Bathymetric responses in functional structure of southern California demersal fish communities to Pacific Decadal Oscillation regimes and an El Niño

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Abstract

During the past 35 years, changing ocean conditions in the Southern California Bight (SCB), due largely to the Pacific Decadal Oscillation (PDO) and two major El Niños, have variably affected the abundance of different fishes. Less well-known are bathymetric changes in species distribution and community organization occurring during these periods. Regional surveys of demersal fishes in the SCB during this period have provided data for assessing changes in fish abundance and bathymetric distribution, as well as for describing the functional organization of communities. This study describes bathymetric shifts in the functional organization of demersal fish communities on the continental shelf during a PDO cycle and an El Niño. The study is based on results of four large-scale surveys of the demersal fish fauna of the southern California shelf (10 - 200 m depth) conducted in 1972-1973 (cold regime), 1994 (warm regime), 1998 (El Niño), and 2003 (cold regime). The latter three studies are compared to a baseline model of the functional organization the communities developed using 1972-1973 data. The functional organization is described in terms of the occurrence of 18 foraging guilds and the depth replacement pattern of their dominant species across the shelf. Although the order of depth replacing species within a given guild relative to depth generally did not change between the surveys, the relative portion of the shelf occupied by a numerically dominant guild members often did change, as well as a variety of pattern shifts. Changes in depth replacement patterns in these oceanic periods varied by guild. El Niño effects on these patterns included expansions or contractions of depth ranges of some guild members, retreats of some guilds or guild members to deeper water, and intrusions of new dominant guild members from the south. Changes between cold and warm regime periods were generally less pronounced but some gradual declines in the occurrence of deep-living guild members during the warm regime were apparent, suggesting decreased recruitment from the north. Patterns of several guilds were identical or nearly so in the two cold regimes, suggesting a resilient return to baseline cold regime patterns. Examination of depth replacement patterns within foraging guilds provides a unique perspective for understanding disruptive effects and resilient responses of demersal fish communities to changing ocean conditions. Understanding how fish populations and communities change in bathymetric distribution in response to natural changes in ocean conditions will contribute to evaluation of anthropogenic (fishing, pollution, habitat alteration) effects on southern California fish populations and communities.

Introduction

Changing ocean conditions during the past 35 years have affected the abundance of many fish species in the SCB. These changes are largely related to the Pacific Decadal Oscillation (Chavez *et al*. 2003) and two major El Niño events. Most studies have focused on changes in the overall abundance of a species or in its occurrence (Allen *et al*. 2004, Jarvis *et al*. 2004). Besides changes in overall abundance, fish species may respond to changes in oceanic regimes by showing changes in their geographic or bathymetric distributions. While changes in the geographic distribution of fishes are often observed during shifts in oceanic regimes or El Niños (Radovich 1961; Mearns 1988; Lea and Rosenblatt 2000; Allen and Groce 2001a,b; Groce *et al*. 2001), less is known about bathymetric changes in species distributions and community organization during these periods. Knowledge of these changes is particularly valuable in assessing the health of demersal

fish populations and communities. Information on bathymetric changes in fish distribution provides the basis for distinguishing between natural and anthropogenic effects on demersal fish populations and communities, and managing populations and communities in a changing oceanic environment. For instance, a decrease in the population of a fish species in an area might be initially attributed to human activity (wastewater discharge, fishing, etc.) occurring there, whereas it may be due to a population shift to deeper water to avoid warmer or less productive waters at location. Alternatively, it may be the result of a reduction in larval recruitment of the species due to decreased strength of currents (e.g., California Current). Regional surveys of demersal fishes in the SCB during the past 35 years have provided data for assessing changes in fish abundance, bathymetric distribution of species, and functional organization of the communities.

The objective of this study was to determine bathymetric changes in functional organization of demersal fish communities on the southern California shelf during a Pacific Decadal Oscillation cycle and the 1997-1998 El Niño event. Specific objectives were to assess changes in bathymetric distribution of fish foraging guilds across the shelf, and assess changes in the bathymetric distribution of expected guild dominants on the shelf in different guilds during these oceanic periods.
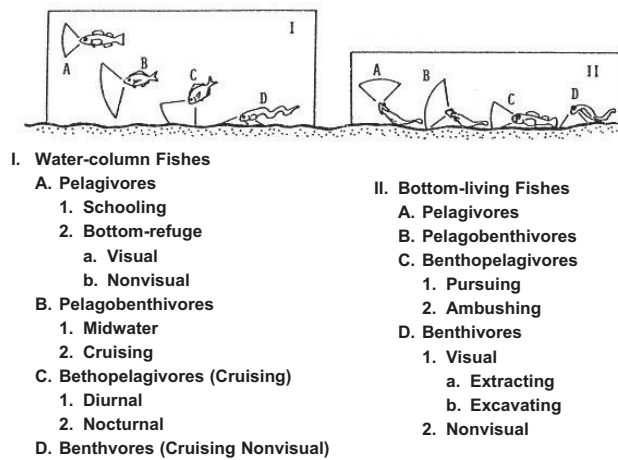
METHODS

Background on Guild Classification and Functional Organization of Fish Community Analysis

Allen (1974) first reported on the potential value of developing a model of the functional structure of demersal fish communities for analysis of pollution effects on southern California fish communities near wastewater discharge sites on the southern California shelf. That paper provided a preliminary description of the methods to be used for construction of such a model. Allen (1982) provided the results of a study conducted to produce such a model for soft-bottom fish communities on the southern California shelf. Data for that study were obtained from 126 fish species representing 43 families collected in 342 trawl samples collected from the southern California shelf during 1972-1973 at depths of 10 - 200 m. That study provided information on the general characteristics of the fauna as well as analyses that lead

to production of a model of the functional structure of the communities.

Allen (1982) used a synthetic approach, beginning with recurrent group analysis (Fager 1957, 1963), then using information on depth distributions, relative abundance, diet, and morphological data collected in the study, as well as behavioral information from the literature, to describe the functional organization of the soft-bottom fish communities of the southern California shelf (10 - 200 m) based on data from 1972-1973. The recurrent group analysis described recurrent groups of 34 fish species (27% of the total species, but 93% of the total fish abundance in the survey). Recurrent groups were generally associated with different depth zones, with a major group associated with each of the three bathymetric life zones on the shelf. Species that were most similar in morphology occurred in different recurrent groups at different depths. Recurrent groups contained species that were dissimilar in their morphology. Morphological differences were associated with feeding and foraging. Stomach content analysis was conducted on 1,013 stomachs of the 40 most common fish species, including the recurrent group species. The primary foraging difference among species that occurred together most frequently (these were typically recurrent groups consisting of two species) was their orientation to the bottom during foraging. These two-species recurrent groups generally consisted of the following combinations of foraging types: a) a water-column fish that feeds in the water-column with a benthic fish that feeds on the bottom; b) a water-column fish that feeds on the bottom with a benthic fish that feeds in the water-column; c) a water-column fish that feeds in the water with a water-column fish that feeds on the bottom; or d) a benthic fish that feeds in the water-column with a benthic fish that feeds on the bottom. Based on foraging orientation relative to the bottom as a point of organization, the 40 most common species were classified into 18 foraging guilds (15 major guilds with one guild divided into four size classes; Figures 1 and 2).

Fish were classified into water-column and benthic lifestyles; within these categories, species were classified according to foraging zones: water-column (pelagivores); bottom (benthivores); and two intermediate foraging zones, mostly water-column with some bottom (pelagobenthivores) and mostly bottom with some water-column (benthopelagivores). All four orientations were found among both water-column

I. Water-column Fishes
  A. Pelagivores
    1. Schooling
    2. Bottom-refuge
      a. Visual
      b. Nonvisual
  B. Pelagobenthivores
    1. Midwater
    2. Cruising
  C. Bethopelagivores (Cruising)
    1. Diurnal
    2. Nocturnal
  D. Benthvores (Cruising Nonvisual)

II. Bottom-living Fishes
  A. Pelagivores
  B. Pelagobenthivores
  C. Benthopelagivores
    1. Pursuing
    2. Ambushing
  D. Benthivores
    1. Visual
      a. Extracting
      b. Excavating
    2. Nonvisual

Figure 1. Foraging guilds of soft-bottom fishes on the southern California shelf (from Allen 1982, 2006).

fishes found near the seafloor and benthic fishes found on the soft-bottom. Some of these orientations were further subclassified by refuge mode (e.g., schooling, bottom-refuge), sensory differences used in foraging (e.g., visual, nonvisual), and foraging behavior (e.g., pursuing, ambushing, extracting, excavating). In one guild (benthic ambushing benthopelagivores), ecological segregation appeared to be related to mouth size, with up to four different species with non-overlapping mouth sizes foraging similarly on the soft-bottom within a given life zone but consuming larger prey species with larger mouth size. Species within the same guild were sometimes morphologically similar due to being congeners (e.g., specklefin midshipman, *Porichthys myriaster*; plainfin midshipman, *Porichthys notatus*) but some were similar due to convergence (e.g., queenfish, *Seriphus politus*; and shortbelly rockfish, *Sebastes jordani*; or Pacific sanddab (*Citharichthys sordidus*), and slender sole (*Lyopsetta exilis*). Some guilds, however, included species that were not morphologically similar (e.g., bigmouth sole, *Hippoglossina stomata*, and California lizardfish, *Synodus lucioceps*) but which foraged similarly and had similar diets. Allen (1982 and 2006) provide more detailed summaries of natural history traits used in this guild classification.
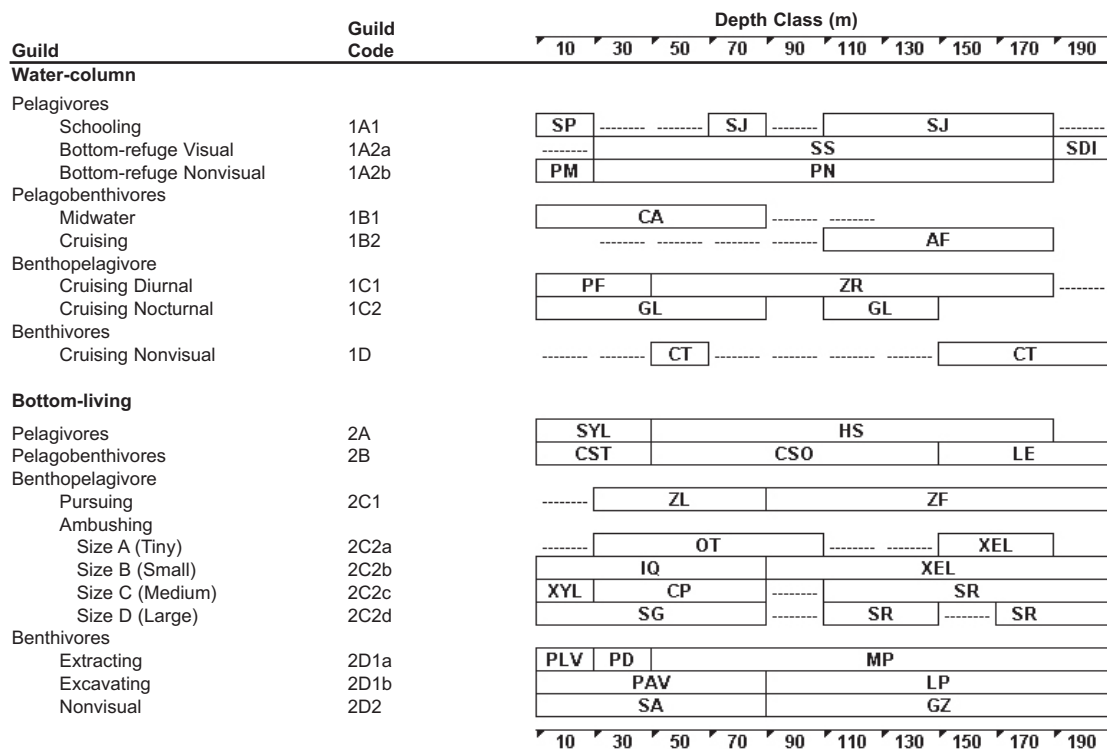
Allen (1982) found that soft-bottom fish species comprising a guild typically replaced each other with depth on the southern California shelf. For instance, in terms of relative abundance of species in a guild, one species may be dominant in abundance on the inner shelf, another on the middle shelf, and a third on the outer shelf. Based on this relationship, a model of the functional structure of the southern California soft-bottom fish communities on the shelf

was developed (Figure 2). The functional structure model included 18 foraging guilds and describes the distribution of these guilds across the mainland shelf from 10 - 200 m, at 20-m depth intervals. The distribution of a guild across the depth range is expressed as a rectangular box to show at what depth range a guild occurred in 20% or more of the samples within each 20-m depth class enclosed by the box. Abbreviations in the guild boxes indicate what guild species is dominant at a particular range of depths. It should be noted that an actual plot of the relative abundance of guild members across depth will show a region of overlap (like the intersection of two normal curves) where both species coexist.

It should also be noted that guild members may replace each other geographically within a life zone, and a similar model has been constructed for soft-bottom fish communities from the California-Oregon border to the tip of Baja California at depths for the inner shelf (10 - 30 m), middle shelf (30 - 100 m), outer shelf (100 - 200 m), and upper slope (200 - 500 m; Allen 2006).

Assessment of Bathymetric Changes in Functional Structure Model Relative to Different Oceanic Regimes

The present study is based on the results of four large-scale regional trawl surveys of the demersal fish fauna on the southern California shelf (10 - 200 m depth): 1972-1973 cold-regime, 342 trawl samples at 99 stations (Allen 1982; Figure 3a); 1994 warm regime, 114 samples at 114 stations (Allen *et al*. 1998; Figure 3b); 1998 El Niño, 314 samples at 314 stations (Allen *et al*. 2002; Figure 3c); and 2003 cold regime, 210 samples at 210 stations in the survey and 182 samples at 182 stations at 5 - 200 m and 28 stations on the upper slope at 201 - 500 m (Figure 3d; Allen *et al*. 2007). These surveys differed somewhat in the regions of the SCB sampled: 1972-1973 -- central mainland shelf and Santa Catalina Island; 1994 -- entire mainland shelf, no islands; 1998 -- entire mainland shelf, Santa Catalina Island and Channel Islands; and 2003, entire mainland shelf and Channel Islands. The surveys differed also somewhat in the depth range sampled (10 - 200 m in 1972-1973 and 1994, 5 - 200 m in 1998, and 5 - 500 m in 2003). The 1972-1973 survey extended from May 1972 to December 1973, with stations repeatedly sampled during this period, resulting in 342 samples being collected from the 99 stations. In contrast, the three regional surveys took one sample

Figure 2. Functional structure of the soft-bottom fish community of the southern California shelf.

Guild	Guild Code	10	30	50	70	90	110	130	150	170	190
Water-column											
Pelagivores											
Schooling	1A1	SP		--------	SJ	--------	SJ				--------
Bottom-refuge Visual	1A2a	--------		SS							SDI
Bottom-refuge Nonvisual	1A2b	PM		PN							
Pelagobenthivores											
Midwater	1B1		CA			--------	--------				
Cruising	1B2	--------	--------	--------	--------		AF				
Benthopelagivore											
Cruising Diurnal	1C1	PF			ZR						--------
Cruising Nocturnal	1C2	GL				GL					
Benthivores											
Cruising Nonvisual	1D	--------	--------	CT	--------	--------	--------	--------	CT		
Bottom-living											
Pelagivores	2A	SYL			HS						
Pelagobenthivores	2B	CST		CSO				LE			
Benthopelagivore											
Pursuing	2C1	--------	ZL			ZF					
Ambushing											
Size A (Tiny)	2C2a	--------	OT			--------	--------	XEL			
Size B (Small)	2C2b	IQ				XEL					
Size C (Medium)	2C2c	XYL	CP			--------	SR				
Size D (Large)	2C2d	SG			--------	SR	--------	SR			
Benthivores											
Extracting	2D1a	PLV	PD	MP							
Excavating	2D1b	PAV			LP						
Nonvisual	2D2	SA			GZ						

Size Classes (mouth length) of fish: A = 1-4 mm; B = 5-8 mm; C = 9-26 mm; and D ≥ 27 mm.

AF = *Anoplopma fimbria*	LP = *Lycodes pacificus*	SG = *Scorpaena guttata*
CA = *Cymatogaster aggregata*	MP = *Microstonus pacificus*	SJ = *Sebastes jordani*
CP = *Chitonotus pugetensis*	OT = *Odontopyxis trispinosa*	SP = *Seriphus politus*
CSO = *Citharichthys sordidus*	PAV = *Parophrys vetulus*	SR = *Sebastes rosenblatti*
CST = *Citharichthys stignaeus*	PD = *Pleuronichthys decurrens*	SS = *Sebastes saxicola*
CT = *Chilara taylori*	PF = *Phanerodon furcatus*	SYL = *Synodus lucioceps*
GL = *Genyonemus lineatus*	PLV = *Pleuronichthys verticalis*	XEL = *Xeneretmus latifrons*
GZ = *Glyptocephalus zachirus*	PM = *Porichthys myriaster*	XYL = *Xystreurys liolepis*
HS = *Hippoglossina stomata*	PN = *Porichthys notatus*	ZF = *Zaniolepis frenata*
IQ = *Icelinus quadriseriatus*	SA = *Symphurus atricaudus*	ZL = *Zaniolepis latipinnis*
LE = *Lyopsetta exilis*	SDI = *Sebastes diplopria*	ZR = *Zalembius rosaceus*

Boxes indicate where guild occurred in 20% or more of samples in each 20-m depth class.

Dotted lines define areas where guild occurred in less than 20% of samples in a 20-m depth class.

The numerically dominant species in a guild at depths enclosed by box is identified by abbreviation in box..

Figure 2. Functional structure of the soft-bottom fish community of the southern California shelf in 1972-1973 (Allen 1982, 2006).

per station, with the survey being conducted in July-August in 1994, July-September in 1998, and July-October in 2003. In the present study, the comparison of all four surveys is focused on bathymetric changes in community organization in the 10 - 200 m zone only, which was sampled in all surveys.

For all four surveys, fishes were sampled using 7.6 m (head rope) semiballoon otter trawls with 1.3 cm cod-end mesh. All fish collected in the surveys were identified to species, measured to centimeter size-class, and weighed in bulk by species to the nearest 0.1 kg.

The distribution of fish species collected at depths of 10 - 200 m in the 1994, 1998, and 2003 surveys were compared to the baseline model of the functional organization of demersal fish communities

on the southern California shelf using 1972-1973 data (Allen 1982). The functional structure was described in terms of the occurrence of 18 foraging guilds and their dominant members across the shelf at depths of 10 - 200 m. The 1972-1973 study provides an expected bathymetric distribution for each guild and for the dominant guild members. The expected pattern was then examined for each guild by oceanic regime.

Species in each survey were sorted into 18 predefined foraging guilds, 15 basic guilds (Figure 1) with one guild (bottom-living benthopelagivores) being further divided into four size-class divisions of the guild, giving a total of 18 guilds (Figure 2). The guild classification of the most common species was defined in Allen (1982). The guild classification of a
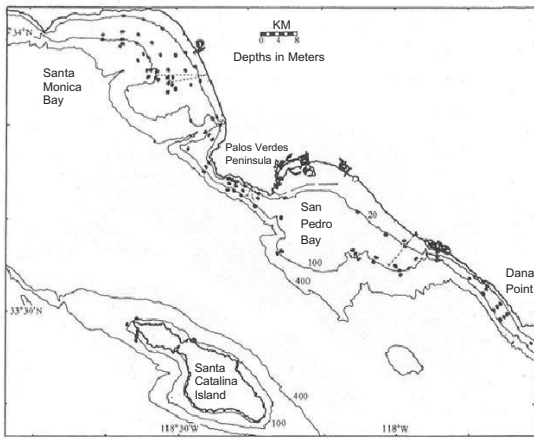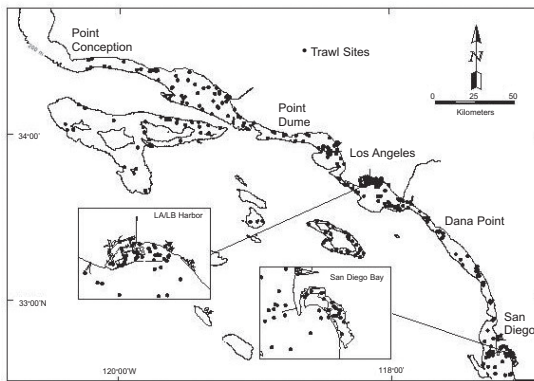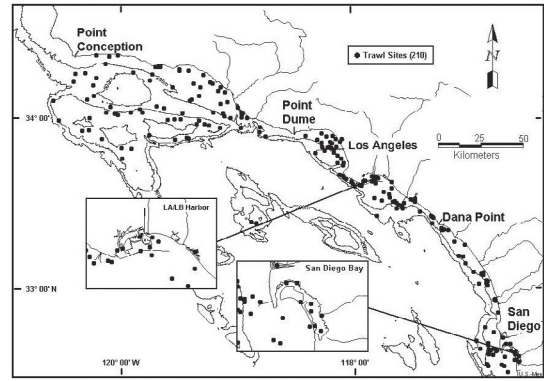
Figure 3a. Map of otter trawl stations sampled at depths of 10 to 190 m on the southern California shelf from May 1972 to December 1973 (99 stations total, 5 at Santa Barbara Island not shown here (342 trawl samples total; from Allen 1982).
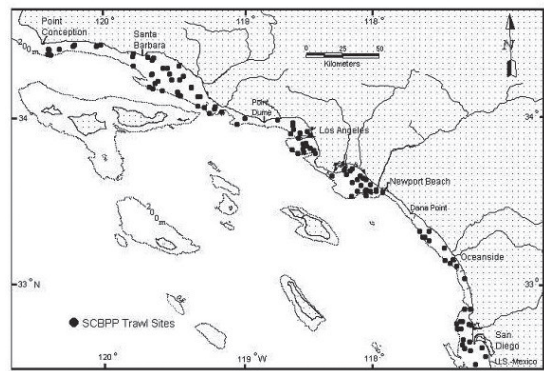
Figure 3b. Map of otter trawl stations sampled at depths of 10 to 200 m on the mainland shelf of southern California in the Southern California Bight Pilot Project survey of July-August 1994 (114 stations and samples total; from Allen *et al*. 1998).

Figure 3c. Otter trawl stations sampled at depths of 2 to 202 m on the southern California shelf in the Southern California Bight 1998 Regional Monitoring Program survey in July-September 1998 (314 stations and samples total; from Allen *et al*. 2002).

Figure 3d. Otter trawl stations sampled at depths of 2 to 476 m on the southern California shelf and upper slope in the Southern California Bight 2003 Regional Monitoring Program survey July-October 2003 (210 stations and samples total, 182 at depths of 2 to 200 m; from Allen *et al*. 2007).

few other species included in the analysis was based on their known foraging behavior or on that inferred from their morphology and/or feeding habits. If more detailed information were available, some of the less frequently occurring species might have been more appropriately classified into specialized guilds not defined in the above study. However, they are conservatively included here in the more general foraging orientation guilds.

The functional organization of the demersal fish assemblages identified in the 1994, 1998, and 2003 surveys was based on the methods developed in Allen (1982), which described the functional organi-

zation of demersal fish communities on the central portion of the southern California shelf at depths of 10 - 200 m in 1972-1973 (Figure 2). Note that the functional organization of the demersal fish assemblages in all four surveys was described at 20-m depth intervals. In this model, the distribution of a guild across depth strata is shown as a box, indicating that a guild occurred at that depth zone in 20% or more of the samples in each 20-m depth class enclosed by the box. The species abbreviation shown within a box indicates the dominant (in relative abundance) species of the guild at those depths. Dotted lines indicate that the guild occurs at the depth but not in 20% or more of the samples. This

organization in 1994, 1998, and 2003 surveys (Allen *et al*. 1998, 2002, 2007) was compared to the model of functional organization for 1972-1973 (Allen 1982) to assess how the organization of the community changed during three oceanic periods .

RESULTS

Most Common Fish Species in Surveys

The four surveys varied somewhat in the numbers of species and families of fishes collected. The 1972-1973 survey collected 126 species of 43 families, the 1994 survey collected 87 species of 34 families, the 1998 survey collected 142 species of 54 families, and the 2003 survey collected 142 species of 52 families. The reports of these surveys include summaries of the survey catch (total species, families, total abundance, biomass). Among the four surveys, 42 fish species occurred in 20% or more of the total samples in at least one of the four surveys or were important foraging guild members in 1972-1973 (Table 1)

Twelve species occurred in 20% or more of the total samples in each of the four surveys (Table 1). These included Dover sole (*Microstomus pacificus*), Pacific sanddab, stripetail rockfish (*Sebastes saxicola*), plainfin midshipman, pink seaperch (*Zalembius rosaceus*), English sole (*Parophrys vetulus*), yellowchin sculpin (*Icelinus quadriseriatus*), speckled sanddab (*Citharichthys stigmaeus*), California tonguefish (*Symphurus atricaudus*), hornyhead turbot (*Pleuronichthys verticalis*), bigmouth sole, and longspine combfish (*Zaniolepis latipinnis*). The remaining species occurred in all four surveys except California skate (*Raja inornata*), which was absent in the 1972-1973 survey; shiner perch (*Cymatogaster aggregata*), absent in the 1994 survey; and sablefish (*Anoplopoma fimbria*), absent in the 1994 and 1998 surveys.

Variation in Guild Occurrence by Survey

Although Allen (1982) provides detailed information on the guild members and guilds from 1972-1973, and information on percent occurrence of the species, it does not give information on the percent occurrence of the guilds on the southern California shelf. For the synoptic regional surveys (1994, 1998, 2003), Allen *et al*. (1998, 2002, 2007) provide this information, yielding an assessment of extent of occurrence by guilds, and changes in this occurrence over time (Table 2). The most widespread guild was the benthic pelagobenthivore

(sanddab) guild, occurring in more than 90% of the samples on the mainland shelf in all three surveys. The next most widespread guild was the benthic extracting benthivore (turbot) guild, with both guilds occurring in more than 80% of the samples from the mainland shelf in all three surveys and in greater than 90% of the samples in 1994 and 2003. Both of these guilds also occurred in more than 90% of the samples in the 2003 if the island shelf and mainland and island upper slope sampled in 2003 are included. These two guilds represent the core members of the soft-bottom fish community of the southern California shelf.

The three surveys represent different oceanic periods: 1994 (warm regime), 1998 (El Niño, very warm), and 2003 (cold regime; Allen *et al*. 2004). Hence, the occurrence pattern of the foraging guilds provides insight into how the guilds and their dominant species respond to different oceanic periods in southern California. Four guilds were notably less frequent during the El Niño period than in the warm and cold regimes (Table 2). These were the turbot, combfish, rockfish, and cusk-eel guilds [note: foraging behavior names of these guilds are also given in Table 2]. In contrast, the lizardfish and croaker guilds were notably more frequent during the El Niño period than in the warm and cold regimes. The sculpin/poacher guild was notably higher in percent occurrence in the cold regime than during the El Niño, and the eelpout, seaperch, and scorpionfish guilds were notably more frequent during the cold regime than in the warm regime and El Niño. The tonguefish guild was notably more frequent during the El Niño period than in the cold regime, but not so relative to the warm regime. The sculpin guild was more frequent than in the warm regime than during the El Niño. The midshipman guild was notably more frequent in both the warm regime and during the El Niño than in the cold regime. Oddly, the pygmy poacher guild was notably more frequent during the El Niño period and the cold regime than in 1994. More detailed reasons for these patterns (recruitment success, adult movements, biogeographic adaptations, etc.) require further study.

Changes in Functional Organization of the Communities Relative to Oceanic Regimes

The description of the functional organization of soft-bottom fish communities on the southern California shelf by Allen (1982) was based on data collected in 1972-1973, a cool regime period.

Table 1. Most common (percent frequency of occurrence) fish species collected at depths of 5 - 200 m in trawl surveys of the Southern California Bight in 1972-1973, 1994, 1998, and 2003 based on data from Allen (1982) and Allen *et al*. (1998, 2002, and 2007).

		Percent Trawl Samples in Survey (= %FO)				
		Oceanic Regime				
Common Name	Scientific Name	Cold 1972-73 (n = 342)	Warm 1994 (n = 114)	El Niño 1998 (n = 314)	Cold 2003 (n = 210)	Mean %FO
Dover sole	*Microstomus pacificus*	68	57	25	52	51
Pacific sanddab	*Citharichthys sordidus*	66	66	40	62	59
stripetail rockfish	*Sebastes saxicola*	66	44	22	42	43
plainfin midshipman	*Porichthys notatus*	61	50	27	38	44
pink seaperch	*Zalembius rosaceus*	59	39	27	43	42
English sole	*Parophrys (=Pleuronectes) vetulus*	54	44	26	46	43
yellowchin sculpin	*Icelinus quadriseriatus*	52	45	28	41	41
speckled sanddab	*Citharichthys stigmaeus*	48	41	26	38	38
curlfin sole	*Pleuronichthys decurrens*	45	3	4	18	17
California tonguefish	*Symphurus atricaudus (=atricauda)*	44	43	45	31	41
hornyhead turbot	*Pleuronichthys verticalis*	40	53	36	47	44
bigmouth sole	*Hippoglossina stomata*	36	49	37	32	38
longspine combfish	*Zaniolepis latipinnis*	35	39	21	42	34
California scorpionfish	*Scorpaena guttata*	31	23	17	22	23
slender sole	*Lyopsetta (=Eopsetta) exilis*	30	32	16	27	26
shortspine combfish	*Zaniolepis frenata*	29	28	18	29	26
shiner perch	*Cymatogaster aggregata*	27	0	10	10	12
rex sole	*Glyptocephalus (=Errex) zachirus*	25	18	5	15	16
bay goby	*Lepidogobius lepidus*	23	32	10	22	22
vermilion rockfish	*Sebastes miniatus*	23	3	3	5	8
roughback sculpin	*Chitonotus pugetensis*	22	11	8	25	16
blackbelly eelpout	*Lycodes (=Lycodopsis) pacificus*	22	13	8	15	14
halfbanded rockfish	*Sebastes semicinctus*	21	13	6	27	17
white croaker	*Genyonemus lineatus*	21	5	29	10	16
pygmy poacher	*Odontopyxis trispinosa*	21	5	6	20	13
spotted cusk-eel	*Chilara taylori*	21	16	8	15	15
shortbelly rockfish	*Sebastes jordani*	20	2	2	11	9
white seaperch	*Phanerodon furcatus*	18	3	12	8	10
California halibut	*Paralichthys californicus*	17	20	38	21	24
longfin sanddab	*Citharichthys xanthostigma*	17	48	35	30	32
splitnose rockfish	*Sebastes diploproa*	16	11	4	13	11
blacktip poacher	*Xeneretmus latifrons*	16	18	6	16	14
sablefish	*Anoplopoma fimbria*	15	0	0	6	5
greenblotched rockfish	*Sebastes rosenblatti*	14	16	6	7	11
California lizardfish	*Synodus lucioceps*	8	51	53	20	33
specklefin midshipman	*Porichthys myriaster*	8	11	17	11	12
fantail sole	*Xystreurys liolepis*	8	24	19	10	15
Pacific hake	*Merluccius productus*	6	14	4	5	7
queenfish	*Seriphus politus*	5	2	20	7	8
bigfin eelpout	*Lycodes cortezianus*	4	2	1	9	4
California skate	*Raja inornata*	0	22	11	16	12
barred sand bass	*Paralabrax nebulifer*	0	4	21	7	8
	Number of Stations	99	114	314	210	
	Depth Range of Survey	10-200 m	10-200 m	5-200 m	5-500 m	
	Mainland Shelf	PD-DP	PC-USM	PC-USM	PC-USM	
	Islands	Ca Is	—	Ch Is	Ch Is	

% FO = percent frequency of occurrence (% total samples in survey with the species); m = meters;
PC-USM = Point Conception to U. S. Mexico International Border; PD-DP = Point Dume to Dana Point
Ca Is = Santa Catalina Island; Ch Is = Channel Islands
n = number of trawl samples

Although the oceanic climate had warmed since the 1980s and then cooled following the 1998 El Niño (Chavez *et al*. 2003, Allen *et al*. 2004, Goericke *et al*. 2005), the model provides a framework for examining changes in the functional organization of the communities with changing ocean regimes. Thus, the organization of the soft-bottom fish communities of the southern California shelf can be compared in four different oceanic periods: 1972-1973 cold regime (Allen 1982); 1994 warm regime (Allen *et al*. 1998); 1998 El Niño period (Allen *et al*. 2002a); and 2003 cold regime (this study). The extent of distribution of the guilds across the shelf (10 - 200 m) and the depth replacement pattern within guilds varied by

Table 2. Percent frequency of occurrence (percent trawl samples where guild occurred) of foraging guilds on the mainland shelf (10 to 200 m) in southern California in 1994, 1998, and 2003 (modified from Allen *et al.* 2007).

Guild No.	Guild Name (Allen 1982)	Identifier	%FO SC Bight 2003 (n = 210)	Mainland Shelf 1994 (n = 114)	Mainland Shelf 1998 (n = 185)	Mainland Shelf 2003 (n=127)
2B	Benthic Pelagobenthivores (1, 1)	sanddab	90	96	93	99
2D1a	Benthic Extracting Benthivores (2, 3)	turbot	91	92	80	94
2C2b	Benthic Ambushing Benthivores, Small (6, 5)	sculpin/poacher	65	65	62	73
2D1b	Benthic Excavating Benthivores (9, 9)	eelpout	62	54	46	71
2A	Benthic Pelagivores (3, 2)	lizardfish	61	75	87	67
2C1	Benthic Pursuing Benthivores (5, 7)	combfish	60	66	51	67
2D2	Benthic Nonvisual Benthivores (4, 4)	tonguefish	64	72	80	65
1C1	Water-Column Diurnal Benthopelagivores (11, 8)	seaperch	49	42	48	63
1A2a	Bottom-refuge Visual Pelagivores (7, 12)	rockfish	59	57	40	61
2C2d	Benthic Ambushing Benthoplagivores, Large (13, 10)	scorpionfish	57	29	43	60
2C2c	Benthic Ambushing Benthivopelagivores, Med. (10, 11)	sculpin	34	53	41	45
1A2b	Bottom-refuge Nonvisual Pelagivores (8, 6)	midshipman	45	56	57	44
1A1	Water-Column Schooling Pelagivores	queenfish	50	38	32	37
2C2a	Benthic Ambushing Benthoplagivores, Tiny	pygmy poacher	20	7	15	22
1D	Water-Column Cruising Benthivores	cusk-eel	20	16	7	19
1C2	Water-Column Nocturnal Benthopelagivores	croaker	20	6	25	12
1B1	Water-Column Schooling Pelagobenthivores	shiner perch	10	0	4	11
1B2	Water-Column Cruising Pelagobenthivores	sablefish	6	0**	0**	1

Occurred in ≥ 10% more trawl samples in this year than in one or both other years

Occurred in ≤ 10% fewer trawl samples in this year than one or more other years

Did not occur in ≥ or ≤ 10% of trawl samples in this year relative to any other year
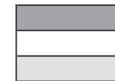
** Barred sand bass, included in this guild in 1994 and 1998, was moved to guild 2C2d in 2003, reducing the guild occurrence to 0.

SC Bight 2003 (n = 210) includes mainland shelf, islands, bays/harbors, and upper slope (2 - 476 m).

Mainland Shelf 2003 (n = 127) includes only 10 - 200 m.

Numbers in parentheses are top 10 rank of guilds in 1994 and in 1998, respectively (rank is listed if it is in the top 10 in either 1994 or 1998).
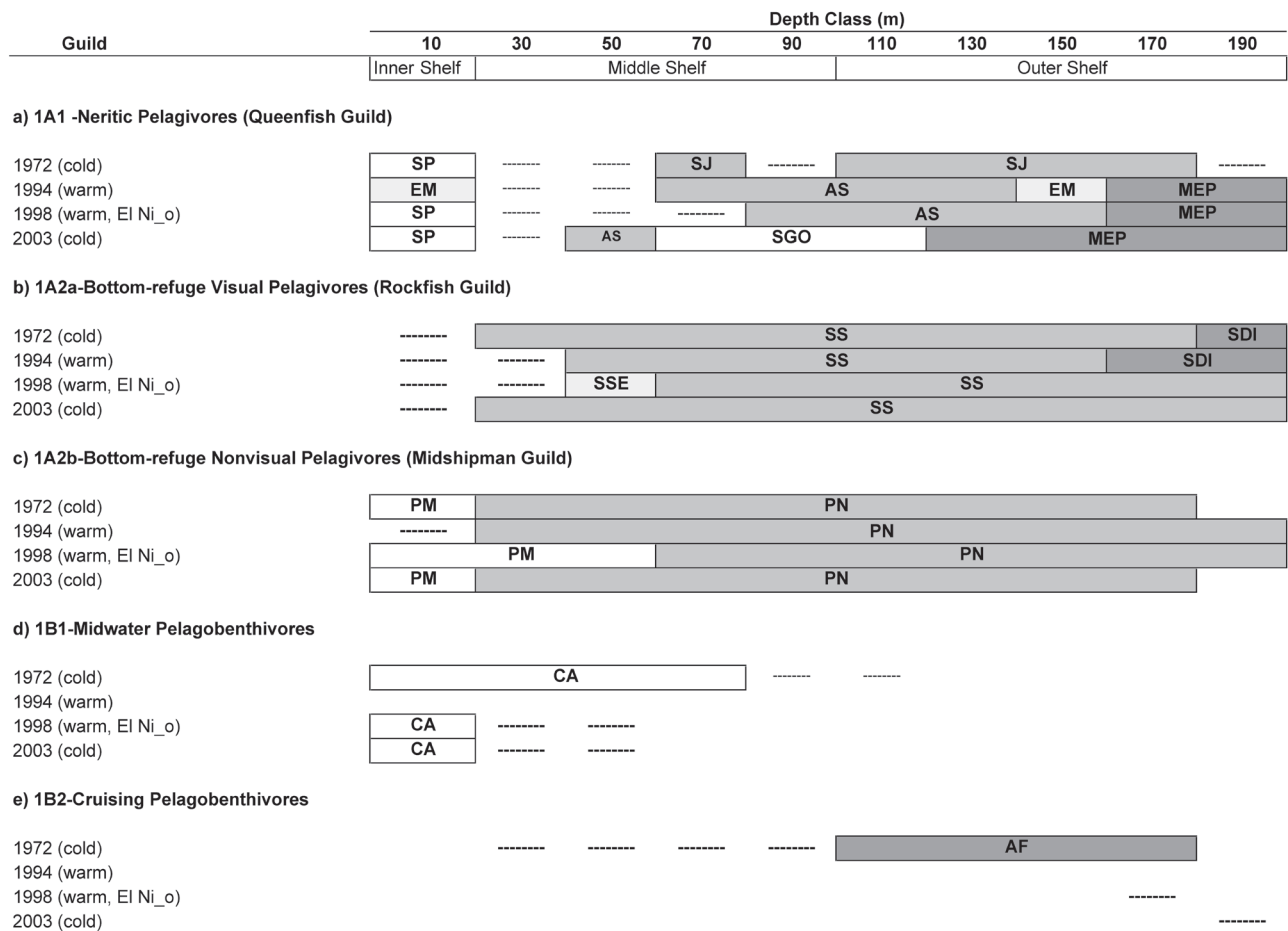
guild. Some guilds occurred across the entire area or most of it in all years. Others had distinct breaks, where a guild occurred infrequently in all years. Some showed such gaps primarily during the El Niño period, suggesting a retreat from some depths. In general, the depth replacement sequence of species within a guild did not change from that described in Allen (1982) but in some cases, another guild member became dominant at a depth. Some of these showed evidence of invasion from the south or north during an oceanic period.

In Guild 1A1 – Water Column Schooling Pelagivores (Figure 4a), the guild distribution pattern showed stable occurrence on the inner part of the inner shelf (5 - 20 m), with the queenfish, a neritic species being dominant except in 1994 when northern anchovy (*Engraulis mordax*), a coastal pelagic species, was more common and abundant on the inner shelf (Allen *et al*. 1998). The guild occurred infrequently (<20% occurrence) in all years at 30 m (20 - 40 m), but relatively common at greater depths, although the dominant species varied. In 1972-1973,

shortbelly rockfish was dominant on the middle and outer shelf. In 1994, 1998, and 2003, Pacific hake (*Merluccius productus*) was the dominant species on the outer shelf. Pacific argentine (*Argentina sialis*), a small species, was dominant on the middle shelf in 1994 and 1998, and to some extent on the outer shelf in 1998. In 2003, juvenile chilipepper (*Sebastes goodei*) were most common and abundant on the middle shelf. Hence, Pacific argentine was the dominant on the middle shelf in warmer periods (1994, 1998) and rockfishes in the colder period (shortbelly rockfish in 1972-1973 and chilipepper in 2003). Except on the inner shelf, the guild appeared to retreat to deeper water in 1998 during the El Niño period.

In Guild 1A2a – Bottom-refuge Visual Pelagivores (Figure 4b), the guild was dominated by planktivorous soft-bottom rockfishes on the middle and outer shelf, but occurred infrequently on the inner shelf. The dominant guild member on the middle shelf in all years was the stripetail rockfish. On the outer shelf, this species was also dominant in 1998 and 2003, but splitnose rockfish (*Sebastes*

	Depth Class (m)									
Guild	10	30	50	70	90	110	130	150	170	190
	Inner Shelf	Middle Shelf				Outer Shelf				

a) 1A1 -Neritic Pelagivores (Queenfish Guild)

	10	30	50	70	90	110	130	150	170	190
1972 (cold)	SP	--------	--------	SJ	--------	SJ			--------	
1994 (warm)	EM	--------	--------	AS				EM	MEP	
1998 (warm, El Ni_o)	SP	--------	--------	--------	AS				MEP	
2003 (cold)	SP	--------	AS	SGO		MEP				

b) 1A2a-Bottom-refuge Visual Pelagivores (Rockfish Guild)

	10	30	50	70	90	110	130	150	170	190
1972 (cold)	--------	SS							SDI	
1994 (warm)	--------	--------	SS					SDI		
1998 (warm, El Ni_o)	--------	--------	SSE	SS						
2003 (cold)	--------	SS								

c) 1A2b-Bottom-refuge Nonvisual Pelagivores (Midshipman Guild)

	10	30	50	70	90	110	130	150	170	190
1972 (cold)	PM	PN								
1994 (warm)	--------	PN								
1998 (warm, El Ni_o)	PM		PN							
2003 (cold)	PM	PN								

d) 1B1-Midwater Pelagobenthivores

	10	30	50	70	90	110	130	150	170	190
1972 (cold)	CA			--------	--------					
1994 (warm)										
1998 (warm, El Ni_o)	CA	--------	--------							
2003 (cold)	CA	--------	--------							

e) 1B2-Cruising Pelagobenthivores

	10	30	50	70	90	110	130	150	170	190
1972 (cold)		--------	--------	--------	--------	AF				
1994 (warm)										
1998 (warm, El Ni_o)								--------		
2003 (cold)										--------

IA1: SP = queenfish (*Seriphus politus*); SJ = shortbelly rockfish (*Sebastes jordani*);

EM = northern anchovy (*Engraulis mordax*); AS = Pacific argentine (*Argentina sialis*)

MEP = Pacific hake (*Merluccius productus*); SGO = chilipepper (*Sebastes goodei*)

IA2a: SS = stripetail rockfish (*Sebastes saxicola*);

SDI = splitnose rockfish (*Sebastes diploproa*); SSE = halfbanded rockfish (*Sebastes semicinctus*)

IA2b: PM = specklefin midshipman (*Porichthys myriaster*); PN = plainfin midshipman (*Porichthys notatus*)

IB1: CA = shiner perch (*Cymatogaster aggregata*)   IB2: AF = sablefish (*Anoplopoma fimbria*)

Boxes indicate where guild occurred in 20% or more of samples in each 20-m depth class.
Dotted lines define areas where guild occurred in less than 20% of samples in a 20-m depth class.
The numerically dominant species in a guild at depths enclosed by box is identified by abbreviation in box.

Figure 4. Comparison of changes in depths of common occurrence of foraging guilds 1A1 to 1B2 of demersal fish communities on the southern California shelf in 1972-1973, 1994, 1998, and 2003 (Allen 1982; Allen *et al*. 1998, 2002, and 2007, respectively).

diploproa) was dominant there in 1972-1973 and 1994. Stripetail rockfish appeared to retreat to deeper water on the shallow side of its occurrence in the warm years of 1994 and 1998, but particularly during 1998. In this year, halfbanded rockfish (*Sebastes semicinctus*) replaced stripetail rockfish on the middle shelf at 50 m (40 - 60 m).

In Guild 1A2b – Bottom-refuge Nonvisual Pelagivores (Figure 4c), the guild was dominated by midshipmen in all years, with specklefin midshipman dominant on the inner shelf (occurring infrequently in 1994) and plainfin midshipman through-

out the middle and outer shelf. The depth replacement pattern was identical in the two cold regime periods (1972-1973, 2003). Specklefin midshipman extended its deepest (to 60 m) inshore dominance in 1998.

In Guild 1B1 – Water-column Midwater Pelagobenthivores (Figure 4d), shiner perch was the only dominant species. This species was dominant on the inner and middle shelf in 1972-1973 was absent in 1994 and dominant only on the inner shelf in 1998 and 2003, occurring infrequently on the middle shelf.

In Guild 1B2 – Water-column Cruising Pelagobenthivores (Figure 4e), sablefish was the only dominant species. This species was dominant on the middle and outer shelf in 1972-1973, absent in 1994, and occurred infrequently on the outer shelf in 1998 and 2003.

In Guild 1C1 – Water-column Cruising Diurnal Benthopelagivores (Figure 5a), white seaperch (*Phanerodon furcatus*) was dominant on the inner shelf in 1972-1973, 1998, and 2003, but was infrequent there in 1994. Pink seaperch was dominant on the middle shelf in all years, and also on the outer

shelf in 1972-1973, 1998, and 2003. It replaced white seaperch as dominant on the inner shelf in 1994. In that year it appeared to shift its range shoreward, being dominant on the inner and middle shelf, but infrequent on the outer shelf. Although white seaperch was dominant on the inner shelf in 1998, pink seaperch appeared to retreat from the inner shelf (occurring only infrequently at 30 m) during this El Niño period.

In Guild 1C2 – Water-column Cruising Nocturnal Benthopelagivores (Figure 5b), white croaker (*Genyonemus lineatus*) was the dominant in
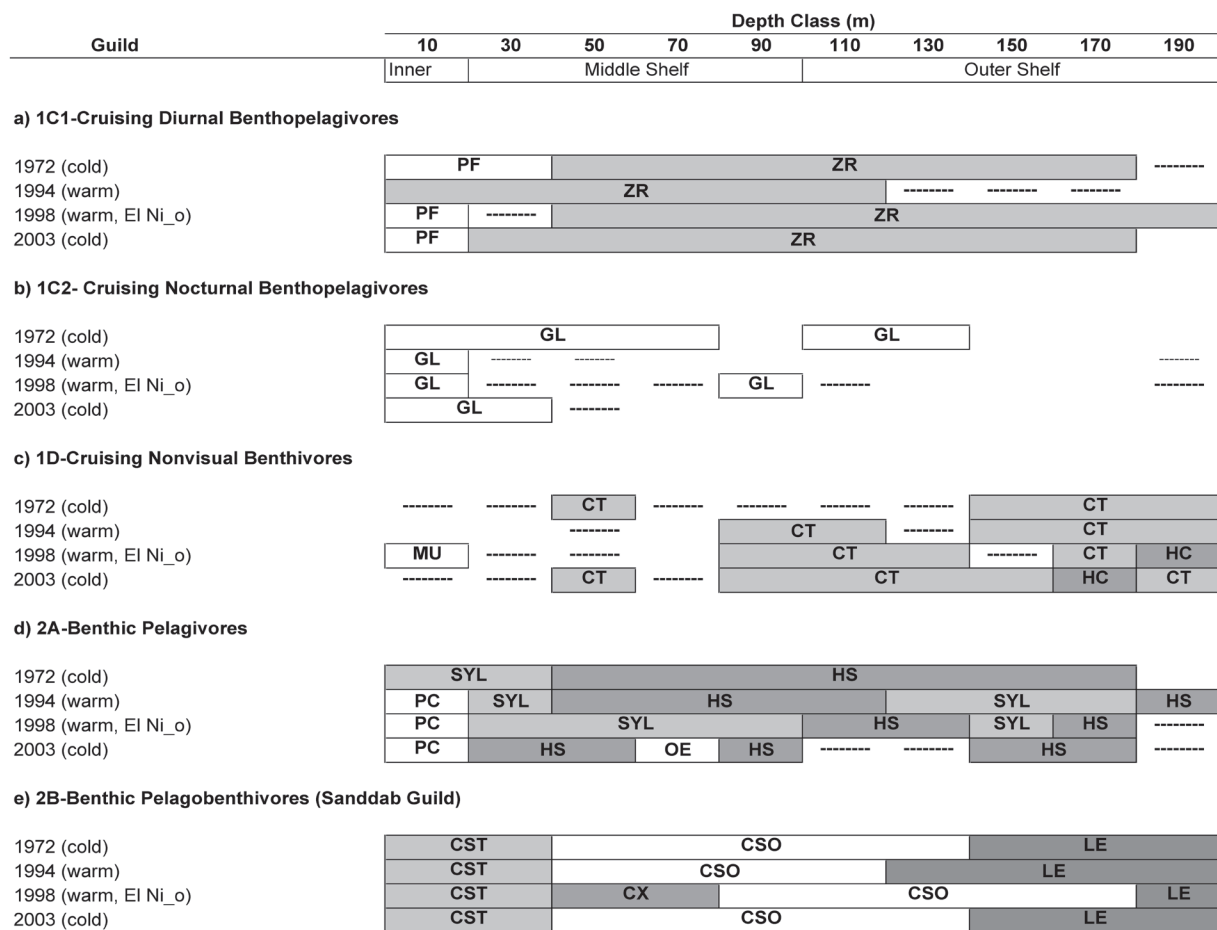
IC1: PF = white seaperch (*Phanerodon furcatus*); ZR = pink seaperch (*Zalembius rosaceus*)
IC2: GL = white croaker (*Genyonemus lineatus*);
ID: CT = spotted cusk-eel (*Chilara taylori*); MU = California corbina (*Menticirrhus undulatus*);
   HC = spotted cusk-eel (*Hydrolagus colliei*)
2A: SYL = California lizardfish (*Synodus lucioceps*); HS = bigmouth sole (*Hippoglossina stomata*)
   PC = California halibut (*Paralichthys californicus*); OE = lingcod (*Ophiodon elongatus*)
2B: CST = speckled sanddab (*Citharichthys stigmaeus*); CSO = Pacific sanddab (*Citharichthys sordidus*);
   LE = slender sole (*Lyopsetta exilis*); CX = longfin sanddab (*Citharichthys xanthostigma*)

Boxes indicate where guild occurred in 20% or more of samples in each 20-m depth class.
Dotted lines define areas where guild occurred in less than 20% of samples in a 20-m depth class.
The numerically dominant species in a guild at depths enclosed by box is identified by abbreviation in box.

Figure 5. Comparison of changes in depths of common occurrence of foraging guilds 1C1 to 2B of demersal fish communities on the southern California shelf in 1972-1973, 1994, 1998, and 2003 (Allen 1982; Allen *et al*. 1998, 2002, and 2007, respectively).

all years. As with the shiner perch in Guild 1B1, it was dominant on the inner and middle shelf in 1972-1973. It was also dominant on the inner shelf in 1994, 1998, and 2003. In 1998, it also was frequent on the outer middle shelf, and in 1972 it was frequent on the outer shelf.
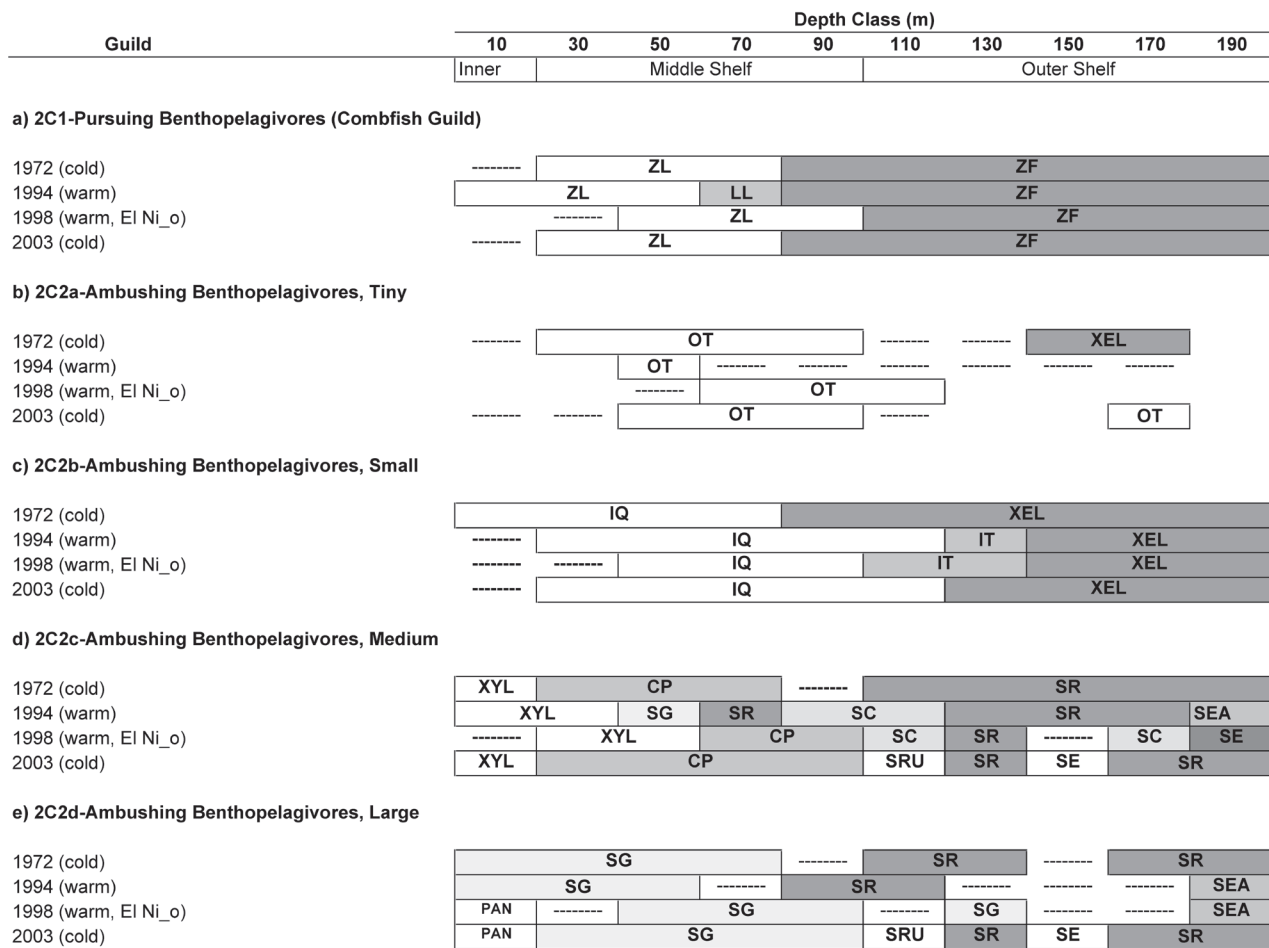
In Guild 1D – Water-column Cruising Nonvisual Benthivores (Figure 5c), spotted cusk-eel (*Chilara taylori*) was the dominant species on much of the area of the middle and outer shelf in 1994, 1998, and 2003. However, in 1972-1973 it occurred only infrequently on the middle shelf, but was frequent on the outer shelf. Because this guild is primarily a cusk-eel guild, some of the low occurrence on the inner and middle shelf may be artifact related to daytime trawling in the surveys. Cusk-eels typically bury in sediments during the day in shallow water and only are out foraging at night. Night trawls may find that this species and its shallow replacement (basketweave cusk-eel, *Ophidion scrippsae*) are common and abundant then. In deeper water where light levels are minimal, spotted cusk-eel actively forages during the day (Allen 1982, 2006). California corbina (*Menticirrhus undulatus*) made a brief appearance as a dominant on the inner shelf in 1998 and spotted ratfish (*Hydrolagus colliei*) as a dominant at locations on the outer shelf in 1998 and 2003.

In Guild 2A – Benthic Pelagivores (Figure 5d) was widespread in occurrence in 1972-1973, 1994, and 1998, but its occurrence was less in 2003. The dominant species on the inner shelf in 1972-1973 was California lizardfish, but was California halibut (*Paralichthys californicus*) in 1994, 1998, and 2003. Bigmouth sole was dominant over the middle and outer shelf in 1972-1973, and on the middle shelf in 1994, but it was frequently replaced as dominant on the middle shelf and outer shelf in 1994 and 1998 by California lizardfish. Allen (2006) split this guild into two guilds foraging in the same way, but differing in body type: flatfishes and roundfishes. Among the flatfishes, the typical pattern was California halibut dominant on the inner shelf and bigmouth sole dominant on the middle and outer shelf. This would generally be the case if California lizardfish (a roundfish) were removed from the comparison; however, bigmouth sole clearly had areas of low occurrence on the outer shelf in 2003. California lizardfish appears to have been an invader during 1972-1973, spreading to deeper water in 1994 and 1998, before becoming less common and abundant in 2003 (when California halibut and bigmouth sole out-

ranked it in dominance). Juvenile lingcod (*Ophiodon elongatus*), a roundfish northern replacement of California lizardfish (Allen 2006), were abundant in a limited area of the middle shelf in 2003. The disjunct regions of California lizardfish dominance on the outer shelf raised concern that these may be spotted lizardfish (*Synodus evermanni*) from southern Baja California. However, that species is the dominant member of the benthic roundfish pelagivores guild on the outer shelf only south of Magdalena Bay, Baja California Sur, whereas California lizardfish is the dominant member of that guild on the outer shelf from Point Conception to Magdalena Bay (Allen 2006).

In Guild 2B – Benthic Pelagobenthivores (Figure 5e) was common and abundant at all depths in all four time periods. Speckled sanddab was the dominant species on the inner shelf in all four years (1972-1973, 1994, 1998, and 2003). Pacific sanddab was the dominant member of the entire middle shelf in 1972-1973, 1994, 1998, and 2003, but was replaced on the inner side of this zone in 1998 by longfin sanddab (*Citharichthys xanthostigma*). The depth range of dominance for Pacific sanddab remained about the same in 1998 as other areas, but it shifted seaward and well on to the outer shelf. Slender sole was the dominant on the outer shelf in 1972-1973, 1994, and 2003, but was replaced by Pacific sanddab as dominant at depths between 120 and 180 m in 1998. The sudden dominance of longfin sanddab and retreat of Pacific sanddab and slender sole to deeper water in 1998 appears to be a strong El Niño response. The depth replacement pattern was identical in the two cold regime periods (1972-1973, 2003).

In Guild 2C1 – Benthic Pursuing Benthopelagivores (Combfish Guild; Figure 6a) the primary pattern was longspine combfish dominant on the middle shelf and shortspine combfish (*Zaniolepis frenata*) on the outer shelf and except for 1998 on the outer part of the middle shelf. In 1994, bay goby (*Lepidogobius lepidus*), a small species of similar body shape and foraging behavior as a juvenile combfish but finds refuge in invertebrate burrows, was more abundant than combfish at 70 m (60 - 80 m). The guild was infrequent or absent on the inner shelf in all years except 1994, when longspine combfish was also common on the inner shelf. This species retreated to the outer middle shelf in 1998. This pattern of expanding onto the inner shelf in 1994 and retreating to the outer middle shelf in 1998 also occurred in Guild 1C1 with pink seaperch. Both species feed

Depth Class (m)

Guild	10	30	50	70	90	110	130	150	170	190
	Inner		Middle Shelf			Outer Shelf				

a) 2C1-Pursuing Benthopelagivores (Combfish Guild)

1972 (cold): -------- ZL | ZF
1994 (warm): ZL | LL | ZF
1998 (warm, El Ni_o): -------- ZL | ZF
2003 (cold): -------- ZL | ZF

b) 2C2a-Ambushing Benthopelagivores, Tiny

1972 (cold): -------- OT -------- -------- XEL
1994 (warm): OT -------- -------- -------- -------- -------- --------
1998 (warm, El Ni_o): -------- OT
2003 (cold): -------- -------- OT -------- OT

c) 2C2b-Ambushing Benthopelagivores, Small

1972 (cold): IQ | XEL
1994 (warm): -------- IQ | IT | XEL
1998 (warm, El Ni_o): -------- -------- IQ | IT | XEL
2003 (cold): -------- IQ | XEL

d) 2C2c-Ambushing Benthopelagivores, Medium

1972 (cold): XYL | CP -------- SR
1994 (warm): XYL | SG | SR | SC | SR | SEA
1998 (warm, El Ni_o): -------- XYL | CP | SC | SR -------- SC | SE
2003 (cold): XYL | CP | SRU | SR | SE | SR

e) 2C2d-Ambushing Benthopelagivores, Large

1972 (cold): SG -------- SR -------- SR
1994 (warm): SG -------- SR -------- -------- -------- SEA
1998 (warm, El Ni_o): PAN -------- SG -------- SG -------- -------- SEA
2003 (cold): PAN | SG | SRU | SR | SE | SR

2C1: ZL = longspine combfish (*Zaniolepis latipinnis*); ZF = shortspine combfish (*Zaniolepis frenata*);
   LL = bay goby (*Lepidogobius lepidus*)
2C2a: OT = pygmy poacher (*Odontopyxis trispinosa*); XEL = blacktip poacher (*Xeneretmus latifrons*) (S = small)
2C2b: IQ = yellowchin sculpin (*Icelinus quadriseriatus*) ; XEL = blacktip poacher (*Xeneretmus latifrons*) (L = large);
    IT = spotfin sculpin (*Icelinus tenuis*)
2C2c: XYL = fantail sole (*Xystreurys liolepis*) (M = medium) ; CP = roughback sculpin (*Chitonotus pugetensis*) (L);
   SR = greenblotched rockfish (*Sebastes rosenblatti*) (S); SG = California scorpionfish (*Scorpaena guttata*) (M);
   SC = greenspotted rockfish (*Sebastes chlorostictus*) (S); SEA = shortspine thornyhead (*Sebastolobus alascanus*) (S)
   SE = pink rockfish (*Sebastes eos*) (S); SRU = flag rockfish (*Sebastes rubrivinctus*) (S)
2C2d: SG (L); SR (L); SEA (L); PAN = barred sand bass (*Paralabrax nebulifer*) (L); SRU (L); SE (L);

Boxes indicate where guild occurred in 20% or more of samples in each 20-m depth class.
Dotted lines define areas where guild occurred in less than 20% of samples in a 20-m depth class.
The numerically dominant species in a guild at depths enclosed by box is identified by abbreviation in box.

Figure 6. Comparison of changes in depths of common occurrence of foraging guilds 2C1 to 2C2d of demersal fish communities on the southern California shelf in 1972-1973, 1994, 1998, and 2003 (Allen 1982; Allen *et al*. 1998, 2002, and 2007, respectively).

primarily on gammaridean amphipods, suggesting that perhaps a shift in abundance of prey and/or a change in bottom temperature may have affected their distributions in these years. The depth replacement pattern for combfishes in this guild was identical in the two cold regime periods (1972-1973, 2003).

In Guild 2C2a – Benthic Ambushing Benthopelagivores Size A (Tiny; Figure 6b) was dominated by pygmy poacher (*Odontopyxis trispinosa*) on the middle shelf and juvenile blacktip poacher (*Xeneretmus latifrons*) on the outer shelf in 1972-1973. In 1998 and 2003, pygmy poacher was the dominant on the middle shelf, but occurred infrequently on much of the middle shelf in 1994. It was a dominant in a small region of the outer shelf in 2003.

In Guild 2C2b – Benthic Ambushing Benthopelagivores Size B (Small; Figure 6c) was largely dominated by yellowchin sculpin on the middle shelf and adult blacktip poacher on the outer shelf. In 1972-1973, yellowchin sculpin was also

dominant on the inner shelf and blacktip poacher also shifted shoreward, replacing yellowchin sculpin on the outer part of the middle shelf. The shallow edge of the region of common occurrence of yellowchin sculpin and blacktip poacher was deeper in 2003. Spotfin sculpin (*Icelinus tenuis*) was dominant at shelf break depths in 1994 and 1998, but not during the cold regime periods of 1972-1973 and 2003.

In Guild 2C2c – Benthic Ambushing Benthopelagivores, Size C (Medium; Figure 6d) the distribution pattern of guild dominants was generally most similar in 1972-1973 and 2003 (both cold regimes). In 1972-1973, fantail sole (*Xystreurys liolepis*) was dominant on the inner shelf, roughback sculpin (*Chitonotus pugetensis*) on the middle shelf, and juvenile greenblotched rockfish (*Sebastes rosenblatti*) on the outer shelf. This is the basic pattern for this guild. This pattern was similar in 2003 except that at some depths on the outer shelf, juvenile greenblotched rockfish was replaced by other rockfishes (greenspotted rockfish, *Sebastes chlorostictus*; flag rockfish, *Sebastes rubrivinctus*; pink rockfish, *Sebastes eos*; and shortspine thornyhead, *Sebastolobus alascanus*). Fantail sole was the dominant species of this guild on the inner shelf in 1972-1973, 1994, and 2003, but the guild was infrequent there in 1998. Fantail sole shifted as a dominant deeper onto the middle shelf in 1998, replacing roughback sculpin as dominant in that area. Although roughback sculpin was generally the dominant on the middle shelf, in 1994 it was infrequent there, being replaced by juveniles of a number of rockfishes of this guild. In general, the typical pattern of this guild was disrupted in all years at the shelf break with the guild either being infrequent (as in 1972-1973) or replaced by juveniles of hard bottom rockfishes in 1994, 1998, and 2003. Juvenile greenblotched rockfishes declined dramatically in distribution on the outer shelf during the period, being widespread in 1972-1973, less so in 1994, dominant at a limited depth (120 - 140 m) in 1998, and increasing in dominance on the outer shelf in 2003.

In Guild 2C2d – Benthic Ambushing Benthopelagivores, Size D (Large; Figure 6e) showed a relatively consistent pattern on the middle shelf, but a similar pattern to Guild 2C2c on the outer shelf. California scorpionfish (*Scorpaena guttata*) was the dominant member of this guild on the inner shelf in 1972-1973 and 1994, but barred sand bass (*Paralabrax nebulifer*) was dominant there in 1998 and 2003. California scorpionfish was dominant on

the middle shelf in all years, although it shifted shallower in 1994 and deeper in 1998. Adult greenblotched rockfish was dominant on the outer shelf in 1972-1973, was more restricted to the shelf break in 1994, but returning to broad distribution on the outer shelf in 2003. The guild was infrequent, usually represented by incidental hard-bottom rockfishes of this guild in 1994 and 1998 (e.g., flag rockfish, pink rockfish) or with shortspine thornyhead. The distribution of greenblotched rockfish in 1994 and 1998 for both adults (this guild) and juveniles (Guild 2C2), indicate a strong negative response to the warm regime and El Niño, perhaps due to poor recruitment of juveniles and movement of adults to deeper water.

In Guild 2D1a – Benthic Extracting Benthivores (Figure 7a) occurred consistently in all depth zones in all years. Dover sole was the consistent dominant on the middle and outer shelf in all years. Hornyhead turbot was generally the dominant on the inner shelf and inner part of the middle shelf. It was dominant on the inner shelf in 1972-1973, 1994, and 2003, but was replaced there by spotted turbot (*Pleuronichthys ritteri*), a shallow species, in 1998. Hornyhead turbot was also dominant on the inner part of the middle shelf in1998 and 2003, but was replaced there by curlfin sole (*Pleuronichthys decurrens*) in 1972-1973. Curlfin sole replaces hornyhead turbot on the inner shelf north of Point Conception and spotted turbot replaces hornyhead turbot on the inner shelf and middle shelf in Baja California Sur (Allen 2006).

In Guild 2D1b – Benthic Excavating Benthivores (Figure 7b) showed a relatively consistent pattern in all years. English sole was typically dominant on the inner and middle shelf and blackbelly eelpout (*Lycodes pacficus*) on the outer shelf. English sole was dominant on the inner shelf in 1972-1973, 1994, and 2003; but the guild was infrequent on the inner shelf in 1998, with English sole retreating to deeper water during the El Niño period. The depth on the middle or outer shelf where it was replaced by blackbelly eelpout increased over the period, being about 80 m in 1972-1973, 120 m in 1994 and 1998, and 140 m in 2003. English sole replaced blackbelly eelpout along parts of the mainland outer shelf in 1998.

Guild 2D2 – Benthic Nonvisual Benthivores (Figure 7c) showed a relatively consistent pattern over the years. California tonguefish was typically dominant on the inner and middle shelf and rex sole (*Glyptocephalus zachirus*) on the outer shelf.

Guild	Depth Class (m)									
	10	30	50	70	90	110	130	150	170	190
	Inner		Middle Shelf			Outer Shelf				

a) 2D1a-Benthic Extracting Benthivores (Turbot Guild)

1972 (cold)	PLV	PD				MP				
1994 (warm)	PLV				MP					
1998 (warm, El Ni_o)	PLR		PLV		MP					
2003 (cold)	PLV				MP					

b) 2D1b-Benthic Excavating Benthivores

1972 (cold)	PAV				LP					
1994 (warm)	PAV					LP				
1998 (warm, El Ni_o)	--------	PAV			LP	PAV		LP		
2003 (cold)	PAV				LP					

c) 2D2-Benthic Nonvisual Benthivores

1972 (cold)	SA				GZ					
1994 (warm)	SA					GZ				
1998 (warm, El Ni_o)	SA			RS	--------	GZ				
2003 (cold)	UH	SA		RI	--------	GZ				

2D1a: PLV = hornyhead turbot, *Pleuronichthys verticalis* ; PD = curlfin sole, *Pleuronichthys decurrens* ; ;

   MP = Dover sole, *Microstomus pacificus* ; PLR = spotted turbot, *Pleuronichthys ritteri*

2D1b: PAV = English sole, *Parophrys vetulus* ; LP = blackbelly eelpout, *Lycodes pacificus.*

2D2: SA = California tonguefish, *Symphurus atricaudus* ; GZ = rex sole, *Glyptocephalus zachirus* ;

   RS = starry skate, *Raja stellulata* (S); UH = round stingray, *Urobatis halleri* ; RI = Caliofrnia skate, *Raja inornata*

Boxes indicate where guild occurred in 20% or more of samples in each 20-m depth.
Dotted lines define areas where guild occurred in less than 20% of samples in a 20-m depth class.
The numerically dominant species in a guild at depths enclosed by box is identified by abbreviation in box.

Figure 7. Comparison of changes in depths of common occurrence of foraging guilds 1D1a to 2D2 of demersal fish communities on the southern California shelf in 1972-1973, 1994, 1998, and 2003 (Allen 1982; Allen *et al*. 1994, 1998, 2002, and 2007, respectively).

California tonguefish was dominant on the inner shelf in 1972-1973, 1994, and 1998, but was replaced there by round stingray (*Urobatis halleri*) in 2003. The depth range of dominance for California tonguefish expanded to the inner part of the outer shelf in 1994, but returned to the middle shelf in 1998 and 2003. Rex sole replaced California tonguefish at 80 m in 1972-1973, but this replacement occurred at 120 m in 1994 and 2003. Rex sole retreated as dominant to 160 m or deeper on the outer shelf in 1998. The guild was infrequent or replaced by juvenile starry skate (*Raja stellulata*) in 1998 and juvenile California skate in 2003 at limited depths near the shelf break.

In general, the distribution of the 18 foraging guilds across the depth range of 10 - 200 m was most complete in 1972-1973, with some guilds showing large gaps in occurrence during the four periods. Among guilds foraging from the water-column, these gaps occurred among schooling pelagivores (Guild 1A1), midwater and cruising pelagobenthivores (Guilds 1B1 and 1B2), cruising nocturnal benthopelagivores (1C2), and cruising benthivores (1D).

Among guilds foraging from the bottom, large gaps in presence occurred among benthic ambushing benthopelagivores sizes A (pygmy poacher guild; 2C2a) and D (scorpionfish guild; 2C2d). The organization was generally stable if a single dominant guild member occupied a broad depth range on the shelf. However, if an expected dominant from Allen (1982) was missing, there may be no good replacement (Allen *et al*. 2002). This is particularly apparent in the outer shelf representative of the sculpin (2C2c) and scorpionfish guilds (2C2d). Whereas the greenblotched rockfish (SR) was dominant on the outer shelf in these guilds in 1972-1973, larger members of this guild (2C2d) were infrequent in 1994 and very infrequent in 1998, with some closely related species (greenspotted rockfish; pink rockfish) and some less closely related species (shortspine thornyhead; California scorpionfish) dominant within the outer shelf. This suggests that the best-adapted species of this guild for the outer shelf soft-bottom habitat of southern California is the greenblotched rockfish.

The depth distribution patterns of several guilds and their guild dominants were identical or nearly so

within a guild in the two cold regimes surveyed (1972-1973 and 2003), suggesting a resilient return to baseline cold-regime patterns. The sanddab, midshipman, and combfish guilds showed identical depth distribution patterns of the guild and depths of dominance of guild dominants within a guild in the two cold regimes. In addition, the soft-bottom rockfish, seaperch, and scorpionfish guilds showed nearly identical patterns to the patterns within these guilds during the two cold regimes.

DISCUSSION

Responses of different foraging guilds to changing ocean conditions varied between different oceanic periods. Although these changes might just represent year-to-year variation, the evidence presented here suggests that they are responses to the different oceanic cycles occurring during the survey periods and during the past 30 years (Chavez *et al*. 2003, Allen *et al*. 2004, Goericke *et al*. 2005). During the warm regime of the Pacific Decadal Oscillation, ocean temperatures increased, upwelling in the California Current decreased, and zooplankton abundance decreased (Roemmich and McGowan 1995, Smith 1995, Chavez *et al*. 2003). In most cases (Figures 4 through 7) there appears to be an El Niño effect in 1998 that is greater than the differences between 1972-1973 and 1994 (e.g. midshipman guild, lizardfish guild, sanddab guild, and turbot guild; Figures 4c, 5d, 5e, and 7a). These responses occur primarily on the inner shelf and shallow middle shelf, but in some guilds, responses occurred at the interface of the middle shelf and outer shelf. During an El Niño, the thermocline deepens and bottom water temperatures are warmer on the shelf (Dark and Wilkins 1994, Hayward 2000), perhaps causing species to expand or contract their bathymetric or geographic ranges. Some changes occurring during this period may be related to zooplankton abundance or decreased transport of larvae in the California Current from the north, whereas others may be due to movement of juveniles and adults to more desirable conditions. In addition, several guilds showed a resilient return in 2003 to 1972-1973 patterns. In guilds 1A2b (midshipman guild), 2B (sanddab guild), and 2C1 (combfish guilds) the patterns in the two cold regime periods (1972-1973 and 2003) were exactly the same (Figures 4c, 5e, and 6a). In guild 1A2a (rockfish) and 1C1 (seaperch), the guilds were almost exactly the same. In general the patterns of these two periods were more similar

than either was to 1994 or 1998 (Figures 4b and 5a). Knowledge of the oceanic regime at the time of a survey may allow prediction of expected community structure at a given depth.

A number of changes are apparent in the functional structure of demersal fish communities as there is a shift from a cold regime to a warm regime. In general, there is a decreased occurrence of some water-column guilds on the middle shelf, relative to that of a cold regime (Figure 4). Also, in a warm regime, there is a decreased occurrence of some benthic guilds on the inner shelf, relative to that of a cold regime (Figure 6), and a decreased occurrence of some outer shelf guild dominants (without replacement; Figures 5 and 6), perhaps due to less recruitment of larvae in the weakened California Current. During cold regimes, the California Current is very strong, resulting in increased transport of larvae of cold-temperate species from the central California coast into southern California. During warm regimes, the California current is weaker, with less transport of larvae of cold temperate species. However, there may be more transport of larvae of warm temperate species from northern Baja California. During the 1970s, high recruitment of young stripetail rockfish occurred during the two coldest years whereas high recruitment of calico rockfish occurred during warmest years (Mearns *et al*. 1980). In addition, there may be more movement of adults of some species into the SCB from the north during a cold regime, and more movement of adults of some species from the south into the SCB during a warm regime. Another factor is that that plankton productivity is higher during cold regimes (due to more upwelling in the California Current) and lower during warm regimes (when upwelling of nutrients is less) (Roemmich and McGowan 1995). Thus warm regimes may be more oligotrophic. In addition, there is more precipitation and hence runoff, during warm regimes than in cold regimes (Chavez *et al*. 2003). The presence of more or less runoff from coastal watersheds causing increased turbidity and deposition of terrestrial sediment on the inner shelf may also affect the occurrence of inner shelf species.

An El Niño event affects the structure of demersal fish communities in a variety of ways. Some guild dominants exhibit expansions or contractions of their depth ranges of dominance. Some guilds retreat to deeper water (perhaps due to a deepening of the thermocline). As noted above, there is also

more precipitation and runoff from coastal water-sheds during El Niño periods which may increase turbidity and deposition of sediment on the inner shelf, causing inner shelf species to move deeper. Intrusions of new dominant guild members may occur from the south, such as in 1998 when longfin sanddab replaced the Pacific sanddab as the numeri-cally dominant species of the sanddab guild on the inner middle shelf (Figure 5e), perhaps due to increased transport of larvae from the south in stronger north-flowing currents. The decreased occurrence of many water-column guilds, particular-ly on the middle shelf may be due to a deepening of the thermocline and reduced plankton productivity. The decreased occurrence of many benthic guilds on the inner shelf is likely due to warmer nearshore waters intruding from the South and perhaps also to runoff effects. The decreased occurrence of some outer shelf guild dominants without replacement is possibly due to movements of adults into deeper water without recruitment of larvae of suitable species from the north. .

Changes in the distribution of dominant guild members between cold and warm regimes are likely in part due to different magnitudes of larval recruit-ment between the two periods and in part due to movements across depths by juvenile and adult fish. Changes that occur in the oceanic environment between a cold and warm regime include increased water temperature, a deeper thermocline depth, decreased plankton productivity, reduced transport of the California Current, and increased coastal runoff (during warm regimes and El Niños).

The results of this study indicates that the distri-bution of fish species within some foraging guilds varies by depth across the shelf during different oceanic regime periods. As a result, the depth pat-tern of the functional organization of the community also varies somewhat between oceanic regimes. Nevertheless, it appears that some guilds showed the same depth replacement patterns of dominant guild members in different cold regimes (1972-1973 and 2003), suggesting that there may be a predictable pattern in cold regimes. As only two surveys in this study had surveyed the same type of regime (in this case, cold regime) in different years, it is not known yet whether the warm regime and El Niño patterns are repeatable. This will not be known until after additional surveys are conducted during one or both of these regimes. In the meantime, the bathymetric replacement patterns of numerically dominant guild

species within a guild, and the distribution of the guilds described for the warm regime and El Niño periods in this study provide the only information on expected changes during these periods. Although the differences in the pattern of functional structure in the different surveys may be due to year-to-year vari-ability, the identical depth replacement patterns of three guilds and the nearly identical patterns of another three guilds, suggest that cold regime pat-terns may be predictable and not simply due to year-to-year variability.

Environmental assessments of anthropogenic activity (fishing, pollution, habitat disruption) would typically attempt to assess differences in the observed conditions in an area likely affected by human activity relative to that of natural conditions. In this, case, an assessment might determine differ-ences in the guild distributions and depth distribution of dominant guild species relative to that expected in the baseline model (Allen 1982). "Baseline" here refers to first model of functional structure of this fauna in this region, which by chance, happened to be in a cold regime period. Whether the typical regime in this area is cold or warm is uncertain, but it is apparent that the alternation of these multi-decadal regimes likely go back many years (Soutar and Isaacs 1969, 1974; Chavez et al. 2003). However, if these patterns vary by oceanic period (cold regime, warm regime, El Niño) then it is important that the assessment chooses a natural base-line appropriate to the oceanic condition at the time of the assessment survey. If this is not done, differ-ences in the observed distribution of guilds and guild species may be misinterpreted as being the result of anthropogenic activities rather than to a shift to a dif-ferent natural oceanic regime. A similar result was shown for populations of species in southern California over a 30-year period, with some species being warm-regime species with population trends increasing during warm periods and decreasing dur-ing cold periods and others being cold-regime species, with populations increasing during cold periods and decreasing during warm periods (Allen et al. 2004). In fact, the population trend response as well as the bathymetric response are both proba-bly occurring during the warm regime, cold regime, and El Niño periods.

The functional structure of soft-bottom fish com-munities approach for describing community organi-zation off southern California has recently (Allen 2006) been extended along the West Coast from the

California-Oregon border to the tip of Cabo San Lucas, Baja California Sur, at depths from 10 - 500 m. That study describes how the functional structure of soft-bottom fish communities change biogeographically within bathymetric life zones and bathymetrically within a biogeographic region. This information may provide the basis for assessing oceanic regime affects on the organization of soft-bottom fish communities to the north and south of the Southern California Bight.

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