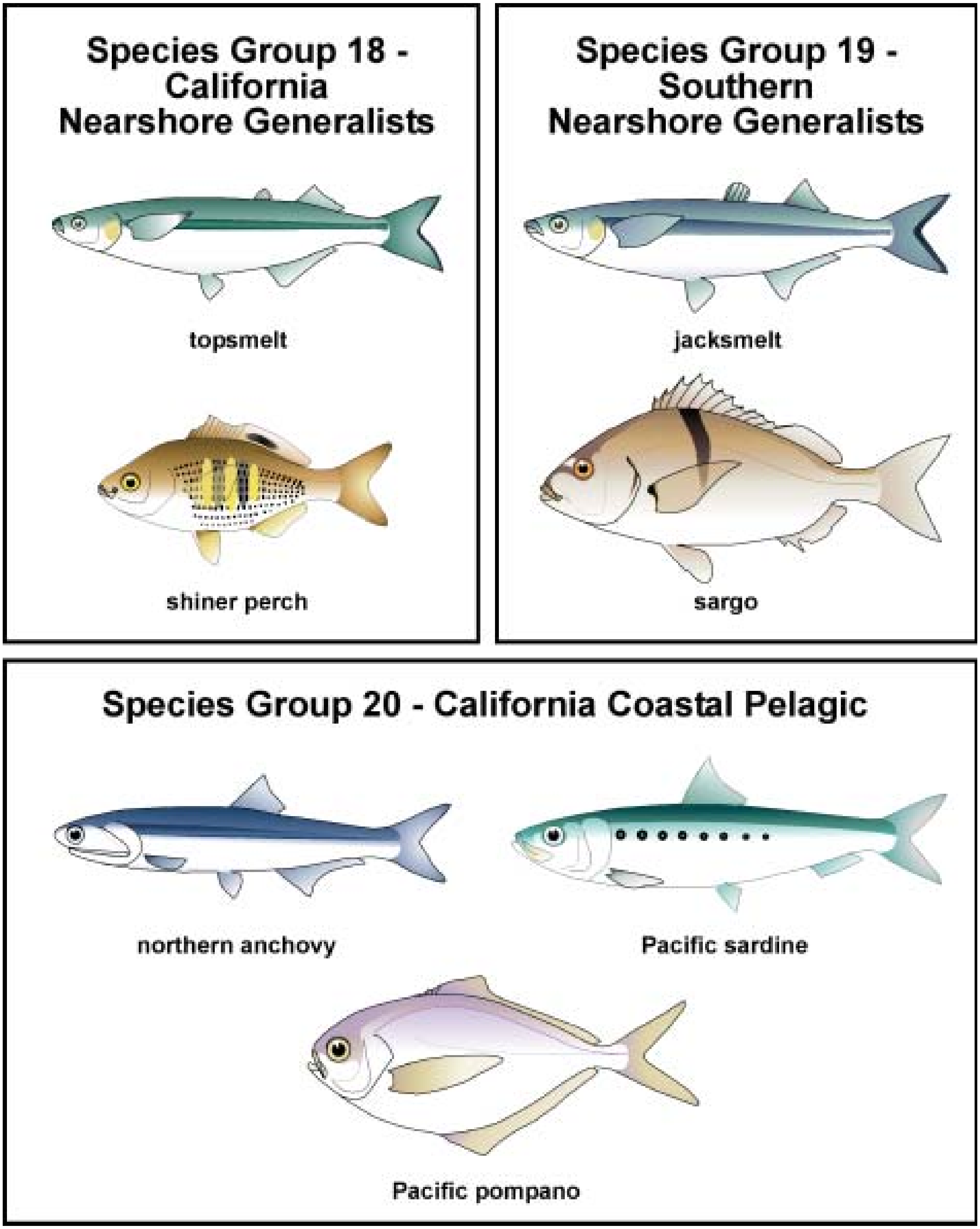

FIGURE 4-9 Widespread members of Species Groups 18–20 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

California and Baja California and include species that are typical of the surf zone environment. Group 23 represented a collection of large, mobile species that are active mainly at night and are often from the rock/sand margins of rocky reef and kelp bed complexes. They may be present in both soft-bottom and rocky nearshore habitats. Six of these 11 species are elasmobranches that contribute a great deal of biomass to nearshore fish assemblages. The nocturnal behavior of these species, in the past, has rendered them inconspicuous to most diver surveys of reef areas. A recent assessment of these habitats

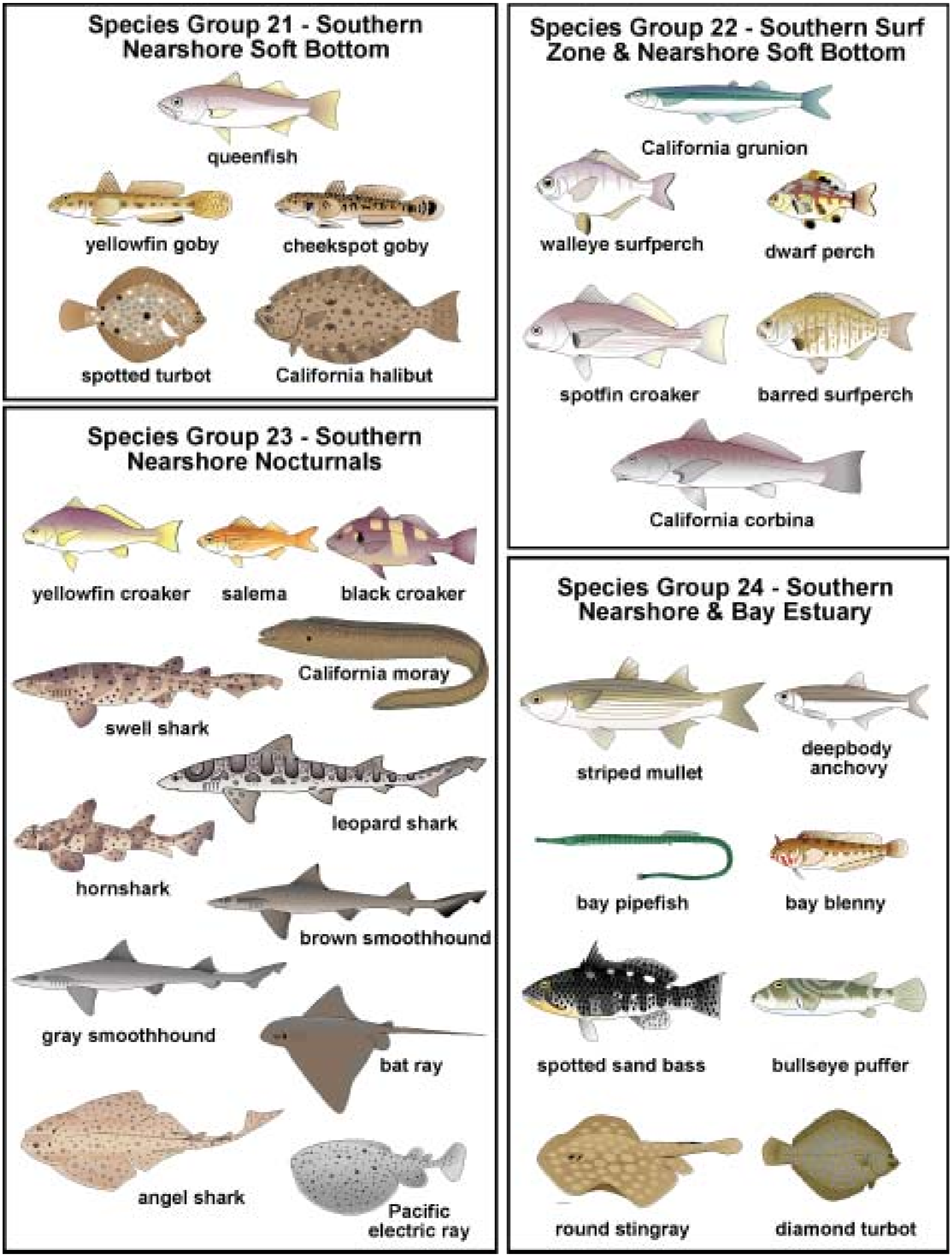

FIGURE 4-10 Nearshore members of Species Groups 21–24 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

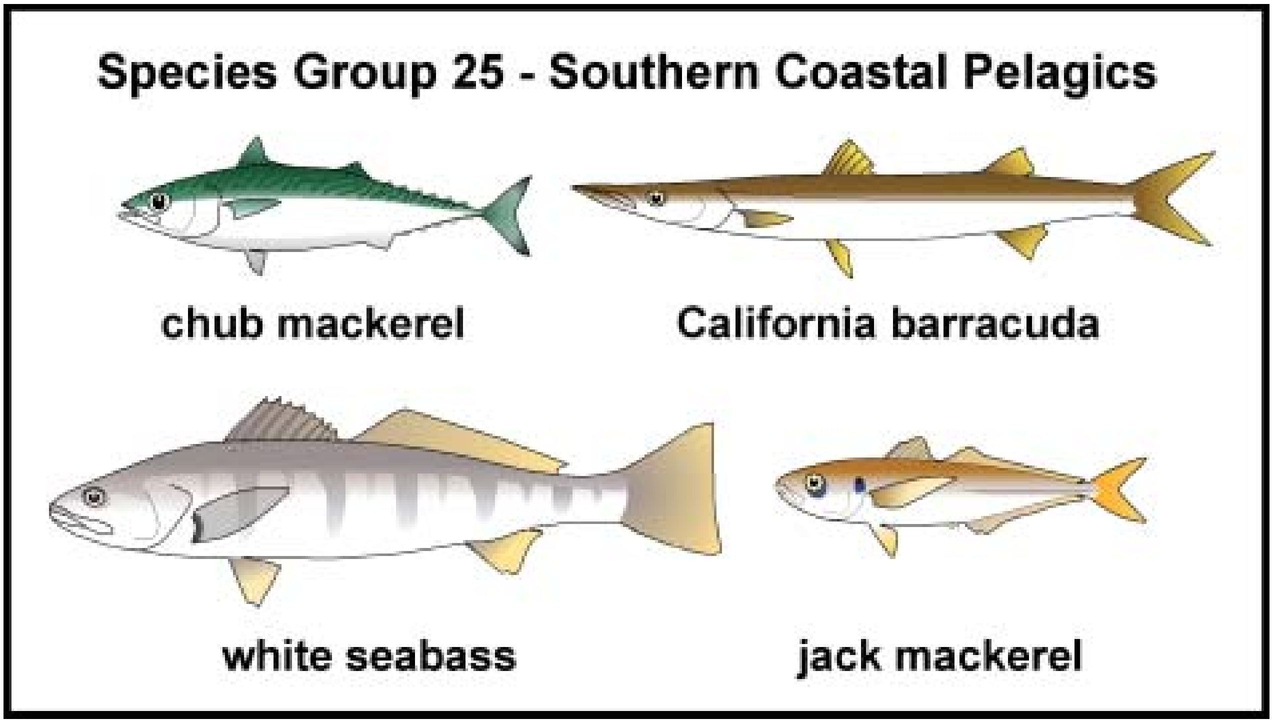

FIGURE 4-11 Southern coastal pelagic members of Species Groups 25 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

by gill net sampling in southern California was solely responsible for the identification of this ecologically important group (Pondella and Allen, 2000). Group 24 included eight species that are commonly from southern bays and estuaries but are also variously found in nearshore, soft-bottom areas of the southern coastline. One of them, the bullseye puffer, was found only in the bays and on the shoreline of central Baja California.

Species Group 25 (fig. 4-11) consisted of four coastal pelagic species, including three (white seabass, California barracuda, and jack mackerel) that are found around kelp beds and reefs in the southern regions of California and in Baja California. They can be found in the same types of habitats as members of Species Group 23.

Species Groups 26–29 contained nearshore soft-bottom species, which are usually encountered along sandy beaches (fig. 4-12). Group 26 included three species found commonly on the shallow inner shelf off southern California and northern Baja California. Group 27 contained four species from similar environments off central California. The four species in Group 28 were found mainly in southern, shallow, soft-bottom habitats, particularly those close to shallow reefs.The giant kelpfish of Group 28 is commonly found in all shallow habitats with algae (live or drift), surf grass, or eelgrass. Group 29 included three widespread members found in the surf zone and shallow inner shelf. The two pipefishes are associated with the drift algae of the surf zone, whereas the speckled sanddab is an abundant species throughout the nearshore soft-bottom environment.

Species Groups 30–32 contained soft-bottom, inner to midshelf generalists (fig. 4-13). White croaker and basketweave cusk-eel of Group 30 are abundant, nocturnal species of the nearshore soft-bottom and inner shelf. Groups 31 and 32 consisted of nine inner shelf and seven midshelf species, respectively.

In Species Group 33, we encounter the first of the truly deep dwelling species, especially in southern waters (fig. 4-13). In general, fishes occur in deeper water in the southern regions of the distribution because of temperature stratification, a phenomenon referred to as submergence (see Chapter 1). The six members of Group 33 are typical of the mid- to outer shelf of the California coastline.

Species Groups 34–39 are composed of deeper reef species (50–250 m) and are dominated by rockfish species (genus *Sebastes*) (figs. 4-14 and 4-15). Group 34 included four species (three rockfishes) common to mid-depth rocky reefs and surrounding soft-bottom areas. Groups 35 and 36 included 11 rockfish species that are widespread over mid to deep rocky reefs. Members of groups 37–39 are typical of deep rocky reefs and deep canyons of central and southern California. Members of Group 38, however, also live in shallower kelp bed and rocky reefs and recruit to subtidal areas north of Point Conception (Burge and Schultz, 1973; Miller and Geibel, 1973; Yoshiyama et al., 1987).

Species Group 40 contained six deep shelf and continental slope species indicative of the soft-bottom areas of the deep waters off California (fig. 4-16). This group included one of the most abundant flatfishes of the deep shelf and slope, the Dover sole, as well as the common rockfish relative, the longspine thornyhead. Also, the two rattails (macrourids) and the slickhead (alepocephalid) of this group are typical of the deep, benthopelagic realm. Finally, Species Groups 41 and 42 contained species that were widespread over deep shelf, slope, and deep bank habitats, usually in excess of 200 m depth (fig. 4-16).

Each major habitat and associated species identified by this analysis and earlier works will be covered in greater detail in Unit II of this volume. Soft substratum habitats are the subjects of chapter 5 (BE-bays and estuaries), chapter 6 (NSB-nearshore soft-bottom, SZ-surf zone, and harbors), chapter 7 (IS-inner shelf and OS-outer shelf), chapter 13 (SLP including SSLP and

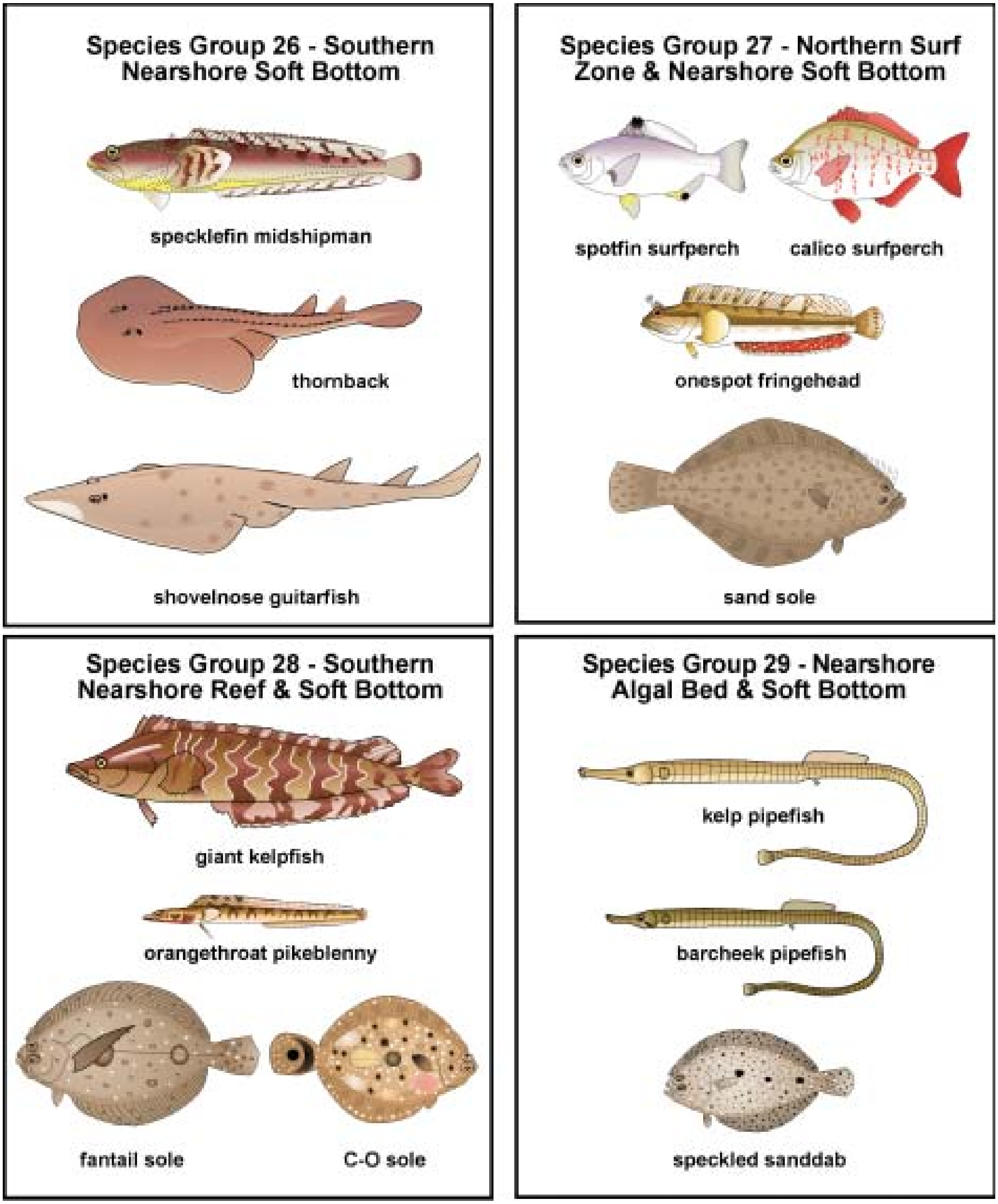

FIGURE 4-12 Nearshore members of Species Groups 26–29 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

DSLP-shallow and deep continental slope) and chapter 12 (CP and PEL-surface waters). The rocky intertidal (RIT) habitat will be discussed in chapter 8, and the rocky subtidal (RST) and kelp bed/rocky reefs (KBRF) are the subjects of chapter 9. Fishes of the deep rocky reefs and banks (MDRF, DRF, and DBNK) are the subjects of chapter 10 in this volume.

Physical Basis for Groups

WHICH PHYSICAL ATTRIBUTES DEFINE THESE HABITATS AND HOW MIGHT THESE INFLUENCE THE FISHES THERE?

The site and species groups covered above were determined strictly by fish species associations. To begin to address the

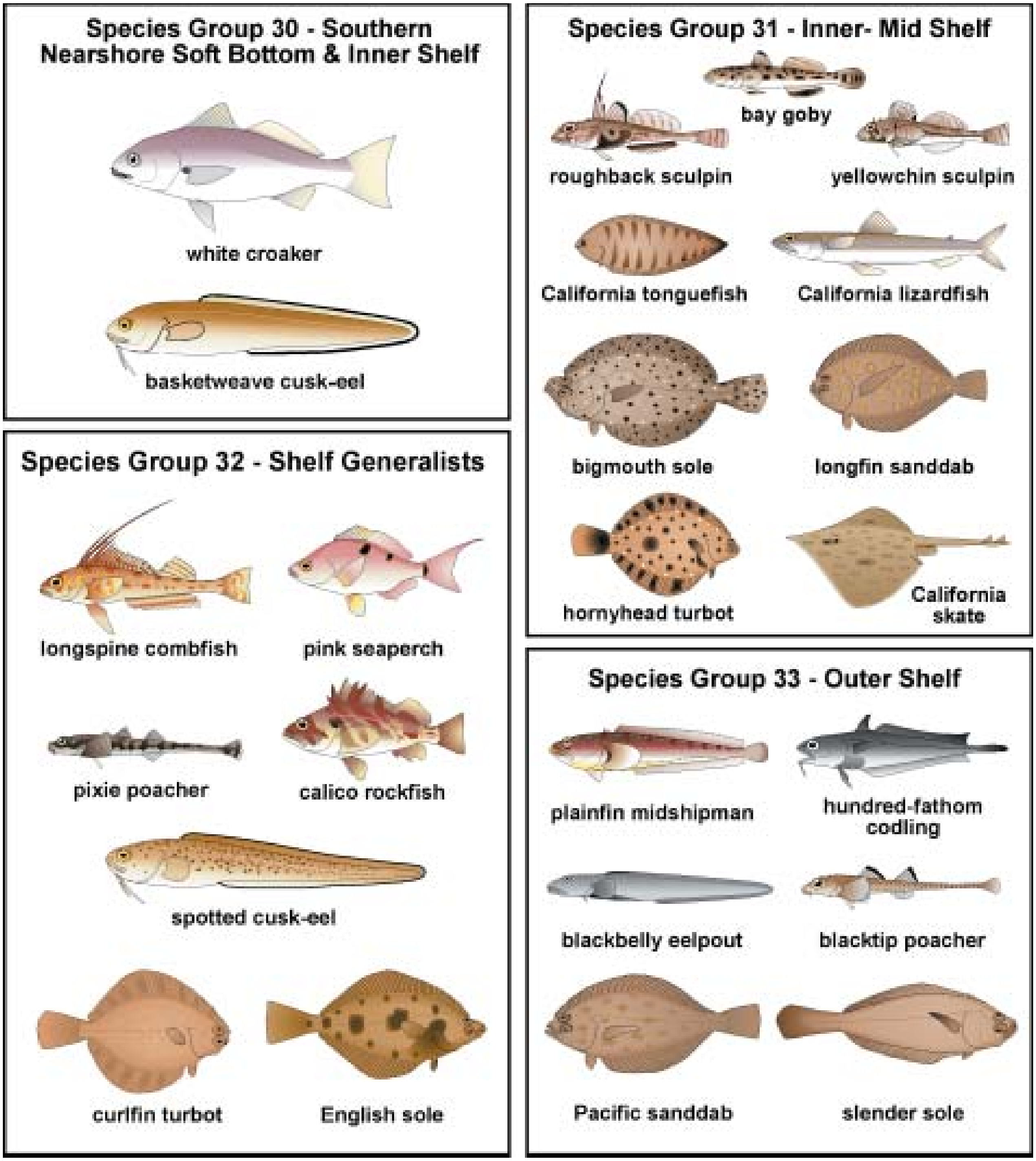

FIGURE 4-13 Shelf associated members of Species Groups 30–33 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

question, information on the substratum type, mean depth, and latitude for each of the original 168 sites was assembled from the literature. Substratum type was represented by an index derived from available information and ranged from 0 (mud) to 5 (bench rock). Cobble and mixed rock/sand or rock/mud substrata fell in the middle of the index range. Depths were recorded as the mean depth (m) of the habitat in question, and latitude (°N) was determined from charts if not otherwise available from the source publication. These data were then used to discriminate among the 15 major types of habitats identified through cluster analysis. In this multivariate analysis, these three physical variables discriminated extremely well among major habitats in a highly significant manner. These three physical variables accounted for as much as 90% ($R^2 = 0.90$) of the variance within the site group model. The differences among the major habitats relative to these physical attributes can be visualized by plotting the mean canonical scores (centroids) of the sites within the major habitats by the three significant discriminant roots (fig. 4-17). Root 1 represented mainly substratum type and ranged from rocky substrata

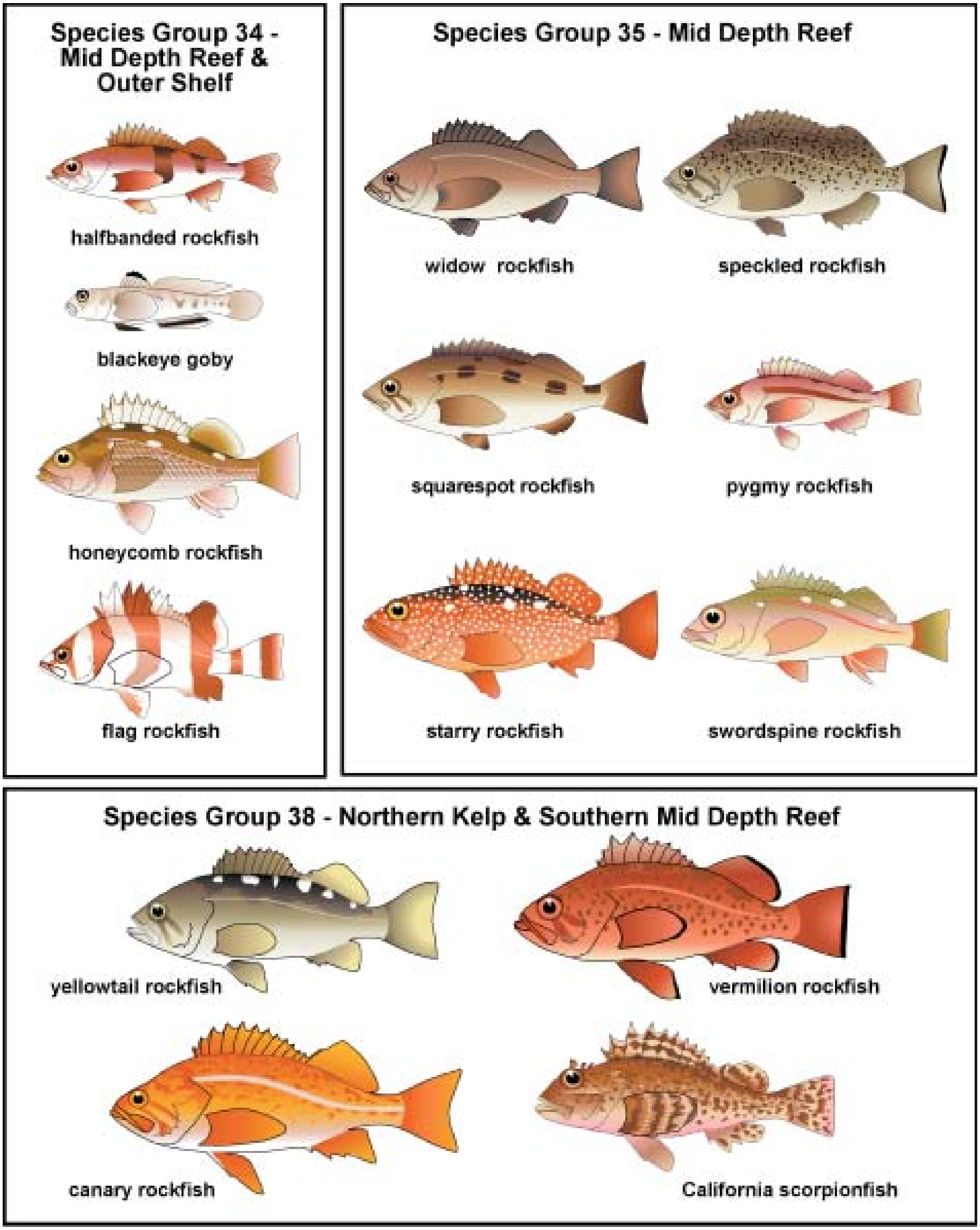

FIGURE 4-14 Shelf and deeper reef associated members of Species Groups 34, 35, and 38 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

on the left and muddy substrata on the right of the axis. Root 2 was loaded heavily on depth and is represented in the graph as shallow (top) to deep (bottom) on this axis. Latitude was the primary influence in root 3 and ranges from north to south on the axis. Therefore, shallow, rocky habitats fall into the upper left, back portion of the three-dimensional space. Conversely, deep, muddy habitats fall into the lower right portion of the space. The deep bank (DBNK) habitat falls in the center of root 1 reflecting the rock/mud mix character of this deep-sea habitat.

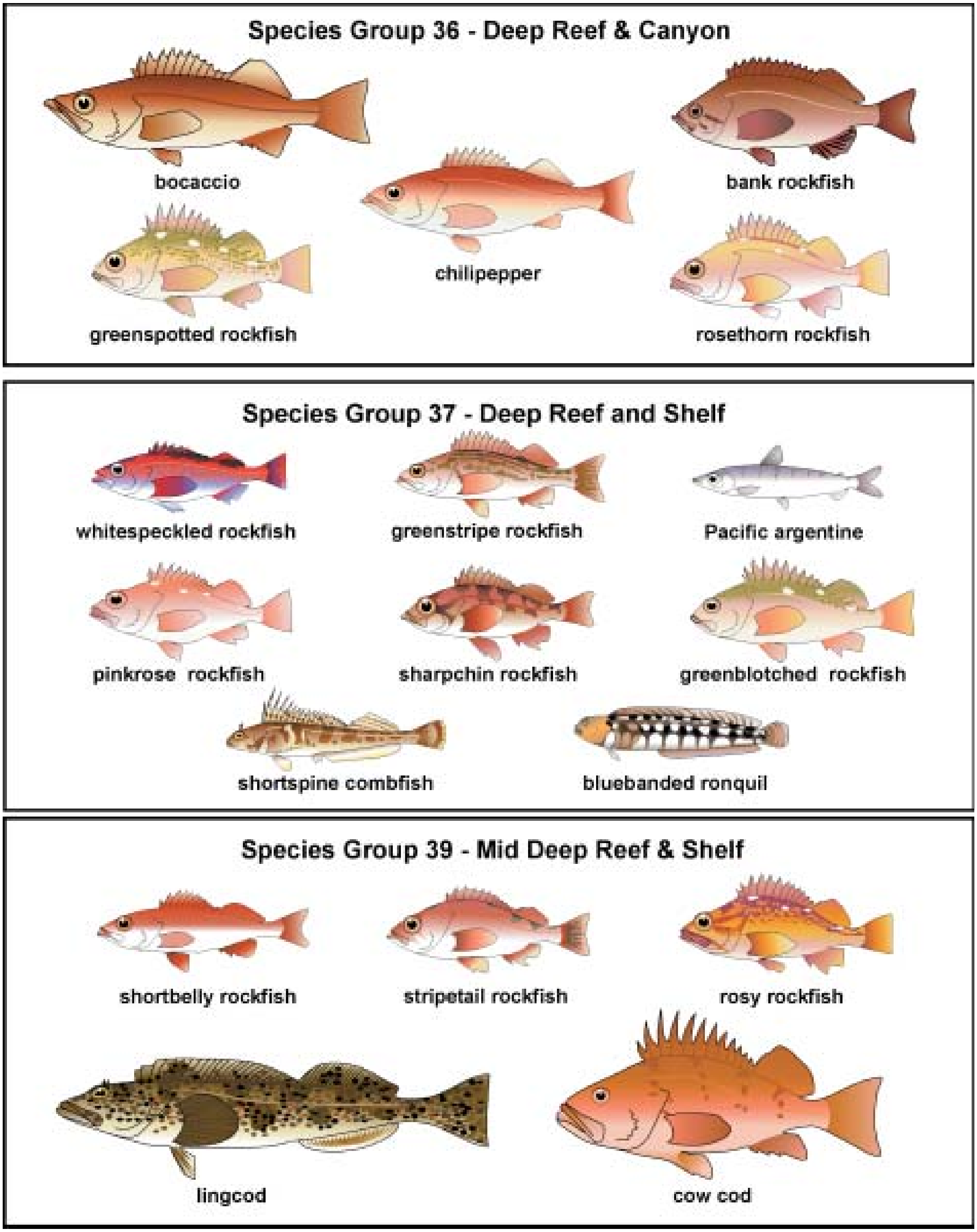

FIGURE 4-15 Deep reef and shelf associated members of Species Groups 36, 37, and 39 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats.

Based on the significant discrimination of site groups by physical attributes, the 42 species groups were also discriminated based on individual species correlations with the same three physical factors, substratum, depth, and latitude. This discrimannt analysis was carried out to link the species groupings directly to the physical attributes of their habitats. Not surprisingly, substratum, depth, and latitude significantly discriminated among the groups of fishes at a level equivalent to that of the major habitat types. The three physical variables, once again, accounted for as much as 90% ($R^2 = 0.90$) of the

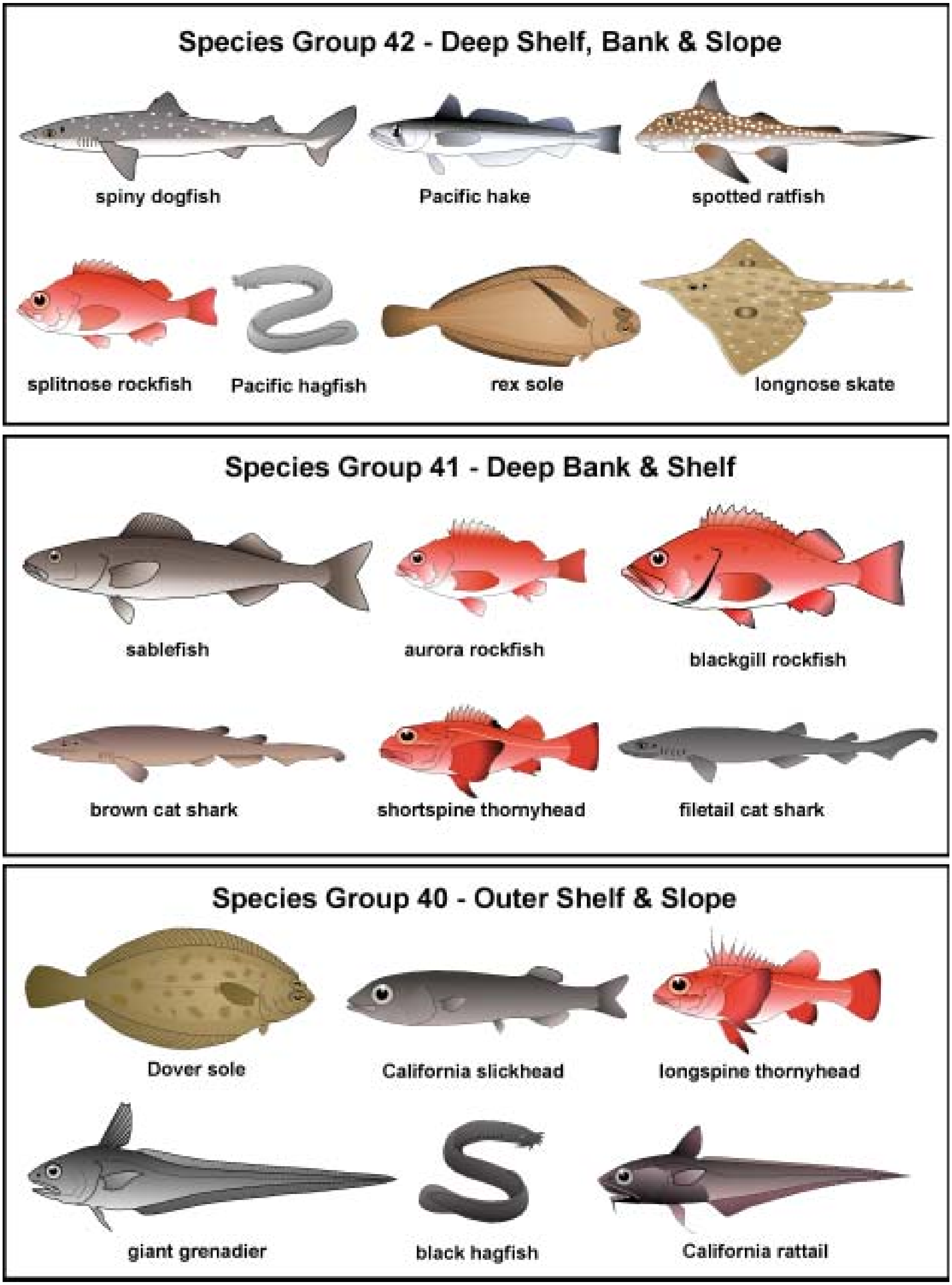

FIGURE 4-16 Deep shelf, bank, and slope associated members of Species Groups 40–42 derived by cluster analysis based on relative abundances and co-occurrence of species within habitats. Groups are arranged by relative depth (top to bottom).

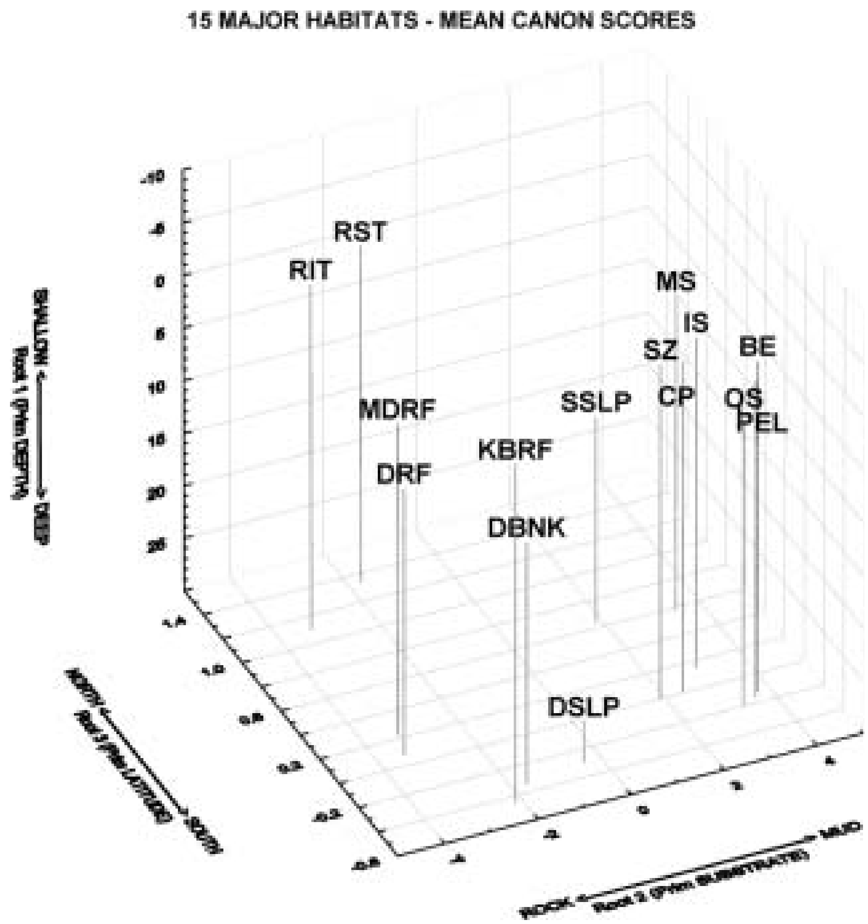

FIGURE 4-17 Plot of mean canonical scores of 15 major habitats derived from discriminate function analysis using substrate, depth, and latitude.

variance within the site group model. This implies that fish species associations are closely allied to the characteristics of their habitat. Again, this is not surprising considering the millions of years in which marine fishes have had to adapt to such conditions (see chapter 2). What it means, in a practical sense, is that we can closely predict which fish assemblages should normally occur at specific latitudes, depths, and substrata off California. As with the site groups, plotting the species groups according to the mean canonical scores on the three significant roots allows us to determine the general habitat of a particular species group directly from its position in the three-dimensional space (fig. 4-18). For example, in Fig. 4-18, species group 5 falls in the back of the upper left quadrant of the plot. Its position indicates (and predicts) that the species in this group occupy shallow, rocky habitats in higher latitudes relative to other species groups in the plot. Similarly, species group 40 is positioned in the middle of the lower right portion of the space indicating that this species group occupies a deep, soft-bottom habitat (slope) throughout California (root 3 score of zero). The cluster of habitats in the upper, right middle of the space represent the 21 species groups that occupy the shallow, nearshore, soft-bottom areas off California. Likewise, the cluster including "rockfish" species groups 34–39 falls in the space representing mid-depth to deep rocky reefs. Therefore, the value of this three-dimensional plot lies mainly in the fact that it represents a heuristic, predictive model of species occurrence in the multivariate space depicting habitat substratum, depth, and latitude. One drawback to this approach at this time is that a number of holes remain in the space. Potential habitat, depth, and latitude combinations (e.g., surf zone in central California) remain unstudied at this time (table 4-4).

Habitat Generalists

ARE ALL SPECIES LINKED TO PARTICULAR HABITATS OR ARE THERE HABITAT GENERALISTS?

The species groups represent a collection of both widespread (generalized) and restricted (specialized) distributions among major habitats. A number of the more common species found off California occur over a wide range of habitats either in shallow water (<30 m) or in deep water (table 4-5). Among the species of shallow water habitats, the black perch was reported from the broadest range of habitats, 24 of the 29 shallow site groups. Kelp bass, pile perch, white seaperch, and barred sand bass also occurred in a large percentage of shallow habitats with both rocky and soft substrata. These species were members of the same nearshore generalist species group (15). Shiner perch and topsmelt were recorded from a large portion of the shallow water site groups as were opaleye, California halibut, and northern anchovy. Blackeye goby, white croaker, and California scorpionfish were also found in a wide variety of habitats and should be considered shallow generalists as well.

Deep-water generalist species were best represented by shortspine thornyhead that occurred in seven of the nine possible deep-water site groups, followed by the spotted ratfish, bank rockfish, shortspine combfish, and Pacific hake. Six other species of rockfish—swordspine, greenstriped, greenblotched,

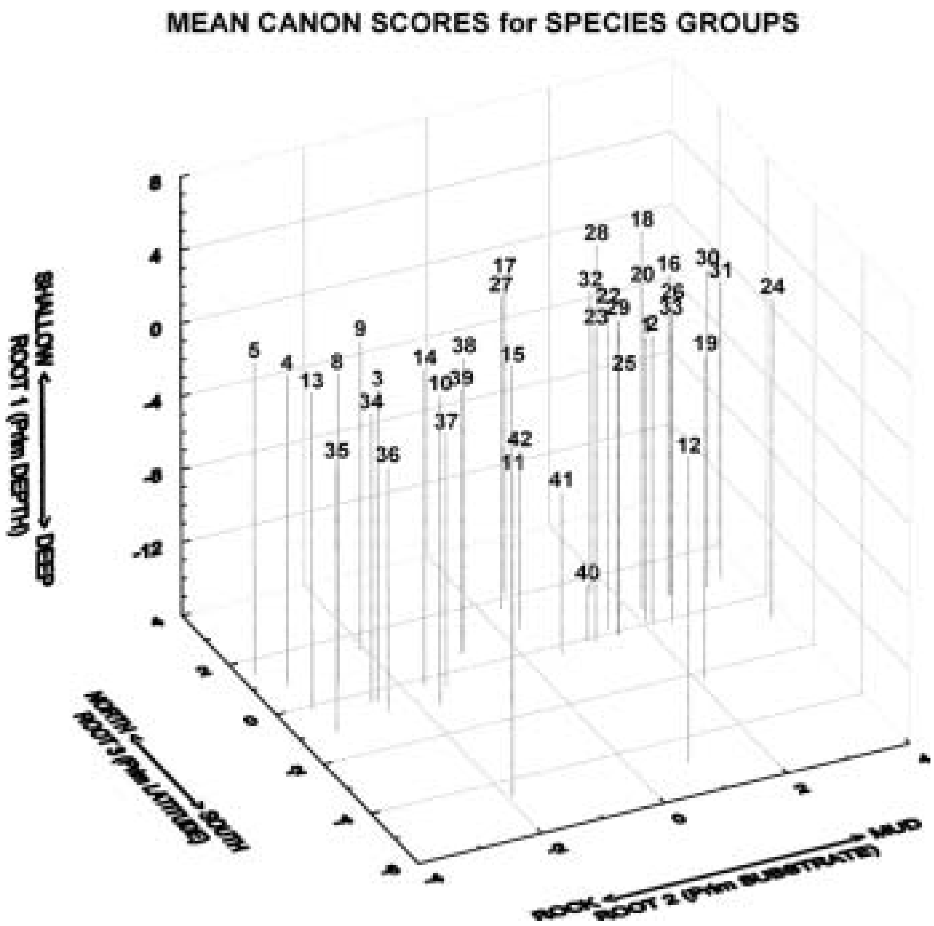

FIGURE 4-18 Plot of mean canonical scores of 42 species groups derived from discriminate function analysis of correlations with substrate, depth, and latitude.

stripetail, splitnose, and boccacio—plus the lingcod were all reported from most deep-water habitats. These deep-water generalists tended to be equally represented in habitats with both rocky and soft substrata.

At the level of species group occurrence within the major habitats, members of species groups 15, 18, 20, 28, and 29 were recorded in more than two-thirds of the shallow major habitats (see table 4-3).

Topsmelt and shiner perch (Species Group 18) were reported from all of the major shallow habitats, save the rocky subtidal, as were the members of group 28 although in much lower abundance. The broad occurrence of species group 28 was largely the result of the widespread distribution of one member, giant kelpfish, that was associated with macrophyte (kelp, drift algae, eelgrass, and surfgrass) substratum in many shallow water habitats. Group 15 was represented in all shallow habitats south of Point Conception except for the rocky intertidal. Four members of this group, black perch, pile perch, kelp bass, and barred sand bass, are ubiquitous in most nearshore habitats in southern California and northern Baja California. White seaperch is common to the nearshore areas throughout California, and the last member, rubberlip seaperch, was more closely associated with reefs over a wide latitudinal range. Large schools containing the members of Species Group 20 were reported from the water column of five major shallow habitats as well as the pelagic habitat offshore. Northern anchovy, Pacific sardine, and Pacific pompano may represent three of the most abundant coastal pelagic species in California waters (Allen and DeMartini, 1983; Cailliet et al., 1979) and range throughout the nearshore waters as both adults and juveniles. Finally, the speckled sanddab, barcheek pipefish, and kelp pipefish (Group 29) occurred in a wide latitudinal range along the coast of the Californias, primarily in the surf zone, nearshore soft-bottom, and inner shelf. The two pipefishes associated mainly with the drift algal beds just outside the surf.

Deep-water generalist species were clustered largely into Species Groups 39 and 42. The species in Group 39 were reported from both mid to deep rocky reefs and deep shelf locations. Lingcod and cowcod occurred over soft substrata mainly as juveniles, and the remaining rockfish species (shortbelly, stripetail, and to some extent rosy) were reported widely from both substrata as adults. Members of Group 42, particularly Pacific hagfish, Pacific hake, spotted ratfish, spiny dogfish, and splitnose rockfish, were reported throughout the deep shelf, shallow slope, deep reef, and deep bank habitats. One member, rex sole, along with Dover sole (Group 40), were the two most abundant and widespread flatfishes of the deep, soft-bottom habitats.

Taxonomic Composition of Assemblages

WHICH FAMILIES AND ORDERS OF FISHES ARE BEST REPRESENTED OVERALL IN THE VARIOUS HABITATS AND FISH FAUNA?

Certain families exhibited great flexibility in habitat requirements and occurred across a wide range of habitats over a

TABLE 4-4

Habitat Analysis Summary Table

Major Habitat	*Northern California*	*Central California*	*Southern California*	*Northern Baja California*	*Central Baja California*
PEL	Hanan et al. (1993), Squire (1983), Mais (1974)	Hanan et al. (1993), Squire (1983), Mais (1974)	Hanan et al. (1993), Squire (1983), Mais (1974)	Hanan et al. (1993), Squire (1983), Mais (1974)	Hanan et al. (1993), Squire (1983), Mais (1974)
RIT	Grossman (1982); Yoshiyama et al. (1987)	Burge and Schultz (1973); Allen and Horn (unpubl. data)	Allen (1985); Crase (1990); Cross (unpubl. data)	Stepien et al. (1991)	No data
RST	Yoshiyama et al. (1987)	Burge and Schultz (1973)	Walker (unpubl. data)	No data	No data
KBRF	No data	Burge and Schultz (1973); Miller and Geibel (1973)	Allen et al. (1992); DeMartini (1981); DeMartini (unpubl. data); DeMartini and Roberts (1981); Ebeling et al. (1980); Love et al. (1999); Stephens and Zerba (1981); Stephens et al. (1986); Stephens et al. (1984); Turner et al. (1969)	Love et al. (1999); Quast (1968)	Love et al. (1999)
MDRF	No data	Yoklavich et al. (2000)	Love and Yoklavich (unpubl. data)	No data	No data
DRF	No data	Yoklavich et al. (2000)	Love and Yoklavich (unpubl. data)	No data	No data
DBNK	No data	No data	Cross (1987)	No data	No data
BE	Ganssle (1966)	Yoklavich et al. (1991); Horn (1980)	Allen (1988); Allen and Horn (1975); Allen et al. (2002); Brooks (1999); Horn and Allen (1981); Lane and Hill (1975); Onuf and Quammen (1983)	Beltran-Felix et al (1986), Rosales-Casian (1996,1997)	Galvan et al. (2000)
SZ	No data	Allen (unpubl. data)	Allen (unpubl. data); Carlisle et al. (1960); Tetra Tech (1977)	No data	No data
CP	No data	No data	Allen and DeMartini (1983)	No data	No data
IS	No data	Allen (unpubl. data)	Allen (1976); Allen et al. (1983); Allen et al. (2002); Lane and Hill (1975); MEC (1988); Pondella and Allen (2000); Stephens et al. (1974)	Rosales-Casian (1997)	No data
MS	No data	Burton et al. (1995)	Allen, L.G. (1976); Allen, M.J. et al. (1999); DeMartini and Allen (1984); LAUSD (unpubl. data)	No data	No data
OS	No data	Burton et al. (1995)	Allen, L.G. (1976); Allen, M.J. et al. (1999); DeMartini and Allen (1984); LAUSD (unpubl. data)	No data	No data
SSLP	NOAA (unpubl. data)	NOAA (unpubl. data)	NOAA (unpubl. data)	No data	No data
DSLP	NOAA (unpubl. data)	NOAA (unpubl. data)	NOAA (unpubl. data)	No data	No data

NOTE: Past studies stratified by habitat and latitude.

TABLE 4-5
Top 15 Shallow and Deep Water Generalist Species

Shallow Generalists

SPP Group	*Species*	*Common Name*	*#Occur Shallow (29)*	*#Occur All (38)*	*#Occur Rocky Bottom (20)*	*#Occur Soft Bottom (16)*
15	*Embiotoca jacksoni*	Black perch	24	24	13	9
15	*Paralabrax clathratus*	Kelp bass	21	21	11	8
15	*Rhacochilus vacca*	Pile perch	20	20	11	7
15	*Paralabrax nebulifer*	Barred sand bass	18	18	9	8
28	*Heterostichus rostratus*	Giant kelpfish	18	18	9	7
13	*Oxyjulis californica*	Senorita	16	17	14	2
15	*Phanerodon furcatus*	White seaperch	16	17	7	8
11	*Girella nigricans*	Opaleye	16	16	11	3
20	*Engraulis mordax*	Northern anchovy	15	16	3	11
18	*Cymatogaster aggregata*	Shiner perch	14	16	4	10
21	*Paralichthys californicus*	California halibut	14	16	1	13
18	*Atherinops affinis*	Topsmelt	14	14	6	6
7	*Rhinogobiops nicholsii*	Blackeye goby	13	15	11	4
30	*Genyonemus lineatus*	White croaker	13	15	2	11
38	*Scorpaena guttata*	California scorpionfish	12	15	7	7

Deep Generalists

SPP Group	*Species*	*Common Name*	*#Occur Deep (9)*	*#Occur All (38)*	*#Occur Rocky Bottom (20)*	*#Occur Soft Bottom (16)*
41	*Sebastolobus alascanus*	Shortspine thornyhead	7	7	4	3
42	*Hydrolagus colliei*	Ratfish	7	8	6	2
36	*Sebastes rufus*	Bank rockfish	6	6	5	1
37	*Zaniolepis frenata*	Shortspine combfish	6	7	5	2
42	*Merluccius productus*	Pacific hake	6	7	3	4
35	*Sebastes ensifer*	Swordspine rockfish	5	5	5	0
36	*Sebastes paucispinis*	Boccacio	5	12	10	2
37	*Sebastes elongatus*	Greenstriped rockfish	5	6	4	2
37	*Sebastes rosenblatti*	Greenblotched rockfish	5	6	4	2
39	*Ophiodon elongatus*	Lingcod	5	11	8	3
39	*Sebastes saxicola*	Stripetail rockfish	5	7	3	4
40	*Microstomus pacificus*	Dover sole	5	8	2	6
42	*Sebastes diploproa*	Splitnose rockfish	5	5	3	2
32	*Pleuronectes vetulus*	English sole	4	11	2	8
32	*Zalembius rosaceus*	Pink seaperch	4	8	3	5

NOTE: Ranked by number of occurrences in 38 shallow and deep site groups.

wide latitudinal range. Overall, rockfishes and close relatives (family Scorpaenidae) represented the most commonly occurring family of fishes off California, they were recorded from 78% of California habitats when they are stratified by region (table 4-6). Surfperches (Embiotocidae) were also widespread, occurring in 70% of the habitats. Other prominent families occurring in over 50% of the regional habitats included the right-eyed flatfishes (Pleuronectidae), sculpins (Cottidae), and kelpfishes (Clinidae).

Sculpins and rockfishes dominated the shallow water habitats north of Point Conception; surfperches and greenlings were also common (table 4-7). The rockfishes also dominated both the deep northern and southern habitats along with pleuronectids. On the other hand, although rockfishes are present in reduced numbers, the shallow, southern habitats tend to be dominated by a different set of families. Species of surfperches, sculpins, kelpfishes, and pleuronectids remain important and are joined by croakers (Sciaenidae), sea chubs (Kyphosidae), silversides (Atherinopsidae), gobies (Gobiidae), and sea basses (Serranidae).

The vast majority of fish species encountered in the coastal marine habitats off California belonged to the superorder Acanthopterygii, including the orders Pleuronectiformes, Scorpaeniformes, and, especially, the Perciformes. Perciform fishes were dominant or well represented in every major habitat attesting to the adaptability of these highly derived bony fishes. Perciform fishes ranged in body form and habits from dorso-ventrally flattened, benthic, hole dwelling forms such as blennies and gobies to laterally compressed, demersally oriented forms such as surfperches (Embiotocidae), croakers (Sciaenidae), and sea basses (Serranidae), to fusiform, midwater swimmers such as bonita, mackerel (Scombridae), and

TABLE 4-6

Top 20 Fish Families

		Family	% Occur
1	Scorpaenidae	Scorpionfishes	78
2	Embiotocidae	Surfperches	70
3	Pleuronectidae	Righteye flounders	68
4	Cottidae	Sculpins	62
5	Clinidae	Clinids	51
6	Gobiidae	Gobies	49
7	Hexagrammidae	Greenlings	46
8	Paralichthyidae	Lefteye flounders	43
9	Sciaenidae	Croakers	43
10	Engraulidae	Anchovies	41
11	Atherinopsidae	Silversides	38
12	Batrachoididae	Toadfishes	35
13	Pomacentridae	Damselfishes	35
14	Clupeidae	Herrings	32
15	Syngnathidae	Pipefishes	32
16	Gobiesocidae	Clingfishes	30
17	Kyphosidae	Sea chubs	30
18	Labridae	Wrasses	30
19	Ophidiidae	Cusk-eels	30
20	Serranidae	Sea basses	30

NOTE: Ranked by percent occurrence within habitats stratified by latitudinal region.

jacks (Carangidae). In general, perciform and scorpaeniform fishes dominated in habitats with rock substrata.

Members of these orders possess the derived acanthopterygian characteristics of fin spines, ctenoid scales (unless secondarily lost), protrusible jaws and, in basal members, deepened, laterally compressed bodies (Helfman et al., 1997). Fin spines and ctenoid scales may offer protection from predators as well as from abrasion by rocks. The deepened body with thoracic pelvic fins and pectorals high on the sides of the fish (particularly in basal perciform fishes) represent adaptations for efficient maneuverability in close quarters. Protrusible jaws were prerequisite for the diversification of feeding strategies seen among these species (see chapter 13). Pleuronectiform fishes dominated the soft substratum habitats (particularly the nearshore soft-bottom, inner shelf, and outer shelf). These fishes are highly specialized for a benthic existence by having both eyes on one side, lying on the other side, and having extensive color and pattern change capabilities. Cryptically colored, scorpaeniform, carcharhiniform, and rajiform fishes were also well represented in habitats with soft substrata. The pelagic habitats (PEL and CP) and the open water within the other habitats were occupied principally by atheriniform, clupeiforrn, and perciform (particularly scombroid) fishes. The pelagic realm also contained an impressive number of carcharhiniform and lamniform sharks. Major adaptations of these water column fishes included elongate, streamlined, or fusiform body shapes. All are relatively fast swimmers that exhibit marked countershading (see Chapter 12).

TABLE 4-7

Top 10 Fish Families

Family		% Occur North Shallow	Family		% Occur North Deep
Cottidae	Sculpins	100	Scorpaenidae	Scorpionfishes	100
Scorpaenidae	Scorpionfishes	82	Pleuronectidae	Lefteye flounders	100
Embiotocidae	Surfperches	82	Merlucciidae	Hakes	100
Hexagrammidae	Greenlings	73	Anoplopomatidae	Sablefishes	80
Clinidae	Clinids	64	Rajidae	Skates	80
Paralichthyidae	Righteye flounders	64	Chimaeridae	Chimaeras	60
Pleuronectidae	Lefteye flounders	55	Macrouridae	Grenadiers	60
Gobiidae	Gobies	55	Squalidae	Dogfish sharks	40
Engraulidae	Anchovies	55	Alepocephalidae	Slickheads	40
Batrachoididae	Toad fishes	45	Embiotocidae	Surfperches	20
Family		**% Occur South Shallow**	**Family**		**% Occur South Deep**
Embiotocidae	Surfperches	93	Scorpaenidae	Scorpionfishes	100
Clinidae	Clinids	86	Pleuronectidae	Lefteye flounders	83
Cottidae	Sculpins	79	Merlucciidae	Hakes	67
Sciaenidae	Croakers	71	Anoplopomatidae	Sablefishes	67
Atherinopsidae	Silversides	71	Chimaeridae	Chimaeras	67
Kyphosidae	Sea chubs	71	Myxinidae	Hagfishes	67
Serranidae	Sea basses	71	Embiotocidae	Surfperches	50
Scorpaenidae	Scorpionfishes	64	Hexagrammidae	Greenlings	50
Pleuronectidae	Lefteye flounders	64	Macrouridae	Grenadiers	50
Gobiidae	Gobies	64	Argentinidae	Argentines	50

NOTE: Ranked by percent occurrence within habitats stratified by region and depth.

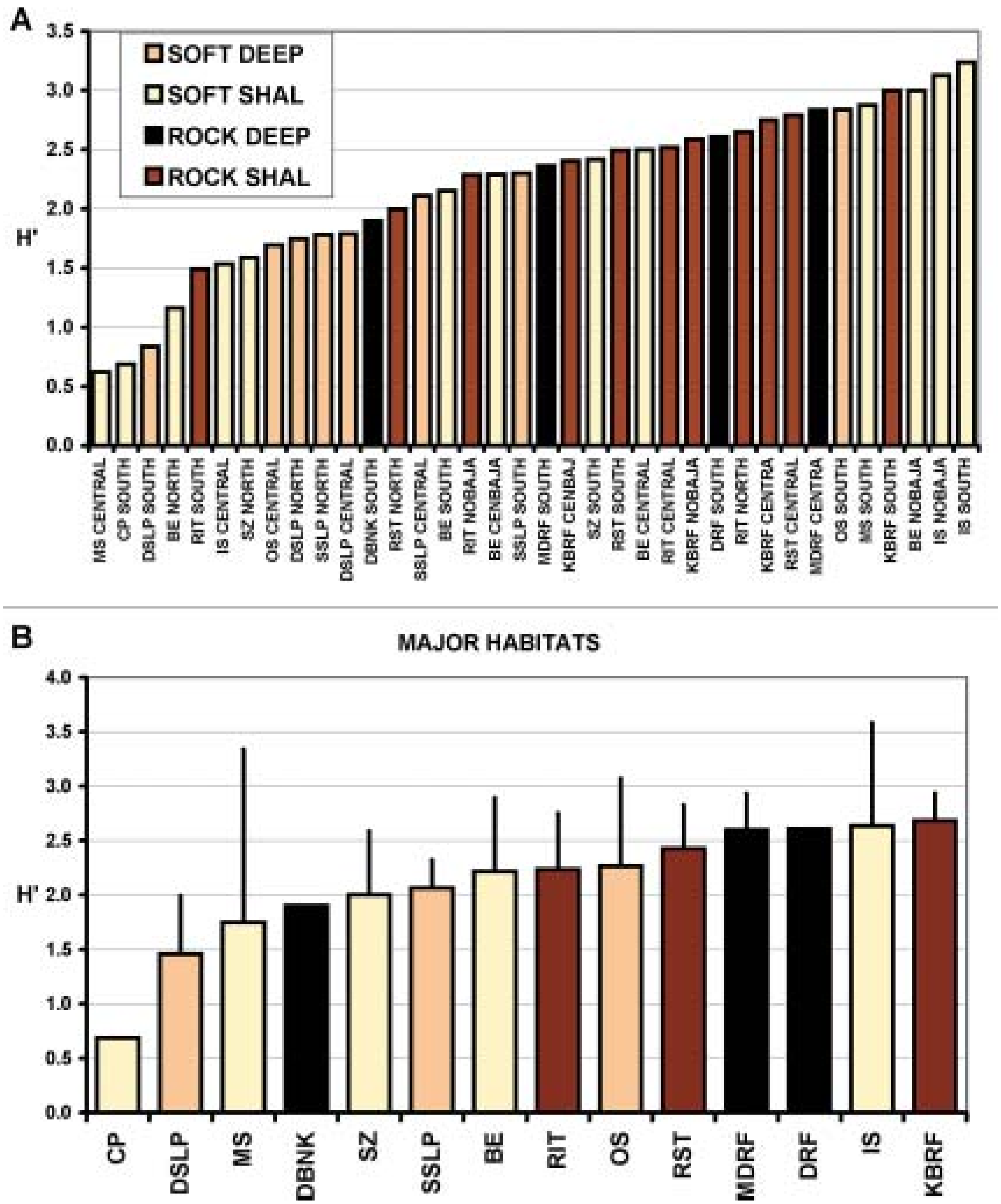

FIGURE 4-19 H′ Diversity from habitats by latitude (top) and major habitats overall (bottom). Habitats are ranked (low to high) and stratified by substrate and depth.

Patterns of Diversity

HOW MANY DIFFERENT SPECIES OCCUR IN THE VARIOUS HABITATS AND IN WHAT RELATIVE ABUNDANCE?

No clear patterns of H′ diversity nor species richness (*S*) among the 168 habitat sites were evident. Neither measure was significantly related to the three major physical factors, which were shown to influence species composition so closely. Neither H′ (canonical correlation, $X^2 = 2.16$, $p = .54$, $R^2 = 0.01$) nor *S* ($X^2 = 4.22$, $p = .24$, $R^2 = 0.03$) varied significantly according to substratum index, depth, or latitude. Individual H′ and *S* values were highly variable among habitat types and the physical variables, particularly depth and latitude.

The H′ diversity index combines measures of richness and evenness; it is, in practice, largely a measure of the equity of species abundance (evenness). Ranking habitats by latitude and major habitats based on mean value of H′ (fig. 4-19) also failed to yield clear patterns of diversity. H′ ranged from 0.62 for the inner shelf off of Monterey to a high of 3.24 for the nearshore soft-bottom in southern California. Values for the

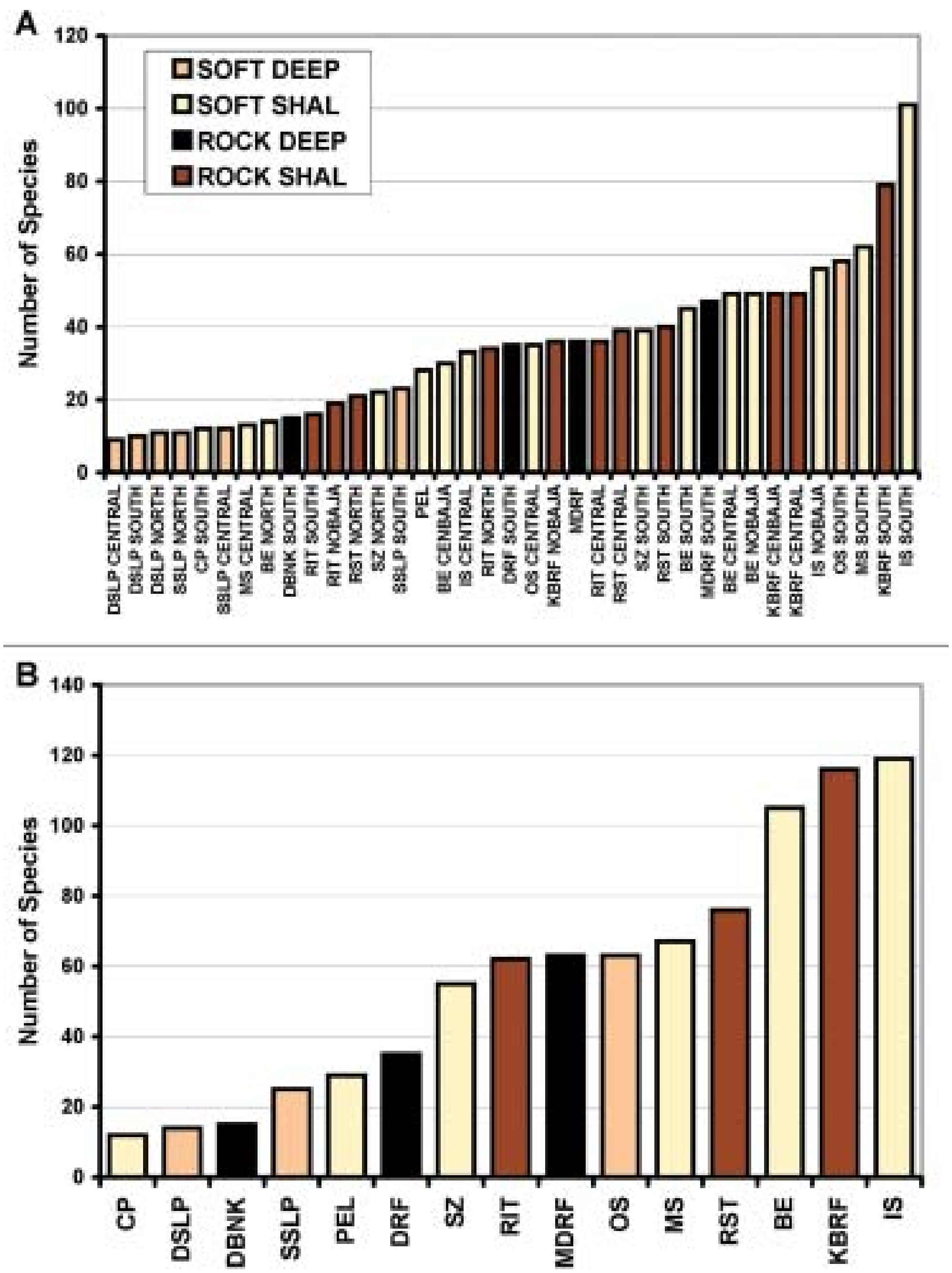

FIGURE 4-20 Number of species recorded from habitats by latitutude (top) and by major habitats overall (bottom). Habitats are ranked (low to high) and stratified by substrate and depth.

majority of habitats ranged between 2.0 and 3.0, and habitats with rocky substrata occurred throughout the ranking. Soft-bottom habitats were well represented at both ends of the H′ diversity spectrum. H′ diversity did not differ significantly over the 14 major types of habitats listed (ANOVA, $F_{[12,22]} = 1.22$, $p = .33$).

The major habitats fell into two groups relative to H′ diversity. The first group included relatively low diversity habitats (CP, DSLP, and possibly DBNK) where assemblages are dominated numerically by one or two species. The second group includes all the remaining major habitats with relatively high diversity ranging only between 2.0 and 2.6 in mean H′. This group includes a very wide range of habitats from shallow to deep and rocky to soft-bottom.

An inescapable and rather surprising conclusion is that most of the major habitats displayed equivalent levels of evenness independent of substratum, depth, and latitude. Some, but not all of those habitats with generally low H′ diversity, particularly the CP south, BE north, and RIT south are highly variable environments with unpredictable rates of disturbance resulting from storm surge, rainfall, patchy resources, shifting water masses, and unpredictable bouts of upwelling (see Chapter 18). A high rate of disturbance may be responsible for the high dominance in their fish assemblages. Important

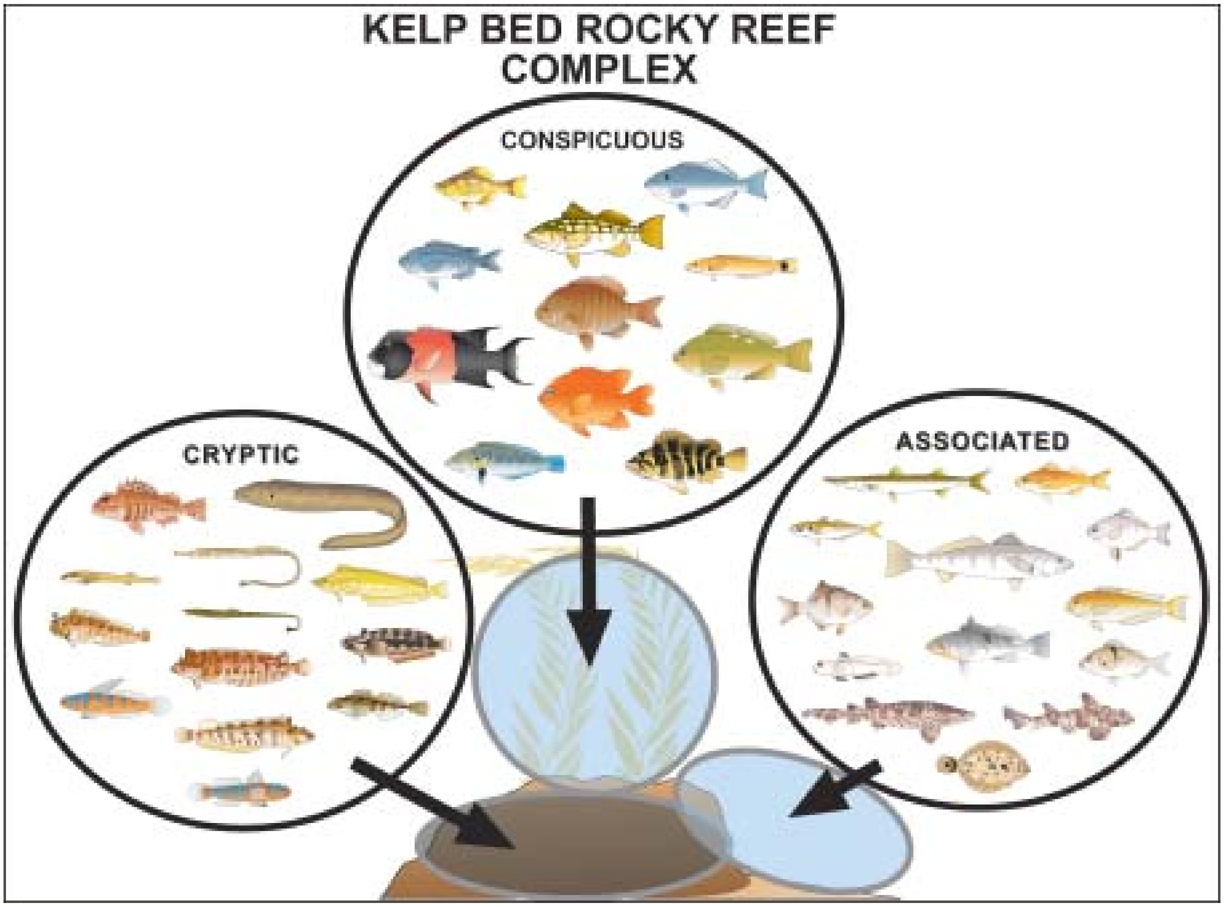

FIGURE 4-21 A diagrammatic representation of the three major components of a kelp bed rocky reef complex. Conspicuous forms are joined by a rich fauna of cryptic and nearshore forms that associate with reefs to varying degrees when present. Historically, most studies have concentrated only on conspicuous forms within habitats.

questions, however, remain. Why do the various California marine fish habitats possess similar H' diversity? Are most of these habitats, saturated with common species? What other physical (e.g. disturbance) and biological factors (e.g. recruitment to nursery areas) may explain the differences or similarities in diversity?

The ranking of species richness within habitats by latitude and major habitats (fig. 4-20) created a pattern similar in some ways to that of H' but different in others. Species richness ranged from a low of 9 species from the deep slope off central California to a high of 101, again, for the nearshore soft bottom in southern California. In general, soft, deep habitats ranked low in richness, whereas shallow and deep rocky and shallow soft habitats tended to rank higher. Values for the majority of habitats ranged between 20 and 50 species. Of the five habitats that recorded more than 50 species, four are found in the south (NSB Baja, OS south, IS south, and NSB south). The kelp bed rocky reefs of southern California ranked highest among the habitats with rocky substrata where 79 species were recorded.

When the major habitats are ranked, the total number of species recorded (Fig. 4-20) and the same general pattern of low richness in deep soft and high in shallow rocky and soft substratum habitats remained. The coastal pelagic (CP) habitat again ranked lowest among the major habitats, although it should be pointed out that this habitat was sampled only in southern California and therefore, had no corresponding sites in other regions. The deep and shallow slope (soft) and deep bank (rock/mud) habitats were also ranked low in species richness. In this view, three shallow, well-studied habitats (BE, KBRF, and NSB) clearly stand out from the others; more than 100 species were recorded from each.

WHY ARE THERE MORE SPECIES IN SOME HABITATS THAN IN OTHERS?

Rocky reefs that support kelp beds are widely recognized as highly diverse habitats. Allen (1985) concluded that these important habitats ranked among the most diverse of all fish habitats within the Southern California Bight, despite the fact that cryptic fish assemblages associated with rocky reefs were not assessed in that study. Interestingly, in the previous analysis, the shelf, soft-bottom habitat ranked as high as the rocky reefs in diversity (Allen, 1985). The problem with that result, as was pointed out at the time, was that the soft-bottom samples represented collections summed over a wide depth range and therefore did not take depth replacement of fish assemblages into account. The current analysis summarized data from the shelf stratified by depth (inner, mid-, and outer shelf), which ultimately clustered into the major habitats designated as inner shelf (IS), middle shelf (MS), and outer shelf (OS). The species richness of the IS habitat was high, but the MS and OS soft-bottom habitats, though on the higher end of the range, were substantially lower than that of the KBRF habitat. The KBRF habitats represented in the current analysis

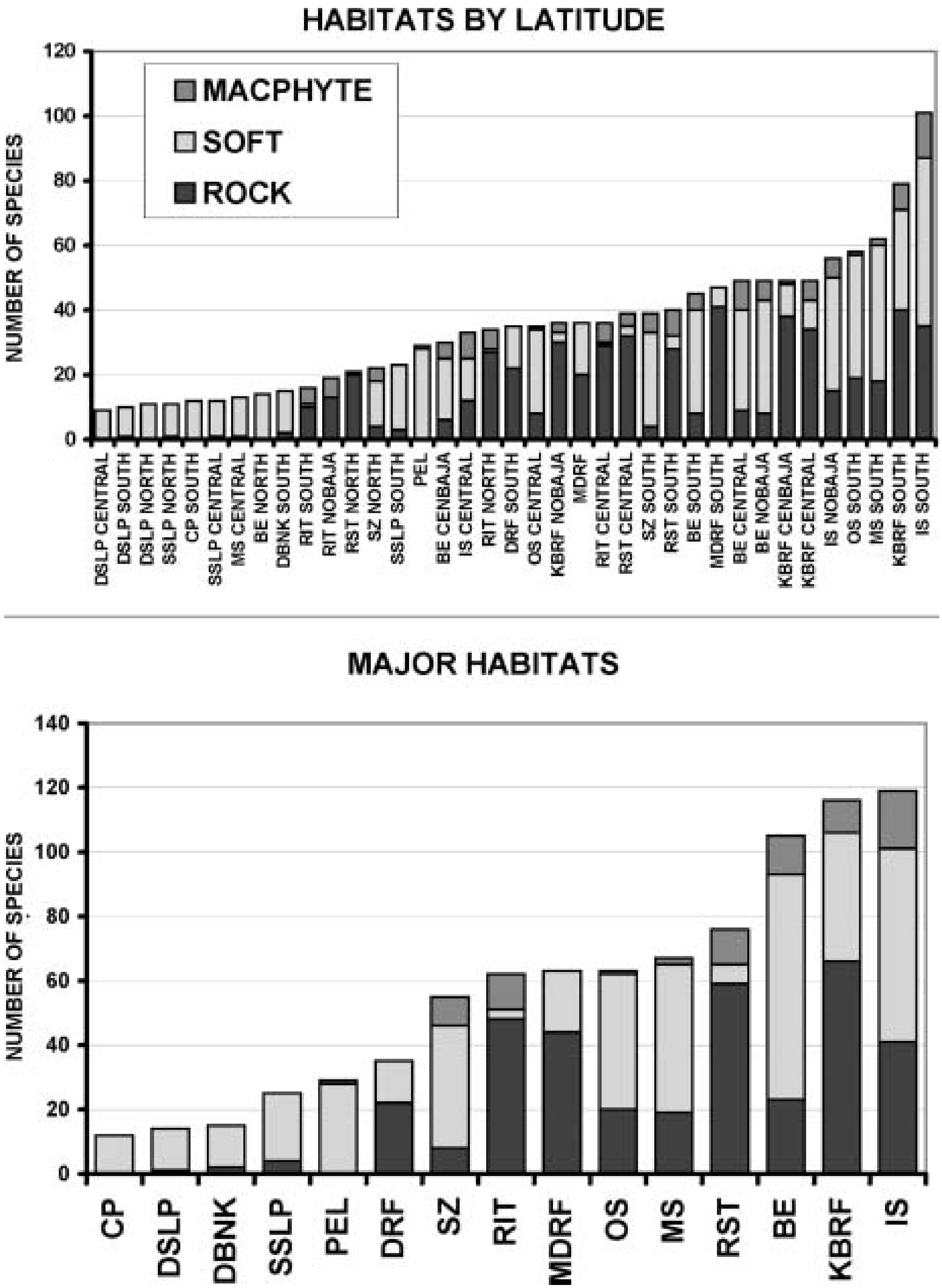

FIGURE 4-22. Number of species associated with macrophytes, reefs, or soft-bottom as adults recorded from habitats by latitutude (top) and by major habitats overall (bottom). Habitats are ranked (low to high) and stratified by substrate and depth.

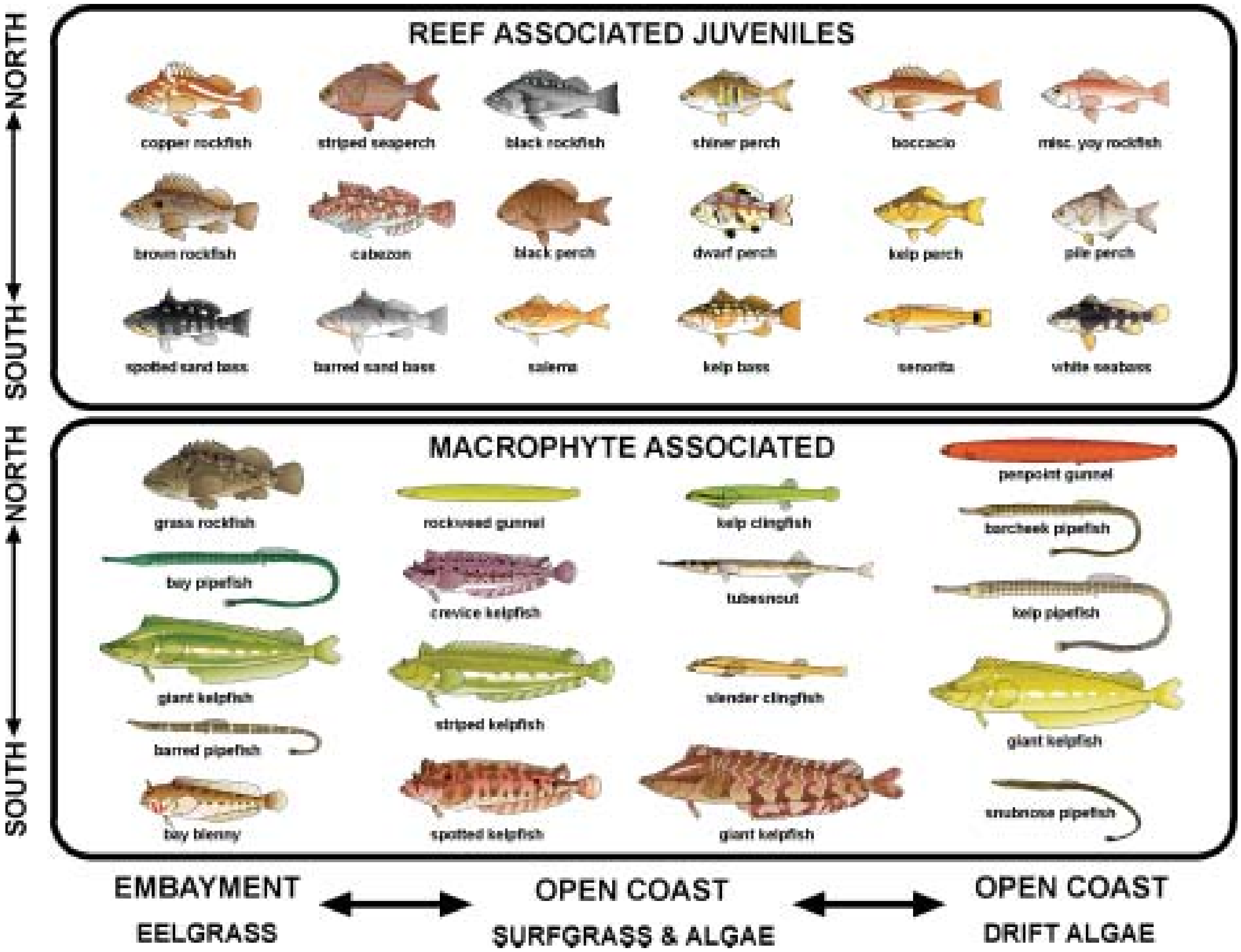

FIGURE 4-23 Species recorded that associate with macrophytes in soft-bottom habitats that greatly enhance species richness. Many species of macrophyte associated fishes recruit to and occur wherever there is a macrophyte structure, regardless of substrate. In addition many species of reef associated fishes recruit to these beds and remain with them for some time, using them as nursery areas.

actually represent complexes of three subhabitats (fig. 4-21). The conspicuous species that are normally recognized as kelp bed or reef species are only one component of the complex. The cobble and rock substratum with its turf algae assemblages provides habitat for a diverse assemblage of cryptic species. The third important component of the reef complex is made up of the primarily soft-bottom species that are associated with the rock/sand margins of the reefs. These include coastal pelagic species as well as many nocturnal species (e.g., members of Species Group 23), which feed on or near the reef at night.

How can shallow, soft-bottom habitats have as many or more species recorded than the highly diverse rocky reef systems with kelp beds? The answer lies partially in the fact that bays and estuaries and nearshore soft-bottom areas are more complex environments than previously thought (fig. 4-22). These habitats represent shallow, productive areas that possess macrophyte structure over sand or mud bottom. In bays, eelgrass beds (*Zostera marinus*) provide structure to an otherwise homogenous substratum. Attached and drift algae provide the same for the nearshore soft-bottom habitat. Protected areas along the coast and in harbors often support beds of filamentous red algal (e.g., *Gracillaria spp*). Open coast sandy beaches provide nearly continuous drift algal bed habitat just outside the surf line over much of California's coastline.

If a variable describing the presence or absence of macrophyte substratum is added to the multivariate analysis involving substratum, depth, and latitude, the number of species recorded from the habitat sites stratified by latitudinal region becomes significantly explained ($X^2 = 9.88$, $p = .04$, $R^2 = 0.06$) by the four-factor model (results for H' diversity remained unchanged). Therefore, at least part of the variability in species richness may be explained by a combination of the four physical factors of substratum, presence of macrophytes, depth, and latitude. The model accounts for only 6% of the variance, however, and generalizations must be tempered by this fact. Nevertheless, there was a tendency for shallow habitats with rocky substrata, combinations of substrata (e.g., rock/sand, rock/mud, cobble/sand, etc.), and/or macrophyte substratum to support more species.

The addition of macrophytes to soft-bottom habitats is important for the enhancement of species richness for two main reasons. First, many species recruit to and occur wherever there is macrophyte structure, regardless of substratum (fig. 4-23). Second, and perhaps more important, many species of reef associated fishes recruit to these beds and remain with them for some time, using them as nursery areas. In the northern regions, juvenile rockfishes and surfperches use eelgrass and drift algal beds extensively. In the south, juvenile surfperches join juvenile croakers, sea basses, sea chubs, and wrasses in using macrophyte beds in bays and along the open coast. The addition of the macrophyte associated species and the juveniles of reef fishes largely accounts for the high species richness in the BE and NSB habitats (fig. 4-23). The significant, multivariate relationship between the number of species at each of the original 168 sites and a combination of substratum, the presence of macrophytes, and depth strongly attests to the overall importance of macrophyte structure to the enhancement of species richness in shallow water habitats.

Recommendations for Future studies

Clearly, several large holes remain in our knowledge of California's fish habitats. Major habitats within latitudinal regions remain unstudied. Thorough quantitative studies have not been carried out or are not published for most of the major habitats in northern California, northern Baja California, and central Baja California. The surf zone, coastal pelagic, deep reef, and deep bank habitats of central California also need further study.

It is important that future ichthyofaunal investigations target each major component of the fish assemblage of the habitat sampled. This will require multiple-gear strategies aimed at the quantitative assessment of species inhabiting both the water column (conspicuous species) and the benthos (cryptic species) of the habitat. Because nocturnal assemblages are sometimes quite different from those that occupy the habitat during the day, future studies may also need to involve nighttime sampling.

A thorough explanation of the factors regulating species diversity within habitats awaits these future studies. Such studies should, wherever possible, employ stratified, saturation sampling of the habitat within some restricted time period. Saturation sampling involves the collection of fishes at least until species accumulation curves level off. Also, such future investigations should preferably be accompanied by assessments of the physical and chemical environment so that objective models may replace subject indexes and ranking strategies. Such undertakings will require considerable effort but need not require large funding sources as long as care is taken to assess the abundance of the fishes accurately within each of the subhabitats of the system.

Literature Cited

Allen, L.G. 1976. Abundance, diversity, seasonality and community structure of fish populatikons in Newport Bay, California. M.A. Thesis. Calif. State Univ., Fullerton.

———. 1983. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California. U.S. Fish. Bull. 80(4):769–790.

———. 1985. A habitat analysis of the nearshore marine fishes from Southern California. Bull. South. Calif. Acad. Sci. 84(3):233–155.

———. 1988. Recruitment, distribution, and feeding habits of young-of-the-year California halibut (*Paralichthys californicus*) in the vicinity of Alamitos Bay, California, 1983–1985. Bull. South. Calif. Acad. Sci. 87:19–30.

Allen, L.G., and M.H. Horn. 1975. Abundance, diversity, and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. Estuarine Coastal Mar. Sci. 3(2):371–380.

Allen, L.G., and E.E. DeMartini. 1983. Temporal and spatial patterns of nearshore distribution and abundance of the pelagic fishes off San Onofre-Oceanside, California. U.S. Fish.Bull. 81(3):569–586.

Allen, L.G., M.H. Horn, F.A. Edmands, and C.A. Usui. 1983. Structure and seasonal dynamics of the fish assemblage in the Cabrillo Beach area of Los Angeles harbor, California. Bull. South. Cal. Acad. Sci. 82(2):47–70.

Allen, L.G., L.S. Bouvier, and R.E. Jensen. 1992. Abundance, diversity and seasonality of cryptic fishes and their contribution to a temperate reef fish assemblage off Santa Catalina Island, California. Bull. South. Calif. Acad. Sci. 91(2):55–69.

Allen, L.G., A.M. Findlay, and C.M. Phalen. 2002. Structure and standing stock of the fish assemblages of San Diego Bay, California from 1994 to 1999. Bull. South. Cal. Acad. Sci. 101(2):49–85.

Allen, M.J., S.L. Moore, K.C. Schiff, S.B. Weisberg, D. Diener, J.K. Stull, A. Groce, J. Mubarak, C.L. Tang, and R. Gartman. 1998. Southern California Bight 1994 Pilot Project: V. Demersal fishes and megabenthic invertebrates. Southern California Coastal Water Research Project, Westminster, CA.

Beltran-Felix, J.L., M.G. Hammann, A. Chagoya-Guzman, and S. Alvarez-Borrego. 1986. Ichthyofauna of Estero de Punta Banda, Ensenada, Baja California, Mexico, before a major dredging operation. Ciencias Marinas 12(1):79–92.

Brooks, A.J. 1999. Factors influencing the structure of an estuarine fish assemblage: the role of interspecific competition. Ph.D. Dissertation. University of California, Santa Barbara.

Burge, R.T., and S.A. Schultz. 1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Cal. Fish Game, Tech. Rep. 19.

Burton, E.J., J. Neer, and T. Sozanski. 1995. Diversity and abundance of soft-bottom fishes in southern Monterey Bay, California. Report for Ford Ord Survey. Moss Landing Marine Laboratories, Moss Landing, CA.

Cailliet, G.M., K.A. Karpov, and D.A. Ambrose. 1979. Pelagic assemblages as determined from purse seine and large midwater trawl catches in Monterey Bay and their affinities with the market squid, *Loligo opalescens*. California Cooperative Oceanic Fisheries Investigations Reports 20:21–30.

Carlisle, J.S., J.W. Schott, and N.J. Abramson. 1960. The barred surfperch (*Amphisticus argenteus* Agassiz) in Southern California. Calif. Fish Game Fish. Bull. 109.

Clifford, H.T., and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, New York.

Crase, M.S. 1992. A survey of the intertidal ichthyofauna of Resort Pt., Palos Verdes, California. M.S. Thesis, California State University, Northridge.

Cross, J.N. 1987. Demersal fishes of the upper continental slope off southern California. CalCOFI Rep. 28:155–167.

DeMartini, E.E. 1981. The spring-summer ichthyofauna of surfgrass (*Phyllospadix*) meadows near San Diego, California. Bull. South. Calif. Acad. Sci. 80(2):81–90.

DeMartini, E.E., and D. Roberts. 1981. An empirical test of biases in the rapid visual technique for species time censuses of reef fish assemblages. Mar. Biol. 70:129–134.

DeMartini, E.E., and L.G. Allen. 1984. Diel influences on the species and size composition, numbers and diversity of fishes caught by a 7.6 in otter trawl in Southern California coastal waters. CalCOFI Reports, Vol. 25.

Ebeling, A.W., R.J. Larson, and W.S. Alevizon. 1980a. Habitat groups and island-mainland distributions of kelp-bed fishes off Santa Barbara, California. In D.M. Power (ed.), Multidisciplinary Symposium on the California Islands. Santa Barbara Museum of Natural History. pp. 403–431.

Ebeling, A.W., R.J. Larson, W.S. Alevizon, and R.N. Bray. 1980b. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California. U.S. Fish. Bull. 78(2):361–377.

Forey, P.L., C.J. Humphries, I.L. Kitching, R.W. Scotland, D.J. Siebert, and D.M. Williams. 1992. Cladistics. Oxford University Press, New York.

Galván, M.F, F.J. Gutierrez, S., L.A. Abitia, C., and J. Rodríguez, R. 2000. The distribution and affinities of the shore fishes of Baja California Sur lagoons. In M. Munawar, S. Lawrence, I.F. Munawar, and D. Malley (eds.), Aquatic ecosystems of Mexico: status and scope. Ecovision World Monograph series. Backhuys, P, Leiden, The Netherlands, pp. 383–398.

Ganssle, D. 1966. Fishes and decapods of San Pablo and Suisun Bays. Calif. Fish Game Fish Bull. 133:64–94.

Grossman, G.D. 1982. Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. Am. Nat. 119(5):611–637.

Hanan, D.A., D.B. Holts, and A.L. Coan, Jr. 1993. The California drift gill net fishery for sharks and swordfish, 1981–82 through 1990–91. Calif. Fish Game Fish Bull. 175.

Hastings, P.A. 2000. Biogeography of the tropical eastern Pacific: distribution and phylogeny of chaenopsid fishes. Zool. J. Linn. Soc. 128:319–335.

Helfman, G.S., B.B. Collette, and D.E. Facey, 1997. The diversity of fishes, Blackwell Science, Malden, MA.

Horn, M.H. 1970. Systematics and biology of the stromateid fishes of the genus *Peprilus*. Bull. Mus. Comp. Zool. 140:165–261.

———. 1980. Diversity and ecological roles of noncommercial fishes in California marine habitats. CalCOF1 21:37–47.

———., and L.G. Allen. 1978. A distributional analysis of California coastal marine fishes. J. Biogeogr. 5:23–42.

Horn, M.H., and L.G. Allen. 1981. Ecology of fishes in upper Newport Bay, California: seasonal dynamics and community structure. Cal. Fish Game, Tech. Rep. 45.

Kluge, A.G., and J.S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zool. 18:1–32.

Lane, E.D., and C.W. Hill (eds.). 1975. Marine resources of Anaheim Bay. Calif. Dept. Fish Game, U. S. Fish. Bull. 65.

Love, M.S., M. Nishimoto, D. Schroeder, and J. Caselle. 1999. The ecological role of natural reefs and oil and gas production platforms on rocky reef fishes in southern California: final interim report. U.S. Dept. Interior, U.S. Geological Survey/Biological Resources Division. USGS/BRD/CR-1999-007.

Mais, K.F. 1974. Pelagic fish surveys in the California Current. Calif Dept. Fish Game, Fish Bull. 162.

MEC Analytical Systems, Inc. 1988. Biological baseline and an ecological evaluation of exisiting habitats in Los Angeles Harbor and adjacent waters, Vol I, final report. Exec. Sum., MEC05088001, Port of Los Angeles, San Pedro, CA.

Miller, D.J., and J.J. Geibel. 1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Fish Game Fish. Bull. No. 158.

Onuf, C.P., and M.L. Quammen. 1983. Fishes in a California coastal lagoon: effects of major storms on distribution and abundance. Mar. Ecol. Prog. Ser. 12:1–14.

Pondella, D.J. II, and L.G. Allen. 2000. The nearshore fish assemblage of Santa Catalina Island. In Proc. Fifth California Islands Symp., D.R. Browne, K.L. Mitchell, and H.W. Chaney (eds.) U.S. Department of the Interior, Mineral Management Service, Pacific OCS Region, MMS 99-0038, pp.394–400.

Quast, J.C. 1968. Fish fauna of the rocky inshore zone. In W.J. North and C.L. Hubbs (eds.), Utilization of kelp-bed resources in Southern California. Calif. Fish Game Fish Bull. 139:109–142.

Rosales-Casian, J.A. 1996. Ichthyofauna of Bahia de San Quintin, Baja California, Mexico, and its adjacent coast. Ciencias Mar. 22(4): 443–458.

———. 1997. Inshore soft-bottom fishes of two coastal lagoons on the northern Pacific coast of Baja California. CalCOFI Rep. 38:180–192.

Shannon, C.E., and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana, IL.

Squire, J.L., Jr. 1983. Abundance of pelagic resources off California, 1963–78, as measured by an airborne fish monitoring program. NOAA Tech. Rep NMFS SSRF-762.

Stephens, J.S., Jr., C. Terry, S. Subber, and M.J. Allen. 1974. Abundance, distribution, seasonality and productivity of the fish populations in Los Angeles Harbor, 1972–73. In Marine Studies of San Pedro Bay, Part IV, Environ. Field Invest., (D. Soule and M. Oguri eds.), Allan Hancock Found. Pub. USC-SG-6-72, pp. 1–42.

Stephens, J.S., Jr., and K.E. Zerba. 1981. Factors affecting fish diversity on a temperate reef. Environ. Biol. Fish. 6:111–121.

Stephens, J.S., Jr., G.A. Jordan, P.A. Morris, M.M. Singer, and G.E. McGowan. 1986. Can we relate larval fish abundance to recruitment or population stability? A preliminary analysis of recruitment to a temperate rocky reef. Calif. Coop. Oceanic Fish. Invest. Rep. 27:65–83.

Stephens, J.S., Jr., P.A. Morris, K. Zerba, and M. Love. 1984. Factors affecting fish diversity on a temperate reef: the fish assemblage of Palos Verdes Point, 1974–1981. Environ. Biol. Fish. 11:259–275.

Stepien, C.L., H. Phillips, J.A. Adler, and P.J. Mangold. 1991. Biogeographic relationships of a rocky intertidal fish assemblage in an area of cold water upwelling off Baja California, Mexico. Pac. Sci. 45(1):63–71.

Swofford, D.L. 1998. Phylogenetic analyses using parsimony (PAUP* 4.0b8). Sinauer Associates, Sunderland, MA.

Tetra Tech, Inc. 1977. MRC Fish Program: Final Report, Appendices, December 1977. Report submitted to the Marine Review Committee of the California Coastal Commission.

Turner, C.H., E.E. Ebert, and R.R. Given. 1969. Man-made reef ecology. Cal. Fish Game Fish Bull. 146.

Yoklavich, M.M., H.G. Green, G.M. Cailliet, D.E. Sullivan, R.N. Lea, and M.S. Love. 2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. U. S. Fish. Bull. 98:625–641.

Yoklavich, M.M., G.M. Cailliet, J.P. Barry, D.A. Ambrose, and B.S. Antrim. 1991. Temporal and spatial patterns in abundance and diversity of fish assemblages in Elkhorn Slough, California. Estuaries 14(4):465–480.

Yoshiyama, R.M., C. Sassaman, and R.N. Lea. 1987. Species composition of rocky intertidal and subtidal fish assemblages in central and northern California, British Columbia-Southeast Alaska. Bull. South. Calif. Acad. Sci. 86(3):136–144.