



A comparison of long-term trends and variability in populations of larvae of exploited and unexploited fishes in the Southern California region: A community approach

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Abstract

We have constructed an “expert-knowledge classification system” to categorize 309 fish taxa in the California Cooperative Oceanic Fisheries Investigations ichthyoplankton database into primary (coastal, coastal-oceanic, and oceanic) assemblages based on their principal ecological domains and subsequently, secondary assemblages according to the habitat affinities of adults. We examined effects of fishing, climate, adult habitat, and age-at-maturation on long-term variation of fish populations. We tested the hypothesis that populations of unexploited taxa track climatic trends more closely than those of exploited taxa insofar as climatic signals may be confounded by fishing effects.

Most oceanic taxa (23/34) showed a significant relationship with environmental variables and followed the trend of the Pacific Decadal Oscillation. Very few coastal (3/10) and coastal-oceanic (3/23) taxa exhibited a significant relationship with environmental signals; **however, several fluctuated coherently**, and age-at-maturation is an important factor. The lack of close correlation between fish populations and environmental signals in the coastal and coastal-oceanic assemblages **indicates that these species might show nonlinear biological responses** to external forcing rather than a simple linear tracking of environmental variables.

We did not find a systematic pattern indicating that fishing influenced population fluctuation of exploited species. Constrained comparisons of exploited to unexploited species living in the same habitat and reaching maturity at the same age revealed evidence of overexploitation for some species but not for all. Our results suggest that considering

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life history and ecological characteristics of fish species and applying a community approach are important in understanding fishing effects on fish populations in the context of a changing environment.

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1. Introduction

Understanding decadal-scale climatic effects on the Northeast Pacific marine ecosystem is an important issue because strong environmental changes have occurred at this time scale (Chavez, Ryan, Lluch-Cota, & Niquen, 2003; Hare & Mantua, 2000; McGowan, Bograd, Lynn, & Miller, 2003; Venrick, McGowan, Cayan, & Hayward, 1987). It has been hypothesized that a regime or an ocean climate condition may persist for 2–3 decades and then undergo a rapid change to another state (Mantua, Hare, Zhang, Wallace, & Francis, 1997; Trenberth & Hurrell, 1994). However, whether these changes are regime shifts generated from underlying nonlinear dynamics or manifestations of red noise is still debated (Pierce, 2001; Rudnick & Davis, 2003). Evidence of warming in the North Pacific since 1976 and a variety of biological responses have been noted (Beamish, Neville, & Cass, 1997; Brinton & Townsend, 2003; Lavaniegos & Ohman, 2003; Roemmich & McGowan, 1995a, 1995b). Cool conditions in the North Pacific continuing after 1998 suggest another transition to a new ocean state (Ohman & Venrick, 2003; Peterson & Schwing, 2003). In addition to these low-frequency effects, biological production is affected by high-frequency El Niño/Southern Oscillation events (Fiedler, Methot, & Hewitt, 1986; Yoklavich, Loeb, Nishimoto, & Daly, 1996).

Clearly, fluctuations of exploited fish populations can be affected by both environmental forcing and fishing mortality (Jacobson et al., 2001; McFarlane, Smith, Baumgartner, & Hunter, 2002), and these factors are inextricably convolved in catch data. From the viewpoints of fisheries management and conservation of marine resources, it is important to determine fishing effects on fish populations and communities within the context of a changing environment. This view is an essential component of ecosystem-based approaches to fisheries management that has gradually become the standard requirement for fisheries management; that is, to base management decisions not only on the status of a fish population but also the ecosystem (Browman & Stergiou, 2004; Garcia, Zerbi, Aliaume, Do Chi, & Lasserre, 2003; NOAA, 1999; Pikitch et al., 2004). One practical issue here is to develop approaches that can be used to separate fishing from environmental effects on fish populations. Analyses of long-term data on the abundance of species taken independently of their fishery offer the best chance to achieve this goal. The larval fish data collected in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) may be useful to separate these effects, because the CalCOFI program is one of the most comprehensive observational oceanography programs in the world and spans more than 50 years (Hewitt, 1988; Ohman & Venrick, 2003).

Larval abundances are primarily measures of the spawning biomass and reproductive effort of the adult stock for the year, because most larvae taken in plankton nets are in a very early stage of development. However, their abundance is not correlated with subsequent year class strength (Peterman, Bradford, Lo, & Methot, 1988). Long-term trends in larval abundance mostly reflect trends in adult biomass; short-term fluctuations are likely related to episodes of high or low reproductive output or geographic shifts due to animal movement (e.g., El Niño effects), since sudden changes in biomass would not be expected (Moser et al., 2000). Several studies have shown that larval abundance is a good indicator of adult biomass (Gunderson, 1993; Moser et al., 2000; Moser et al., 2001b; Moser & Watson, 1990). The common use of larval indices in stock assessment models also supports this conclusion. Given that there are no long-term

survey data of adult populations, and fisheries data are confounded by changing fishing mortality, the CalCOFI larval fish data are one of best sources of information for monitoring the relative sizes of adult populations along the west coast of the United States.

One possible use of larval fish data is to consider the larvae as representatives of the various communities of adult fishes that produced them. Fish communities can be determined based on adult habitats, assuming that species using the same habitats should interact. In the southern California region, community ecology of coastal fishes has been studied (Allen, 1982; Horn & Allen, 1985), and both biogeography and habitat use documented (Horn, 1980; Horn & Allen, 1978; Miller & Lea, 1972). However, this study is the first attempt to categorize all fish species whose larvae are collected in the CalCOFI program into distinct communities according to the adult habitat. We use “assemblage” instead of “community” to represent species that live in the same biogeographic region and habitat, and thus, “potentially” interact with each other, because a community cannot be defined from our data.

Species living in the same habitat should experience the same environmental forcing. Long-term variability of fish population size is a product of species interactions and species responses to the environment as well as fisheries. In order to understand this variability, we propose to examine assemblages of species rather than individual species. In addition to habitat, life history traits are known to affect the responses of fish populations to fisheries and the environment (Adams, 1980). Here, we examined only age-at-maturation, because data for other factors are sparse, especially for noncommercial species. Our approach was to compare within and between groups of species, with group membership constrained by their habitats and life history traits in order to reduce confounding effects.

We started with a description of fish assemblages in the Southern California Region (SCR). We used the ichthyoplankton time series to examine species co-variation (cross-correlations among taxa) for each assemblage and determined factors affecting that co-variation. We tested the hypothesis that populations of unexploited taxa track climatic trends more closely than those of exploited taxa, because climatic signals may be confounded by fishing effects. Finally, we compared exploited and unexploited taxa within an assemblage living in the same habitat and reaching maturity at about the same age in the SCR. The potential and limitation of this community approach based on the CalCOFI data are discussed.

2. Materials and methods

2.1. The expert-knowledge classification system

We constructed an “expert-knowledge classification system” to categorize species (or higher taxa) in the CalCOFI ichthyoplankton database into assemblages (Table 1 and Supplementary Table 1). This system included a panel of experts (Allen, Hunter, Lea, Moser, Rosenblatt, and Watson) and the literature where available. Three primary assemblages (coastal, coastal-oceanic, and oceanic) were defined based on their cross-shore distribution. These three assemblages are considered the principal ecological divisions of the fish species in the SCR. Within each primary assemblage, secondary assemblages were categorized based on adult habitats.

2.2. Life history data

We compiled information on age-at-maturation for species whose larvae commonly occur in coastal and coastal-oceanic habitats (Supplementary Table 2). Our best choice was to use studies based on California specimens. Lacking that, in order of preference, we used:

Table 1

Summary of criteria used in the “expert-knowledge classification system” to determine fish assemblages

Oceanic (seaward of the slope)*Depth*

Epipelagic (upper 200 m)

Epi-mesopelagic migrator

Mesopelagic

Bathypelagic

Region

World wide

North Pacific

Pacific

Coastal-oceanic

Region

North: north of Point Conception

Bight: characteristic of the Southern California Bight (SCB: defined for this purpose as Point Conception, California, to Punta Eugenia, Baja California, Mexico)

South: south of Punta Eugenia

Broad north: broadly distributed from the SCB northward

Broad south: broadly distributed from the SCB southward

All: found in all regions above

Coastal (continental shelf and upper slope)

*Shore*Nearshore: ≤ 30 mOffshore: not restricted to ≤ 30 m*Region*

As defined in the coastal-oceanic group

Bottom

Kelp/hard: kelp and/or hard bottom

Both: both hard and soft bottom

Soft: soft bottom

Water: water column (bottom type unimportant)

Fishing status

Fished (targeted, recreational and/or commercial)

Bycatch (not targeted but subject to fishery mortality)

Unfished (no significant fishing mortality)

Note that the order of the listed criteria does not imply any priority except the three primary assemblages.

1. Studies on the species from elsewhere in the world.
2. Studies on species of similar size within the same genus.
3. Estimates from relationships between maximum-body-length and age-at-maturation.

The age-at-maturation is defined as the age at which 50% of the population reaches maturity. When the age-at-maturation was reported as a range, we used the median age. Life history data for most oceanic species are lacking and were not included in the analyses.

2.3. Data processing

The spatial coverage of CalCOFI surveys has changed through time. For consistency, we restricted our analyses to the current array of 66 stations in the SCR (Fig. 1(a)) and to samples collected in oblique tows.

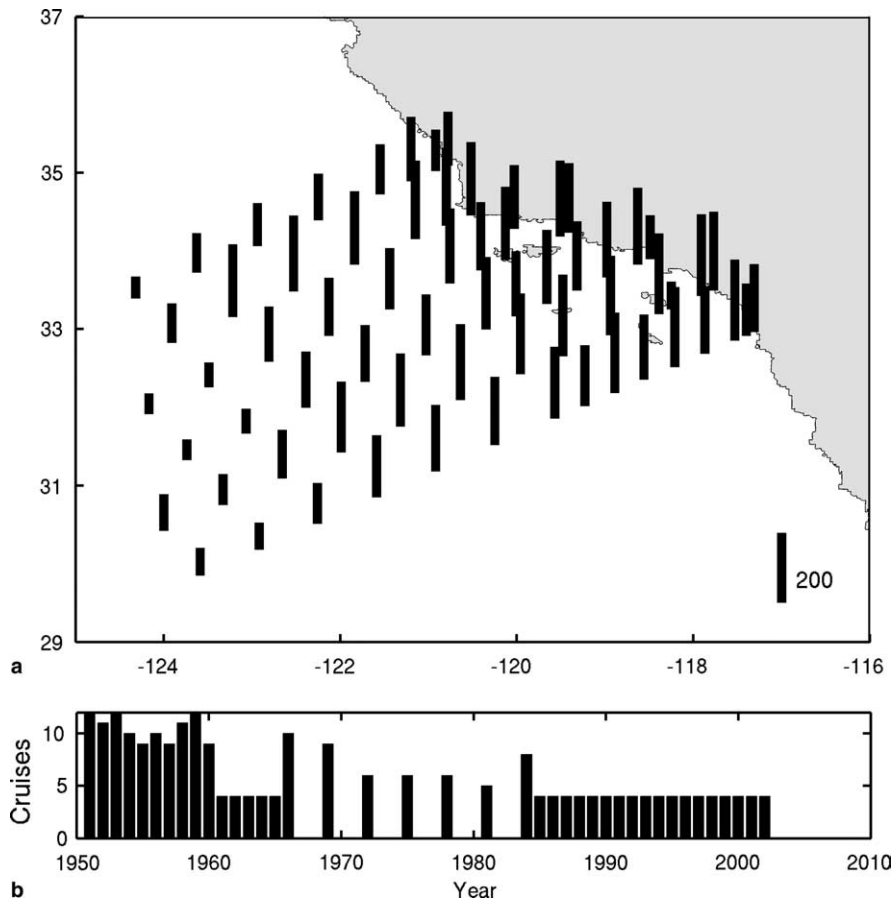


Fig. 1. Maps showing (a) spatial pattern of CalCOFI stations used in this study and number of samples at each station, and (b) temporal sampling frequency.

The abundance time series for each species is composed of net tows taken from 1951 to 2002 (40 sampling years). The occupation numbers for each station are shown in Fig. 1(a). The abundance time series was calculated by taking the spatial average for each cruise, and then the annual average was calculated based on the known spawning period of each species according to Moser et al. (2001a). Note that the sampling was triennial from 1966 to 1984 (Fig. 1(b)). In constructing the time series, we assumed that spatial heterogeneity and sampling errors are insignificant after the averaging process (we shall come back to this point in Section 4).

2.4. Changes in taxonomic knowledge

Since the inception of the CalCOFI program, fish larvae have been identified to species or the lowest taxon that prevailing knowledge permitted. In the 1980s, the ability to identify larvae in the California Current region was greatly improved as a result of a concerted effort to provide better taxonomic resolution (Moser, 1996). The taxonomic history of each species is reconstructed here according to the records in the CalCOFI database, as well as the current knowledge of experts in larval fish taxonomy. Note that some species were combined early on, but later were resolved to the species level (Supplementary Table 1). For

taxonomic consistency through time, species without continuous identification records were aggregated back to the generic, familial, or even ordinal level whenever necessary in analyses.

2.5. Changes in sampling methods

There have been two major changes in ichthyoplankton sampling methods in the CalCOFI program (Ohman & Smith, 1995): (1) the depth of hauls was increased from 140 to 210 m in 1969; (2) sampling gear was changed from a 1.0-m-diameter ring net to a 0.71-m-diameter bridle-less bongo net in 1978.

The increase in sampling depth in 1969 would bias abundances toward higher estimates for taxa whose larval distributions are substantially deeper than 140 m. This change should have had little effect on the coastal and coastal-oceanic assemblages because their larval distributions are generally shallower than 140 m (Moser & Pommeranz, 1999). For the oceanic assemblage, some mesopelagic species have deeper larval distributions. We compiled the limited information from studies of vertical distributions of larvae off southern California (Ahlstrom, 1959). Among the 34 oceanic taxa examined, 13 had no information on vertical distributions, 17 had distributions shallower than 140 m, and four had distributions deeper than 140 m (Table 2). Among the four deep taxa, California flashlightfish (*Protomyctophum crockeri*) and the scopelarchids range much deeper than 210 m and the bias should be less significant. Although we have limited information on larval vertical distributions, we believe this bias is minor.

The bias of abundance estimates due to the net change should also be minor. Hewitt (1980) compared the catch efficiency of the Bongo and ring net for anchovy larvae and found no significant difference in estimated total abundance, although larger size classes were collected more effectively by the Bongo net. No similar comparison has been made for other taxa, but we assume their larvae had similar responses to the net change.

2.6. Time series of abundances

To examine climatic and fishing effects on larval fish abundances (inds./10 m²), we (1) examined species co-variation for the oceanic, coastal-oceanic, and coastal assemblages; (2) determined the effects of habitat factors (Table 1), fishing, and age-at-maturation on species co-variation; and (3) examined the relationship between abundance and environmental variables for each taxon. We chose taxa with a high-frequency of occurrence (>30 of the 40 sampling years) for our time series analysis because taxa with a lower frequency of occurrence might not be sampled representatively. Based on this criterion, 67 taxa were used in the following analyses.

Species exhibiting a significant correlation are likely driven by the same dynamics. To examine species co-variation, we computed pair-wise correlation coefficients between taxa of an assemblage. A stationary bootstrap procedure was used to compute the 95% confidence interval of the correlation coefficient and perform the hypothesis test. This approach is nonparametric and accounts for autocorrelation in the time series (Politis & Romano, 1994; Politis, 2003).

To examine the effects of habitat, fishing, and age-at-maturation on species co-variation, we calculated the number of significant correlations out of all possible comparisons within and between categories (e.g., species within the same habitat: water, kelp/hard bottom, soft bottom and both, and between different habitats). If a given categorization factor significantly affects the species co-variation, the proportion of significant correlations within categories will be higher than between categories. This was tested by Fisher's exact statistics at $\alpha = 0.05$. Age-at-maturation was categorized for the coastal and coastal-oceanic assemblages as: age 1–2, 2–3, 3–4, 3.5 and above.

In order to determine whether environmental forcing has driven the coherent fluctuations of species abundances, we investigated the relationship between abundance and environmental variables using a forward-stepwise multiple regression. Again, the stationary bootstrap test was used to account for serial

Table 2

Larval vertical distributions compiled from the literature showing their upper limit (up), modal depth (mode), and lower limit (low)

	Moser and Smith (1993)	Ahlstrom (1959)
	Up-mode-low	Up-mode-low
<i>Aristostomias scintillans</i>		72, from 1 cruise (only one individual)
<i>Bathylagus ochotensis</i>	75-87.5-400	
<i>Bathylagus pacificus</i>		
<i>Bathylagus wesethi</i>	50-87.5-250	2-88-138, from 6 cruises
<i>Ceratoscopelus townsendi</i>	0-37.5-175	
<i>Chauliodus macouni</i>	0-212.5-400	105, from 2 cruises (one individual in each cruise)
<i>Chiasmodon niger</i>		
<i>Cyclothone</i> spp.	0-87.5-200	2-56-88, from 6 cruises
<i>Diaphus theta</i>	25-62.5-225	
<i>Diogenichthys atlanticus</i>	50-87.5-300	8-72-72, from one cruise
<i>Hygophum reinhardtii</i>		
<i>Idiacanthus antrostomus</i>		105-138, from 1 cruise
<i>Melamphaes</i> spp.	25-87.5-300 (850) ^a	56-72-138, from 6 cruise
<i>Microstoma</i> spp.		56-105-105, from 3 cruises
Myctophidae		
<i>Myctophum nitidulum</i>		
<i>Nannobranchium</i> spp.	25-37.5-300	2-50-138, from 19 cruises
<i>Nansenia candida</i>		
<i>Notolychnus valdiviae</i>		
<i>Notoscopelus resplendens</i>		
Paralepididae	25-187.5-250	
<i>Poromitra</i> spp.		
<i>Protomyctophum crockeri</i>	175-212.5-550	
Scopelarchidae	300-1000-1000	72-138-215, from 5 cruises
<i>Scopelogadus bispinosus</i>		
<i>Scopelosaurus</i> spp.		
<i>Stenobranchius leucopsarus</i>	75-87.5-200	
Sternoptychidae		
<i>Stomias atriventer</i>	25-37.5-200	41-72, from 2 cruises
<i>Symbolophorus californiensis</i>	25-112.5-300	
<i>Tactostoma macropus</i>		
<i>Tarletonbeania crenularis</i>	75-137.5-400	28-56-138, from 6 cruises
<i>Triphoturus mexicanus</i>	0-62.5-300	
<i>Vinciguerrria lucetia</i>	0-62.5-125 (1000) ^a	2-41-105, from 5 cruises

The taxa indicated with bold have a distribution deeper than 140 m determined by the mode.

^a For *Melamphaes* spp. and *Vinciguerrria lucetia*, one extra deep sample was found but main distribution remained in the shallow layer.

dependence in the time series. We used two local variables, CalCOFI sea-surface temperature and the upwelling index, and three large-scale variables, the Southern Oscillation Index (SOI), the Pacific Decadal Oscillation Index (PDO), and the North Pacific Index (NPI), as well as their lags up to three years. The CalCOFI sea-surface temperature is based on the spatial average over our sampling domain (Fig. 1(a)). The upwelling index (Bakun, 1990) anomaly in the center of the Southern California Bight (33N, 119W) is associated with the local nutrient and hydrographic dynamics within the CalCOFI sampling domain. The SOI is based on atmospheric pressure differences between Tahiti and Darwin (Trenberth, 1984), indicating the state of the El Niño/Southern Oscillation (ENSO). The PDO is based on the first empirical orthogonal function of sea-surface temperature in the North Pacific (Mantua et al., 1997). The NPI is the area-weighted sea level pressure over the region 30N–65N, 160E–140W (Trenberth & Hurrell, 1994).

The PDO and NPI track the leading patterns of sea surface temperature variability and North Pacific sea-level pressure, respectively. We applied a permutation test (Manly, 1997) to determine whether there was a significant change in abundance between the cold (1951–1976) and warm (1977–1998) period for each taxon. We excluded 1999–2002 from the between-period comparisons because we cannot be sure that a transition occurred in 1999.

2.7. Constrained pair-wise comparisons

To further investigate fishing effects on exploited species, we applied “constrained comparisons”: comparing exploited to unexploited species living in the same habitat and reaching maturity at about the same age. These constraints were used to minimize confounding effects. We normalized each time series (to zero mean and unit variance), and plotted the exploited (y -axis) against unexploited (x -axis) species for two periods: before and after 1976. If the two species varied coherently, the data would scatter along the 1:1 line. We assume that fluctuation of the unexploited species reflects natural variation. The exploited species would fluctuate coherently with the unexploited species (i.e., the data fall along the 1:1 line) if fishing pressure did not significantly affect natural variation. The data would fall below the 1:1 line if the population of the exploited species was greatly reduced by strong fishing pressure.

3. Results

3.1. The expert-knowledge classification system and three primary assemblages

The “expert-knowledge classification system” was used to categorize 309 fish taxa into assemblages (Supplementary Table 1). Subsequent aggregation to higher taxonomic levels in order to assure taxonomic consistency resulted in 178 taxa. Percentages of fished, bycatch, or unfished taxa in each of the three primary assemblages are summarized in Table 3, before and after taxonomic aggregation. There were no fishing-targeted species in the oceanic assemblage, except as occasional bycatch. Fewer than half of the taxa in the coastal-oceanic assemblage were targeted, but those targeted species were commercially important: northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), Pacific chub mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and Pacific sardine (*Sardinops sagax*). About half of the taxa in the coastal assemblage were exploited.

Table 3

Number of taxa and percentage of the fished, bycatch, and unfished in the three primary assemblages before and after taxonomic aggregation

Group	Fished	Bycatch	Unfished	Number of taxa
<i>Before aggregation</i>				
Coastal	0.363	0.153	0.382	157
Coastal-oceanic	0.333	0	0.417	24
Oceanic	0	0.016	0.984	128
<i>After aggregation</i>				
Coastal	0.493	0.155	0.183	71
Coastal-oceanic	0.350	0	0.450	20
Oceanic	0	0.023	0.977	87

The sum of each row is not equal to 1 because fishing status cannot be determined for some of the higher taxonomic complexes.

3.2. Species co-variation

For the time series analyses, we categorized 67 taxa with a high-frequency of occurrence into oceanic (34 taxa), coastal-oceanic (10 taxa), and coastal (23 taxa) assemblages, and then sub-categorized them into fished, bycatch, and unfished groups (Fig. 2). Note that all the oceanic taxa are unfished. To examine their

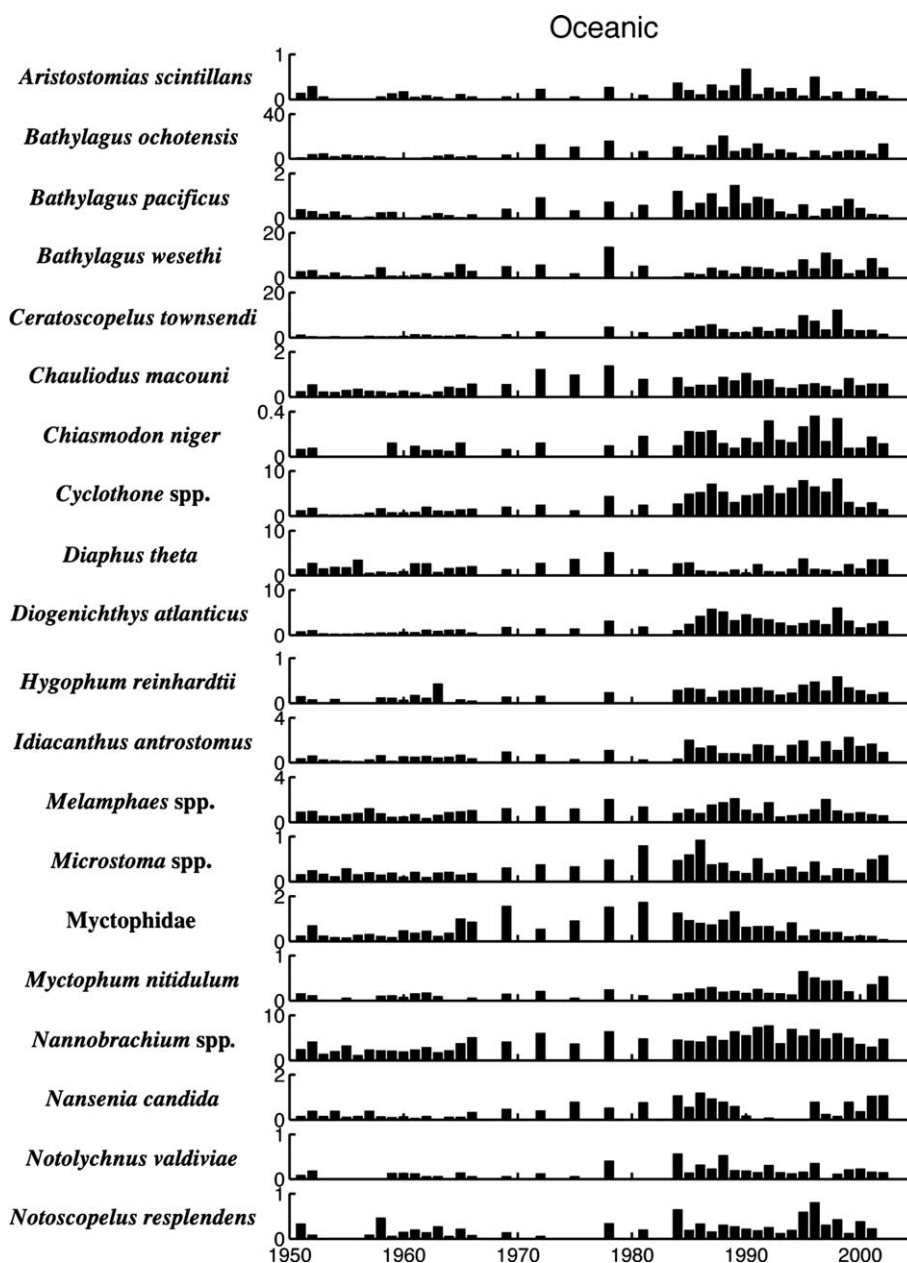


Fig. 2. Abundance time series of the taxa with a high-frequency of occurrence grouped into oceanic, coastal-oceanic-fished, coastal-oceanic-unfished, coastal-fished, coastal-bycatch, and coastal-unfished categories. (Arrows indicate low abundances after ENSO events.)

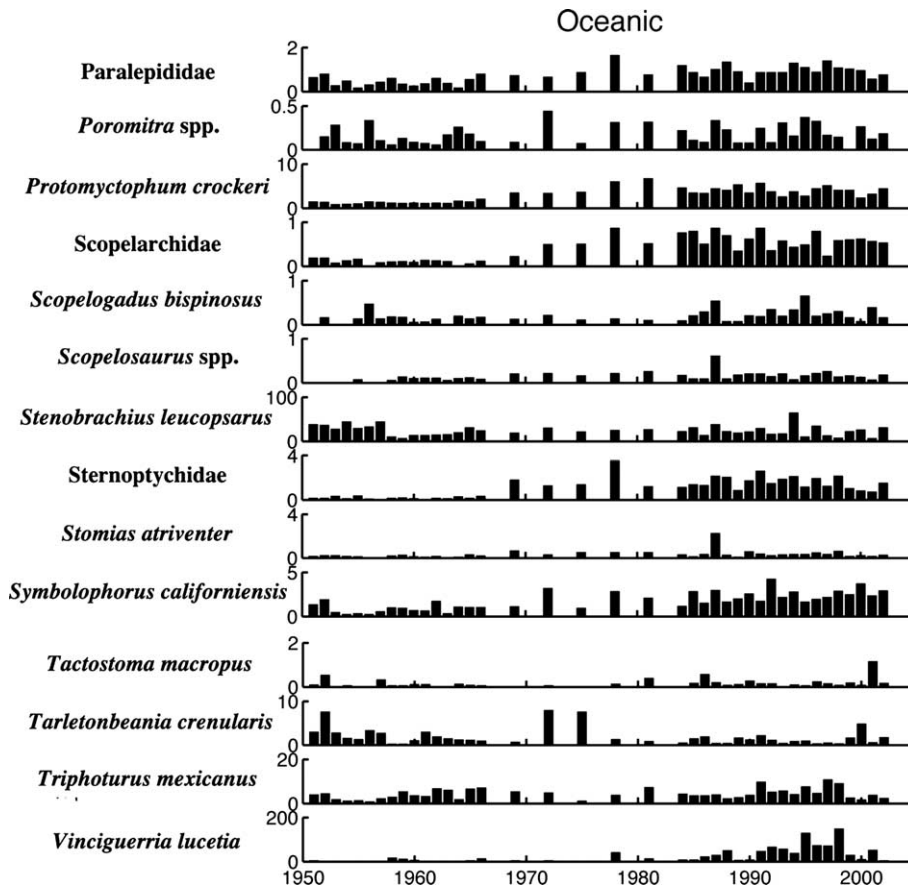


Fig. 2 (continued)

long-term coherence and factors affecting their co-variation, we tested pair-wise correlations between taxa within each of the three primary assemblages (Table 4). For each primary assemblage, the same matrix was reorganized according to fishing status, habitat, geographic distribution, and age-at-maturation for revealing the correlation structure. Based on Fisher's exact test, habitat depth was an important factor determining species co-variation in the oceanic assemblage ($p = 0.0150$) (Table 4). For the coastal-oceanic assemblage, age-at-maturation was marginally significant ($p = 0.1522$) (Table 4). For the coastal assemblages, age-at-maturation was the only significant factor ($p = 0.0306$) (Table 4).

3.3. Time series of fish abundances and climatic signals

To investigate climatic effects, we examined the relationship between fish abundances and environmental variables, and compared abundance between the cold (1951–1976) and warm (1977–1998) period. The five environmental variables that we examined are correlated. In the regression analysis, we selected variables that produced the best regression model. Among the 34 oceanic taxa, 29 increased in abundance from the cold to warm period, and 23 were correlated with the PDO index or the Cal-

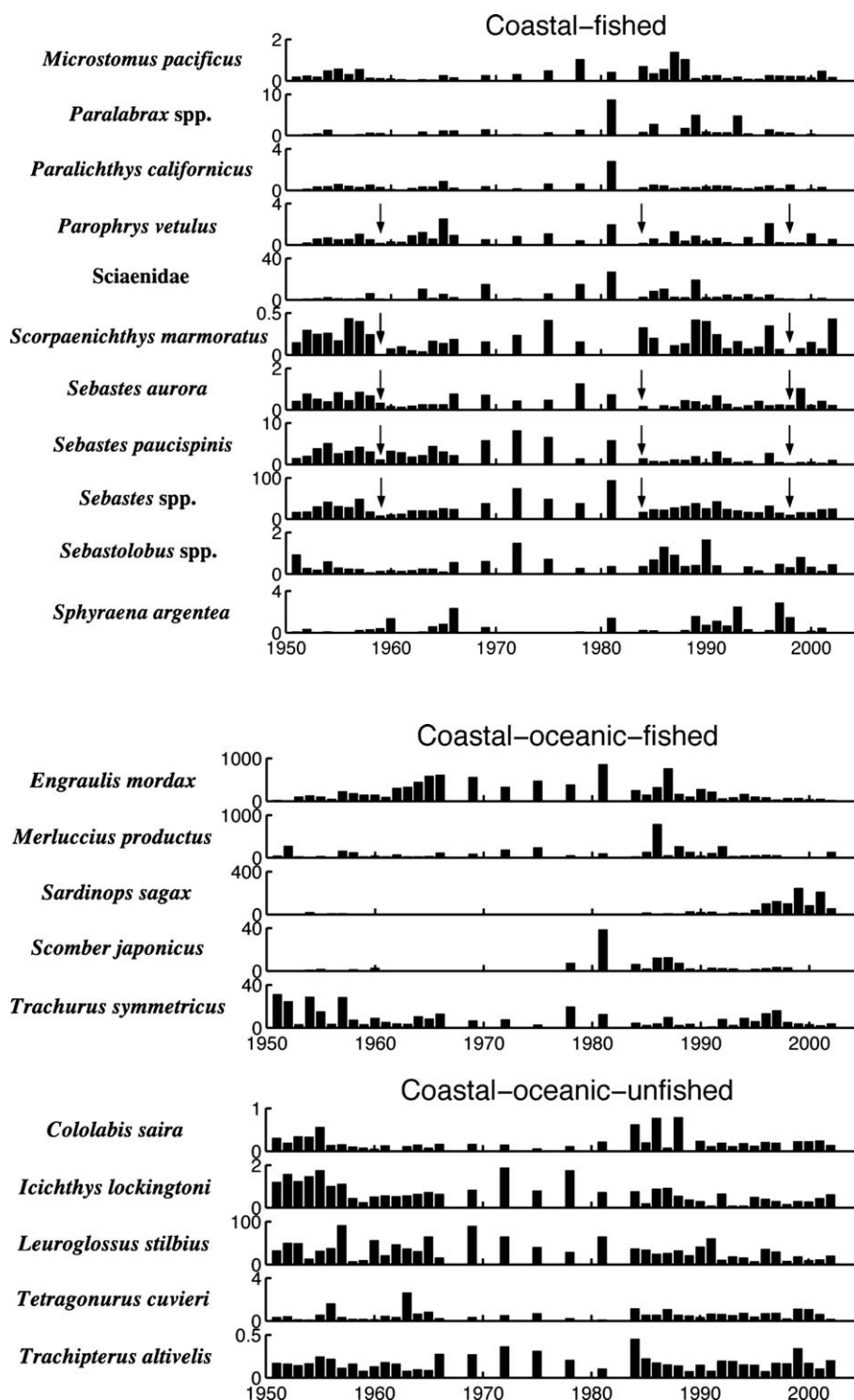


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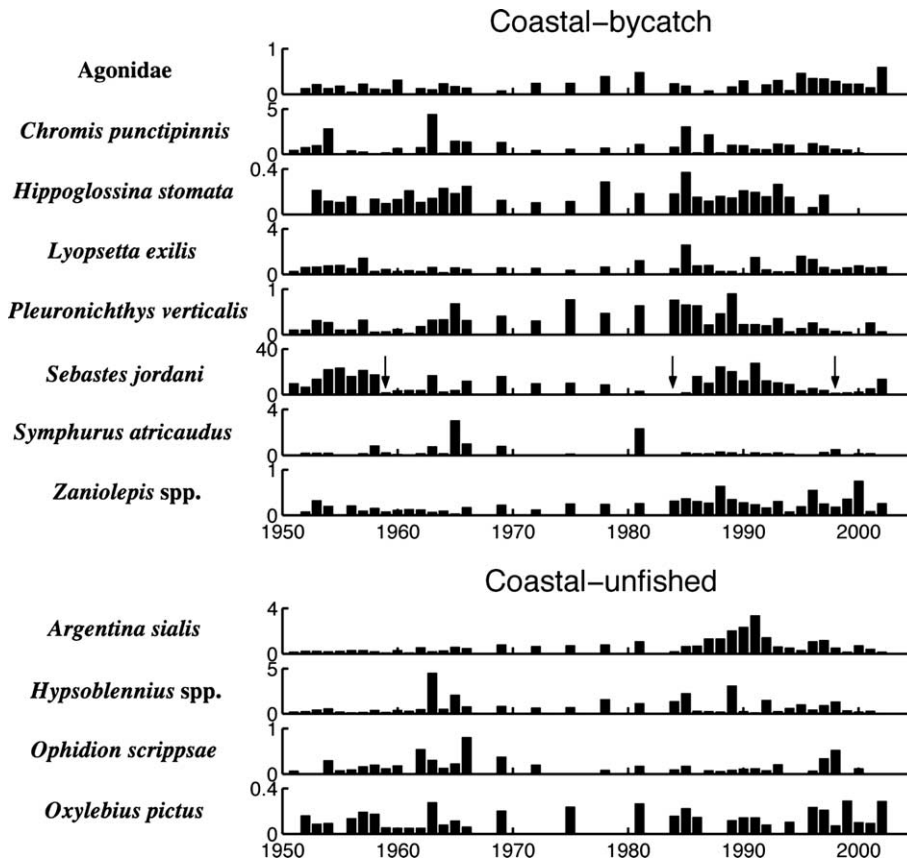


Fig. 2 (continued)

COFI SST (Table 5 and Fig. 2). Mexican lampfish (*Triphoturus mexicanus*) is the only species correlated with the SOI (Table 5). Larvae of tropical–subtropical taxa consistently increased in abundance in the warm period (Table 5 and Fig. 2). One might expect decreasing abundances for subarctic–transitional taxa during the warm period, but this occurred only in blue lanternfish (*Tarletonbeania crenularis*); on the contrary, nine among the 12 subarctic–transitional taxa also increased in abundance during the warm period (Table 5 and Fig. 2). Four species, Dogtooth lampfish (*Ceratoscopelus townsendi*), Pacific blackdragon (*Idiacanthus antrostomus*), topside lampfish (*Notolychnus valdiviae*), and patchwork lampfish (*Notoscopelus resplendens*), all widely distributed from temperate to tropical regions, also increased in abundance in the warm period (Table 5 and Fig. 2). These results suggest that the fluctuations in abundance of the oceanic taxa were highly associated with the temperature pattern in the Northeast Pacific.

Among the coastal–oceanic assemblage, Pacific sardine and Pacific chub mackerel increased and medusafish (*Ichthyos lockingtoni*) decreased in abundance in the warm period (Table 5 and Fig. 2). Abundance of Pacific chub mackerel was positively correlated with the PDO, jack mackerel negatively correlated with the PDO with lag two years, and medusafish positively correlated with the CalCOFI SST (Table 5). Only these three among the 10 coastal–oceanic species exhibited a significant correlation with the environmental

variables examined. We did not find that unexploited species are more strongly correlated than exploited species with the environmental variables.

Among the coastal assemblage, Pacific argentine (*Argentina sialis*), kelp and sand basses (*Paralabrax* spp.), and combfishes (*Zaniolepis* spp.) increased significantly and bocaccio (*Sebastes paucispinis*) decreased significantly in abundance from the cold to warm period (Table 5 and Fig. 2). Only three among the 23 coastal species exhibited a significant correlation with environmental variables examined. Abundance of kelp and sand basses was positively correlated with the PDO, cabezon (*Scorpaenichthys marmoratus*) positively correlated with the NPI, and bocaccio negatively correlated with the CalCOFI SST (Table 5). Abundances of English sole (*Parophrys vetulus*), cabezon, aurora rockfish (*Sebastes aurora*), bocaccio, unidentified rockfishes (*Sebastes* spp.), and shortbelly rockfish (*Sebastes jordani*) fluctuated with an irregular, shorter period corresponding to ENSO events. Particularly low abundances occurred after the 1958, 1983, and 1997 El Niños (Fig. 2, indicated by arrows). Although these taxa responded similarly in timing to the ENSO events, their correlations with the SOI were not significant (Table 5 and Fig. 2). The reductions of larval abundance after the ENSO events are likely due to the low reproductive output for these years. Again, we did not find that unexploited species are more strongly correlated than exploited species with the environmental variables.

Table 4

Correlation matrices for oceanic, coastal-oceanic, and coastal assemblages showing correlations between species (1: significant; 0: otherwise)

The oceanic group

Geographic regions:

North Pacific	<i>Aristostomias scintillans</i>																Within: 72/146 Between: 113/260 Fisher's Exact: p = 0.1509	
	<i>Bathylagus ochotensis</i>	1																
	<i>Bathylagus pacificus</i>	1	1															
	<i>Ceratoscopelus townsendi</i>	0	0	1														
	<i>Chauliodus macouni</i>	1	1	1	0													
	<i>Diaphus theta</i>	0	0	0	0	0												
	<i>Idiacanthus antrostomus</i>	0	0	1	1	0	0											
	<i>Nansenia candida</i>	0	1	0	0	1	0	0										
	<i>Protomyctophum crockeri</i>	1	1	1	1	1	0	1	1									
	<i>Stenobrachius leucopsarus</i>	0	0	0	0	0	0	0	0	0								
	<i>Stomias atriventer</i>	1	1	1	1	0	0	0	0	1	0							
	<i>Symbolophorus californiensis</i>	1	1	1	1	1	0	1	0	1	0	1						
	<i>Tactostoma macropus</i>	0	0	0	0	0	0	0	1	0	0	0	0					
<i>Tarletonbeania crenularis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0				
Pacific	<i>Bathylagus wesethi</i>	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0 1 0 1 1 0 1 1 1 1		
	<i>Hypogomphus reinhardtii</i>	1	0	1	1	0	0	1	0	1	0	0	1	0	0			
	<i>Scopelogadus bispinosus</i>	0	0	0	1	0	0	1	0	0	0	0	1	0	0			
	<i>Triphoturus mexicanus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0			
	<i>Vinciguerria lucetia</i>	0	0	0	1	0	0	1	0	1	0	0	0	0	1			
World	<i>Chiasmodon niger</i>	1	0	1	1	0	0	1	0	1	0	0	1	1	1	1	1 1 1 1 0 1 1 1 0 1 1 0 1 1 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1	
	<i>Diogenichthys atlanticus</i>	1	1	1	1	1	0	1	1	1	0	1	1	0	0			
	<i>Microstoma</i> spp.	0	1	0	1	1	0	0	1	1	0	0	0	1	0			
	<i>Myctophum nitidulum</i>	0	0	0	1	0	0	1	0	1	0	0	1	0	0			
	<i>Notolychnus valdiviae</i>	1	1	1	1	1	0	0	1	1	0	0	1	0	0			
	<i>Notoscopelus resplendens</i>	1	0	0	1	0	0	0	1	0	0	0	0	0	1			
	<i>Poromitra</i> spp.	0	1	0	1	0	0	0	0	0	0	0	0	0	0			
	Scopelarchidae	1	1	1	1	1	0	1	1	1	0	1	1	0	0			
	<i>Scopelosaurus</i> spp.	1	1	1	1	1	0	1	0	1	0	1	1	0	0			
	Sternoptychidae	1	1	1	1	1	0	1	0	1	0	1	1	0	0			

Table 4 (continued)

Depth:		Within: 112/214 Between: 105/251 Fisher's Exact: p = 0.015	
Migrator	<i>Ceratoscopelus townsendi</i> <i>Diaphus theta</i> <i>Hygophum reinhardtii</i> <i>Myctophum nitidulum</i> <i>Nannobranchium</i> spp. <i>Notolychnus valdiviae</i> <i>Notoscopelus resplendens</i> <i>Protomystophum crockeri</i> <i>Stenobranchius leucopsarus</i> <i>Symbolophorus californiensis</i> <i>Tarletonbeania crenularis</i> <i>Triphoturus mexicanus</i> <i>Vinciguerrria lucetia</i>	0 1 0 1 0 1 1 0 1 1 1 0 1 0 1 1 0 1 1 1 1 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0 1 0 1 1 1 1 0 1 0 0 1 0 0 0 0 1 0 0 0 1 0 1 1 1 0 0 0 0 0 0 1 0 1 1 1 0 1 0 0 1 1	
Mesopelagic	<i>Aristostomias scintillans</i> <i>Bathylagus ochotensis</i> <i>Bathylagus pacificus</i> <i>Bathylagus wesethi</i> <i>Chauliodus macouni</i> <i>Diogenichthys atlanticus</i> <i>Idiacanthus antrostomus</i> <i>Melamphaes</i> spp. <i>Microstoma</i> spp. <i>Nansenia candida</i> <i>Poromitra</i> spp. <i>Scopelarchidae</i> <i>Scopelogadus bispinosus</i> <i>Scopelosaurus</i> spp. <i>Sternoptychidae</i> <i>Stomias atriventer</i> <i>Tactostoma macropus</i>	0 0 1 0 1 1 1 1 0 1 0 0 0 0 0 0 0 1 1 0 1 0 1 0 0 0 1 0 1 0 1 1 0 1 0 1 0 0 0 1 0 0 1 1 0 0 1 0 1 0 1 1 0 0 0 0 1 1 0 1 0 1 0 0 0 1 0 1 1 1 1 1 1 0 1 0 0 1 1 0 1 1 1 0 0 1 0 1 0 0 1 0 0 0 0 1 0 0 1 0 1 0 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 1 1 1 1 0 1 0 0 1 1 0 0 1 1 0 0 0 0 1 0 0 1 1 0 0 1 1 0 0 1 0 1 0 1 0 1 0 1 1 1 1 0 1 0 1 0 0 1 1 0 0 1 1 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 1 1 0 1 0 1 0 1 0	1 1 1 0 0 0 1 1 1 0 1 1 1 1 1 0 0 1 1 0 1 0 1 1 1 1 1 0 0 1 0 0 1 1 0 0 0 1 0 0 1 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 0 1 1 1 0 0 1 0 1 1 0 0 0 1 0 1 1 1 1 1 1 1 1 0 0 1 1 0 1 1 1 1 1 1 1 1 1 0 1 0 1 1 1 1 0 0 1 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 1 1 0 0 0 0 0
Bathypelagic	<i>Chiasmodon niger</i>	1 0 1 1 1 1 1 1 1 0 1 0 1	1 1 0 1 1 0 1 1 0 1 0 1 0 0 1 1 1 1 0

The coastal-oceanic group**Fishing status:**

Fished	<i>Engraulis mordax</i> <i>Merluccius productus</i> <i>Sardinops sagax</i> <i>Scomber japonicus</i> <i>Trachurus symmetricus</i>	0 1 0 0 0 0 0 0 0 0	Within: 2/20 Between: 4/25 Fisher's Exact: p = 0.4473
Unfished	<i>Cololabis saira</i> <i>Icichthys lockingtoni</i> <i>Leuroglossus stilbius</i> <i>Tetragonurus cuvieri</i> <i>Trachipterus altivelis</i>	0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0

Geographic regions:

Broad north	<i>Merluccius productus</i> <i>Cololabis saira</i> <i>Icichthys lockingtoni</i> <i>Leuroglossus stilbius</i> <i>Tetragonurus cuvieri</i> <i>Trachipterus altivelis</i>	0 0 0 0 0 1 0 0 0 0 0 0 0 0 0	Within: 2/21 Between: 4/24 Fisher's Exact: p = 0.4001
All	<i>Engraulis mordax</i> <i>Sardinops sagax</i> <i>Scomber japonicus</i> <i>Trachurus symmetricus</i>	0 0 0 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0	1 0 0 0 0 0 0 0 0

(continued on next page)

Table 4 (continued)

Age-at-maturation:													
1	<i>Engraulis mordax</i>											Within: 5/25	
1.5	<i>Cololabis saira</i>	0										Between: 1/20	
2	<i>Sardinops sagax</i>	1	0									Fisher's Exact: p = 0.1522	
2	<i>Scomber japonicus</i>	0	0	0									
2.5	<i>Leuroglossus stilbius</i>	1	0	1	0								
3	<i>Trachurus symmetricus</i>	0	0	0	0	0	0						
3	<i>Icichthys lockingtoni</i>	0	0	1	0	1	1						
3.5	<i>Merluccius productus</i>	0	0	0	0	0	0	0	0				
3.5	<i>Tetragonurus cuvieri</i>	0	0	0	0	0	0	0	0	0			
4.5	<i>Trachipterus altivelis</i>	0	0	0	0	0	0	0	0	0	0		

The coastal group													
Fishing status:													
Fished	<i>Microstomus pacificus</i>											Within: 13/89	
	<i>Paralabrax</i> spp.	0										Between: 22/164	
	<i>Paralichthys californicus</i>	0	0									Fisher's Exact: p = 0.4660	
	<i>Parophrys vetulus</i>	0	0	0									
	Sciaenidae	0	1	1	1								
	<i>Scorpaenichthys marmoratus</i>	0	0	0	0	0	0						
	<i>Sebastes aurora</i>	0	0	0	0	0	0	0					
	<i>Sebastes paucispinis</i>	0	0	0	1	0	0	0	0				
	<i>Sebastes</i> spp.	0	0	0	1	1	0	1	1				
	<i>Sebastolobus</i> spp.	0	0	0	0	0	0	0	0	0	0		
	<i>Sphyræna argentea</i>	0	1	0	0	0	0	0	0	0	0		
Bycatch	Agonidae	0	0	0	0	0	0	0	0	0	0	0	
	<i>Chromis punctipinnis</i>	0	0	0	1	0	0	0	0	0	0	0	0
	<i>Hippoglossina stomata</i>	0	1	0	0	1	0	0	0	0	0	0	0
	<i>Lyopsetta exilis</i>	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Pleuronichthys verticalis</i>	1	1	1	1	1	0	0	0	1	0	0	0
	<i>Sebastes jordani</i>	0	0	0	0	0	1	0	0	0	0	0	0
	<i>Symphurus atricaudus</i>	0	1	0	0	1	0	0	0	0	0	0	0
	<i>Zaniolepis</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0
Unfished	<i>Argentina sialis</i>	0	0	0	0	0	0	0	0	0	0	1	
	<i>Hypsoblennius</i> spp.	0	1	0	0	1	0	0	0	0	0	0	0
	<i>Ophidion scrippsae</i>	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Oxylebius pictus</i>	0	0	0	0	0	0	0	0	0	0	0	0

3.4. Constrained pair-wise comparisons

Knowledge of adult habitats and age-at-maturation of coastal and coastal-oceanic species enables us to perform constrained comparisons (Fig. 3). For the coastal-oceanic assemblage, we compared northern anchovy to Pacific saury (*Cololabis saira*), both mature about age 1–2 and compared Pacific sardine and Pacific chub mackerel to California smoothtongue (*Leuroglossus stilbius*), all of which mature around age 2. No significant pattern was found in comparing northern anchovy with Pacific saury (Fig. 3(a)). In comparing the Pacific sardine and Pacific chub mackerel with California smoothtongue, most points are below the 1:1 line before 1976 and above it after 1976, indicating depletion of the exploited species before 1976 and a recovery afterward (Fig. 3(b) and (c)). In comparing jack mackerel to medusafish (both with age-at-matu-

Table 4 (continued)

Geographic regions:																Within: 13/104 Between: 17/127 Fisher's Exact: p = 0.5009			
Broad north	<i>Lyopsetta exilis</i>																		
	<i>Microstomus pacificus</i>	0																	
	<i>Parophrys vetulus</i>	0 0																	
	<i>Scorpaenichthys marmoratus</i>	0 0 0																	
	<i>Sebastes aurora</i>	0 0 0 0																	
	<i>Sebastes paucispinis</i>	0 0 1 0 0																	
	<i>Sebastolobus</i> spp.	0 0 0 0 0 0																	
	Agonidae	0 0 0 0 0 0 0																	
	<i>Pleuronichthys verticalis</i>	0 1 1 0 0 0 0 0																	
	<i>Sebastes jordani</i>	0 0 0 1 0 0 0 1 0																	
<i>Zaniolepis</i> spp.	0 0 0 0 0 0 0 0 0																		
<i>Argentina sialis</i>	0 0 0 0 0 0 0 0 0 1																		
<i>Oxylebius pictus</i>	0 0 0 0 0 0 0 0 0 0 0																		
Bight	<i>Chromis punctipinnis</i>	0 0 1 0 0 0 0 0 0 0 0 0 0														1 1 0			
	<i>Hippoglossina stomata</i>	0 0 0 0 0 0 0 0 1 0 0 0 0																	
	<i>Ophidion scrippsae</i>	0 0 0 0 0 0 0 0 0 1 0 0 0																	
Broad south	<i>Paralabrax</i> spp.	0 0 0 0 0 0 0 0 1 1 0 0 0														0 1 1 1 0 1 1 0 0 0			
	<i>Paralichthys californicus</i>	0 0 0 0 0 0 0 0 1 0 0 0 0																	
	Sciaenidae	0 0 1 0 0 0 0 0 1 1 0 0 0																	
	<i>Hypsoblennius</i> spp.	0 0 0 0 0 0 0 0 1 1 0 0 0																	
	<i>Sphyræna argentea</i>	0 0 0 0 0 0 0 0 0 0 1 0 0																	
All	<i>Symphurus atricaudus</i>	0 0 0 0 0 0 0 0 1 0 0 0 0														0 0 0 0	0 0 0 0 0	0	

Bottom habitats:

Water	<i>Microstomus pacificus</i>											Within: 7/67																		
	<i>Sebastes paucispinis</i>	0										Between: 22/165																		
	<i>Sphyræna argentea</i>	0 0										Fisher's Exact: p = 0.3587																		
	<i>Sebastes jordani</i>	0 0 0																												
	<i>Argentina sialis</i>	0 0 1 0																												
Kelp/Hard	<i>Paralabrax</i> spp.	0	0	1	0	0	0																							
	<i>Scorpaenichthys marmoratus</i>	0	0	0	1	0	0																							
	<i>Chromis punctipinnis</i>	0	0	0	0	0	0	0	0																					
	<i>Hypsoblennius</i> spp.	0	0	0	0	0	1	0	1																					
	<i>Oxylebius pictus</i>	0	0	0	0	0	0	0	0	0																				
Soft	<i>Lyopsetta exilis</i>	0	0	0	0	0	0	0	0	0	0																			
	<i>Paralichthys californicus</i>	0	0	0	0	0	0	0	0	0	0	0																		
	<i>Parophrys vetulus</i>	0	1	0	0	0	0	0	0	1	0	0	0	0																
	<i>Sebastes aurora</i>	0	0	0	0	0	0	0	0	0	0	0	0	0																
	<i>Sebastolobus</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0																
	<i>Hippoglossina stomata</i>	0	0	0	0	0	1	0	1	0	0	0	0	0	0															
	<i>Pleuronichthys verticalis</i>	1	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1													
	<i>Symphurus atricaudus</i>	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1												
	<i>Zaniolepis</i> spp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0												
	<i>Ophidion scrippsae</i>	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0											
Both	Sciaenidae	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0	0										
	Agonidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								

(continued on next page)

ration around three years), the data fell along the 1:1 line, suggesting that jack mackerel was under light fishing pressure (Fig. 3(d)). This result agrees with Mason and Bishop's (2001) report on the status of the fishery.

For the coastal assemblage, an exploited flatfish, English sole, was compared with three bycatch flatfishes, bigmouth sole (*Hippoglossina stomata*), slender sole (*Lyopsetta exilis*), and hornyhead turbot

Table 4 (continued)

Age-at-maturation:																			
1	<i>Symphurus atricaudus</i>																	Within: 15/81	
1	<i>Hypsoblennius</i> spp.	1																Between: 7/90	
1	<i>Ophidion scrippsae</i>	1	0															Fisher's Exact: p = 0.0306	
2	<i>Sphyræna argentea</i>	0	0	1															
2	<i>Chromis punctipinnis</i>	0	1	1	0														
2.5	<i>Zaniolepis</i> spp.	0	0	0	0	0													
2.5	<i>Argentina sialis</i>	0	0	0	1	0	1												
3	<i>Lyopsetta exilis</i>	0	0	0	0	0	0	0											
3	<i>Hippoglossina stomata</i>	0	0	0	0	1	0	0	0										
3	<i>Sebastes jordani</i>	0	0	0	0	0	0	0	0	0									
3	<i>Oxylebius pictus</i>	0	0	0	0	0	0	0	0	0	0								
4	<i>Paralabrax</i> spp.	1	1	0	1	0	0	0	0	0	1	0	0						
4	<i>Parophrys vetulus</i>	0	0	0	0	1	0	0	0	0	0	0	0	0					
4	<i>Sebastes paucispinis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
4	<i>Pleuronichthys verticalis</i>	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0			
4.5	<i>Paralichthys californicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
4.5	<i>Scorpaenichthys marmorat</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
5	<i>Sebastes aurora</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
5.5	<i>Microstomus pacificus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Matrices are organized according to adult habitat, geographic distribution, fishing status, or age-at-maturation. Number of significant correlations out of all possible comparisons within and between categories are computed. Fisher's exact test is applied to determine whether the factor is affecting the species correlation structure.

(*Pleuronichthys verticalis*). All four are associated with soft bottom and mature around age 3–4. In the comparison with bigmouth sole, no pattern was found (Fig. 3(e)). The comparisons with slender sole and hornyhead turbot suggested that English sole was not under very strong fishing pressure in the SCB (Fig. 3(f) and (g)), as would be expected given that the fishery is primarily north of Point Conception and that females begin spawning at a smaller size than that targeted by the fishery (Pearson, Owen, & Thomas, 2001). In comparing bocaccio to shortbelly rockfish (both living in the water column, primarily over rocky bottom, and with age-at-maturation of 4 and 3 years, respectively), we found that these species fluctuated coherently before 1976. However, most data points fell below the 1:1 line after 1976, indicating depletion of bocaccio (Fig. 3(h)). This supports Ralston's (1998) stock assessments for a group of rockfish species showing that the bocaccio biomass has been declining since 1970.

4. Discussion

4.1. Time series of fish abundances and species co-variation

Long-term variability in abundance of the oceanic species of larval fish taken in the CalCOFI surveys was strongly affected by climate. Among these taxa, 85% increased in abundance from the cold to warm period and 71% exhibited a significant relationship with environmental signals (Table 5). Increased abundance of oceanic taxa during the warm period is most likely due to movement of adults into the CalCOFI sampling grid, although increased reproductive effort or larval survival may play a role. Bograd and Lynn (2003) examined long-term variability in the southern California Current system and suggested more frequent incursion of the central gyre water into the offshore part of the CalCOFI grid during the warm per-

Table 5

Average larval abundances in the cold (1951–1976) and warm (1976–1998) periods and selected environmental variables in the regression model for each taxon

Species	Mean abundances		Permutation		
	1951–1976	1977–1998	<i>p</i> -Value ^a	Selected variables ^b	Distribution ^c
Oceanic					
<i>Aristostomias scintillans</i>	0.080	0.239	0.001	PDO lag1(+)	Subarctic-transitional
<i>Bathylagus ochotensis</i>	3.171	7.958	0.002	NS	Subarctic-transitional
<i>Bathylagus pacificus</i>	0.223	0.658	0.001	PDO lag1(+)	Subarctic-transitional
<i>Bathylagus wesethi</i>	2.335	4.774	0.004	NS	Transitional
<i>Ceratoscopelus townsendi</i>	0.747	4.611	0.001	PDO lag1(+), NPI(–)	Temperate to tropical
<i>Chauliodus macouni</i>	0.388	0.661	0.006	NS	Subarctic-transitional
<i>Chiasmodon niger</i>	0.043	0.189	0.001	PDO(+)	Tropical–subtropical
<i>Cyclothone</i> spp.	1.113	5.296	0.001	PDO lag1(+)	
<i>Diaphus theta</i>	1.786	1.689	0.793	CalCOFI SST(–)	Subarctic-transitional
<i>Diogenichthys atlanticus</i>	0.765	3.358	0.001	PDO lag1(+)	Tropical–subtropical
<i>Hygophum reinhardtii</i>	0.091	0.288	0.001	CalCOFI SST(+)	Subtropical
<i>Idiacanthus antrostomus</i>	0.408	1.127	0.001	CalCOFI SST(+)	Temperate to tropical
<i>Melamphaes</i> spp.	0.817	1.228	0.013	PDO(+)	
<i>Microstoma</i> spp.	0.198	0.397	0.001	PDO lag1(+)	Subarctic-transitional
Myctophidae	0.483	0.819	0.015	NS	
<i>Myctophum nitidulum</i>	0.079	0.264	0.001	PDO(+)	Tropical–subtropical
<i>Nannobranchium</i> spp.	2.837	5.532	0.001	PDO lag1(+)	
<i>Nansenia candida</i>	0.235	0.457	0.049	NS	Subarctic-transitional
<i>Notolychnus valdiviae</i>	0.062	0.228	0.001	PDO lag1(+)	Temperate to tropical
<i>Notoscopelus resplendens</i>	0.121	0.325	0.001	CalCOFI SST(+)	Temperate to tropical
Paralepididae	0.495	1.009	0.001	PDO lag1(+), NPI(–)	
<i>Poromitra</i> spp.	0.143	0.209	0.062	NS	Cosmopolitan
<i>Protomyctophum crockeri</i>	1.627	4.327	0.001	PDO lag1(+)	Subarctic-transitional
Scopelarchidae	0.153	0.605	0.001	PDO lag1(+)	
<i>Scopelogadus bispinosus</i>	0.130	0.247	0.016	NS	Tropical
<i>Scopelosaurus</i> spp.	0.081	0.195	0.001	PDO(+)	
<i>Stenobranchius leucopsarus</i>	24.910	24.224	0.887	NS	Subarctic-transitional
Sternoptychidae	0.389	1.770	0.001	PDO lag1(+)	
<i>Stomias atriventer</i>	0.207	0.469	0.004	PDO	Tropical
<i>Symbolophorus californiensis</i>	0.989	2.299	0.001	NS	Subarctic-transitional
<i>Tactostoma macropus</i>	0.090	0.170	0.100	NS	Subarctic-transitional
<i>Tarletonbeania crenularis</i>	2.603	0.959	0.005	CalCOFI SST(–)	Subarctic-transitional
<i>Triphoturus mexicanus</i>	3.708	5.396	0.038	SOI(–)	Subtropical
<i>Vinciguerria lucetia</i>	4.039	47.538	0.001	CalCOFI SST(+)	Tropical
Coastal-oceanic-fished					
<i>Engraulis mordax</i>	253.529	238.249	0.827	NS	All
<i>Merluccius productus</i>	78.507	126.365	0.326	NS	Broad north
<i>Sardinops sagax</i>	3.382	30.130	0.002	NS	All
<i>Scomber japonicus</i>	0.587	6.228	0.001	PDO(+)	All
<i>Trachurus symmetricus</i>	11.219	6.929	0.118	PDO lag2(–)	All
Coastal-oceanic-fished					
<i>Cololabis saira</i>	0.169	0.242	0.280	NS	Broad north
<i>Icichthys lockingtoni</i>	0.925	0.504	0.004	CalCOFI SST(–)	Broad north
<i>Leuroglossus stilbius</i>	41.155	28.741	0.080	NS	Broad north
<i>Tetragonurus cuvieri</i>	0.548	0.552	0.976	NS	Broad north
<i>Trachipterus altivelis</i>	0.178	0.167	0.694	NS	Broad north
Coastal-fished					
<i>Microstomus pacificus</i>	0.236	0.425	0.144	NS	Broad north
<i>Paralabrax</i> spp.	0.465	1.770	0.026	PDO(+)	Broad south

(continued on next page)

Table 5 (continued)

Species	Mean abundances		Permutation		
	1951–1976	1977–1998	<i>p</i> -Value ^a	Selected variables ^b	Distribution ^c
<i>Paralichthys californicus</i>	0.326	0.495	0.129	NS	Broad south
<i>Parophrys vetulus</i>	0.699	0.610	0.793	NS	Broad north
Sciaenidae	3.075	6.654	0.078	NS	Broad south
<i>Scorpaenichthys marmoratus</i>	0.194	0.164	0.811	NPI(+)	Broad north
<i>Sebastes aurora</i>	0.464	0.347	0.445	NS	Broad north
<i>Sebastes paucispinis</i>	3.491	1.377	0.001	CalCOFI SST(–)	Broad north
<i>Sebastes</i> spp.	27.732	28.478	0.631	NS	
<i>Sebastolobus</i> spp.	0.383	0.467	0.815	NS	Broad north
<i>Sphyræna argentea</i>	0.382	0.792	0.120	NS	Broad south
Coastal-bycatch					
Agonidae	0.145	0.225	0.062	NS	Broad north
<i>Chromis punctipinnis</i>	0.879	0.942	0.866	NS	Bight
<i>Hippoglossina stomata</i>	0.127	0.165	0.168	NS	Bight
<i>Lyopsetta exilis</i>	0.513	0.785	0.219	NS	Broad north
<i>Pleuronichthys verticalis</i>	0.256	0.376	0.122	NS	Broad north
<i>Sebastes jordani</i>	11.165	9.909	0.613	NS	Broad north
<i>Symphurus atricaudus</i>	0.408	0.295	0.562	NS	All
<i>Zaniolepis</i> spp.	0.128	0.290	0.001	NS	Broad north
Coastal-unfished					
<i>Argentina sialis</i>	0.343	1.139	0.001	NS	Broad north
<i>Hypsoblennius</i> spp.	0.711	0.964	0.426	NS	Broad south
<i>Ophidion scrippsae</i>	0.198	0.128	0.255	NS	Bight
<i>Oxylebius pictus</i>	0.106	0.111	0.859	NS	Broad north

A permutation test is applied to determine whether there was a significant difference in abundance between the warm and cold periods. CalCOFI SST: the CalCOFI sea-surface temperature (www.calcofi.org/data/data.html).

Upwelling: the upwelling index anomaly (33N, 119W) (www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html); SOI: the Southern Oscillation Index (www.cgd.ucar.edu/cas/catalog/climind/soi.html); PDO: the Pacific Decadal Oscillation Index (www.jisao.washington.edu/pdo/PDO.latest); NPI: the North Pacific Index (www.cgd.ucar.edu/~jhurrell/np.html); NS: no significant variable was selected.

^a Bold indicating statistical significant at $\alpha = 0.05$ for the permutation test.

^b The selected variables are listed in the order of explanatory power for each taxon. Signs (+) and (–) indicate significant positive and negative correlation, respectively.

^c Specific distributions are given for the oceanic taxa based on Moser (1996). For other taxa, distributions are defined in Table 1. Blanks indicate that the specific distribution cannot be decided for some higher taxonomic complexes.

iod. The association of oceanic species and water masses is well known (Moser et al., 2001a; Moser, Smith, & Eber, 1987; Smith & Moser, 2003). Eastward incursion of the central gyre could bring more oceanic fishes closer to shore and therefore into the CalCOFI domain. Significantly increased abundance of many oceanic taxa during the warm period suggests that these species are indicators of climate-driven change in circulation in the SCB. Although the physical mechanism is not fully understood at this time, these species can serve as indicators of the change in circulation we have described and hence can be useful in monitoring climate effects in the California Current Ecosystem.

The oceanic species within the mesopelagic assemblage often co-varied, and so did the species within the vertical-migrating assemblage (Table 4). Significant co-variation of species between the mesopelagic and vertical-migrating assemblages is less frequent than that within assemblage ($p = 0.0150$, based on Fisher's exact test). The oceanic species appeared to react to different environmental signals depending on whether they migrate or not. It is likely that the mesopelagic species only experienced the deep-water environment, while the migrating species responded to environmental signals of the whole upper water column.

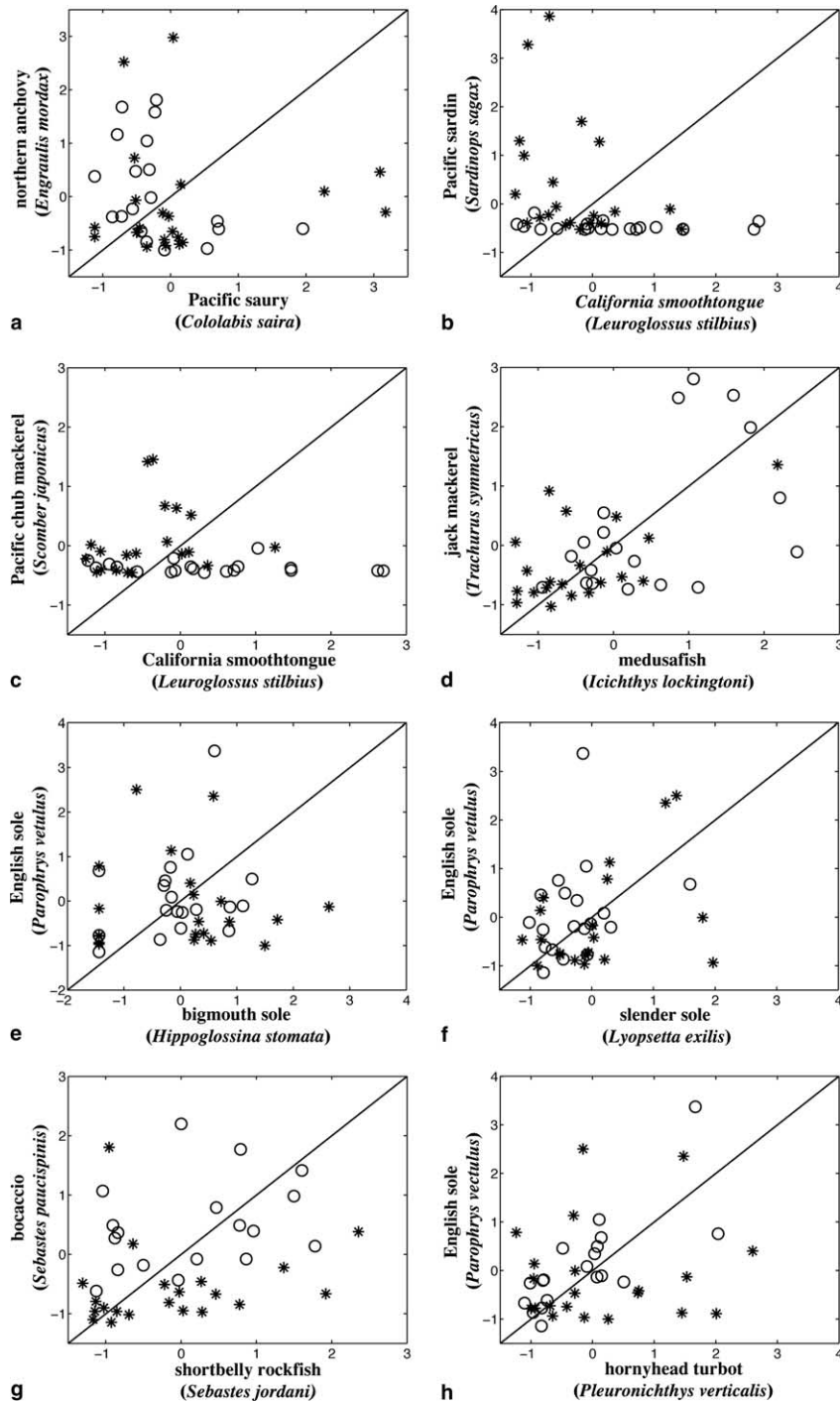


Fig. 3. Scatter plots of selected exploited (y-axis) versus unexploited (x-axis) species living in the same habitat and reaching maturity at about the same age (circles, data before 1976; stars, data after 1976). Each time series was standardized to zero mean and unit variance. If the two species varied coherently, the data scatter along the 1:1 line. The data fall below the 1:1 line when the population size of the exploited species was greatly reduced by strong fishing pressure.

Among the coastal-oceanic taxa, two exploited species, Pacific sardine and Pacific chub mackerel, increased in abundance in the warm period (Table 5 and Fig. 2). However, it is not clear to what extent these recoveries were associated with climate or with reduction in fishing effort. Declining abundance of jack mackerel and medusafish in the warm period (Table 5 and Fig. 2) might be due to declining food availability (zooplankton biomass) during the warm period (Roemmich & McGowan, 1995a, 1995b), but there was no consistent pattern for other species. Among the coastal taxa, some species responded to ENSO or decadal-scale climatic signals, but others showed coherent trends without any correlation with the environmental signals examined (Tables 4 and 5, and Fig. 2).

We hypothesized before the analysis that fluctuations in abundances of unexploited taxa would follow climatic trends, and those of exploited taxa would not, or at least would do so less distinctly, because of overwhelming effects of strong fishing mortality. Significant correlations between the environmental variables and larval fish abundances were found for 71% of the oceanic taxa (Table 5), but no fisheries exist for the oceanic taxa. The abundances of coastal and coastal-oceanic taxa, which contain both exploited and unexploited species, were less often correlated with environmental variables than were oceanic species. In addition, unexploited coastal and coastal-oceanic species were no more likely to be correlated with environmental variables than were exploited ones (Table 5). Only 18% of the coastal and coastal-oceanic species responded clearly to environmental signals, suggesting that these species may respond to environmental signals in a nonlinear way. Dixon, Milicich, and Sugihara (1999) showed that episodic larval fish recruitment requires nonlinear combinations of unrelated forcings: lunar phase, turbulence and wind direction. Analogously, high fish abundance in the CalCOFI time series can be a result of several factors (e.g., food availability, temperature, advection, and others) acting simultaneously.

Among the coastal and coastal-oceanic taxa, species that reached maturity at about the same age fluctuated coherently (Table 4), possibly in response to the same environmental signals. In a year of good oceanic conditions, high recruitment success can result in a strong year-class, which may sustain the population for several years. This has been observed in Pacific hake (Quirollo, Wespestad, & Dorn, 2001) and sockeye salmon (Ricker, 1997) as well as freshwater fishes (Townsend, 1989). The quasi-cycles seen in some of the fish populations in the CalCOFI time series could be due to interaction between age-at-maturation and environmental conditions. Interestingly, not all of these coherent fluctuations responded to ENSO events. It is likely that critical conditions of both biological and physical factors need to be met simultaneously so that a strong year class can be established. A better understanding of the interplay between biological and physical factors should help to shed light on the mechanisms.

4.2. A comparison with larval recurrent groups

Previous studies of larval fish assemblages in the CalCOFI domain were based on species co-occurrence (Loeb, Smith, & Moser, 1983a, 1983b; Moser & Smith, 1993; Moser et al., 1987). Recurrent group analyses have been widely used to study larval assemblages (Moser, Smith, & Fuiman, 1993). We compared the larval recurrent groups of Moser et al. (1987) with our expert-knowledge classification system for adult fishes (Table 6). Their southern complex consists mainly of oceanic species, their southern coastal complex contains four coastal species, and their northern complex is a mixture of coastal, coastal-oceanic, and oceanic species as defined in our system. Their northern complex reflects northern species based on adult distributions, except for Gulf sanddab (*Citharichthys fragilis*), longfin sanddab (*Citharichthys xanhostigma*), Pacific sardine, and Pacific chub mackerel; their southern complex also is not entirely consistent with known adult distributions. Clearly, species co-occurring in their larval stage frequently live in different habitats as adults. Larval distributions are determined by advection, diffusion and buoyancy, and to a lesser extent

Table 6

A comparison between the larval recurrent groups (Moser et al., 1987) and the assemblages described by the “expert-knowledge classification system”

Recurrent groups	Expert knowledge classification system
Northern complex	
<i>Leuroglossus</i> group	
<i>Leuroglossus stilbius</i>	Coastal-oceanic, broad north
<i>Merluccius productus</i>	Coastal-oceanic, broad north
<i>Sebastes</i> spp.	Coastal
<i>Bathylagus ochotensis</i>	Oceanic, North Pacific, mesopelagic
<i>Stenobranchius leucopsarus</i>	Oceanic, North Pacific, migrator
<i>Tarletonbeania</i> group	
<i>Tarletonbeania crenularis</i>	Oceanic, North Pacific, migrator
<i>Icichthys lockingtoni</i>	Coastal-oceanic, broad north
<i>Citharichthys</i> group	
<i>Engraulis mordax</i>	Coastal-oceanic, broad north
<i>Citharichthys fragilis</i>	Offshore, broad south, soft
<i>Citharichthys xanthostigma</i>	Offshore, broad south, soft
<i>Sardinops</i> group	
<i>Sardinops sagax</i>	Coastal-oceanic, all
<i>Scomber japonicus</i>	Coastal-oceanic, all
Southern complex	
<i>Symbolophorus</i> group	
<i>Bathylagus wesethi</i>	Oceanic, North Pacific, mesopelagic
<i>Symbolophorus californiensis</i>	Oceanic, North Pacific, migrator
<i>Nannobranchium ritteri</i>	Oceanic, Pacific, migrator
<i>Cyclothone</i> spp.	Oceanic, world
<i>Diogenichthys atlanticus</i>	Oceanic, world, mesopelagic
<i>Triphoturus</i> group	
<i>Triphoturus mexicanus</i>	Oceanic, Pacific, migrator
<i>Protomyctophum crockeri</i>	Oceanic, North Pacific, migrator
<i>Trachurus symmetricus</i>	Coastal-oceanic, all
<i>Ceratoscopelus</i> group	
<i>Ceratoscopelus townsendi</i>	Oceanic, North Pacific, migrator
<i>Lampadena urophaos</i>	Oceanic, North Pacific, bathypelagic
<i>Vinciguerria</i> group	
<i>Gonichthys tenuiculus</i>	Oceanic, North Pacific, migrator
<i>Hygophum atratum</i>	Oceanic, North Pacific, migrator
<i>Diogenichthys laternatus</i>	Oceanic, Pacific, mesopelagic
<i>Vinciguerria lucetia</i>	Oceanic, North Pacific, migrator
Southern coastal complex	
<i>Synodus</i> group	
<i>Ophidion scrippsae</i>	Nearshore, Bight, soft
<i>Symphurus atricaudus</i>	Offshore, all, soft
<i>Synodus lucioceps</i>	Offshore, broad south, soft
<i>Prionotus</i> spp.	Offshore, south, soft

by adult spawning habitats. In addition, the integrated tows used in CalCOFI surveys “smear” the vertical distributions of the larvae. Therefore, constructing fish assemblages based on adult habitat is a step forward to understanding how climatic and fishing effects influence the organization of fish communities.

4.3. Potential and limitation of the community approach

As our ideas move away from single species fisheries management strategies to ecosystem-based approaches to management, long-term monitoring data sets will become more important. They will provide an historical context for strategies to balance ecosystem effects derived from fishing and from environmental change. Approaches based on retrospective analyses of long-term monitoring need to be developed.

Few marine monitoring programs are as extensive as the CalCOFI, and thus its data set provides a unique opportunity to examine techniques to separating the effects on fish populations of fisheries exploitation from those of the environment. This is the first time that larval fish data have been used to investigate this question. A key element of such analyses is the constrained comparison of the abundances of paired exploited and unexploited species within a habitat class and reaching maturity at about the same age. To achieve such comparisons, we constructed the expert-knowledge classification system (Supplementary Table 1) to identify habitat class, and compiled data on age-at-maturation (Supplementary Table 2) for each species. Our ability to perform such comparisons was enhanced by the fact that the CalCOFI time series contain both exploited and unexploited species and provide data of sufficient length.

We found evidence for strong fishing pressure on Pacific sardine and Pacific chub mackerel before 1976 (Fig. 3(b) and (c)) and on bocaccio after 1976 (Fig. 3(h)) when we performed the constrained comparisons. Jack mackerel and English sole appear to have been much more lightly exploited, and remain in a good condition (Fig. 3(d), (f), and (g)). These results are consistent with the current understanding of the status of the fish populations according to anecdotal information and rigorous stock assessments (Mason & Bishop, 2001; Pearson et al., 2001; Ralston, 1998). Our comparative approach reveals patterns of fishing effects on fish populations for six of eight comparisons (Fig. 3). One should keep in mind that a perfect species pair (one exploited and the other unexploited) is unlikely to exist. Incorporating other life history traits in addition to habitat and age-at-maturation will help to interpret the dynamics of fish populations. For example, fecundity, growth rate, trophic level, and other traits might influence the response of fish populations to environmental signals and fishing effects (King & McFarlane, 2003).

In addition to a lack of information for many fish species, spatial heterogeneity and sampling errors intrinsically associated with plankton surveys also cause difficulty. To examine this, we computed spatial variance of fish abundance. We used coefficient of variation to represent spatial variance associated with each CalCOFI cruise (CV_{cr}) for each of the selected species in the constrained comparisons. The annual mean coefficient of variation (CV_{yr}) was computed as follows:

$$CV_{yr} = \frac{\sum_{cr=1}^k CV_{cr} \times x_{cr}}{\sum_{cr=1}^k x_{cr}},$$

where CV_{cr} and x_{cr} are the coefficient of variation and the mean abundance of a given cruise, respectively, and k is the total number of cruises of the year. As such, the CV_{yr} was calculated from abundance-weighted CV_{cr} to account for the seasonal variation. The long-term (1951–2002) arithmetic mean CV_{yr} ranges from 1.8 to 5.7 (Table 7), indicating that the CalCOFI time series have high variance. This variance consists of spatial heterogeneity and sampling errors. Spatial heterogeneity can be caused by predation, food supply, advection, specific bottom features and other factors. Although the spatial variance is high, our averaging process within the sampling grid should have resulted in time series that reasonably estimated long-term trends of abundance. Our finding of a significant relationship between species co-variation and their age-at-maturation is one validation (Table 4), and the trend of larval fish abundance following fisheries data for some species is another (Moser et al., 2000, 2001b; Moser & Watson, 1990). Larval abundance time series are a good indicator of adult biomass for some species but might be extremely noisy for others.

Another constraint of the method was the lack of data on the life history of unexploited species. Constrained comparisons of exploited and unexploited species can be a powerful tool for separating fishing

Table 7

The long-term (1951–2002) average spatial coefficient of variation (CV) of larval fish abundances for the species used in the pair-wise comparisons

Species	Average spatial CV	SD
<i>Cololabis saira</i>	5.5074	1.4855
<i>Engraulis mordax</i>	2.3822	0.8696
<i>Sardinops sagax</i>	4.3384	1.5136
<i>Scomber japonicus</i>	4.8103	1.351
<i>Trachurus symmetricus</i>	3.1289	0.7697
<i>Ichthyos lockingtoni</i>	4.0586	1.5156
<i>Leuroglossus stilbius</i>	1.8604	0.3208
<i>Lyopsetta exilis</i>	3.9908	1.0081
<i>Parophrys vetulus</i>	4.8183	1.498
<i>Hippoglossina stomata</i>	5.7165	1.2908
<i>Pleuronichthys verticalis</i>	5.6114	1.4095
<i>Sebastes paucispinis</i>	3.2811	1.2734
<i>Sebastes jordani</i>	3.1502	1.0649

Standard deviation (SD) was calculated from annual CVs.

from environmental effects, but this tool is effective only if adequate life history data exist. Unfortunately, life history data on noncommercial species are rare, and hence data from proxy species or a general relationship must be used, adding variance and decreasing the power of the analysis. Regardless of the problems, the noisy data and lack of life history information, this study indicates that adult-based analysis of ichthyoplankton time series has great potential as a way to evaluate the long-term effects of fishing and the environment on fish communities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.pocean.2005.05.002](https://doi.org/10.1016/j.pocean.2005.05.002).

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