

UNIVERSITY OF CALIFORNIA, SAN DIEGO

Separating environmental effects from fishing impacts on the dynamics of
fish populations of the Southern California region

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy

in

Oceanography

by

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To
Chang-tai Shih,
who brought me on board science,
and pointed me in the direction of life.

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ABSTRACT OF THE DISSERTATION

Separating environmental effects from fishing impacts on the dynamics of fish populations of the Southern California region

by

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Professor George Sugihara, Co-Chair

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Disentangling environmental variability from fishing effects on the dynamics of fish populations is essential for sound fisheries management. This is an important component of ecosystem approaches to fisheries. Toward this goal, I compare exploited with unexploited species living in the same environment. Using greater than 50-year long larval fish time series collected in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) from the southern California region, I consider fishing as a treatment effect in a long-term ecological experiment. I construct an “expert-knowledge classification system” to categorize southern California fish species collected during the CalCOFI surveys into communities based on the habitat affinities of adults (coastal, coastal-oceanic, and oceanic), and incorporate their life history traits, phylogeny, and status of exploitation into analyses.

Fisheries exploitation occurs only in the coastal and coastal-oceanic communities. Within these communities, very few species exhibit a significant linear correlation with environmental variables, and exploited species are not more responsive to climate than unexploited species. However, the long-term variability in the abundance of exploited species is higher than that of unexploited species, after accounting for life history effects, phylogeny, and a changing environment. The increased variability of the exploited populations is likely caused by fishery-induced truncation of age-structure, which reduces the capability of populations to dampen the effects of environmental variability. This inference is substantiated by analyzing age or length composition in catch data for the exploited species used in this study, which clearly indicate a declining trend in average age or length through time. Furthermore, the latitudinal distributions of exploited species are more responsive to climate changes than those of unexploited species, suggesting that fishing may reduce the resilience of fish populations facing environmental variation. The reduced resilience may be caused by fishery-induced truncation of age-structure or constriction of spatial distributions.

My results indicate that fishing is likely to magnify uncertainty of fish populations and therefore, increase the probability of dramatic shifts of the populations facing environmental variations. A precautionary management approach is warranted not only because of normal uncertainties associated with estimates of stock size but because fishing magnifies population variability. Therefore, in addition to maintaining total viable biomass, management strategies should be implemented to conserve fish population structures in order to prevent fishing from increasing population variability.

Chapter 1. Introduction to the Dissertation

Introduction

Evidence on archeological and historical time scales reveals that fisheries have had dramatic impacts on target species and coastal ecosystems (Jackson et al. 2001). In 2004, the FAO estimated that among the world's fisheries 77% are heavily exploited, over-exploited, depleted, or recovering from depletion (Fig. 1.1) (FAO 2005). These alarming numbers and recent evidence, including decreased stocks of predatory fishes (Myers and Worm 2003), fishing down of marine food webs (Pauly et al. 1998), and decreased world fisheries landings (Watson and Pauly 2001), indicate that many commercially-important fish populations have been declining in the past several decades. However, some studies suggest that in some cases, the declines of fish populations are due to environmental effects alone. For example, paleobiological records show that large fluctuations in the abundance of sockeye salmon (Finney et al. 2002) from Alaska and Pacific sardine and northern anchovy off the California coast occurred prior to the industrialized fisheries (Baumgartner et al. 1992). World fisheries data show synchronized fluctuations of catch of various sardine and anchovy stocks in the world ocean (Lluch-Belda et al. 1992; Chavez et al. 2003).

It has been believed that fluctuations of the fish populations are caused by both fishing and environmental forcing. However, the extent to which the fluctuations of fish populations are due to fishing, or to environmental change, or to some combination of these effects is still a matter of debate (Mantua et al. 1997; Finney et al. 2002; Beaugrand et al. 2003). In order to have sound fisheries management, it is important to separate

environmental effects from fishing impacts on fish populations and understand the effects of exploitation on fish populations within the context of a changing environment.

In order to separate fishing effects on fish populations from environmental forcing, it is necessary to investigate the environmental signals of the system under study. During the past century, there was a warming trend in the Northeast Pacific Ocean (Field et al. 2006) superimposed on decadal-scale (e.g. the Pacific Decadal Oscillation (Mantua et al. 1997)) and interannual-scale (e.g. the El Niño/Southern Oscillation (Trenberth 1984)) fluctuations (Fig. 1.2). These large-scale climatic signals have significant influences on the physical environment of southern California marine ecosystem as reflected in the local ocean temperature (Fig. 1.2). A study based on the planktonic foraminifera of the California Current indicates an anomalous warming trend in the 20th century not seen in previous centuries and attributes this trend to anthropogenic effects (Field et al. 2006). In addition, studies on fishes (Beamish et al. 1997; Hare and Mantua 2000; Beamish et al. 2004) and zooplankton (Roemmich and McGowan 1995a; 1995b; Brinton and Townsend 2003; Lavaniegos and Ohman 2003) reveal high-amplitude fluctuations of marine populations possibly caused by decadal-scale climate variation. Besides the low-frequency climatic effects, marine populations are also affected by higher-frequency El Niño/Southern Oscillation events (Fiedler et al. 1986; Yoklavich et al. 1996). These climatic effects may have significant impacts on California fish populations.

Clearly, fluctuations of exploited fish populations can be affected by both environmental forcing and fishing mortality (Jacobson et al. 2001; McFarlane et al. 2002). Separating the effects of environmental variability from the impacts of fishing on

the dynamics of fish populations is important for sound fisheries management (Garcia et al. 2003; Browman and Stergiou 2004; Hutchings and Reynolds 2004; Pikitch et al. 2004; Daan et al. 2005). This view is an essential component of ecosystem-based approaches to fisheries which is becoming a standard requirement in fisheries management; that is, to base decisions not only on the status of a fish population but also the condition of the ecosystem and the environment as well as inter-specific interactions (Garcia et al. 2003; Browman and Stergiou 2004; Pikitch et al. 2004). Increasing effort has been devoted to developing indicators for assessing impacts of fisheries (Daan et al. 2005). In Table 1.1, I compile 52 indicators at the level of populations, assemblages, and ecosystems from the literature. Although this list is by no means comprehensive, it reveals some interesting patterns. Among the 52 indicators, only 26 have a predicted outcome as a basis to determine whether fishing effects exist. In addition, only four population-level indicators have reference points that can be explicitly defined without referring to the “pristine” state of the population or the ecosystem. These statistics point out the impracticality in applying many of these indicators because pristine conditions prior to fishing are generally unknown. Even for those indicators that have defined reference points, it is difficult to determine whether the trends of the indicators are caused by fishing effects or by environmental change. Furthermore, time series data used to develop these indicators are usually too short, and therefore, efficacy of these indicators is unknown.

To overcome some of these problems, I develop approaches to evaluate the effects of exploitation on fish populations within the context of a changing environment. I studied the larval fish time series (1951-2002) from the southern sector of the California

Current System, which is maintained by NOAA, NMFS, as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). CalCOFI is one of the most ambitious and longest running observational oceanography programs in the world (Hewitt 1988; Ohman and Venrick 2003). Starting with monthly cruises in 1949, with tri-annual sampling from the late 60's to early 80's, it remains on-going on a quarterly basis. Each cruise covers a spacious region (usually 66 stations) off the southern California coast, and at each sampling station a suite of physical and chemical measurements are made to characterize the environment and map the distribution and abundance of phytoplankton, zooplankton, fish eggs and larvae. Since the inception of the CalCOFI surveys in 1949, larval fishes collected at each sampling station of each cruise have been identified to species or the lowest taxonomic level that the prevailing knowledge permitted for both exploited and unexploited species. (Consistent larval fish data are only available since 1951 due to the change of sampling depth). The CalCOFI surveys provide one of the only long-term and large-scale fisheries-independent surveys along the west coast of the United States. This dataset provides fishery-independent data that are free from confounding effects (changes in fishing gears or areas) commonly associated with fishery catch data in estimating fish abundances. Because the CalCOFI program spans more than 50 years, the fish data reflect how fish populations respond to various scales (from annual to decadal) of environmental forcing, as well as to fishing. In addition, because the fish populations live in the same area, they experience much of the same large-scale environmental variability. Since their responses to environmental forcing might vary depending on their life history traits, ecological traits, or phylogeny

(Winemiller and Rose 1992), I integrate the data of life history traits, ecological traits, and phylogeny of fish species into analyses. These properties allow me to separate fishing effects from environmental effects on fish dynamics.

In this study, I assume that trends in larval fish abundances taken over the 50 year CalCOFI time series are proportional to changes in the standing stock of the adults that produced them. 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. Long-term trends in larval abundance mostly reflect trends in adult biomass (Moser et al. 2000); short-term fluctuations are likely related to episodes of high or low reproductive output or geographic shifts due to animal movement (e.g. El Nino effects), since sudden changes in biomass would not be expected (Moser et al. 2000). The agreement between the larval abundance and spawning biomass is illustrated in Figure 1.3, using bocaccio (*Sebastes paucispinis*) as an example (Pearson correlation, $r = 0.718$, $p < 0.001$). Several studies have shown that larval abundance is a good indicator of adult biomass (Moser and Watson 1990; Gunderson 1993; Moser et al. 2000; Moser et al. 2001). The common use of larval indices in stock assessment models also supports this conclusion (Barnes et al. 1992; Deriso et al. 1996; Butler et al. 2003). Given that there are no long-term survey data of adult populations, and fisheries data are confounded by changes in fishing effort, economic and regulatory changes, and many other factors, 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.

Thesis outline

I focus on examining how fishing might affect the resilience of exploited populations that is important in facing climate change (environmental forcing). I examine fishing effects on the dynamics of exploited populations by comparing exploited to unexploited species living in the southern sector of the California Current ecosystem. The essential idea of my analyses is to consider fishing as an experimental factor, using unexploited species as a control. Certainly, fishing effort and fishing mortality for a given species varies through time, and considering fishing as a treatment effect is an oversimplified approach. However, for many exploited species, fishing effort and fishing mortality is difficult to quantify. Thus, as an initial attempt, I categorize fish species into exploited and unexploited groups. In addition, it is important to point out that no perfect unexploited controls exist because fishing is a selective process and fished and unfished groups are not formed randomly. To perform a reasonable comparison of the exploited to the unexploited species, possible intrinsic biases associated with fishing, for example, life history traits, ecological traits, and phylogeny, are taken into consideration.

In chapter 2, I describe an “expert-knowledge classification system” that categorizes 309 fish taxa in the CalCOFI larval fish database into primary (coastal, coastal-oceanic, and oceanic assemblages) based on their principal ecological domains and subsequently, secondary assemblages according to the habitat affinity of adults. This system provides biologically meaningful fish assemblages that are useful for ecosystem-based management of fisheries (Garcia et al. 2003; Browman and Stergiou 2004; Pikitch

et al. 2004). The oceanic assemblage includes no fishery-targeted species, while the coastal and coastal-oceanic assemblage includes both exploited and unexploited species. In the coastal and coastal-oceanic assemblage, respectively, I test the null hypothesis that abundances of both exploited and unexploited taxa show a similar trend in fluctuations. For this test, I use only 33 taxa that were consistently enumerated from the CalCOFI surveys. I also compare exploited to unexploited species living in the same habitat (i.e. belonging to the same secondary assemblage) and reaching maturity at about the same age. Here, I consider the unexploited species as a reference reflecting natural fluctuations.

The understanding gained in chapter 2 forms the basis to further study the species in the coastal and coastal-oceanic assemblages in which exploitation occurs. In chapter 3, I examine fishing effects by comparing variability in the abundance of exploited to that of unexploited species living in the same ecosystem. In addition, potential confounding effects due to species' life history traits, ecological traits, and phylogeny are taken into consideration in the analysis. This approach allows me to separate environmental effects from fishing effects on fish populations. The idea is to examine fishing effects using analysis of covariance: considering fishing as a treatment effect and life history traits, ecological traits, and phylogeny as covariates. I test the null hypothesis that no difference in the variability of the abundance exists between the exploited and unexploited species, after accounting for life history effects and a changing environment.

In chapter 4, I extend a similar idea to spatial distributions. I examine the geographic distribution center of each species in relation to climate variability (in

particular, sea surface temperature). I test the null hypothesis that the geographic distributions of exploited species are not more responsive to climate than unexploited species. I also examine whether or not the species showing a clear distributional response to climate have particular life history traits, ecological traits, or phylogenetic relationships.

In Chapter 5, I examine a suite of biological and physical data in the northeastern Pacific Ocean. The results indicate that marine biological populations have great potential to show abrupt shifts in response to stochastic environmental forcing. If indeed fishing reduces the resilience of exploited populations, fishing processes may elevate the probability that the fish populations could collapse under harsh environmental conditions (Scheffer et al. 2001).

Chapter 6 synthesizes my results and discusses the implications of these studies. Comparisons of exploited to exploited species suggest that fishing reduces the resilience of exploited populations. I speculate that this is because fishing might have changed the population structure of exploited species. Fisheries tend to truncate the age-structure of fish populations by removing large and old individuals through size (age)-selective fishing mortality (Berkeley et al. 2004; Hutchings and Reynolds 2004). (I provide relevant evidence for the species examined in this study in chapter 3.) Truncating the age-structure of a fish population may undermine the bet-hedging ability of the population to survive under harsh environmental conditions. These results have far-reaching management implications. Reduced resilience of exploited fish populations due to fishing may make a population more prone to abrupt changes in abundance and,

potentially, catastrophic declines. I end by discussing directions of future research and management concerns in order to minimize the probability of collapse of fish populations.

Table 1.1. Indicators to detect fishing effects on a population, assemblage, or ecosystem.

Indicators	Expected effect of fishing	Reference point	Literature
<u>Population level</u>			
Population growth rate (r)	Negative	0	Rochet and Trenkel (2003)
Total mortality (Z)	Increase	$Z^* = \frac{(L - L_m)k}{L_m - L_c}$	Rochet and Trenkel (2003)
Exploitation rate (F/Z)	Increase	0.5	Rochet and Trenkel (2003)
Catch per unit fishing effort	Decrease	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Average length of population	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Average length of catch	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Median age at maturation	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Change in F to reverse population growth (ΔF)	Decrease	Depends on variability in r	Rochet and Trenkel (2003)
Biomass relative to unexploited level	Decrease	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Reproductive success	Decrease	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Spatial distribution	Unknown	Compare to the pristine state	Bertrand <i>et al.</i> (2005)
The ratio of fished area and distribution area by species	Depending on the state of fisheries	Compare to the pristine state	Freon <i>et al.</i> (2005)
<u>Assemblage level</u>			
Species richness	Unknown	Compare to the pristine state	Rochet and Trenkel (2003)
Species diversity	Unknown	Compare to the pristine state	Rochet and Trenkel (2003)
k-dominance curve	Unknown	Compare to the pristine state	Rochet and Trenkel (2003)
Partial dominance curve	Unknown	Compare to the pristine state	Trenkel and Rochet (2003)
Species composition	Unknown	Compare to the pristine state	Rochet and Trenkel (2003)

Table 1.1 continued

Average growth rate	Increase	Compare to the pristine state	Rochet and Trenkel (2003)
Average maximum length	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Average age at maturation	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Average size at maturation	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Mean length distribution	Shifted to the left	Compare to the pristine state	Rochet and Trenkel (2003)
Size-biomass spectrum	Decreased slope	Compare to the pristine state	Rochet and Trenkel (2003)
Ordination of species traits	Smaller and faster traits	Compare to the pristine state	Rochet and Trenkel (2003)
Total biomass/abundance	Unknown	Compare to the pristine state	Rochet and Trenkel (2003)
Biomass variability	Increase	Compare to the pristine state	Rochet and Trenkel (2003)
Proportion of piscivorous fish	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Pelagic to demersal ratio	Increase	Compare to the pristine state	Rochet and Trenkel (2003)
Mean trophic level	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Fishing in balance cross trophic levels	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Proportion of noncommercial species	Increase	Compare to the pristine state	Rochet and Trenkel (2003)
Average weight (length) in the community	Decrease	Compare to the pristine state	Rochet and Trenkel (2003)
Discard rate	Increase	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Proportion of the stock that are juveniles	Increase	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Abundance biomass comparison curve	Unknown	Compare to the pristine state	Yemane <i>et al.</i> (2005)
<u>Ecosystem level</u>			
Foodweb structure	Unknown	Compare to the pristine state	Rochet and Trenkel (2003)

Table 1.1 continued

Chlorophyll a	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Detrital dominance	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Dissolved Inorganic Nitrogen	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Ecotrophic efficiency	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Infauna to epifauna ratio	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Benthic invertebrate biomass and production	Unknown	Compare to the pristine state	Duplisea <i>et al.</i> (2005)
Labile to refractory detritus ratio	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Light level at sediment surface	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Net primary production	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
System omnivory index	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Total system throughput	Unknown	Compare to the pristine state	Fulton <i>et al.</i> (2005)
Primary production required to support catch/primary production available	Unknown	Compare to the pristine state	Cury <i>et al.</i> (2005)
Mixed trophic impact	Unknown	Compare to the pristine state	Cury <i>et al.</i> (2005)
Exploited fraction of ecosystem surface	Depending on the state of fisheries	Compare to the pristine state	Freon <i>et al.</i> (2005)
Mean bottom depth of catches	Depending on the state of fisheries	Compare to the pristine state	Freon <i>et al.</i> (2005)
Mean distance of catch from the coast	Depending on the state of fisheries	Compare to the pristine state	Freon <i>et al.</i> (2005)

Notations in the table:

r: population growth rate.

F: fishing mortality.

Z: natural mortality.

$Z^* = \frac{(L - L_m)k}{L_m - L_c}$: k and L are parameters of the von Bertalanffy model, L_m is the length

at maturation, L_c is the length at first capture.

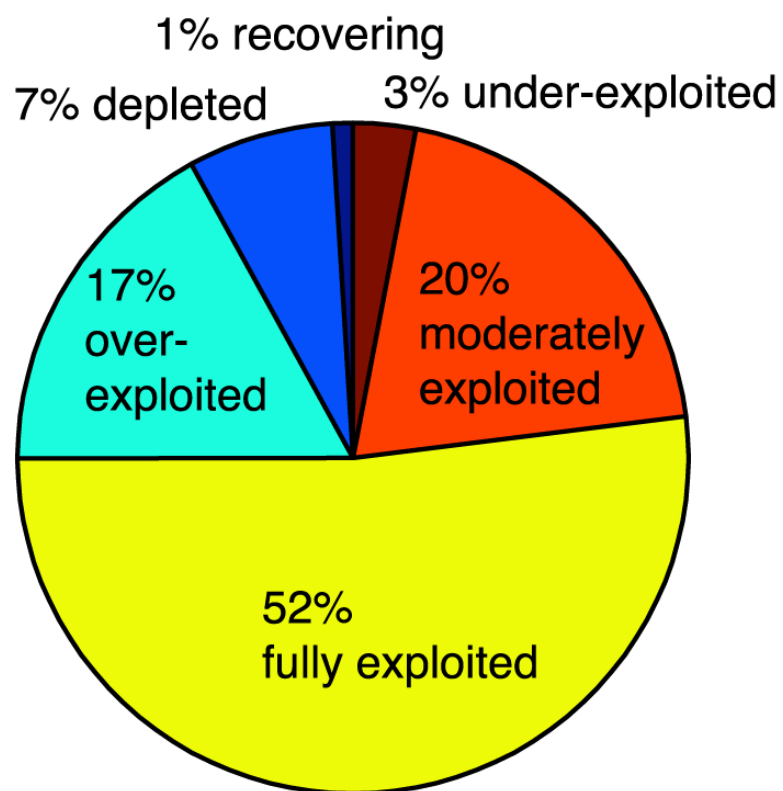


Figure 1.1. The current state of world marine fishery resources as estimated by FAO for the year 2004.

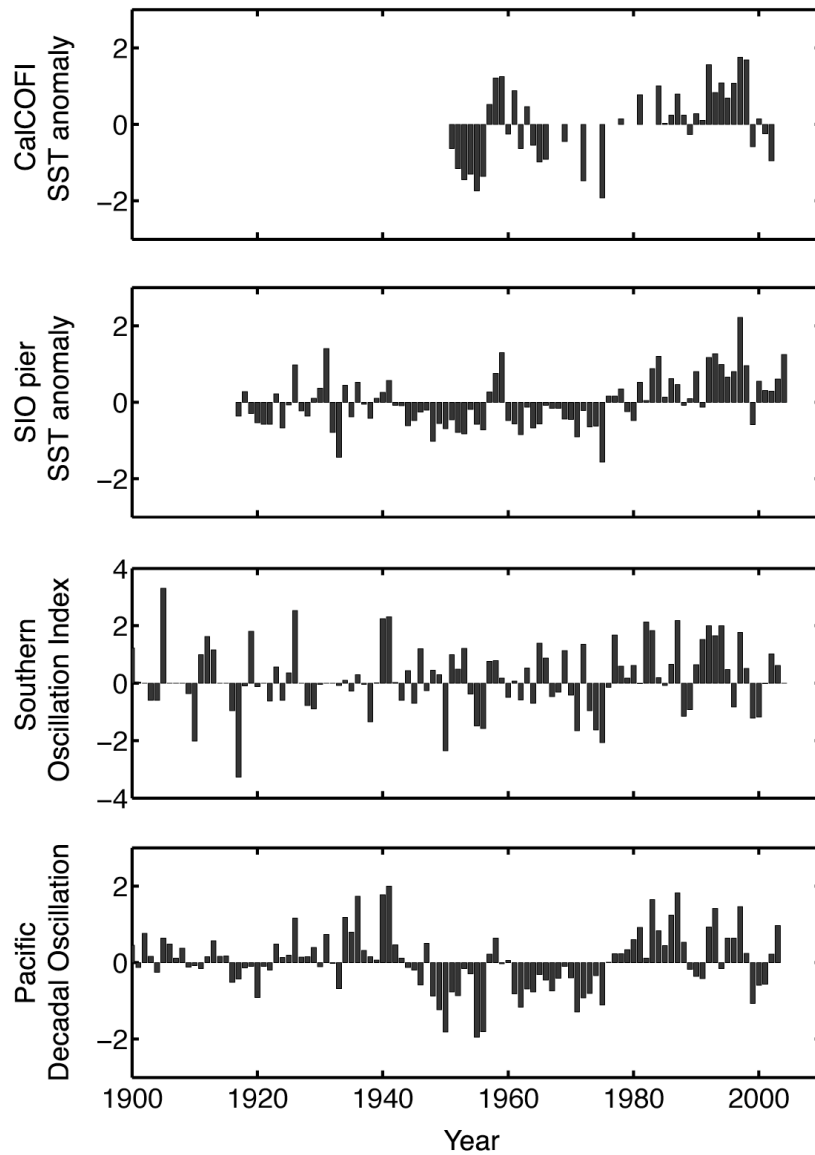


Figure 1.2. Environmental variability associated with the southern California bight marine ecosystem. The CalCOFI and Scripps pier SSTs represent local environmental variability. CalCOFI SST and SIO pier SST are normalized to unit mean and variance. The Southern Oscillation Index (SOI) is widely used for tracking the state of the El Niño Southern Oscillation, which is the leading source of North Pacific interannual climate variations. The Pacific Decadal Oscillation Index (PDO) tracks the leading patterns of North Pacific sea surface temperature variability. The SOI and PDO represent large-scale climate variability.

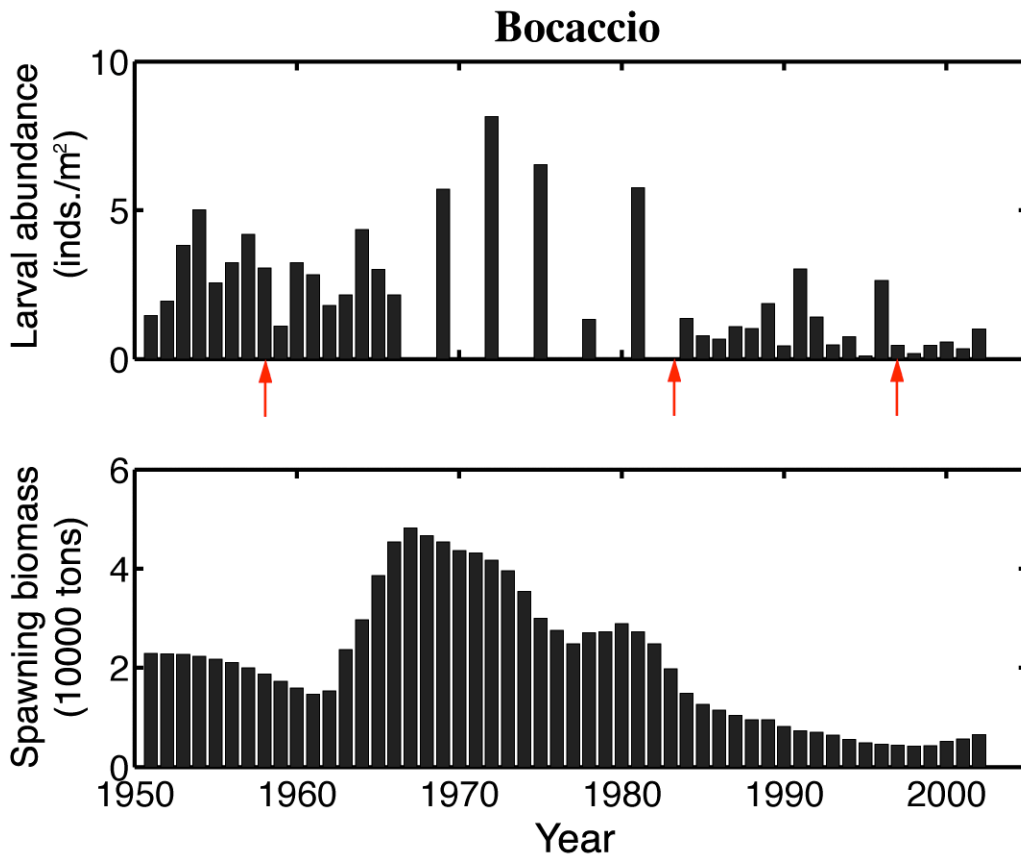


Figure 1.3. An example showing that CalCOFI larval abundance is a good indicator of adult spawning biomass. The spawning biomass of bocaccio is extracted from the stock assessment report of MacCall (2003). Arrows indicate major ENSO events. The long-term trend in larval abundance reflects the trend in adult spawning biomass, while short-term fluctuations may be related to low reproductive output or geographic shifts due to animal movement caused by El Niño effects. Significant correlation is found between larval abundance and adult spawning biomass (Pearson correlation, $r = 0.718$, $p < 0.001$).

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Chapter 2. 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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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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Keywords: Fish assemblages; CalCOFI time series; Fishing effects; Climate; Age-at-maturation

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, & Niuen, 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 m
Offshore: 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.

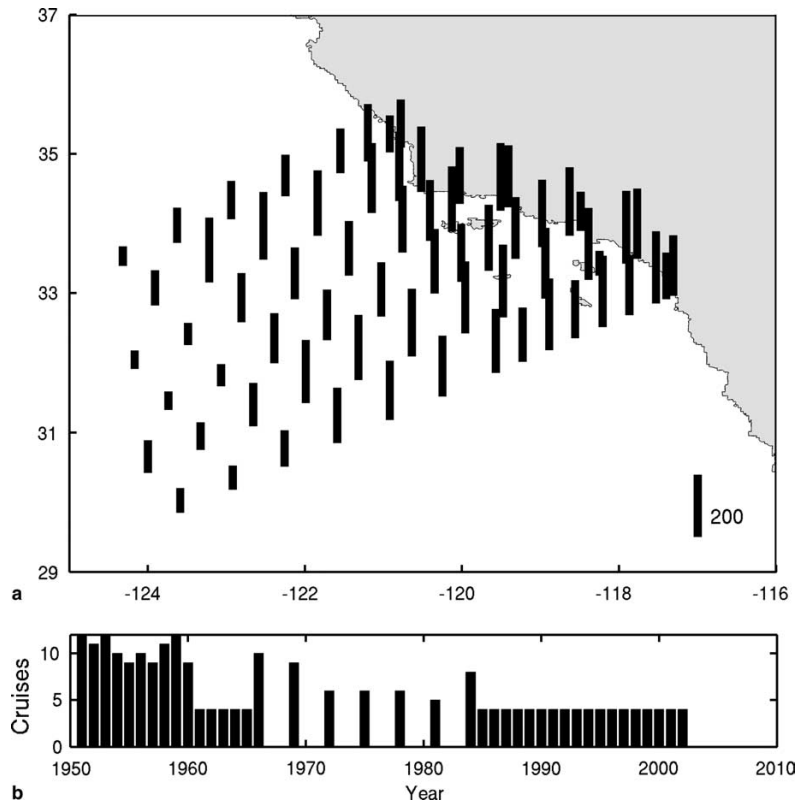


Fig. 1. Maps showing (a) spatial pattern of CalCOFI stations used in this study and number of samples at each station, and (b) temporal sampling frequency.

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)	\\hlstrom (1959)
	U p-mode-low	U p-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>Ceratoscopus 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	
Poromitra 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>Vinciguerria 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 *Vinciguerria 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
Before aggregation				
Coastal	0.363	0.153	0.382	157
Coastal-oceanic	0.333	0	0.417	24
Oceanic	0	0.016	0.984	128
After aggregation				
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

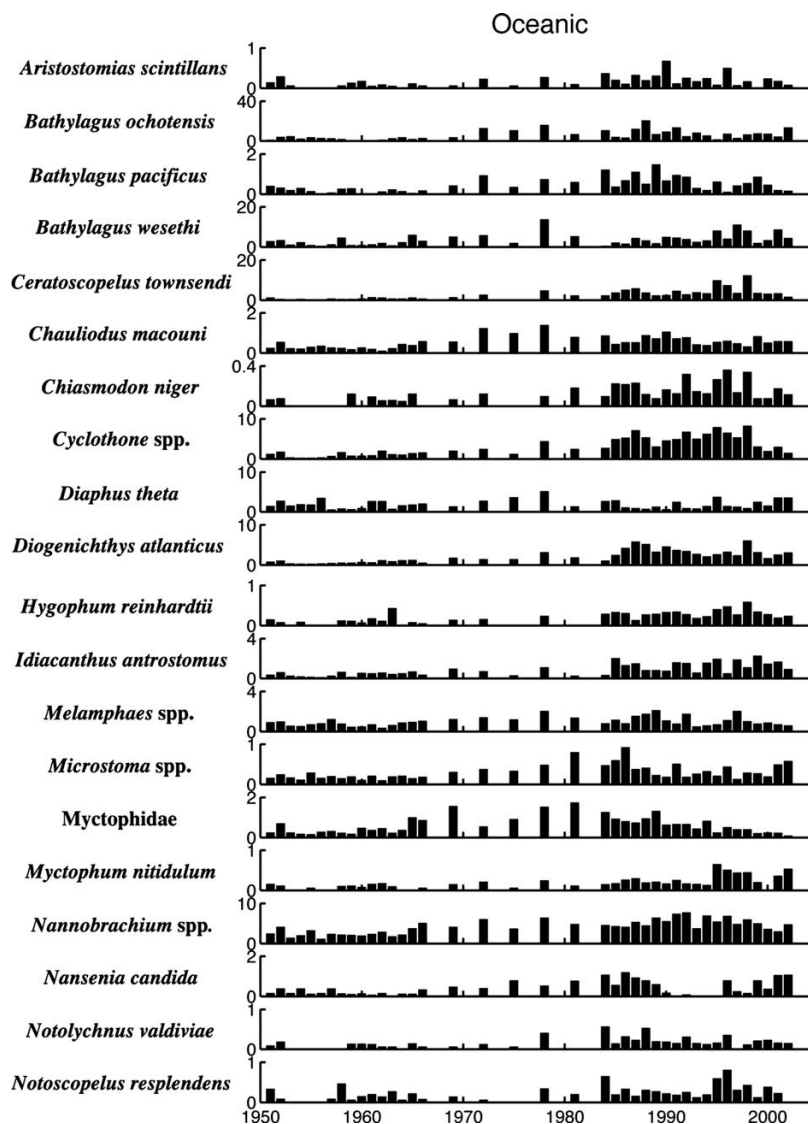


Fig. 2. Abundance time series of the taxa with a high-frequency of occurrence grouped into oceanic, coastal-oceanic-fished, coastal-oceanic-unfished, coastal-fished, coastal-bycatch, and coastal-unfished categories. (Arrows indicate low abundances after ENSO events.)

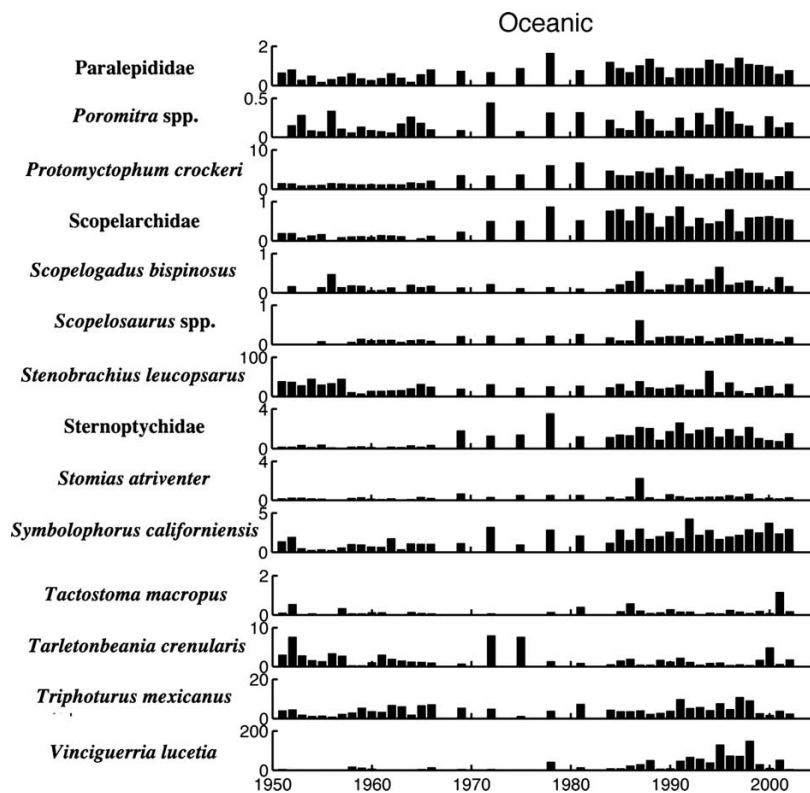


Fig. 2 (continued)

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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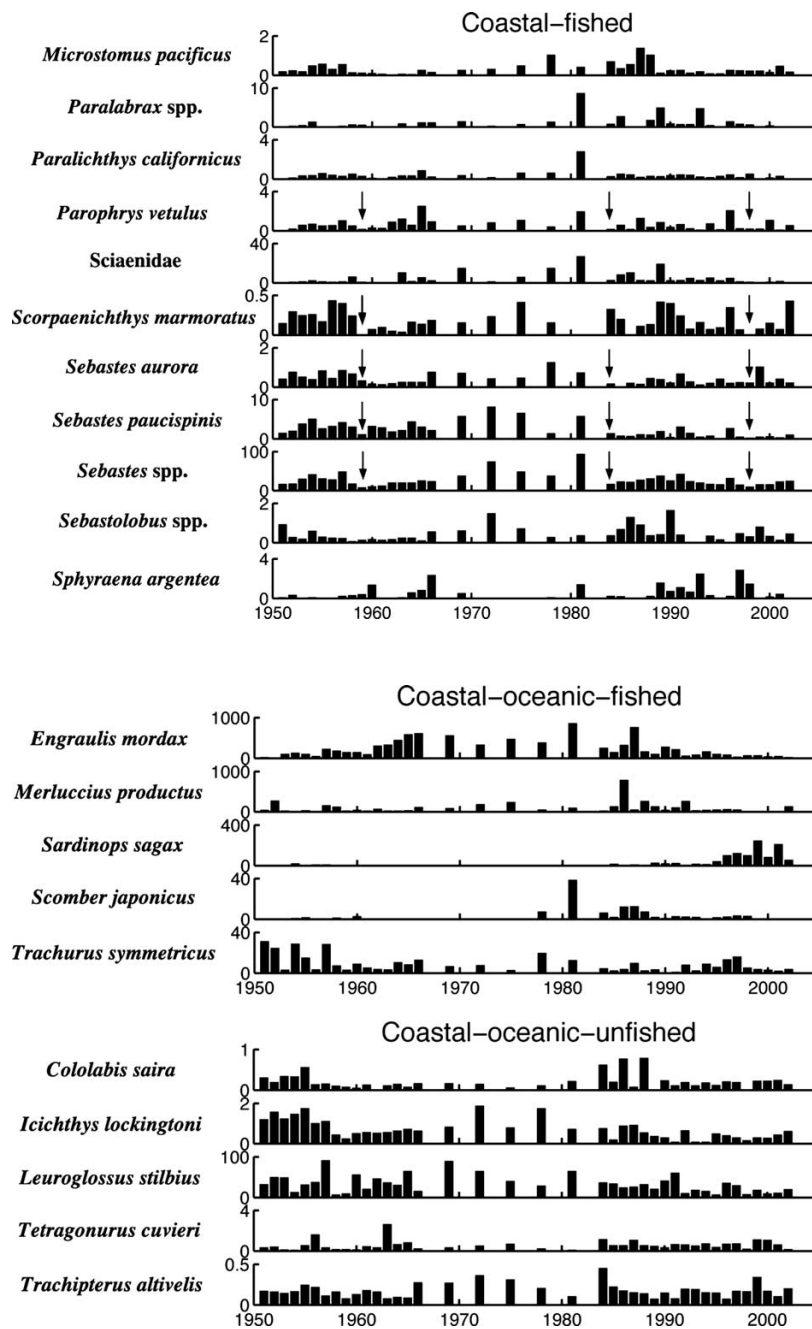


Fig. 2 (continued)

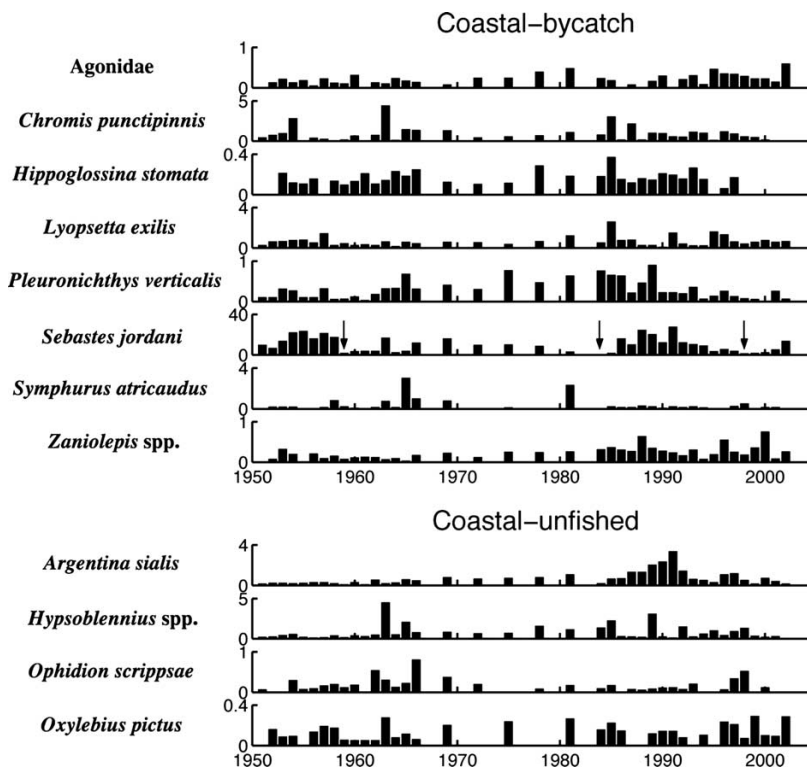


Fig. 2 (continued)

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 valdiviaæ*), 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 (*Icichthys 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 jordanii*) 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>	1	
	<i>Bathylagus ochotensis</i>	1 1	
	<i>Bathylagus pacificus</i>	1 1 1 0	
	<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>Stenobranchius 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	
Pacific	<i>Bathylagus wesethi</i>	0 0 0 1 0 0 1 0 1 0 0 1 0 0	
	<i>Hygophum reinhardtii</i>	1 0 1 1 0 0 1 0 1 0 0 1 0 0	0
	<i>Scopelogadus bispinosus</i>	0 0 0 1 0 0 1 0 0 0 0 1 0 0	1 0
	<i>Triphoturus mexicanus</i>	0 0 0 1 0 0 0 0 0 0 0 0 0 0	1 1 0
	<i>Vinciguerria lucetia</i>	0 0 0 1 0 0 1 0 1 0 0 0 0 1	1 1 1 1 1
World	<i>Chasmodon niger</i>	1 0 1 1 0 0 1 0 1 0 1 1 0 0	1 1 1 1 1 1
	<i>Diogenichthys atlanticus</i>	1 1 1 1 1 0 1 1 1 0 1 1 0 0	1 1 1 0 1 1
	<i>Microstoma</i> spp.	0 1 0 1 1 0 0 1 1 0 0 0 1 0	0 0 0 0 0 0 1 1
	<i>Myctophum nitidulum</i>	0 0 0 1 0 0 1 0 1 0 0 1 0 0	1 1 1 1 1 1 1 1 0
	<i>Notolychnus valdiviae</i>	1 1 1 1 1 0 0 1 1 0 0 1 0 0	0 1 0 0 0 1 1 1 1 0
	<i>Notoscopelus resplendens</i>	1 0 0 1 0 0 0 0 1 0 0 0 0 1	0 1 0 0 1 1 1 1 0 1 1
	<i>Poromitra</i> spp.	0 1 0 1 0 0 0 0 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0 0
	Scopelarchidae	1 1 1 1 1 0 1 1 1 0 1 1 0 0	1 1 0 0 1 1 1 1 1 1 1 1
	<i>Scopelosaurus</i> spp.	1 1 1 1 1 0 1 0 1 0 1 1 0 0	1 0 0 1 0 1 1 0 1 0 0 1 1
	Sternoptychidae	1 1 1 1 1 0 1 0 1 0 1 1 0 0	1 1 0 0 1 1 1 1 1 1 0 1 1 1

Within: 72/146
Between: 113/260
Fisher's Exact: p = 0.1509

Table 4 (continued)

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

The coastal-oceanic group

Fishing status:

Fished	<i>Engraulis mordax</i>	0	
	<i>Merluccius productus</i>	1 0	
	<i>Sardinops sagax</i>	0 0 0	
	<i>Scomber japonicus</i>	0 0 0 0	
	<i>Trachurus symmetricus</i>		
Unfished	<i>Cololabis saira</i>	0 0 0 0 0 0	
	<i>Icichthys lockingtoni</i>	0 0 1 0 1 0	
	<i>Leuroglossus stilbius</i>	1 0 1 0 0 0	0 1
	<i>Tetragonurus cuvieri</i>	0 0 0 0 0 0	0 0 0
	<i>Trachipterus altivelis</i>	0 0 0 0 0 0	0 0 0 0

Within: 2/20
Between: 4/25
Fisher's Exact: p = 0.4473

Geographic regions:

Broad north	<i>Merluccius productus</i>	0	
	<i>Cololabis saira</i>	0 0	
	<i>Icichthys lockingtoni</i>	0 0 1	
	<i>Leuroglossus stilbius</i>	0 0 0 0	
	<i>Tetragonurus cuvieri</i>	0 0 0 0 0	
	<i>Trachipterus altivelis</i>		
All	<i>Engraulis mordax</i>	0 0 0 1 0 0	
	<i>Sardinops sagax</i>	0 0 1 1 0 0	1
	<i>Scomber japonicus</i>	0 0 0 0 0 0	0 0
	<i>Trachurus symmetricus</i>	0 0 1 0 0 0	0 0 0

Within: 2/21
Between: 4/24
Fisher's Exact: p = 0.4001

(continued on next page)

Table 4 (continued)

Age-at-maturation:												Within: 5/25
1	<i>Engraulis mordax</i>											Between: 1/20
1.5	<i>Cololabis saira</i>	0										Fisher's Exact: p = 0.1522
2	<i>Sardinops sagax</i>	1	0									
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	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												Within: 13/89
Fishing status:												Between: 22/164
Fished												Fisher's Exact: p = 0.4660
	<i>Microstomus pacificus</i>											
	<i>Paralabrax</i> spp.	0										
	<i>Paralichthys californicus</i>	0	0									
	<i>Parophrys vetulus</i>	0	0	0								
	Sciaenidae	0	1	1	1							
	<i>Scorpaenichthys marmoratus</i>	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				
	<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		
	<i>Sphyrna argentea</i>	0	1	0	0	0	0	0	0	0	0	
Bycatch	Agonidae	0	0	0	0	0	0	0	0	0	0	
	<i>Chromis punctipinnis</i>	0	0	0	1	0	0	0	0	0	0	
	<i>Hippoglossina stomata</i>	0	1	0	0	1	0	0	0	0	0	
	<i>Lyopsetta exilis</i>	0	0	0	0	0	0	0	0	0	0	
	<i>Pleuronichthys verticalis</i>	1	1	1	1	1	0	0	0	1	0	
	<i>Sebastes jordani</i>	0	0	0	0	1	0	0	0	0	0	
	<i>Symphurus atricaudus</i>	0	1	0	0	1	0	0	0	0	0	
	<i>Zaniolepis</i> spp.	0	0	0	0	0	0	0	0	0	0	
Unfished	<i>Argentina sialis</i>	0	0	0	0	0	0	0	0	0	1	
	<i>Hypsoblemius</i> spp.	0	1	0	0	1	0	0	0	0	0	
	<i>Ophidion scrippsae</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	

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>	0												
	<i>Microstomus pacificus</i>	0 0												
	<i>Parophrys vetulus</i>	0 0 0												
	<i>Scorpaenichthys marmoratus</i>	0 0 0 0												
	<i>Sebastes aurora</i>	0 0 1 0 0												
	<i>Sebastes paucispinis</i>	0 0 0 0 0 0												
	<i>Sebastolobus</i> spp.	0 0 0 0 0 0 0												
	Agonidae	0 0 0 0 0 0 0 0												
	<i>Pleuronichthys verticalis</i>	0 1 1 0 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 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												
Bight	<i>Chromis punctipinnis</i>	0 0 1 0 0 0 0 0 0 0 0 0												
	<i>Hippoglossina stomata</i>	0 0 0 0 0 0 0 0 1 0 0 0										1		
	<i>Ophidion scrippsae</i>	0 0 0 0 0 0 0 0 1 0 0 0										1 0		
Broad south	<i>Paralabrax</i> spp.	0 0 0 0 0 0 0 1 1 0 0 0										0 1 0		
	<i>Paralichthys californicus</i>	0 0 0 0 0 0 0 0 1 0 0 0										0 0 0		
	Sciaenidae	0 0 1 0 0 0 0 0 1 1 0 0 0										0 1 0		
	<i>Hypsoblennius</i> spp.	0 0 0 0 0 0 0 0 1 1 0 0 0										1 0 1		
	<i>Sphyaena argentea</i>	0 0 0 0 0 0 0 0 0 0 1 0										0 0 1 1 0 0 0		
All	<i>Symphurus atricaudus</i>	0 0 0 0 0 0 0 1 0 0 0 0										0 0 0 0 0 0		
Bottom habitats:												Within: 7/67 Between: 22/165 Fisher's Exact: p = 0.3587		
Water	<i>Microstomus pacificus</i>	0												
	<i>Sebastes paucispinis</i>	0 0												
	<i>Sphyaena argentea</i>	0 0 0												
	<i>Sebastes jordani</i>	0 0 1 0												
	<i>Argentina sialis</i>	0 0 1 0												
Kelp/Hard	<i>Paralabrax</i> spp.	0 0 1 0 0												
	<i>Scorpaenichthys marmoratus</i>	0 0 0 1 0 0												
	<i>Chromis punctipinnis</i>	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 0												
	<i>Paralichthys californicus</i>	0 0 0 0 0 0 0 0 0 0 0										0		
	<i>Parophrys vetulus</i>	0 1 0 0 0 0 0 1 0 0 0										0 0		
	<i>Sebastes aurora</i>	0 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 0 0		
	<i>Hippoglossina stomata</i>	0 0 0 0 0 1 0 1 0 0 0										0 0 0 0 0		
	<i>Pleuronichthys verticalis</i>	1 0 0 0 0 1 0 0 1 0 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 0		
	<i>Ophidion scrippsae</i>	0 0 1 0 0 0 0 1 0 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		

(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:														Within: 15/81		
1	<i>Symphurus atricaudus</i>															Between: 7/90
1	<i>Hypsoblennius</i> spp.	1														Fisher's Exact: p = 0.0306
1	<i>Ophidion scrippsae</i>	1	0													
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	0							
3	<i>Hippoglossina stomata</i>	0	0	0	0	1	0	0	0	0						
3	<i>Sebastes jordani</i>	0	0	0	0	0	0	0	0	0	0					
3	<i>Oxylebius pictus</i>	0	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	1	
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	1
4.5	<i>Scorpaenichthys marmorat</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
5	<i>Sebastes aurora</i>	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

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	p-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>Stenobrachius 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-unfished					
<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	p-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.

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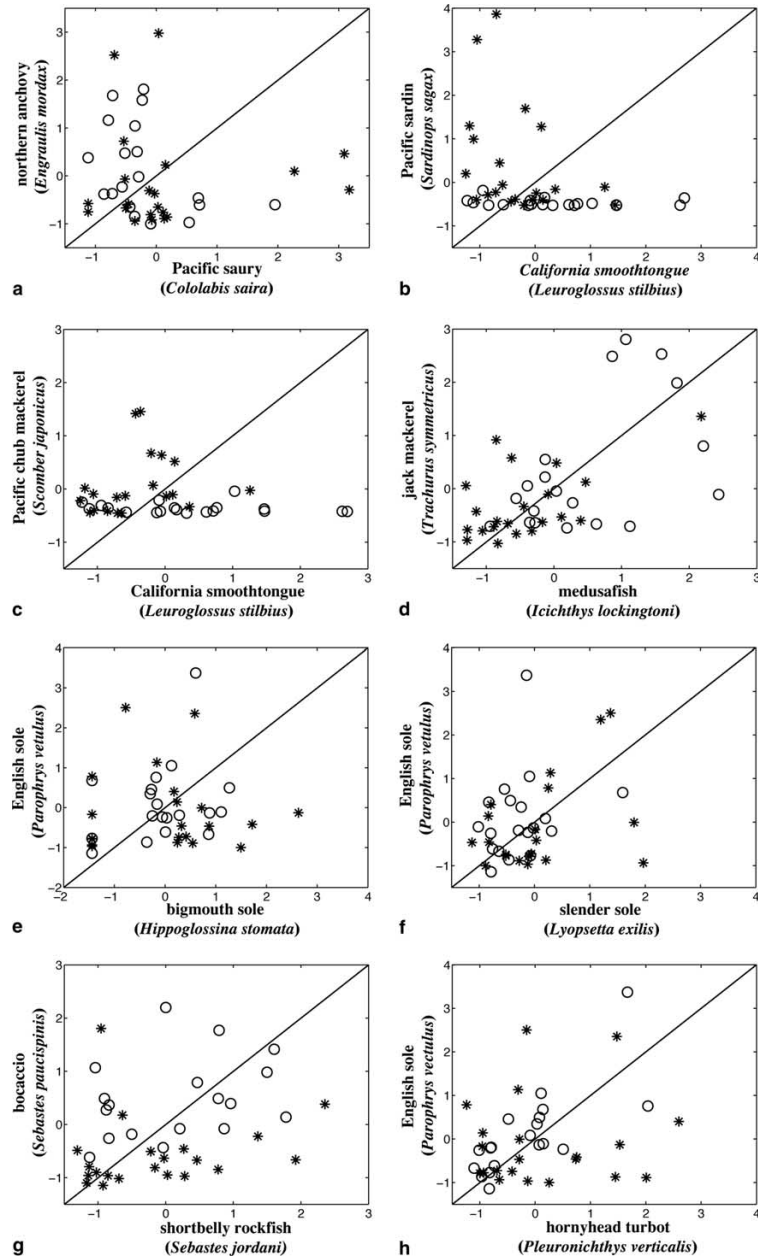


Fig. 3. Scatter plots of selected exploited (y-axis) versus unexploited (x-axis) species living in the same habitat and reaching maturity at about the same age (circles, data before 1976; stars, data after 1976). Each time series was standardized to zero mean and unit variance. If the two species varied 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 (Quirolo, 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 xanthostigma*), 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	
Leuroglossus group	
Leuroglossus stilbius	Coastal-oceanic, broad north
Merluccius productus	Coastal-oceanic, broad north
Sebastes spp.	Coastal
Bathylagus ochotensis	Oceanic, North Pacific, mesopelagic
Stenobranchius leucopsarus	Oceanic, North Pacific, migrator
Tarletonbeania group	
Tarletonbeania crenularis	Oceanic, North Pacific, migrator
Icichthys lockingtoni	Coastal-oceanic, broad north
Citharichthys group	
Engraulis mordax	Coastal-oceanic, broad north
Citharichthys fragilis	Offshore, broad south, soft
Citharichthys xanthostigma	Offshore, broad south, soft
Sardinops group	
Sardinops sagax	Coastal-oceanic, all
Scomber japonicus	Coastal-oceanic, all
Southern complex	
Symbolophorus group	
Bathylagus wesethi	Oceanic, North Pacific, mesopelagic
Symbolophorus californiensis	Oceanic, North Pacific, migrator
Nannobranchium ritteri	Oceanic, Pacific, migrator
Cyclothone spp.	Oceanic, world
Diogenichthys atlanticus	Oceanic, world, mesopelagic
Triphoturus group	
Triphoturus mexicanus	Oceanic, Pacific, migrator
Protomyctophum crockeri	Oceanic, North Pacific, migrator
Trachurus symmetricus	Coastal-oceanic, all
Ceratoscopelus group	
Ceratoscopelus townsendi	Oceanic, North Pacific, migrator
Lampadena urophaos	Oceanic, North Pacific, bathypelagic
Vinciguerria group	
Gonichthys tenuiculus	Oceanic, North Pacific, migrator
Hygophum atratum	Oceanic, North Pacific, migrator
Diogenichthys laternatus	Oceanic, Pacific, mesopelagic
Vinciguerria lucetia	Oceanic, North Pacific, migrator
Southern coastal complex	
Synodus group	
Ophidion scrippsae	Nearshore, Bight, soft
Symphurus atricaudus	Offshore, all, soft
Synodus lucioceps	Offshore, broad south, soft
Prionotus 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 arval 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>Icichthys 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.

Acknowledgments

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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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Appendix

Table A2.1. Larval fish species in the CalCOFI database with coding describing habitat affinities of adult fishes and the taxonomic history of each taxon (see Materials and Methods for details). The ranks were based on the abundance (larvae under 10 m² of sea surface) from 1951-2002.

SCIENTIFIC NAME	COMMON NAME	RANK	GRP	NRSHORE	REGION	DEPTH	BOTTOM	FISHED	TAXONOMIC HISTORY	USED NAME
<i>Engraulis mordax</i>	Northern anchovy	1	2		4		13	14	1951-	always
<i>Merluccius productus</i>	Pacific hake or whiting	2	2		1.5		13	14	1951-	always
<i>Leuroglossus stilbius</i>	California smoothtongue	3	2		1.5		13	16	1951-	always
<i>Sebastes</i> spp.	Rockfishes	4	1	0	0		0	14	1951-	always
<i>Vinciguerra lucetia</i>	Panama lightfish	5	3		23	7	13	16	1951-	always
<i>Stenobranchius leucopsarus</i>	Northern lampfish	6	3		22	7	13	16	1951-	always
<i>Sardinops sagax</i>	Pacific sardine (pilchard)	7	2		4		13	14	1951-	always
<i>Trachurus symmetricus</i>	Jack mackerel	8	2		4		13	14	1951-	always
<i>Sebastes jordani</i>	Shortbelly rockfish	9	1	2	1.5		13	15	1951-	always
<i>Bathylagus ochotensis</i>	Popeye blacksmelt	10	3		22	8	13	16	1951-	always
<i>Triphoturus mexicanus</i>	Mexican lampfish	11	3		23	7	13	16	1951-	always
<i>Bathylagus wesethi</i>	Snubnose blacksmelt	12	3		22	8	13	16	1951-	always
Sciaenidae	Croakers	13	1	0	2.5		11	14	1951-	always
<i>Protomyctophum crockeri</i>	California flashlightfish	14	3		22	7	13	16	1951-	always
<i>Ceratoscopelus townsendi</i>	Dogtooth lampfish	15	3		22	7	13	16	1951-	always
<i>Citharichthys stigmaeus</i>	Speckled sanddab	16	1	1	1.5		12	15	1954-	<i>Citharichthys</i> spp.
<i>Nannobranchium ritteri</i>	Broadfin lampfish	17	3		23	7	13	16	1954-	<i>Nannobranchium</i> spp.
<i>Tarletonbeania crenularis</i>	Blue lanternfish	18	3		22	7	13	16	1951-	always
<i>Diogenichthys atlanticus</i>	Longfin lanternfish	19	3		21	8	13	16	1951-	always
<i>Symbolophorus californiensis</i>	California lanternfish	20	3		22	7	13	16	1951-	always
<i>Citharichthys</i> spp.	Sanddabs	21	1	0	1.5		12	0	1951-	always
<i>Scomber japonicus</i>	Pacific chub mackerel (Pacific mackerel)	22	2		4		13	14	1951-	always
<i>Sebastes paucispinis</i>	Bocaccio	23	1	2	1.5		13	14	1951-	always
<i>Cyclothone signata</i>	Showy bristlemouth	24	3		22	7	13	16	1985-	<i>Cyclothone</i> spp.
<i>Nannobranchium</i> spp.		25	3		21	7	13	16	1951-	always
<i>Citharichthys sordidus</i>	Pacific sanddab	26	1	2	1.5		12	14	1954-1960 and 1984-	<i>Citharichthys</i> spp.
<i>Diaphus</i> spp.	Headlightfishes	27	3		21	7	13	16	1951-	always
<i>Genyonemus lineatus</i>	White croaker	28	1	2	1.5		12	14	1981-	Sciaenidae
Disintegrated fish larvae		29	0						1951-	always
<i>Cyclothone</i> spp.		30	3		21	0	13	16	1951-	always

Table A2.1 continued

<i>Vinciguerria poweriae</i>	Highseas lightfish	31	3		21	7	13	16	1951-	always
Unidentified		32	0						1951-	always
<i>Icichthys lockingtoni</i>	Medusafish	33	2		1.5		13	16	1951-	always
<i>Melamphaes</i> spp.		34	3		21	8	13	16	1951-	always
<i>Sebastes diploproa</i>	Splitnose rockfish	35	1	2	1.5		12	14	1951-1969 and 1987-	<i>Sebastes</i> spp.
<i>Idiacanthus antrostomus</i>	Pacific blackdragon	36	3		22	8	13	16	1951-	always
Myctophidae	Lanternfishes	37	3		21	0	13	16	1951-	always
<i>Argentina sialis</i>	Pacific argentine	38	1	2	1.5		13	16	1951-	always
<i>Chauliodus macouni</i>	Pacific viperfish	39	3		22	8	13	16	1951-	always
<i>Oxyjulis californica</i>	Senorita	40	1	1	1.5		10	16	1961-	Labridae
Gobiidae	Gobies	41	1	0	0		11	0	1951-	always
Sternoptychidae	Hatchetfishes	42	3		21	8	13	16	1951-	always
<i>Lestidiops ringens</i>	Slender barracudina	43	3		22	8	13	16	1961-	Paralepididae
<i>Tetragonurus cuvieri</i>	Smalleye squaretail	44	2		1.5		13	16	1951-	always
<i>Parophrys vetulus</i>	English sole	45	1	2	1.5		12	14	1951-	always
<i>Lyopsetta exilis</i>	Slender sole	46	1	2	1.5		12	15	1951-	always
<i>Sebastes aurora</i>	Aurora rockfish	47	1	2	1.5		12	14	1951-	always
<i>Chromis punctipinnis</i>	Blacksmith	48	1	1	2		10	15	1951-	always
<i>Paralabrax</i> spp.	Kelp and sand basses	49	1	1	2.5		11	14	1951-	always
<i>Paralichthys californicus</i>	California halibut	50	1	2	2.5		12	14	1951-	always
Cottidae	Sculpins	51	1	0	1.5		11	0	1951-	always
<i>Bathylagus</i> spp.		52	3		21	8	13	16	1951-	always
<i>Hypsoblennius</i> spp.		53	1	1	2.5		10	16	1951-	always
<i>Danaphos oculatus</i>	Bottlelight	54	3		21	8	13	16	1972-	Gonostomatidae
<i>Argyropelecus sladeni</i>	Lowcrest hatchetfish	55	3		22	8	13	16	1985-	Sternoptychidae
<i>Microstoma</i> spp.	Dusky pencilsmelt	56	3		21	8	13	16	1951-	always
<i>Sphyræna argentea</i>	Pacific barracuda (California barracuda)	57	1	2	2.5		13	14	1951-	always
<i>Nannobranchium regale</i>	Pinpoint lampfish	58	3		23	7	13	16	1954-	<i>Nannobranchium</i> spp.
<i>Pleuronichthys verticalis</i>	Hornyhead turbot	59	1	2	1.5		12	15	1951-	always
<i>Melamphaes lugubris</i>	Highsnout bigscale	60	3		22	8	13	16	1985-	<i>Melamphaes</i> spp.
<i>Peprilus simillimus</i>	Pacific pompano	61	1	1	1.5		13	14	1951-	always
<i>Stomias atriventer</i>	Blackbelly dragonfish	62	3		22	8	13	16	1951-	always
Labridae	Wrasses	63	1	0	0		10	0	1951-	always
<i>Sebastolobus</i> spp.	Thornyheads	64	1	2	1.5		12	14	1951-	always
<i>Bathylagus pacificus</i>	Pacific blacksmelt	65	3		22	8	13	16	1951-	always
<i>Rhinogobius nicholsii</i>	Blackeye goby	66	1	2	1.5		11	16	1985-	Gobiidae

Table A2.1 continued

<i>Sebastes goodei</i>	Chilipepper	67	1	2	1.5		13	14	1951-1969 and 1987-	<i>Sebastes</i> spp.
<i>Seriphus politus</i>	Queenfish	68	1	1	1.5		12	14	1981-	Sciaenidae
<i>Nansenia candida</i>	Bluethroat argentine	69	3		22	8	13	16	1951-	always
<i>Sternoptyx</i> spp.	Dollar hatchetfishes	70	3		21	8	13	16	1951-	always
<i>Microstomus pacificus</i>	Dover sole	71	1	2	1.5		12	14	1951-	always
Paralepididae	Barracudinas	72	3		21	0	13	16	1951-	always
<i>Diogenichthys laternatus</i>	Diogenes lanternfish	73	3		23	8	13	16	1951-	always
<i>Hygophum reinhardtii</i>	Slender lanternfish	74	3		23	7	13	16	1951-	always
<i>Notoscopelus resplendens</i>	Patchwork lampfish	75	3		21	7	13	16	1951-	always
Ophidiiformes		76	1	0	0		11	0	1951-	always
<i>Myctophum nitidulum</i>	Pearly lanternfish	77	3		21	7	13	16	1951-	always
<i>Symphurus atricaudus</i>	California tonguefish	78	1	2	4		12	15	1951-	always
<i>Scopelogadus bispinosus</i>	Twospine bigscale	79	3		23	8	13	16	1951-	always
<i>Cololabis saira</i>	Pacific saury	80	2		1.5		13	16	1951-	always
Trachipteridae	Ribbonfishes	81	2		0		13	16	1951-	always
<i>Argyropelecus affinis</i>	Slender hatchetfish	82	3		21	8	13	16	1985-	Sternoptychidae
Clinidae	Kelpfishes	83	1	0	0		10	0	1951-	always
<i>Electrona risso</i>	Chubby flashlightfish	84	3		22	8	13	16	1951-	always
<i>Hypsoblennius jenkinsi</i>	Mussel blenny	85	1	1	2		10	16	1985-	<i>Hypsoblennius</i> spp.
<i>Cyclothone acclinidens</i>	Benttooth bristlemouth	86	3		21	7	13	16	1985-	<i>Cyclothone</i> spp.
<i>Scorpaenichthys marmoratus</i>	Cabezon	87	1	2	1.5		10	14	1951-	always
<i>Scopelosaurus</i> spp.	Paperbones	88	3		21	8	13	16	1951-	always
<i>Notolychnus valdiviae</i>	Topside lampfish	89	3		21	7	13	16	1951-	always
<i>Aristostomias scintillans</i>	Shiny loosejaw	90	3		22	8	13	16	1951-	always
<i>Ophidion scrippsae</i>	Basketweave cusk-eel	91	1	1	2		12	16	1951-	always
<i>Arctozenus risso</i>	White barracudina	92	3		21	8	13	16	1961-	Paralepididae
<i>Hypsypops rubicundus</i>	Garibaldi	93	1	1	2		10	16	1951-	always
<i>Chiasmodon niger</i>	Black swallower	94	3		21	9	13	16	1951-	always
<i>Hippoglossina stomata</i>	Bigmouth sole	95	1	2	2		12	15	1951-	always
<i>Icelinus quadriseriatus</i>	Yellowchin sculpin	96	1	2	1.5		12	16	1985-	Cottidae
<i>Sebastes levis</i>	Cow rockfish (cowcod)	97	1	2	1.5		11	14	1951-	always
<i>Brosmophycis marginata</i>	Red brotula	98	1	2	1.5		10	16	1951-	always
<i>Argyropelecus hemigymnus</i>	Spurred hatchetfish	99	3		21	8	13	16	1985-	Sternoptychidae
<i>Ruscarius creaseri</i>	Roughcheek sculpin	100	1	1	1.5		10	16	1985-	Cottidae
<i>Lepidogobius lepidus</i>	Bay goby	101	1	2	1.5		12	16	1985-	Gobiidae
<i>Tactostoma macropus</i>	Longfin dragonfish	102	3		22	8	13	16	1951-	always
Agonidae	Poachers	103	1	0	1.5		11	15	1951-	always

Table A2.1 continued

<i>Benthalbella dentata</i>	Northern pearleye	104	3		22	8	13	16	1972-	Scopelarchidae
<i>Oxylebius pictus</i>	Painted greenling	105	1	1	1.5		10	16	1951-	always
<i>Lampadena urophaos</i>	Sunbeam lampfish	106	3		22	9	13	16	1951-	always
<i>Chilara taylori</i>	Spotted cusk-eel	107	1	2	1.5		12	15	1951-	always
<i>Glyptocephalus zachirus</i>	Rex sole	108	1	2	1.5		12	14	1951-	always
<i>Argyropelecus lychnus</i>	Tropical hatchetfish	109	3		21	8	13	16	1985-	Sternoptychidae
<i>Poromitra crassiceps</i>	Crested bigscale	110	3		21	8	13	16	1985-	<i>Poromitra</i> spp.
<i>Poromitra</i> spp.		111	3		21	8	13	16	1951-	always
<i>Melamphaes parvus</i>	Little bigscale	112	3		23	8	13	16	1985-	<i>Melamphaes</i> spp.
<i>Zaniolepis</i> spp.		113	1	2	1.5		12	15	1951-	always
<i>Pleuronichthys coenosus</i>	C-O sole	114	1	1	1.5		11	15	1951-	always
Gonostomatidae	Bristlemouths	115	3		21	0	13	16	1951-	always
<i>Semicossyphus pulcher</i>	California sheephead	116	1	1	4		10	14	1961-	Labridae
<i>Rosenblattichthys volucris</i>	Chubby pearleye	117	3		23	8	13	16	1972-	Scopelarchidae
<i>Trachipterus altivelis</i>	King-of-the-salmon	118	2		1.5		13	16	1985-	Trachipteridae
<i>Diogenichthys</i> spp.		119	3		21	8	13	16	1951-	always
Scopelarchidae	Pearleyes	120	3		21	8	13	16	1951-	always
<i>Howella</i> spp.	Pelagic basslet	121	3		21	8	13	16	1951-	always
<i>Zaniolepis latipinnis</i>	Longspine combfish	122	1	2	1.5		12	15	1985-	<i>Zaniolepis</i> spp.
<i>Scopelarchus analis</i>	Blackbelly pearleye	123	3		23	8	13	16	1985-	<i>Scopelarchus</i> spp.
<i>Rathbunella</i> spp.	Ronquils (Stripefin, Bluebanded)	124	1	0	1.5		11	16	1985-	Blennioidei
<i>Cataetyx rubrirostris</i>	Rubynose brotula	125	1	2	1.5		12	16	1961-	Bythitidae
<i>Bathophilus flemingi</i>	Highfin dragonfish	126	3		22	8	13	16	1951-	always
Stomiiformes		127	3		21	0	13	16	1951-	always
<i>Bathylagus milleri</i>	Robust blacksmelt	128	3		22	8	13	16	1951-	always
<i>Pleuronichthys ritteri</i>	Spotted turbot	129	1	1	2		12	16	1951-	always
<i>Synodus lucioceps</i>	California lizardfish	130	1	2	2.5		12	15	1951-	always
<i>Vinciguerra</i> spp.		131	3		21	7	13	16	1951-	always
<i>Nannobranchium hawaiiensis</i>		132	3		23	8	13	16	1985-	<i>Nannobranchium</i> spp.
<i>Ichthyococcus irregularis</i>	Bulldog lightfish	133	3		23	8	13	16	1951-	always
<i>Cryptotrema corallinum</i>	Deepwater blenny	134	1	2	2		11	16	1985-	Clinidae
<i>Cyclothone pseudopallida</i>	Slender bristlemouth	135	3		21	8	13	16	1985-	<i>Cyclothone</i> spp.
Stichaeidae	Pricklebacks	136	1	0	1		11	0	1987-	Blennioidei
Pleuronectiformes		137	1	0	0		11	0	1951-	always
<i>Pleuronichthys decurrens</i>	Curlfin sole	138	1	2	1.5		12	14	1951-	always
<i>Loweina rara</i>	Dwarf lanternfish	139	3		23	7	13	16	1951-	always

Table A2.1 continued

<i>Citharichthys xanthostigma</i>	Longfin sanddab	140	1	2	2.5	12	14	1954-1960 and 1984-	<i>Citharichthys</i> spp.	
<i>Lythrypnus dalli</i>	Bluebanded goby	141	1	1	2.5	10	14	1985-	Gobiidae	
<i>Brama japonica</i>	Pacific pomfret	142	3		22	8	13	15	1951-	always
<i>Sebastolobus altivelis</i>	Longspine thornyhead	143	1	2	1.5		12	14	1985-	<i>Sebastolobus</i> spp.
<i>Xystreurus liolepis</i>	Fantail sole	144	1	1	2		12	14	1951-	always
<i>Gigantactis</i> spp.	Whipnoses	145	3		21	9	13	16	1951-	always
Cyclopteridae	Snailfishes, Lumpsuckers	146	1	0	1		0	0	1951-	always
<i>Medialuna californiensis</i>	Halfmoon	147	1	1	2		13	14	1951-	always
Blennioidei		148	1	0	0		0	0	1951-	always
<i>Argyropelecus</i> spp.		149	3		21	8	13	16	1985-	Sternoptychidae
<i>Girella nigricans</i>	Opaleye	150	1	1	2		10	14	1951-	always
<i>Artedius lateralis</i>	Smoothhead sculpin	151	1	1	1		10	16	1985-	Cottidae
<i>Pleuronichthys</i> spp.	Turbots	152	1	0	1.5		11	14	1951-	always
<i>Typhlogobius californiensis</i>	Blind goby	153	1	1	2		10	16	1985-	Gobiidae
<i>Scopelarchus</i> spp.	Pearleyes	155	3		21	8	13	16	1972-	Scopelarchidae
Atherinopsidae	New world silversides	156	1	1	1.5		13	14	1951-	always
<i>Oneirodes</i> spp.	Dreamers	157	3		21	9	13	16	1985-	Oneirodidae
<i>Psettichthys melanostictus</i>	Sand sole	158	1	1	1		12	14	1951-	always
<i>Zaniolepis frenata</i>	Shortspine combfish	159	1	2	1.5		12	15	1985-	<i>Zaniolepis</i> spp.
Ceratioidei		160	3		21	9	13	16	1951-	always
<i>Pleuronichthys guttulata</i>	Diamond turbot	161	1	1	2		12	14	1951-	always
<i>Icosteus aenigmaticus</i>	Ragfish	162	2		1.5		13	16	1951-	always
<i>Neoclinus stephensae</i>	Yellowfin fringehead	163	1	1	2		10	16	1985-	Blennioidei
<i>Diaphus theta</i>	California headlightfish	164	3		22	7	13	16	1951-	<i>Diaphus</i> spp.
<i>Lythrypnus zebra</i>	Zebra goby	165	1	1	2		10	16	1985-	Gobiidae
<i>Scopelarchus guentheri</i>	Staring pearleye	166	3		23	8	13	16	1985-	<i>Scopelarchus</i> spp.
<i>Parvilux ingens</i>	Giant lampfish	167	3		22	9	13	16	1969-	Myctophidae
<i>Xeneretmus latifrons</i>	Blacktip poacher	168	1	2	1.5		12	15	1985-	Agonidae
Macrouridae	Grenadiers	169	2		0		12	0	1951-	always
<i>Scopeloberyx robustus</i>	Longjaw bigscale	170	3		21	8	13	16	1951-	always
<i>Rathbunella alleni</i>	Stripefin ronquil	171	1	0	0		11	16	1995-	Blennioidei
Bathylagidae	Deepsea smelts	172	3		21	8	13	16	1951-	always
<i>Lamppanyctus steinbecki</i>	Longfin lampfish	173	3		23	7	13	16	1985-	<i>Nannobranchium</i> spp.
<i>Hygophum atratum</i>	Thickhead lanternfish	174	3		22	7	13	16	1951-	always
<i>Halichoeres semicinctus</i>	Rock wrasse	175	1	1	2		10	16	1961-	Labridae
<i>Etrumeus teres</i>	Round herring	176	1	1	3		13	16	1951-	always
Haemulidae	Grunts	177	1	1	2.5		0	14	1951-	always

Table A2.1 continued

<i>Icelinus</i> spp.		178	1	2	1.5		0	0	1985-	Cottidae
<i>Hypsoblennius gentilis</i>	Bay blenny	179	1	1	2		10	16	1985-	<i>Hypsoblennius</i> spp.
<i>Nannobranchium bristori</i>		180	3		23	8	13	16	1985-	<i>Nannobranchium</i> spp.
<i>Hygophum</i> spp.		181	3		21	7	13	16	1951-	always
<i>Liparis mucosus</i>	Slimy snailfish	182	1	1	1		10	16	1951-	always
<i>Chitonotus pugetensis</i>	Roughback sculpin	183	1	2	1.5		12	16	1985-	Cottidae
<i>Lepidopsetta bilineata</i>	Rock sole	184	1	2	1.5		11	14	1961-	Pleuronectidae
<i>Ophiodon elongatus</i>	Lingcod	185	1	2	1.5		11	14	1951-	always
<i>Atherinopsis californiensis</i>	Jacksmelt	186	1	1	1.5		13	14	1985-	Atherinidae
<i>Odontopyxis trispinosa</i>	Pygmy poacher	187	1	2	1.5		12	15	1985-	Agonidae
<i>Orthonopias triacis</i>	Snubnose sculpin	188	1	1	1.5		10	16	1987-	Cottidae
<i>Xenistius californiensis</i>	Salema	189	1	1	2.5		13	14	1980-	Haemulidae
Melanostomiinae	Scaleless dragonfishes	190	3		21	8	13	16	1951-	always
<i>Sebastolobus alascanus</i>	Shortspine thornyhead	191	1	2	1.5		12	14	1985-	<i>Sebastolobus</i> spp.
<i>Seriola lalandi</i>	Yellowtail jack	192	1	2	2.5		13	14	1951-	always
Anguilliformes	Eels	193	2	2	0		0	16	1951-	always
<i>Melamphaes simus</i>		194	3		23	8	13	16	1985-	<i>Melamphaes</i> spp.
<i>Arteidius harringtoni</i>	Scalyhead sculpin	195	1	2	1		10	16	1985-	Cottidae
<i>Plectobranchus evides</i>	Bluebarred prickleback	196	1	2	1.5		12	16	1985-	Blennioidei
<i>Arteidius fenestralis</i>	Padded sculpin	197	1	2	1		10	16	1985-	Cottidae
<i>Sarda chiliensis</i>	Pacific bonito	198	1	1	1.5		13	14	1956-	Scombridae
<i>Sebastes melanostomus</i>	Blackgill rockfish	199	1	2	1.5		12	14	1997-	<i>Sebastes</i> spp.
<i>Atractoscion nobilis</i>	White seabass	200	1	2	1.5		13	14	1984-	Sciaenidae
<i>Hexagrammos decagrammus</i>	Kelp greenling	201	1	1	1.5		10	14	1989-	Hexagrammidae
<i>Desmodema lorum</i>	Whiptail ribbonfish	202	3		22	8	13	16	1987-	Trachipteridae
Pleuronectidae	Righteye Flounders	203	1	0	1.5		11	0	1951-	always
<i>Valenciennellus tripunctulatus</i>	Constellationfish	204	3		21	8	13	16	1972-	Gonostomatidae
<i>Citharichthys fragilis</i>	Gulf sanddab	205	1	2	2.5		12	15	1954-	<i>Citharichthys</i> spp.
<i>Macroramphosus gracilis</i>	Slender snipefish	206	2		2.5		13	16	1951-	always
Hexagrammidae	Greenlings	207	1	0	1		11	0	1951-	always
<i>Anisotremus davidsonii</i>	Sargo	208	1	1	2		11	14	1985-	Haemulidae
<i>Gonichthys tenuiculus</i>	Slendertail lanternfish	209	3		22	7	13	16	1951-	always
<i>Photonectes</i> spp.		210	3		21	8	13	16	1961-	Melanostomiinae
Melamphidae	Big scales	211	3		21	8	13	16	1951-	always
Gempylidae	Snake Mackerels	212	3		21	7	13	16	1951-	always
<i>Dolichopteryx longipes</i>	Brownsnout spookfish	213	3		21	8	13	16	1951-	always
<i>Diplospinus multistriatus</i>	Striped escolar	214	3		23	7	13	16	1985-	Gempylidae

Table A2.1 continued

<i>Scorpaena guttata</i>	California scorpionfish (sculpin)	215	1	2	2		11	14	1951-	always
<i>Cyema atrum</i>	Bobtail eel	216	3		21	9	13	16	1951-	always
<i>Eopsetta jordani</i>	Petrale sole	217	1	2	1.5		11	14	1951-	always
<i>Cheilotrema saturnum</i>	Black croaker	218	1	1	2		11	14	1981-	Sciaenidae
<i>Leptocottus armatus</i>	Pacific staghorn sculpin	219	1	1	1.5		12	16	2001-	Cottidae
<i>Hypsoblennius gilberti</i>	Rockpool blenny	220	1	1	2		10	16	1985-	<i>Hypsoblennius</i> spp.
<i>Centrobranchus nigroocellatus</i>	Roundnose lanternfish	221	3		23	7	13	16	1951-	always
<i>Stemonosudis macrura</i>	Sharpchin barracudina	222	3		23	8	13	16	1961-	Paralepididae
<i>Oligocottus</i> spp.		223	1	1	1		10	16	1989-	Cottidae
<i>Xeneretmus leiops</i>	Smootheye poacher	224	1	2	1		12	15	1985-	Agonidae
<i>Paricelinus hoptiticus</i>	Thornback sculpin	225	1	1	1		12	16	1985-	Cottidae
<i>Caristius maderensis</i>	Manefin	226	3		21	8	13	16	1951-	always
Oneirodidae	Dreamers	227	3		21	9	13	16	1951-	always
<i>Nansenia crassa</i>	Stout argentine	228	3		23	8	13	16	1951-	always
<i>Psenes pellucidus</i>	Bluefin driftfish (blackrag)	229	3		23	6	13	16	1951-	always
<i>Platichthys stellatus</i>	Starry flounder	230	1	1	1		12	14	1951-	always
<i>Ruscarius meanyi</i>	Puget Sound sculpin	231	1	1	1		10	16	1999-	Cottidae
<i>Isopsetta isolepis</i>	Butter sole	232	1	1	1		12	14	1951-	always
<i>Anoplarchus purpureus</i>	High cockscomb	233	1	1	1		10	16	1987-	Blennioidei
<i>Bathyagonus pentacanthus</i>	Bigeye poacher	234	1	2	1		12	15	1987-	Agonidae
<i>Magnisudis atlantica</i>	Duckbill barracudina	235	3		21	7	13	16	1985-	Paralepididae
<i>Leuresthes tenuis</i>	California grunion	236	1	1	1.5		13	14	1985-	Atherinidae
<i>Atherinops affinis</i>	Topsmelt	237	1	1	1.5		13	14	1985-	Atherinidae
<i>Diplophos taenia</i>		238	3		23	8	13	16	1951-	always
<i>Neoclinus</i> spp.	Fringeheads	239	1	1	2		0	16	1985-	Blennioidei
<i>Dolopichthys</i> spp.		240	3		21	8	13	16	1997-	Oneirodidae
<i>Cheilopogon pinnatibarbatus</i>	Smallhead flyingfish	241	2		2.5		13	14	1977-	Exocoetidae
<i>Chaenopsis alepidota</i>	Orangethroat pikeblenny	242	1	1	3		12	16	1980-	Clinidae
<i>Caulolatilus princeps</i>	Ocean whitefish	243	1	2	4		11	14	1951-	always
<i>Nezumia</i> spp.		244	1	2	2		12	15	1986-	Macrouridae
<i>Artedius</i> spp.		245	1	0	1.5		11	16	1985-	Cottidae
Exocoetidae	Flyingfishes	246	2		2.5		13	0	1951-	always
<i>Clinocottus analis</i>	Woolly sculpin	247	1	1	2		10	16	1980-	Cottidae
<i>Eutaeniophorus festivus</i>	Festive ribbontail	248	3		21	8	13	16	1951-	<i>Eutaeniophorus</i> spp.
Perciformes		249	2		0		0	0	1951-	always

Table A2.1 continued

<i>Lepidopus fitchi</i>	Pacific scabbardfish	250	1	2	2.5		13	16	1972-	Trichiuridae
<i>Macropinna microstoma</i>	Barreleye	251	3		22	8	13	16	1951-	always
Zoarcoidei		252	2		0		0	0	1985-	Blennioidei
<i>Embassichthys bathybius</i>	Deepsea sole	253	1	2	1.5		11	15	1991-	Pleuronectidae
<i>Cubiceps baxteri</i>		254	3		23	8	13	16	1972-	Nomeidae
<i>Gonostoma atlanticum</i>	Atlantic fangjaw	255	3		21	8	13	16	1951-	always
Carangidae	Jacks	256	2		0		13	14	1951-	always
<i>Gonostoma</i> spp.	Fangjaws	257	3		21	8	13	16	1951-	always
<i>Coryphaena hippurus</i>	Common dolphinfish	258	2		3		13	14	1951-	always
<i>Leptocephalus holti</i>		259	3		23	8	13	16	1985-	Anguilliformes
Pomacentridae	Damselfishes	260	1	1	2.5		10	0	1951-	always
<i>Roncador stearnsii</i>	Spotfin croaker	261	1	1	2		12	14	1981-	Sciaenidae
<i>Liparis</i> spp.		262	1	1	1		11	16	1951-	Cyclopteridae
<i>Mugil cephalus</i>	Striped mullet	263	1	1	2.5		12	14	1951-	always
<i>Gobiesox maeandricus</i>	Northern clingfish	264	1	1	1		10	16	1991-	Gobiesocidae
<i>Gibbonsia</i> spp.		265	1	1	1.5		10	16	1994-	Blennioidei
Bythitidae	Viviparous Brotulas	266	1	2	0		0	16	1951-	always
<i>Lampanyctus tenuiformis</i>		267	3		23	7	13	16	1985-	<i>Nannobranchium</i> spp.
<i>Ophichthus zophochir</i>	Yellow snake eel	268	1	1	3		12	16	1998-	Ophidiiformes
<i>Hermosilla azurea</i>	Zebraperch	269	1	1	2.5		10	14	1951-	always
Gobiesocidae	Clingfishes	270	1	1	1.5		10	16	1951-	always
<i>Triphoturus nigrescens</i>	Highseas lampfish	271	3		21	7	13	16	1951-	always
<i>Anoplopoma fimbria</i>	Sablefish (blackcod)	272	1	2	1.5		12	14	1951-	always
Trichiuridae	Cutlassfishes	273	1	2	0		13	0	1951-	always
<i>Neoclinus blanchardi</i>	Sarcastic fringehead	274	1	1	2		11	16	1985-	Blennioidei
<i>Bolinichthys longipes</i>	Popeye lampfish	275	3		21	7	13	16	1972-	Myctophidae
<i>Eustomias</i> spp.		276	3		21	8	13	16	1961-	Melanostomiinae
Clupeiformes		277	2		0		13	0	1951-	always
<i>Lampanyctus omostigma</i>		278	3		23	7	13	16	1985-	<i>Nannobranchium</i> spp.
Pholidae	Gunnels	279	1	1	1.5		10	16	1989-	Blennioidei
<i>Albatrossia pectoralis</i>	Giant grenadier	280	1	2	1.5		12	15	1994-	Macrouridae
<i>Prionotus</i> spp.	Searobins	281	1	2	3		12	16	1951-	always
<i>Bathophilus filifer</i>	Threadfin dragonfish	282	3		23	8	13	16	1951-	always
<i>Coryphaena equiselis</i>	Pompano dolphinfish	283	3		21	6	13	16	1951-	always
<i>Lepidocybium flavobrunneum</i>	Escolar	284	3		21	7	13	15	1951-	always
<i>Lythrypnus</i> spp.		285	1	1	2.5		10	0	1985-	Gobiidae

Table A2.1 continued

<i>Poromitra megalops</i>		286	3		23	8	13	16	1985-	<i>Poromitra</i> spp.
<i>Myctophum lychnobium</i>		287	3		23	7	13	16	1951-	always
<i>Coryphaenoides acrolepis</i>	Pacific grenadier	288	1	2	1.5		12	14	1985-	Macrouridae
<i>Coryphaenoides leptolepis</i>	Ghostly grenadier	289	1	2	1		12	16	1985-	Macrouridae
<i>Nealotus tripes</i>	Black snake mackerel	290	3		21	8	13	16	1951-	always
<i>Aulorhynchus flavidus</i>	Tubesnout	291	1	1	1		13	16	1951-	always
<i>Caulophryne</i> spp.	Fanfins	292	3		21	9	13	16	1951-	always
<i>Eutaeniophorus</i> spp.		293	3		21	8	13	16	1951-	<i>Eutaeniophorus</i> spp.
Cyematidae	Bobtail Eels	294	3		21	9	13	16	1951-	always
<i>Umbrina roncadora</i>	Yellowfin croaker	295	1	1	2		12	14	1991-	Sciaenidae
<i>Ronquilus jordani</i>	Northern ronquil	296	1	2	1		10	16	1987-	Blennioidei
<i>Liparis fucensis</i>	Slipskin snailfish	297	1	1	1		11	16	1951-	Cyclopteridae
<i>Leptocephalus giganteus</i>		298	3		23	8	13	16	1985-	Anguilliformes
<i>Taaningichthys minimus</i>		299	3		21	9	13	16	1951-	always
<i>Coryphaenoides</i> spp.	Grenadiers	300	2		0		12	0	1985-	Macrouridae
<i>Gonostoma ebelingi</i>	Ebeling's fangjaw	301	3		23	8	13	16	1951-	always
<i>Menticirrhus undulatus</i>	California corbina	302	1	1	2		12	14	1988-	Sciaenidae
<i>Radiicephalus elongatus</i>	Tapertail	303	3		21	8	13	16	1951-	always
<i>Cryptopsaras couesii</i>	Triplewart seadevil	304	2		1.5		13	16	1951-	always
<i>Ilypnus gilberti</i>	Cheekspot goby	305	1	1	2		12	16	1993-	Gobiidae
<i>Hemilepidotus spinosus</i>	Brown Irish lord	306	1	2	1		10	16	1993-	Cottidae
<i>Howella pammelas</i>		307	3		21	8	13	16	1951-	always
<i>Enophrys bison</i>	Buffalo sculpin	308	1	2	1		10	16	1996-	Cottidae
<i>Clevelandia ios</i>	Arrow goby	309	1	1	1.5		12	16	1980-	Gobiidae
<i>Agonopsis sterletus</i>	Southern spearnose poacher	310	1	2	1.5		11	15	1999-	Agonidae
<i>Physiculus</i> spp.		311	1	2	2.5		12	16	1972-	Moridae
<i>Pronotogrammus multifasciatus</i>	Threadfin bass	312	1	2	3		11	16	1951-	always

Table A2.1 continued

GRP:

- 1 = coastal (shelf and upper slope)
- 2 = coastal-oceanic
- 3 = oceanic

NRSORE:

- 1 = $\leq 30\text{m}$
- 2 = not restricted to $\leq 30\text{m}$

REGION:

For the coastal and coastal-oceanic groups:

- 1 = north of Point Conception
- 1.5 = broadly distributed to the north
- 2 = characteristic of the Southern California Bight
- 2.5 = broadly distributed to the south
- 3 = south of Punta Eugenia
- 4 = found in regions 1–3

For the oceanic group:

- 21 = world wide
- 22 = North Pacific
- 23 = Pacific

DEPTH:

- 6 = epipelagic (upper 200m)
- 7 = epi-mesopelagic migrator
- 8 = mesopelagic
- 9 = bathypelagic

BOTTOM:

- 10 = kelp and/or hard bottom
- 11 = both hard and soft bottom
- 12 = soft bottom
- 13 = water column (bottom type unimportant)

FISHED:

- 14 = fished (targeted, recreational and/or commercial)
- 15 = bycatch (not targeted but subject to fishery mortality)
- 16 = unfished (no significant fishing mortality)

0 = unknown

Blanks = not applicable

Table A2.2. Compiled data of age-at-maturation for the coastal and coastal-oceanic species used in the analyses.

Species	Max body length (cm)	ln(max body length)	Age-at-maturation	References and remark
<i>Engraulis mordax</i>	24.8	3.21	1.0	1
<i>Merluccius productus</i>	91	4.51	3.5	1
<i>Sardinops sagax</i>	39.5	3.68	2.0	1
<i>Scomber japonicus</i>	60	4.09	2.0	1
<i>Trachurus symmetricus</i>	81	4.39	3.0	1
<i>Cololabis saira</i>	40	3.69	1.5	Suyama (2002)
<i>Icichthys lockingtoni</i>	46	3.83	3.0	3
<i>Leuroglossus stilbius</i>	15	2.71	2.5	Childress <i>et al.</i> (1980)
<i>Tetragonurus cuvieri</i>	70	4.25	3.0	3
<i>Trachipterus altivelis</i>	183	5.21	4.5	3
<i>Lyopsetta exilis</i>	35	3.56	3.0	2
<i>Microstomus pacificus</i>	76	4.33	5.5	Hunter <i>et al.</i> (1992)
<i>Paralabrax clathratus</i> *	72	4.28	4.0	Love <i>et al.</i> (1996)
<i>Paralichthys californicus</i>	152	5.02	4.5	1
<i>Parophrys vetulus</i>	57	4.04	4.0	Sampson & Al-Jufaily (1999)
<i>Scorpaenichthys marmoratus</i>	99	4.60	4.5	1
<i>Sebastes aurora</i>	41	3.71	5.0	Love <i>et al.</i> (2002)
<i>Sebastes paucispinis</i>	91	4.51	4.0	1
<i>Sphyræna argentea</i>	122	4.80	2.0	1
<i>Chromis punctipinnis</i>	30	3.40	2.0	2
<i>Hippoglossina stomata</i>	40	3.69	3.0	Martinez-Munoz & Ortega-Salas (2001)
<i>Pleuronichthys verticalis</i>	37	3.61	4.0	2
<i>Sebastes jordani</i>	31	3.43	3.0	Pearson <i>et al.</i> (1991)
<i>Symphurus atricaudus</i>	21	3.04	1.0	2

Table A2.2 continued

<i>Zaniolepis frenata</i> *	25	3.22	2.5	3
<i>Argentina sialis</i>	22	3.09	2.5	3
<i>Hypsoblennius jenkinsi</i> *	13	2.56	1.0	Stephens <i>et al.</i> (1970)
<i>Ophidion scrippsae</i>	28	3.33	1.0	4
<i>Oxylebius pictus</i>	25	3.22	3.0	DeMartini & Anderson (1980)

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3. Estimates from the relationship between ln(max-length) and age-at-maturation ($r = 0.48$, $p = 0.0096$) based on the Expectation-Maximization algorithm (Little & Rubin, 2002).

4. Using the estimate from *Ophidion welshi* (Retzer, 1991).

* *Paralabrax clathratus* is used to represent *Paralabrax* spp. because *Paralabrax* larvae in the CalCOFI collections appear to be predominantly *Paralabrax clathratus*. *Zaniolepis frenata* is used to represent *Zaniolepis* spp. and *Hypsoblennius jenkinsi* to represent *Hypsoblennius* spp. for the same reason.

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Chapter 3. Fishing elevates variability in the abundance of exploited species: long-term evidence that fishing magnifies uncertainty in a changing environment

Abstract

Separating the effects of environmental variability from the impacts of fishing on the dynamics of fish populations is essential for sound fisheries management (Beddington and May 1977; Garcia et al. 2003; Berkeley et al. 2004; Browman and Stergiou 2004; Hutchings and Reynolds 2004; Pikitch et al. 2004; Daan et al. 2005; Hsieh et al. 2005b). We distinguish environmental effects from fishing effects by comparing variability in the abundance of exploited versus unexploited species living in the same environments. Using the 50-year-long larval fish time series from the California Cooperative Oceanic Fisheries Investigations (Hsieh et al. 2005b), we regard fishing as a treatment effect in a long-term ecological experiment. Here we present the first direct large-scale evidence from the marine environment that exploited species exhibit higher temporal variability in abundance than unexploited species. This remains true after accounting for life history effects, abundance, ecological traits and phylogeny. The increased variability of exploited populations is likely caused by fishery-induced truncation of the age structure, which reduces the capacity of populations to dampen environmental variability (Murphy 1967; Murawski et al. 2001; Berkeley et al. 2004; Hutchings and Reynolds 2004). Thus, to avoid collapse, fisheries must be managed not only to sustain the total viable biomass but also to prevent the truncation of age structure (Murphy 1967; Murawski et al. 2001; Berkeley et al. 2004; Hutchings and Reynolds 2004). A precautionary management approach (Scheffer et al. 2001; Hsieh et al. 2005a) is warranted not only because of normal uncertainties associated with estimates of stock size but also because fishing itself magnifies population variability (Beddington and May 1977).

Main Text

As estimated by FAO in 2004, among the world's fisheries 52% were heavily exploited and 25% were over-exploited, depleted, or recovering from depletion (FAO 2005). Thus, FAO statistics and recent studies (Hutchings 2000; Watson and Pauly 2001; Garcia et al. 2003; Myers and Worm 2003) indicate that many commercially-important fish populations have been declining in the past several decades. However, the extent to which such declines are due to fishing, or to environmental change, or to some combination of these effects is still a matter of debate (Mantua et al. 1997; Finney et al. 2002; Beaugrand et al. 2003). Clearly, it is important to understand the effects of exploitation on fish populations within the context of a changing environment (Hsieh et al. 2005b). This view is an essential component of ecosystem-based approaches to fisheries management; that is, to base decisions not only on the status of a fish population but also the condition of the ecosystem and the environment, and interspecific interactions (Garcia et al. 2003; Browman and Stergiou 2004; Pikitch et al. 2004). Increasing effort has been devoted to developing indicators for assessing impacts of fisheries (Daan et al. 2005). However, the efficacy of these indicators has not been well established because time series data are often too short, objective reference points are difficult to define since conditions prior to fishing are poorly known, and the effects of the environment and fishing are confounded (Daan et al. 2005).

To overcome some of these problems, we evaluate fishing effects by comparing variability in the larval abundance of exploited to that of unexploited species living in the

same ecosystem. Understanding sources of variability in fish abundance (fluctuations of populations through time) is important in determining reference points, decision making and risk assessment in precautionary fisheries management (Hilborn et al. 2001), and in evaluating the extinction risk of a population (Pimm 1991).

Whether fishing may increase or decrease the population variability of exploited species has been a classic debate (Beddington and May 1977; May et al. 1978) whose origins trace back to the late 60's and 70's. This discussion, though lively, was largely theoretical, because at the time no data existed to resolve the controversy. These data are now available from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) larval fish time series (1951-2002) and covers the southern sector of the California Current System. We use the coefficient of variation (CV) of annual larval abundance to represent temporal variability for the adults of 29 coastal and neritic species, including 13 exploited and 16 unexploited species that were abundant and consistently enumerated from CalCOFI (Hsieh et al. 2005b) (Table 3.1).

Clearly fishing is a selective process, thus the fished and unfished groups might not be formed randomly with respect to other possible explanatory variables that relate to CV. That is to say, fished and unfished groups may selectively differ with respect factors such as life-history traits that apart from fishing can themselves influence the CV. To isolate the effect of fishing as the explanatory variable we use multiple regression analysis to factor out the possible ancillary biases associated with fishing. These, variables include life history effects, abundance, ecological traits, and phylogeny (Methods). We consider life history traits that are known to influence population

responses to fishing and the environment (Winemiller and Rose 1992). In theory (Pimm 1991; Winemiller and Rose 1992; Mertz and Myers 1994; Mertz and Myers 1996), CV is negatively related to maximum length, length-at-maturation, age-at-maturation, spawning duration, and trophic level, and positively related to fecundity (Methods). In addition, one may presume that higher variability would be statistically associated with higher abundance (Pimm 1991), and therefore, abundance is included in the regression model. Furthermore, possible confounding effects of ecological traits (geographic region, habitat, and spawning mode) and phylogenetic constraints are also examined (see Methods and Appendix).

When data from exploited and unexploited species are lumped together, two of the six life history traits appear not to show the expected relationship to the CVs (Appendix). The CVs appear to be positively correlated with maximum length and length-at-maturation while theory (Pimm 1991; Winemiller and Rose 1992; Mertz and Myers 1994; Mertz and Myers 1996) predicts a negative correlation. However, the relationships between the CVs and life history traits follow the theoretical predictions when analyses are performed on exploited and unexploited species separately (Fig. 3.1). Except for fecundity (where data for unexploited species are too sparse to be conclusive, $n = 4$), the predicted relationship between life history traits and CVs is stronger for the unexploited species dataset. The relationship between life history traits and CVs is somewhat weaker for the exploited species dataset, because fishing pressure varies among species and this in itself might obscure the predicted relationships (Fig. 3.1).

The most important result is that the CVs for exploited species are significantly higher than those for unexploited species, after accounting for life history effects, abundance, ecological traits, and phylogeny (multiple regression, $p < 0.001$). In addition, age-at-maturation and geographic region emerge as the significant factors in the full model ($p = 0.015$, and $p < 0.001$, respectively). When accounting for all effects, the overall significance of the multiple regression is $p < 0.001$. Age-at-maturation is likely the best proxy for generation time, which should be important in determining population variability. The remaining life history traits and abundance are highly correlated with age-at-maturation, and therefore, it is not surprising to find them redundant (and eliminated) in the regression model. The warm-water species exhibit higher CVs than the cool-water and widely-distributed species (Fig. 3.2). Phylogeny is not a significant variable affecting CVs (Appendix).

One may suspect that higher variability in the exploited species is caused largely by a long-term declining trend in the larval abundance of exploited species. Contrary to this speculation, we found no systematic differences between the fished and unfished groups in the prevalence of declining trends in larval abundances (Appendix). Out of 13 exploited species, only 2 had significant declines, which is similar to the number (2 out of 16) of unexploited species that showed significant declines. However, for safe measure, we remove low-frequency trends in the abundance time series and recalculate the CVs using de-trended data. Repeating the above analyses on the recalculated CVs still shows that the exploited species exhibit higher variability after accounting for life history traits, abundance, ecological traits, and phylogeny (Appendix). All these results indicate that

the exploited species are more variable than the unexploited species, and our evidence suggests that this difference is caused by fishing and not by the biases associated with the life history traits, abundance, ecological characteristics or phylogeny, although there might be other possible factors not examined in this study.

How can fisheries increase variability in the abundance of exploited populations? An early analysis of this problem was done by Beddington and May (1977) nearly 30 years ago. In many fish populations, the main source of variability lies in recruitment: the transition from the larval stage to the adult stage. This can be shown in a simple population model:

$$N_{t+1} = N_t e^{-(M+F)} + R_t$$

where N_t is the adult abundance and R_t is the recruitment at time t , and M and F is natural and fishing mortality, respectively. Clearly, as the level of fishing mortality increases, the population dynamics are increasingly dominated by recruitment, and at the limit the population variability is equal to the variability of recruitment. Thus, one would expect fishing to increase population variability.

However, beyond this effect recruitment variability itself will be further amplified through the effect that fisheries have on truncating the age-size structure of a population (Murphy 1967; Murawski et al. 2001; Berkeley et al. 2004; Hutchings and Reynolds 2004). It is believed that fisheries operate by selectively removing large and old individuals through size–age selective fishing mortality (Berkeley et al. 2004; Hutchings and Reynolds 2004). This is supported by our analysis, where declining trends in average age or length through time are seen for all exploited species (Figure 3.3, Appendix).

Reducing the average length and age of populations increases recruitment variability by diminishing its capacity to weather short-term unfavorable environmental conditions. Many fish species employ bet-hedging strategies to increase the survival rate of larvae under harsh and variable environmental conditions. Such hedging strategies are associated with long-tailed age structures (a long tail of old individuals in the age distribution), and include: (i) age-related differences in spawning locations and time (Lambert 1987; Hutchings and Myers 1993), and (ii) increased quantity and quality of eggs produced by older (experienced) or larger fish (Marteinsdottir and Steinarsson 1998). A long-tailed age structure can dampen environmental stochasticity and thus stabilize fish populations. In contrast, as fishing truncates age structure, fish populations become more variable as bet-hedging strategies are undermined and the populations more closely track short-term environmental variability. This well-documented mechanism (Lambert 1987; Hutchings and Myers 1993; Marteinsdottir and Steinarsson 1998) suggests how fishing can make populations more susceptible to extrinsic environmental forcing. We call this phenomenon the age-truncation-effect (ATE).

Our results are the first empirical evidence to show that fishing increases variability in the abundance of exploited populations, even after accounting for life history effects, ecological traits, phylogeny, and a changing environment. The elevated variability of exploited populations is likely the result of the increased importance of recruitment and elevated variability of recruitment caused by fishery-induced truncation of their age structure (Murphy 1967; Murawski et al. 2001; Berkeley et al. 2004; Hutchings and Reynolds 2004) (ATE). Greater variability (and therefore reduced resilience) can

increase the probability of collapse of a fish population due to stochastic environmental events (Scheffer et al. 2001).

These findings indicate that an additional level of uncertainty exists in the management of fisheries; that is, decreased stability due to the fishing process itself. To maintain stable fish populations, the age structure of the populations must be conserved (Murphy 1967; Berkeley et al. 2004; Hutchings and Reynolds 2004). Where practical, it may be useful to regulate the minimum and maximum fish size limits in harvesting (Berkeley et al. 2004) and include an age-based biological reference point in the management plans for some species (Murawski et al. 2001) (consider age-specific egg production, egg viability, and spawning duration in stock assessments). These would be particularly important in groups of fishes where it seems likely that truncation of age classes could increase environmental sensitivity of the populations due to loss of bet-hedging capabilities. This management objective could be accomplished with marine reserves (Roberts et al. 2001) that protect older and larger individuals (potentially useful for management of some ground fishes). Such reserves have potential not only to conserve biomass and reproductive potential of the populations but also to stabilize fish populations by preserving their ability to smooth out environmental variation.

Methods

The larval fish data used here were collected in the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The CalCOFI program is one of the most comprehensive observational oceanography programs in the world with at least four

cruises per year (except for tri-annual cruises between 1966 and 1984) and sixty-six stations per cruise, beginning in 1949 (Hsieh et al. 2005b). This dataset provides fishery-independent data that are free from confounding effects (changes in fishing gear or areas) commonly associated with fishery catch data in estimating fish abundances. Because the CalCOFI program spans more than 50 years, they reflect how fish populations respond at various time scales (from annual to decadal) of environmental forcing as well as to fishing. Because the fish populations live in the same area, they experience much the same large-scale environmental forcing. Importantly, both exploited and unexploited species were consistently sampled. These properties allow us to separate fishing effects from environmental effects on fish dynamics: we use unexploited species as an objective reference and consider fishing as a treatment in a long-term experiment.

In this study, we adopt the well-documented assumption that larval fish abundances are proportional to the standing stock of the adults that produced them (Hsieh et al. 2005b). Evidence for this includes studies of the correlation of larval counts with estimates of adult biomass from other surveys and fisheries assessment models (see justification in Appendix). In addition to changes in adult biomass, counts of larvae may vary due to changes in reproductive effort of the adults, mortality rates of eggs and early larvae, and large scale movements of reproducing adults in and out of the CalCOFI survey grid. Owing to these additional sources of variability, larval fish time series have a large variance, but the larval data have been found to track long-term variation in adult biomass in most species (Appendix).

We use coefficients of variation (CVs) of larval fish annual abundance to represent temporal variability for fish species. The CV is a desirable measurement of temporal variability because it is unitless (and therefore is suitable for cross-species comparison (Pimm 1991)) and each time series contains the same sample size (Pimm 1991). Stepwise multiple regression analysis (general linear model) is used to test the effect of fishing, life history traits, larval abundance, ecological traits, and phylogeny on the CVs. Ideally, one would include all dependent variables in the model. However, due to limited sample sizes, we perform regression separately on three sets of data: life history traits (including abundance), ecological traits, and phylogeny. The significant variables selected from the three sets are then combined into a single model. We assume there are no systematic differences between exploited and unexploited populations with regard to interspecific interactions. By-catch effects on unexploited species are assumed to be minimal (Hsieh et al. 2005b).

Missing data on life history traits in the multiple regressions were accounted for using the multiple imputation method (Little and Rubin 2002) (1000 imputations). Because life history traits are correlated (Winemiller and Rose 1992), we use their correlation structure to impute the missing data, assuming a multivariate normal distribution (Little and Rubin 2002). The statistical inferences are generated by combining results of the 1000 analyses (Little and Rubin 2002).

Table 3.1. Life history traits and ecological traits of fish species.

	Species	Common name	Maximum length (cm)	Length-at-maturation (cm)	Age-at-maturation (year)	Fecundity (# of eggs/year)	Spawn duration (year)	Trophic level	Habitat	Region	Spawning mode
Exploited	<i>Engraulis mordax</i>	Northern anchovy	24.8	9	1	150000	12	3.1	Water	All	Planktonic
	<i>Merluccius productus</i>	Pacific hake or whiting	91	40	3.5	2500000	4	3.8	Water	All	Planktonic
	<i>Microstomus pacificus</i>	Dover sole	76	33.2	5.5	83000	6	3.4	Soft	Cool	Planktonic
	<i>Paralabrax clathratus</i>	Kelp bass	72	23	3	81000	5	4.0	Kelp	Warm	Planktonic
	<i>Paralichthys californicus</i>	California halibut	152	41	4.5	2200000	12	4.5	Soft	Warm	Planktonic
	<i>Parophrys vetulus</i>	English sole	57	23	4	1500000	6	3.5	Soft	Cool	Planktonic
	<i>Sardinops sagax</i>	Pacific sardine	39.5	15.8	2	1300000	8	2.6	Water	Warm	Planktonic
	<i>Scomber japonicus</i>	Pacific chub mackerel	60	32	2	1120000	7	3.4	Water	Warm	Planktonic
	<i>Scorpaenichthys marmoratus</i>	Cabezon	99	50	4.5	152000	7	3.5	Kelp	Cool	Demersal
	<i>Sebastes aurora</i>	Aurora rockfish	41	28	5	N/A	7	N/A	Soft	Cool	Live-bearer
	<i>Sebastes paucispinis</i>	Bocaccio	91	36	4	1160000	5	3.5	Water	Cool	Live-bearer
	<i>Sphyræna argentea</i>	Pacific barracuda	122	56	2	225000	6	4.5	Water	Warm	Planktonic
	<i>Trachurus symmetricus</i>	Jack mackerel	81	31	3	1856000	6	3.9	Water	All	Planktonic
	Unexploited	<i>Argentina sialis</i>	Pacific argentine	22	N/A	N/A	N/A	11	3.1	Water	All
<i>Chromis punctipinnis</i>		Blacksmith	30	N/A	2	N/A	4	2.7	Kelp	Warm	Demersal
<i>Cololabis saira</i>		Pacific saury	40	27	1.5	215000	11	3.7	Water	All	Planktonic
<i>Hippoglossina stomata</i>		Bigmouth sole	40	16.2	3	N/A	8	N/A	Soft	Warm	Planktonic
<i>Hypsoblennius jenkinsi</i>		Mussel blenny	13	4.6	1	900	7	N/A	Kelp	Warm	Demersal
<i>Icichthys lockingtoni</i>		Medusafish	46	N/A	N/A	N/A	7	3.6	Water	All	Planktonic
<i>Leuroglossus stilbius</i>		California smoothtongue	15	8	2.5	N/A	6	3.2	Water	All	Planktonic
<i>Lyopsetta exilis</i>		Slender sole	35	N/A	3	N/A	6	3.4	Soft	Cool	Planktonic
<i>Ophidion scrippsae</i>		Basketweave cusk-eel	28	16	1	N/A	6	3.5	Soft	Warm	Planktonic
<i>Oxylebius pictus</i>		Painted greenling	25	14	3	1780	9	3.4	Kelp	Cool	Demersal
<i>Pleuronichthys verticalis</i>		Hornyhead turbot	37	17	4	N/A	11	N/A	Soft	Warm	Planktonic
<i>Sebastes jordani</i>		Shortbelly rockfish	31	14	3	50000	4	3.22	Water	Cool	Live-bearer

Table 3.1 continued

<i>Symphurus atricaudus</i>	California tonguefish	21	N/A	1	N/A	5	3.3	Soft	Warm	Planktonic
<i>Tetragonurus cuvieri</i>	Smalleye squaretail	70	N/A	N/A	N/A	12	3.78	Water	All	Planktonic
<i>Trachipterus altivelis</i>	King-of-the-salmon	183	N/A	N/A	N/A	12	3.9	Water	All	Planktonic
<i>Zaniolepis frenata</i>	Shortspine combfish	25	N/A	N/A	N/A	9	3.44	Soft	All	Live-bearer

Exploited species are defined as fisheries targeted species (Hsieh et al 2005b). Data for life history and ecological traits are described in Appendix 3.1. N/A indicates data not available. Water, pelagic species; Kelp, species associated with kelps or hard bottom; Soft, species associated with soft bottom.

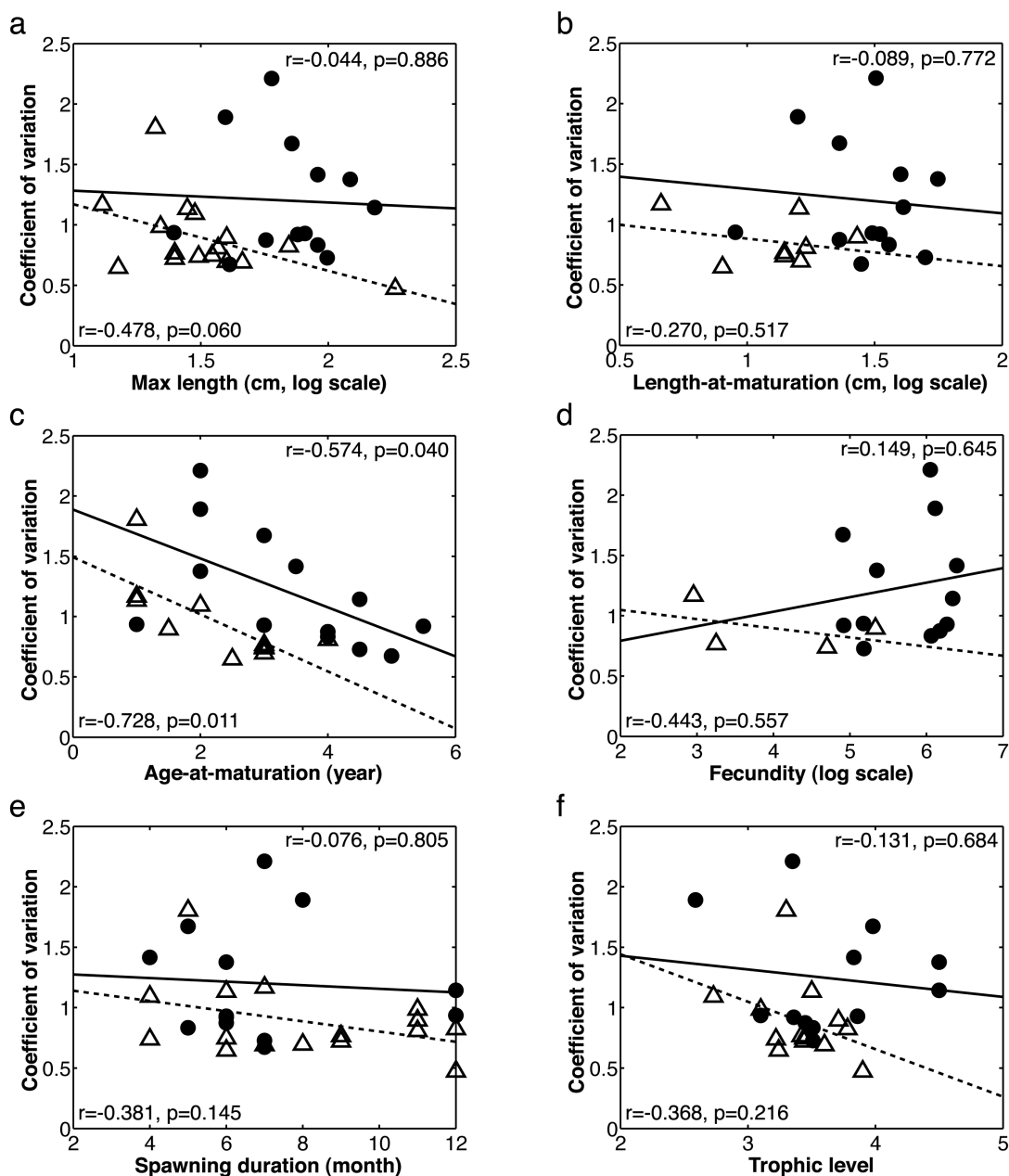


Figure 3.1. Relationships between CVs and life history traits for exploited and unexploited species separately. Exploited species: filled circles, solid line; correlation coefficient and p-value for each trait separately in the upper-right corner. Unexploited species: open triangles, dashed line; correlation coefficient and p-value for each trait separately in the lower-left corner. The trends follow theoretical predictions for all life history traits (except for the fecundity of unexploited species with only four data points). Combining these results into the multiple regression, the CVs of exploited species are higher than those of unexploited species ($p < 0.001$). Note that an analysis of covariance based on individual traits would have been invalid because life history traits are correlated.

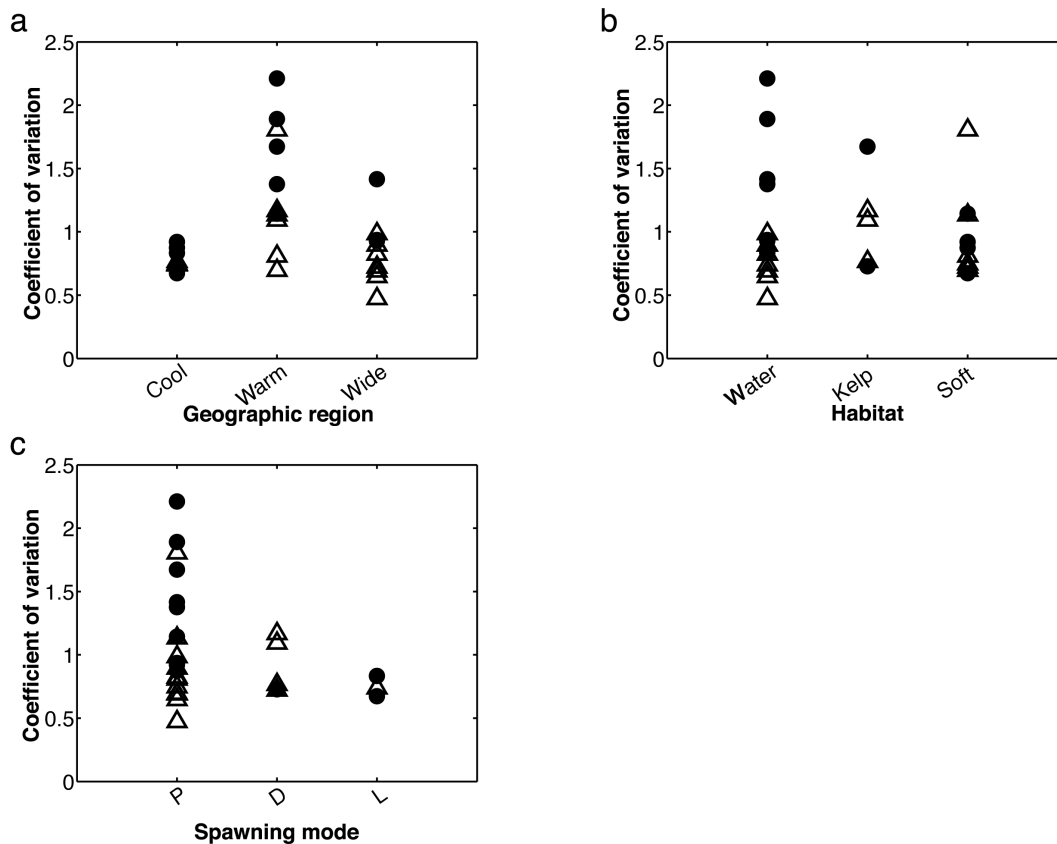


Figure 3.2. CVs of exploited (filled circles) and unexploited (open triangles) species associated with geographic regions (a), habitats (b), and spawning modes (c). In (c), P: pelagic spawners; D: demersal spawners; L: live-bearers. No significant association between CVs and habitats and spawning modes are found. For geographic regions (a), CVs for warm-water species are higher than those for cool-water and widely-distributed species. However, after accounting for the effect of regions, the CVs for the fished species are still higher than those for the unfished ones (multiple regression, $p = 0.005$).

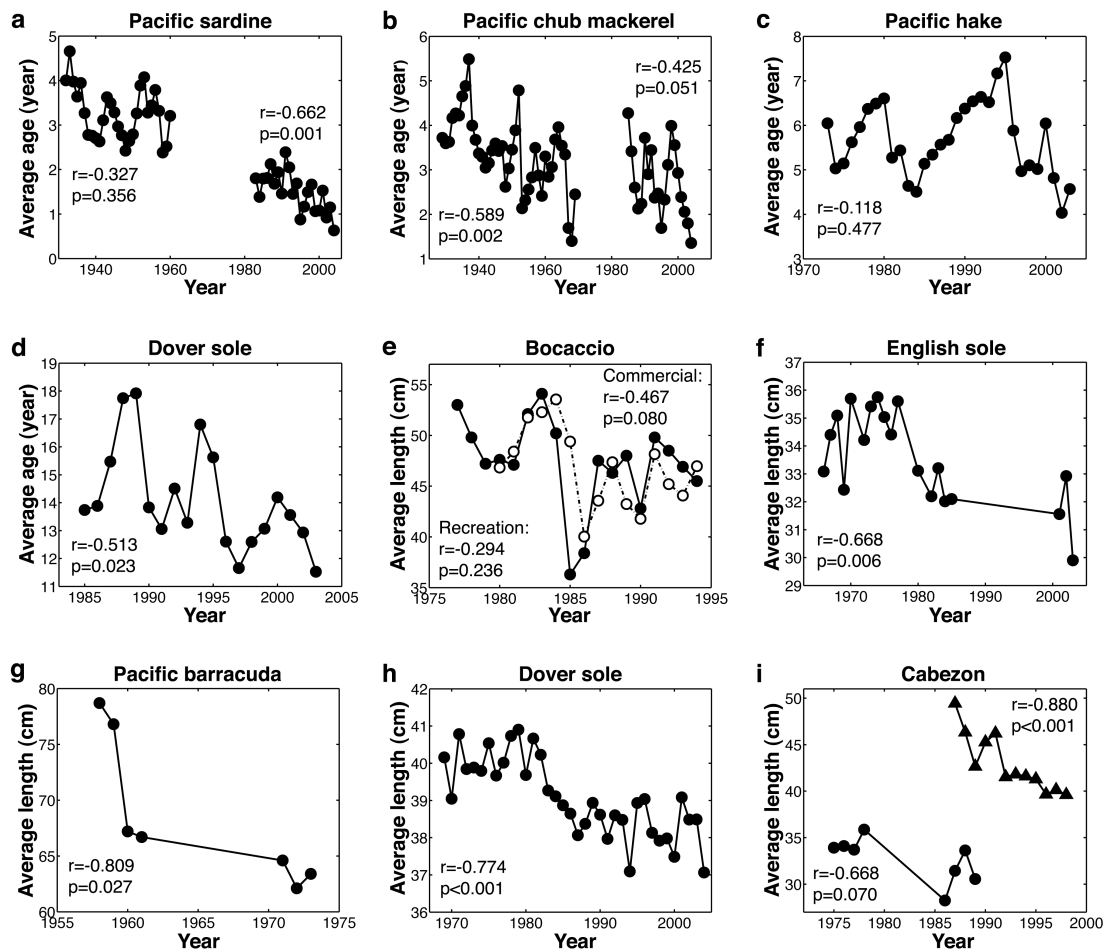


Figure 3.3. Long-term declining trends in the average age (a-d) and length (e-i) of exploited species. In (a) and (b), analysis is carried out separately in the period before and after a moratorium on fishing. In (e), filled and open circles represent data from recreational and commercial fisheries, respectively. In (i), circles and triangles represent data from southern and northern California, respectively. The p values are corrected for serial dependence in the time series. Although only 7 out of 13 time series show a significant trend at $p < 0.05$, all exhibit a declining trend which is highly significant as an ensemble result (binomial test, $p < 0.005$).

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Appendix

Justification for using larval abundances to infer adult populations

Several studies in the southern California area have shown that larval abundance is a good indicator of adult biomass (Moser and Watson 1990; Moser et al. 2000; Moser et al. 2001b). To further establish this relationship, we calculate rank correlations between larval abundances and spawning biomasses estimated from stock assessment models for seven species that contain data significantly overlapping with the CalCOFI time series in time and space. We use the following order to select the data: 1) data from southern California, 2) data from California, and 3) data from the U.S. West coast.

A significant correlation between the CalCOFI larval abundance and spawning biomass is found in *Merluccius productus*, *Sardinops sagax*, *Scomber japonicus*, and *Sebastes paucispinis* (Table A3.1). A low correlation in *Microstomus pacificus* and *Parophrys vetulus* (Table A3.1) might arise because these two species are northern species and are not migratory, and therefore, the spawning biomass estimates for the whole U.S. West coast are not comparable to the CalCOFI larval indices that are obtained from southern California. The lack of a correlation in *Scorpaenichthys marmoratus* (Table A3.1) might be due to the high uncertainty in the stock assessment model for the southern California population (due to a paucity of data), as pointed out by Cope and Punt (2005). Note that the data from stock assessment models also contain high uncertainty. Given that no long-term survey data of adult populations exist, and fisheries data are confounded by changing fishing gear, the CalCOFI larval fish record represents a

unique source of information for monitoring the relative sizes of adult populations along the coast of southern California.

Life history data

Life history parameter estimates for each species were compiled from the primary literature (Table A3.2), FishBase (Froese and Pauly 2005), and research reports of the California Department of Fish and Game (Leet et al. 2001; CDFG 2002). Values were from southern California specimens where possible, and otherwise, data were used for the same species from other regions. The only exception is *Ophidion scrippsae*, whose age-at-maturation is estimated from a congener species, *Ophidion welshi*, having a similar maximum length as *Ophidion scrippsae*. The maximum length (maximum observed length) and trophic level of each species were obtained from FishBase. The length-at-maturation was defined as the length at which 50% of the population reaches maturity. The same criteria were applied to the selection of age-at-maturation data. The fecundity was determined as the total number of eggs produced per fish per year. When the value for length-at-maturation, age-at-maturation, or fecundity was reported as a range, we used the median value. The spawning durations were estimated from the CalCOFI data (see next sections). Ecological traits, including geographic distribution, habitat, and spawning mode, are determined according to FishBase (Froese and Pauly 2005), Hsieh et al(2005) and Moser (1996).

Determining the spawning duration

To determine the spawning duration of each species, we 1) calculate the average abundance per cruise, 2) standardize the cruise values for each year (0 to 1) relative to the maximum value (where maximum value = 1) to obtain the normalized seasonal pattern (Fig. A3.1), and 3) calculate the long-term mean abundance level of each month by averaging the seasonal patterns. We define the spawning period (principal seasons of larval occurrences) as the months with mean abundance level > 0.1 (Fig. A3.1). The spawning duration is calculated as the number of months in which significant larval abundance (mean abundance level > 0.1) was observed. The spawning periods of those species objectively determined here are consistent with those obtained by expert opinion (Moser et al. 2001a).

Examining long-term trends in the abundance of fish populations

Fluctuations of exploited populations are affected by fishing and the environment. One might suspect high variability of exploited populations simply arises from long-term declining trends due to fishing. However, our analysis indicates that no systematic declining trends exist in the fished populations (Table A3.3). Among the exploited species, only jack mackerel (*Trachurus symmetricus*) and bocaccio (*Sebastes paucispinis*) exhibits a significant declining trend, and Pacific sardine (*Sardinops sagax*) exhibits a significant increasing trend. Among the unexploited species, medusafish (*Icichthys lockingtoni*) and California smoothtongue (*Leuroglossus stilbius*) shows a significant declining trend, and Shortspine combfish (*Zaniolepis frenata*) and Pacific argentine

(*Argentina sialis*) shows a significant increasing trend. These results indicate that the variability of exploited populations are not due to long-term depletion trends of stocks.

Effects of fishing and life history traits on variability in the abundance of fish populations

For all species combined (both fished and unfished together), the CVs positively correlate with maximum length (Fig. A3.2a), length-at-maturation (Fig. A3.2b), and fecundity (Fig. A3.2d), and negatively correlate with age-at-maturation (Fig. A3.2c), spawning duration (Fig. A3.2e), and trophic level (Fig. A3.2f). The relationship is significant only between CVs and age-at-maturation ($p = 0.0457$, Fig. A3.2c).

Analysis of covariance based on individual traits is technically invalid because life history traits are correlated. The results are provided here for their heuristic value only (Table A3.4).

The correct procedure is to use multiple regression analysis (general linear model (McCullagh and Nelder 1989)) to test the effects of fishing, life history traits, larval abundance, ecological traits, and phylogeny on the CVs. In the multiple regression, fishing effect is treated as a dummy variable and ecological traits, and phylogeny are categorical variables (McCullagh and Nelder 1989). Due to the limitation of sample size, we perform regression separately on three sets of data: life history traits (including abundance), ecological traits, and phylogeny. The significant variables selected (using a stepwise procedure) from the three sets are then combined into a single model. The results of multiple regression analysis indicate that CVs for exploited species are higher

than those for unexploited species, after accounting for life history effects, ecological traits, abundance, and phylogeny (Table A3.5).

No systematic declining or increasing trend is found in the abundance of the fish populations examined in this study (Table A3.3). For the two species (*Trachurus symmetricus* and *Sebastes paucispinis*) showing significant depletion trends, the CVs are actually low compared to other exploited species (Fig. A3.3). However, to definitively dismiss the possibility that the higher CVs of exploited populations are a trivial artifact of secular trends associated with fishing, we repeat the multiple regression analysis on the de-trended data.

We use two approaches to de-trend the time series: 1) estimating trends using the locally weighted scatter plot smoother (LOWESS) (Cleveland and Devlin 1988) and calculating the magnitudes of residuals deviated from the trends, and 2) taking the first-difference (Thompson and Pagel 1989) ($|N_{t+1}-N_t|$). The LOWESS approach accounts for autocorrelation structure in the fish abundance time series and is less sensitive to outliers than first-differencing. For the LOWESS approach, we investigate a moving window of 11 and 15 years, respectively, which are reasonable lengths for our data (a total of 50 years). Regardless of moving windows used, repeating the multiple regression analysis using recalculated CVs based on de-trended data still shows that the exploited species exhibit higher variability (Table A3.5).

Similar results were obtained with first differenced time series. We note that CV calculated from first-differenced time series is sensitive to outliers because any large deviation would be counted twice during the procedure. With small sample sizes first-

differencing tends to amplify noise from outliers. Nevertheless, multiple regression analysis based on first-differenced data (de-trending only exploited populations and de-trending both) shows qualitatively similar results (Table A3.5).

Effects of phylogenetic constraints

Results of multiple regression analysis indicate that phylogeny is not a significant variable affecting CVs. To further examine the possible effects of phylogenetic constraints on CVs, we examine the phylogenetic relationships of fish species. Results of Monte-Carlo two-way contingency table analysis (Romesburg and Marshall 1985) indicate no taxonomic preference (taxonomic order) of exploitation (Table A3.6). As can be seen in Figure A3.4, the appearances of exploited and unexploited species are scattered on the phylogenetic dendrogram. We also perform comparisons of exploited and unexploited species within an order (only for the three orders containing both exploited and unexploited species, Table A3.6) to test whether the pattern holds up when the phylogeny is taken into consideration. We show the pattern by averaging the CVs and the values of life history traits within an order for exploited and unexploited species, respectively.

The within-order comparisons largely support our conclusion that exploited populations are more variable than unexploited populations (Fig. A3.5). The mean maximum length of exploited species is larger than that of unexploited species for each of the three orders (Fig. A3.5a). In theory and also in our results (Fig. 3.1), the greater the length is, the lower the expected CV. However, in the within-order comparison, the

mean CV of the exploited species is not smaller than that of the unexploited species for any of the three orders, and is in some cases even higher, suggesting that variability in the abundance of exploited species is higher than that of unexploited species. Similar conclusions are found for the length-at-maturation (Fig. A3.5b), age-at-maturation (Fig. A3.5c), trophic level (Fig. A3.5f), although less clear in spawning duration (Fig. A3.5e). In the analysis of fecundity we expect to find a higher average CV in exploited species because of their higher average fecundity; however, this is less clear in our results (Fig. A3.5d). A similar conclusion can be obtained by contrasting pairs of phylogenetically related fished and unfished species (e.g. contrasting *Paralichthys californicus* and *Pleuronichthys verticalis*, Fig, A3.4). One should keep in mind that the power of comparative analyses with phylogeny is always limited by the sample size.

Fishing-induced reduction of average age or length in exploited fish populations

To test whether declining trends exist in the average age and length of exploited fish populations, we examine the age and length composition in catch data for eight exploited species where data are available (Table A3.7). We use the following order to select the data: 1) data from southern California, 2) data from California, and 3) data from the U.S. West coast. In addition, we select the catch data that avoid bias potentially caused by changes of fishing gear or changes of aging methods. For each species, the average age or length of each year is calculated as the abundance-weighted average or is obtained directly from the value provided in the literature. Correlation analysis between average age (length) and time is used to test whether there is a long-term declining trend.

All species show declining trends in length and age (Fig 3.3). Although high short-term variability is found in the average age and length data, possibly due to sampling error, changes in fishers' fishing behavior (e.g. fishing in a deeper area), or recruitment of a new cohort to the fishery (potentially reducing the average age and length), the long-term declining trend is most likely caused by fishing (Jennings and Dulvy 2005).

Table A3.1. Results of correlation analyses between CalCOFI larval abundances and spawning biomasses from stock assessment models

Species	r	p	Domain of assessment	Source
<i>Merluccius productus</i>	0.566	0.003	US west coast	(Helser et al. 2003)
<i>Sardinops sagax</i>	0.751	<0.001	California	(MacCall 1979; Conser et al. 2004)
<i>Scomber japonicus</i>	0.690	<0.001	US west coast	(Hill and Crone 2005)
<i>Microstomus pacificus</i>	0.017	0.918	US west coast	(Sampson 2005)
<i>Parophrys vetulus</i>	0.244	0.115	US west coast	(Stewart 2005)
<i>Scorpaenichthys marmoratus</i>	0.244	0.129	Southern California	(Cope and Punt 2005)
<i>Sebastes paucispinis</i>	0.758	<0.001	California	(MacCall 2003)

Table A3.2. Literature used to obtain life history information.

Species	Maximum length	Length-at-maturation	Age-at-maturation	Fecundity	Trophic level
<i>Engraulis mordax</i>	1	1	2	(Hunter et al. 1985)	1
<i>Merluccius productus</i>	1	1	2	(Smith 1995)	1
<i>Sardinops sagax</i>	1	(Macewicz et al. 1996)	2	(Macewicz et al. 1996)	1
<i>Scomber japonicus</i>	1	1	2	(Dickerson et al. 1992)	1
<i>Trachurus symmetricus</i>	1	1	2	(Macewicz and Hunter 1993)	1
<i>Cololabis saira</i>	1	(Suyama 2002)	(Suyama 2002)	(Suyama 2002)	1
<i>Icichthys lockingtoni</i>	1				1
<i>Leuroglossus stilbius</i>	1	(Childress et al. 1980)	(Childress et al. 1980)		1
<i>Tetragonurus cuvieri</i>	1				1
<i>Trachipterus altivelis</i>	1				1
<i>Lyopsetta exilis</i>	1		3		1
<i>Microstomus pacificus</i>	1	(Hunter et al. 1992)	(Hunter et al. 1992)	(Hunter et al. 1992)	1
<i>Paralabrax clathratus</i>	1		(Love et al. 1996)	3	1
<i>Paralichthys californicus</i>	1		2	(Caddell et al. 1990)	1
<i>Parophrys vetulus</i>	1	(Sampson and Al-Jufaily 1999)	(Sampson and Al-Jufaily 1999)	(Emmett et al. 1991)	1
<i>Scorpaenichthys marmoratus</i>	1	3	3	2, 3	1
<i>Sebastes aurora</i>	1	(Love et al. 2002)	(Love et al. 2002)		1
<i>Sebastes paucispinis</i>	1	(Love et al. 2002)	2	(Love et al. 2002)	1
<i>Sphyræna argentea</i>	1	2	2	2	1
<i>Chromis punctipinnis</i>	1		3		1
<i>Hippoglossina stomata</i>	1		(Martinez-Munoz and Ortega-Salas 2001)		1

Table A3.2 continued

<i>Pleuronichthys verticalis</i>	1		3		1
<i>Sebastes jordani</i>	1	2	(Pearson et al. 1991)	2	1
<i>Symphurus atricaudus</i>	1		3		1
<i>Zaniolepis frenata</i>	1				1
<i>Argentina sialis</i>	1				1
<i>Hypsoblennius jenkins</i>	1	(Stephens et al. 1970)	(Stephens et al. 1970)	(Stephens et al. 1970)	1
<i>Ophidion scrippsae</i>	1		(Retzer 1991)		1
<i>Oxylebius pictus</i>	1		(DeMartini and Anderson 1980)		1

1. FiahBase.

2. Leet, W.S., Dewees, C.M., Klingbeil, R., & Larson, E.J. (eds) (2001). *California's Living Marine Resources: A Status Report*. Oakland: California Department of Fish and Game.

3. California Department of Fish and Game (2002). *Nearshore Fisheries Management Plan*. (<http://www.dfg.ca.gov/mrd/nfmp/>)

Table A3.3. Results of correlation analysis between fish abundance and time

Species	r	p-value
<i>Engraulis mordax</i>	-0.126	0.439
<i>Merluccius productus</i>	0.072	0.659
<i>Sardinops sagax</i>	0.583	< 0.001*
<i>Scomber japonicus</i>	0.159	0.327
<i>Trachurus symmetricus</i>	-0.451	0.004*
<i>Microstomus pacificus</i>	0.105	0.521
<i>Paralabrax clathratus</i>	0.179	0.270
<i>Paralichthys californicus</i>	-0.010	0.950
<i>Parophrys vetulus</i>	-0.050	0.758
<i>Scorpaenichthys marmoratus</i>	-0.097	0.550
<i>Sebastes aurora</i>	-0.243	0.131
<i>Sebastes paucispinis</i>	-0.505	0.001*
<i>Sphyraena argentea</i>	0.230	0.154
<i>Cololabis saira</i>	0.037	0.822
<i>Icichthys lockingtoni</i>	-0.569	< 0.001*
<i>Leuroglossus stilbius</i>	-0.359	0.023*
<i>Tetragonurus cuvieri</i>	0.100	0.539
<i>Trachipterus altivelis</i>	0.040	0.809
<i>Chromis punctipinnis</i>	-0.099	0.544
<i>Lyopsetta exilis</i>	0.172	0.289
<i>Hippoglossina stomata</i>	-0.097	0.554
<i>Pleuronichthys verticalis</i>	0.069	0.673
<i>Sebastes jordani</i>	-0.206	0.203
<i>Symphurus atricaudus</i>	-0.123	0.448
<i>Zaniolepis frenata</i>	0.541	< 0.001*
<i>Argentina sialis</i>	0.437	0.005*
<i>Hypsoblennius jenkins</i>	0.042	0.799
<i>Ophidion scrippsae</i>	-0.167	0.303
<i>Oxylebius pictus</i>	0.189	0.244

* Correlation is significant at $p < 0.05$. Results are prone to Type I error because serial dependence in the time series data are not accounted for.

Table A3.4. Results of the analysis of covariance on each individual life history trait

P-values	Model without interaction term			
	Full model Interaction (β_3)	Intercept (β)	Fishing (β_1)	Life history (β_2)
Max size	0.492	0.004	0.018	0.203
Size-at-maturation	0.977	0.040	0.093	0.623
Age-at-maturation	0.796	<0.001	0.005	0.002
Fecundity	0.562	0.261	0.410	0.902
Spawning duration	0.650	<0.001	0.070	0.276
Trophic level	0.537	0.033	0.026	0.345

Full model: $CV = \beta + \beta_1 * Fishing + \beta_2 * Life + \beta_3 * Fishing * Life$.

Model without interaction term: $CV = \beta + \beta_1 * Fishing + \beta_2 * Life$.

Here, *Fishing* is a dummy variable. The interaction term is not significant in any test of the life history traits. The effect of fishing is significant ($p < 0.1$) in all cases after accounting for the life history effect, except for fecundity.

Table A3.5. Results of multiple regression analyses

Raw data	□	□	□
□	Fishing	Age-at-maturation	Region
Life history traits	0.002	0.003	
Ecological traits	0.005		P < 0.001
Combined	P < 0.001	0.015	P < 0.001

De-trending both exploited and unexploited species using a moving window of 11 years			
□	Fishing	Age-at-maturation	Region
Life history traits	0.019	0.019	
Ecological traits	0.014		P < 0.001
Combined	0.022	0.091	0.016

De-trending both exploited and unexploited species using a moving window of 15 years			
□	Fishing	Age-at-maturation	Region
Life history traits	0.025	0.023	
Ecological traits	0.021		0.001
Combined	0.030	0.094	0.031

De-trending only exploited species using first differencing			
□	Fishing	Age-at-maturation	Region
Life history traits	0.001	0.002	
Ecological traits	0.012		0.017
Combined	0.001	0.009	0.073

De-trending both exploited and unexploited species using first differencing			
□	Fishing	Age-at-maturation	Region
Life history traits	0.093	0.007	
Ecological traits	0.102		0.049
Combined	0.130	0.022	0.279

Table A3.6. The contingency table showing numbers of exploited and unexploited species in each order.

Order	Exploited	Unexploited
Clupeiformes	2	0
Gadiformes	1	0
Perciformes	4	4
Beloniformes	0	1
Osmeriformes	0	2
Lampriformes	0	1
Pleuronectiformes	3	4
Scorpaeniformes	3	3
Ophidiiformes	0	1

Results of the Monte-Carlo two-way contingency table analysis indicate no significant association between phylogeny of fishes and exploitation preference ($p = 0.468$).

Table A3.7. Data sources for calculating time series of average age and length in catch for eight exploited species.

Measure	Species	Common name	Region	Time	Source
Age composition	<i>Merluccius productus</i>	Pacific hake	US west coast	1973-2003	Commercial fishing(Helser et al. 2003)
	<i>Sardinops sagax</i> ^a	Pacific sardine	California	1932-1960	Commercial fishing(Murphy 1966)
				1983-2004	Commercial fishing(Conser et al. 2004)
	<i>Scomber japonicus</i> ^b	Pacific chub mackerel	US west coast	1929-1970	Commercial fishing(Hill and Crone 2005)
			1985-2004	Commercial fishing(Hill and Crone 2005)	
	<i>Microstomus pacificus</i> ^c	Dover sole	California	1985-2003	Commercial fishing(Sampson 2005)
Length composition	<i>Parophrys vetulus</i>	English sole	California	1966-2003	Commercial fishing(Stewart 2005)
	<i>Scorpaenichthys marmoratus</i> ^d	Cabezon	Northern California	1987-1998	Recreational fishing(Cope and Punt 2005)
			Southern California	1975-1989	Recreational fishing(Cope and Punt 2005)
	<i>Sebastes paucispinis</i>	Bocaccio	Central California	1977-1994	Recreational and commercial fishing(Mason 1998)
	<i>Microstomus pacificus</i>	Dover sole	Southern California	1969-2004	Commercial fishing(Sampson 2005)
	<i>Sphyraena argentea</i> ^e	Pacific barracuda	Southern California	1958-1973	Recreational fishing(MacCall et al. 1976)

a. A moratorium for Pacific sardine lasted from 1967 to 1985. Aging methods are different in the period before and after moratorium. Therefore, the data in the two periods are analyzed separately.

b. A moratorium and recovery period for Pacific chub mackerel lasted from 1970 to 1985. Data before and after the moratorium are analyzed separately.

- c. The age data for Dover sole started from 1967, but the data are only reliable since the use of the break and burn otolith age-readings in 1985(Sampson 2005).
- d. The length composition data for cabezon are sparse in the southern California region. Therefore, the data from the northern California region are included for comparison.
- e. The average length data for Pacific barracuda from commercial fishing are not used because they are biased due to changes of fishing gear(MacCall et al. 1976).

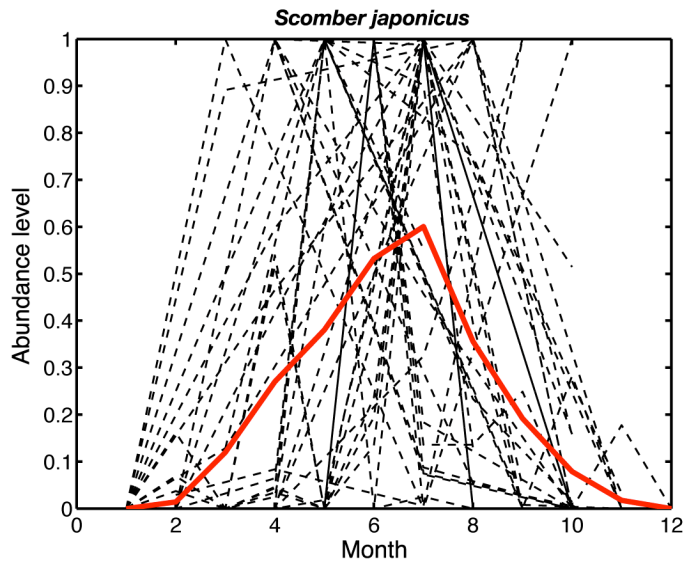


Figure A3.1. An example illustrating spawning seasonality using *Scomber japonicus*. Each dashed line represents annual variation of the standardized larval abundance level of each year, and the solid red line represents the long-term (1951-2002) mean. The spawning period is defined as the months with mean abundance level > 0.1 .

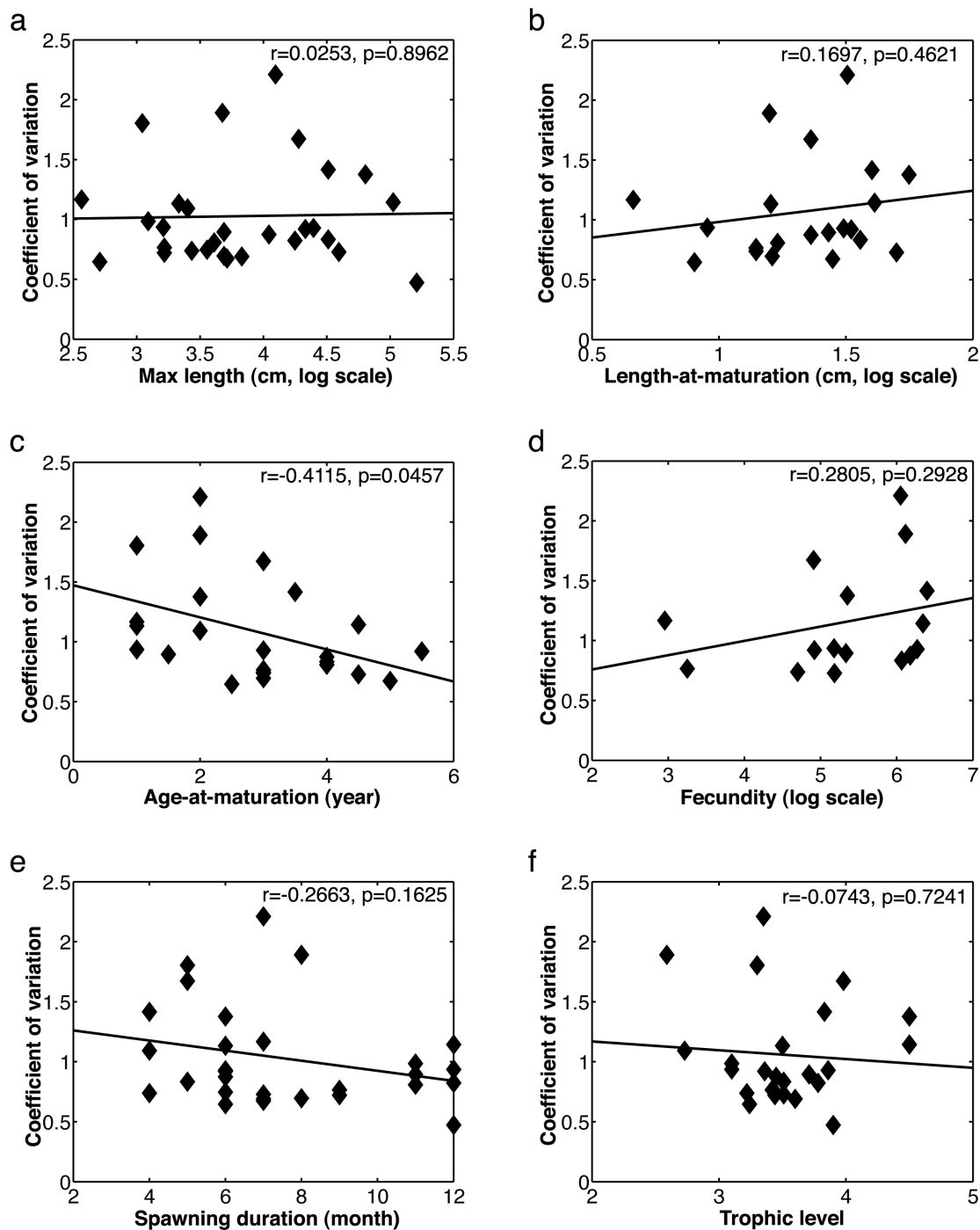


Figure A3.2. Relationships between CVs and life history traits for all species combined.

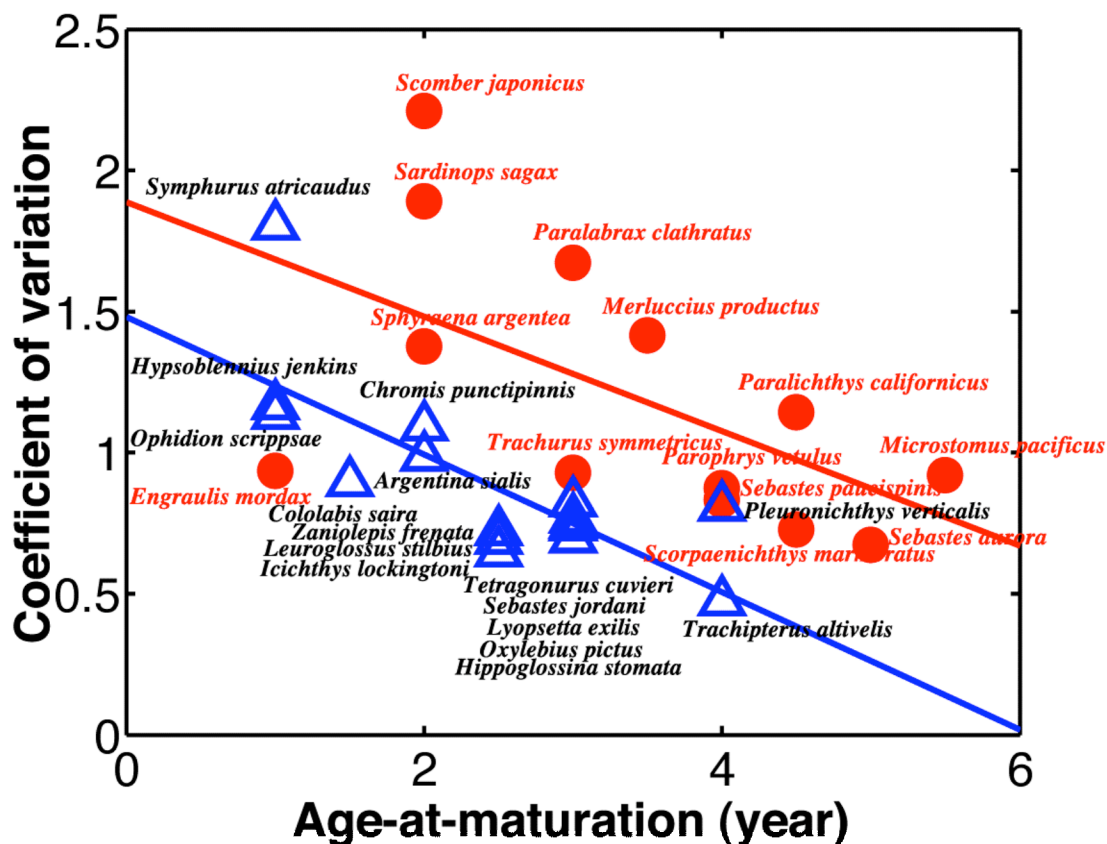


Figure A3.3. Relationships between CVs and age-at-maturation for exploited (circle) and unexploited (triangle) species. Missing data of age-at-maturation (five unexploited species) are imputed using expectation maximization algorithm (Little and Rubin 2002). The imputation of missing data does not significantly change the slope of regression lines.

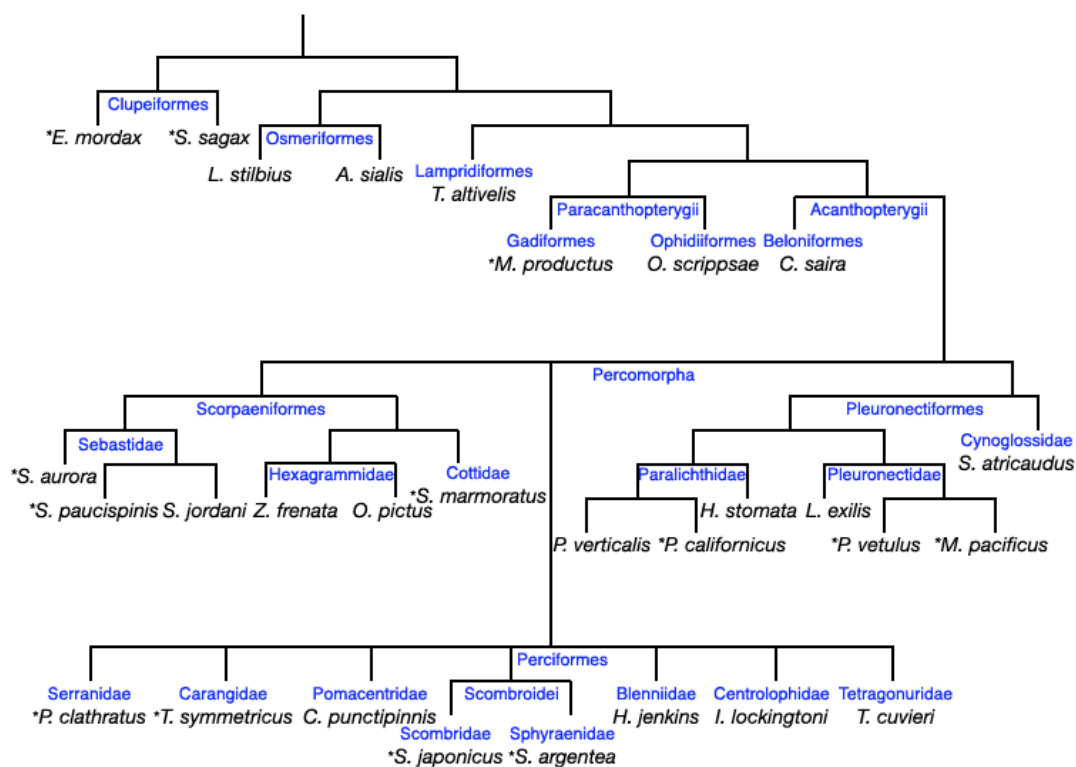


Figure A3.4. Dendrogram showing the phylogenetic relationships among the species used in this study. Exploited species are prefixed with an asterisk and unexploited species are not. Their taxonomic affiliations are also shown. The phylogenetic status of each species is based on Nelson (1994).

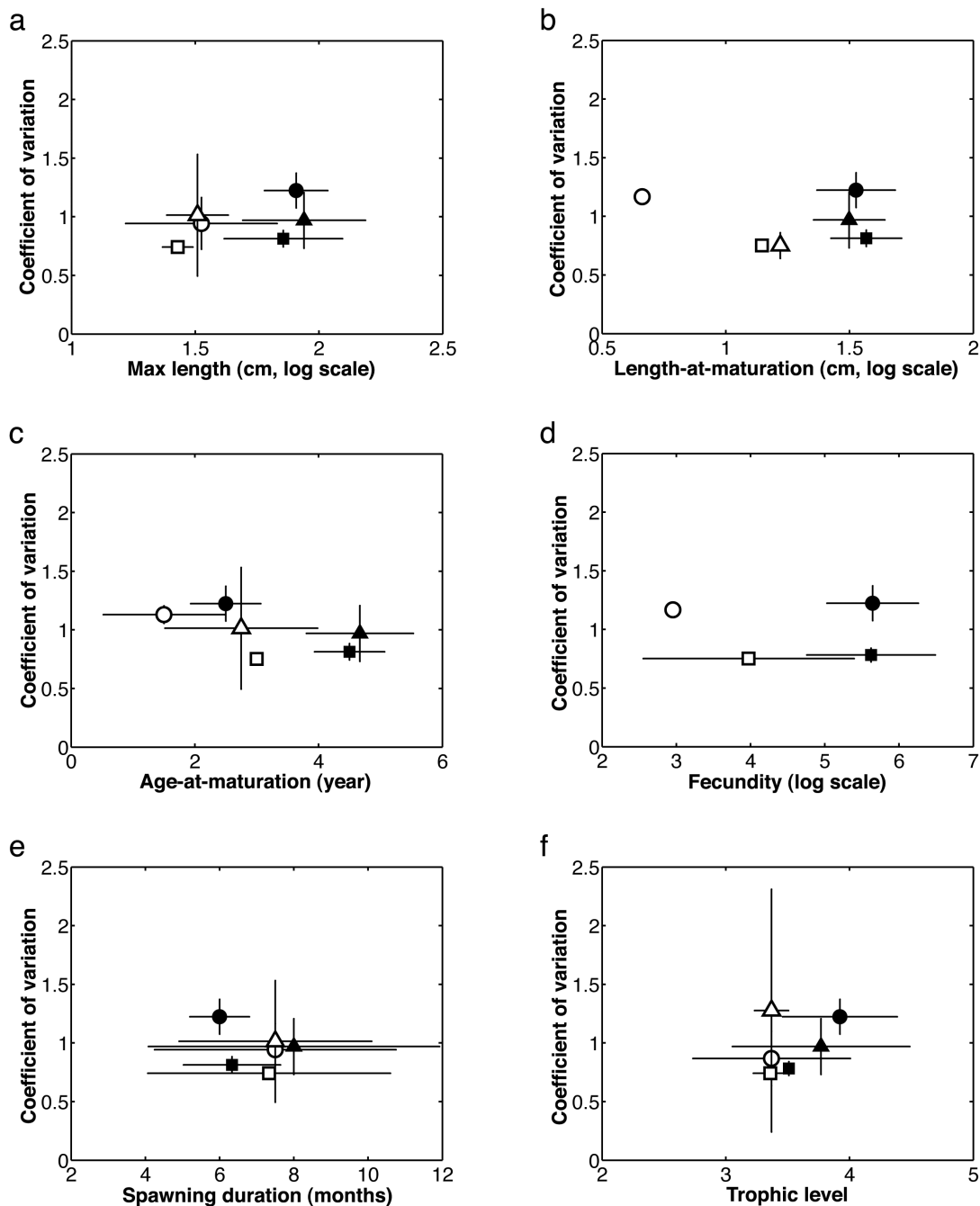


Figure A3.5. Scatter plots showing the relationships between CVs and life history traits. Each symbol represents the average CV and the life history trait within an order for exploited (filled symbols) and unexploited (open symbols) species, respectively. The vertical and horizontal bars represent 2 standard errors for the CVs and the life history traits, respectively. Symbol: circles indicate Perciformes, triangles indicate Pleuronectiformes, and squares indicate Scorpaeniformes.

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Chapter 4. Climatic and fishing effects on shifts in spawning distribution of marine fishes

Abstract

Understanding how fishing changes fish population structure and distributions in response to climate change is important for fisheries management. To examine the synergistic effects of fishing and climate on fish populations, we analyze 29 fish species in the southern California area, including both exploited and unexploited species. Our results indicate that climate change has significant impacts on the geographic distribution of these fishes. At an annual scale, 10 species significantly shift their distribution in mean latitude or boundary in response to sea surface temperature. At a bi-decadal scale, 9 species significantly move poleward from the cold to the warm period. Considering the annual and bi-decadal scales together, a total of 12 species show a clear distributional shift in response to environmental change. More importantly, exploited species show a clearer distributional shift in response to environmental change than unexploited species. This result is not due to biases associated with life history traits, ecological traits, or phylogeny of fish species. We propose two hypotheses explaining why fishing may increase sensitivity of exploited populations in response to environmental change. 1) Fishing truncates age-size structures of populations by selectively removing old or large individuals, which reduces the capacity of populations to dampen environmental variability. 2) Fishing reduces the fish population size and causes constriction of fish spatial distribution, which strengthens signals in their spawning locations. These results indicate that fishing might have reduced the resilience of fish populations and, therefore, made the exploited species more vulnerable to a changing climate.

Introduction

Understanding the synergistic effects of anthropogenic and climatic impacts on biological populations is important for ecosystem conservation and management (Walther et al. 2002; Harley et al. 2006). Climatic fluctuations have had profound impacts on the abundance, distribution, and phenology of species (Beebee 1995; Crick et al. 1997; Mackas et al. 1998; Beaugrand et al. 2002; Stenseth et al. 2002; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Richardson and Schoeman 2004; Perry et al. 2005). At the extreme, climate change may increase the probability of extinction of species by reducing suitable habitats (Thomas et al. 2004). In addition, differential responses of different trophic levels to climate may cause trophic mismatch in space or time (Beaugrand et al. 2003; Edwards and Richardson 2004). Moreover, a prolonged change in climatic conditions (e.g. the protracted warm condition in the north Pacific ocean after 1976) can potentially lead to abrupt shifts of population sizes (Mantua et al. 1997; Scheffer et al. 2001; Hsieh et al. 2005a). Although biological responses to environmental variations have been extensively studied, how anthropogenic effects may alter the structure of biological populations and thus their sensitivity to environmental variations is not well known and warrants investigation.

For marine fishes, the most serious anthropogenic impact is fishing. Because fishing pressure may reduce the resilience of exploited populations facing climate variation (Murphy 1967; Harley et al. 2006), climatic effects may have more severe impacts on commercially-exploited species. Therefore, an important improvement to the management of fisheries is for the processes to take into account how fishing affects the

ability of fish populations to respond to climate changes (Pikitch et al. 2004). By comparing exploited to unexploited fish species living in the same environment, in the previous chapter (Hsieh et al. in prep.) we showed that fishing elevates the variability of exploited populations, presumably by truncating their age structure. Here, we extend the comparative approach to examine how fishing affects the distributional responses of fish populations to climate.

In the northeastern Pacific, climatic effects on fish abundance have been extensively studied (Hare and Mantua 2000; e.g. Benson and Trites 2002; Smith and Moser 2003), and effects on fish assemblages have been observed (Holbrook et al. 1997). However, understanding climatic effects on the geographic distributions of fishes is limited to only a few species, for example, Pacific sardine and northern anchovy (Rodriguez-Sanchez et al. 2002) and Pacific hake (Benson et al. 2002). This is the first large-scale study to compare the geographic distributions of a suite of fish species in response to climate in the northeastern Pacific. In this study, we examine climatic effects on the distribution of fish spawning populations using the larval fish data collected from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) in the southern sector of the California Current System. Here we use the sea surface temperatures (SSTs) from the CalCOFI region as a proxy for climate, because the CalCOFI SSTs have been shown to reflect both interannual and decadal climatic variations in the northeastern Pacific, as well as the global warming trend (Di Lorenzo et al. 2005; Schneider et al. 2005).

The most important question in this study is whether exploited species are more sensitive to climate change in their spatial distributions. To test this hypothesis, we compare distributional responses of exploited and unexploited species to a climate proxy. Clearly fishing is a selective process, and the exploited and unexploited groups might not be formed randomly. To perform a reasonable comparison of the exploited to the unexploited species, possible intrinsic biases associated with fishing must be taken into consideration. Therefore, we examine potential factors, including life history traits, ecological traits, and phylogeny. We then suggest the mechanisms explaining the differential responses of exploited and unexploited species.

Methods

Spatial data

To examine how climate affects spatial distributions of fishes, we study the larval fish time series (1951-2002) developed by CalCOFI from the southern sector of the California Current System. We examine 29 coastal and neritic species that are abundant and consistently enumerated in the CalCOFI surveys (Hsieh et al., 2005b), including 13 exploited and 16 unexploited species (Table 4.1). The CalCOFI surveys have collected comprehensive oceanographic and biological data since 1949 (consistent larval fish data are only available since 1951) with at least four quarterly cruises per year (except for triennial sampling from 1967 to 1984), and the time series is based on fixed grid of sixty-six stations per cruise (Fig. 4.1) (Hsieh et al. 2005b). Because most larvae collected by plankton nets during the CalCOFI surveys are in very early stages of development, the

spatial distribution of larvae is primarily indicative of the distribution of the adult spawning population (although advection of larvae by currents might play a role). Thus, we use the distribution of larvae to infer the distribution of the spawning population for each species.

We use only data landward of Station 90 of the standard CalCOFI grid in this study (the inner box illustrated in Figure 4.1) in order to avoid statistical bias due to missing data in examining the spatial distribution of fish, as sampling offshore of Station 90 was less consistent through time. While the CalCOFI sampling methods changed over time, these changes would not bias the spatial statistics used here. (The effects of changing sampling methods on larval fishes were assessed by Hsieh et al. (2005b)). In addition, although the sampling frequency is higher than quarterly from 1951 to 1984, we use only the quarterly data in this study so that the variance associated with the spatial data is not biased due to the difference in sampling effort of each year.

We determine the distribution-center (mean latitude and longitude) of each year for each taxon, first by averaging the station values across the principal season in which the larvae occur (i.e., spawning season of the species), and then calculating the distribution-center as the abundance-weighted average of the annual map. Thus, a time series of the distribution-center is obtained for each taxon. In addition, the southern/northern boundary is calculated as the minimum/maximum latitude in which a species occurs for each year.

We use average sea surface temperature (SST) within our study region (Fig. 4.1, the inner box) as a proxy for climatic signals. The SST data are from the CalCOFI stations

(<http://www.calcofi.org/newhome/data/data.htm>). When analyzing the correlation between SST and the geographic distribution of a fish species, we use only the SST data corresponding to the spawning season of that species. The annual average SST is calculated by averaging the spatial and temporal data (quarterly data within the spawning seasons). Hereafter, we use SST to refer to the annual average SST.

Data analyses

For each taxon, regression analysis is used to investigate the relationship between the mean latitude and SST and 1-year time-lagged SST. We also examine the southern boundaries for cool water species and northern boundaries for warm water species (Table 4.1) in relation to the SSTs. For species where mean latitudes (or boundaries) are significantly correlated with abundances, we control for abundance and test for the partial correlation between the mean latitude (or boundaries) and SSTs, because the geographic extent of marine populations may be correlated with population size (MacCall 1990).

We also examine the bi-decadal scale variation in fish distributions because climatic variability is important at this time scale in the North Pacific (Mantua et al. 1997; Biondi et al. 2001). We define the cold (1951-1976) and the warm (1977-1998) period following the definition of the Pacific Decadal Oscillation (Mantua et al. 1997). (A transition back to another cold period might have occurred in 1999 (Ohman and Venrick 2003; Peterson and Schwing 2003), but the time series are too short to assure that; therefore, data beyond 1998 are omitted in the analyses at the bi-decadal scale). For each taxon, the centroids of the cold and warm periods are calculated from the time series of the distribution-center

using the robust method of 50% convex hull peeling with all data equally weighted (Zani et al. 1998). This method is robust to the bias caused by outliers. We track the direction and magnitude of the movement from the cold to the warm period for each taxon. To test whether the change in larval distribution domain from the cold to the warm period is statistically significant, we use an ANOVA-like nonparametric test by comparing all pairwise distances of distribution-centers within and between the two periods (illustrated in Fig. 4.2). The statistic is computed as follows:

1) We compute the sum of all pairwise distances between distribution-centers

$$\text{within period 1: } \Omega_1 = \sum \|x_{i1} - x_{j1}\|, \quad i \neq j; i > j,$$

$$\text{and period 2: } \Omega_2 = \sum \|x_{i2} - x_{j2}\|, \quad i \neq j; i > j,$$

where x_{i1} and x_{i2} represent points in two-dimensional Euclidean space in periods 1 and 2, respectively, and i and j are indices for years (Fig. 4.2c).

We then compute the average of pairwise distances within periods:

$$W = \frac{1}{N(N-1)/2 + M(M-1)/2} (\Omega_1 + \Omega_2),$$

where there are N and M points in period 1 and 2, respectively.

2) We compute the average of pairwise distances between periods:

$$B = \frac{1}{NM} \sum \|x_{k1} - x_{l2}\|, \quad k = 1 \text{ to } N, l = 1 \text{ to } M \text{ (Fig. 4.2d)}.$$

3) The statistic $T = W/B$ is used to determine whether there is a significant change in distribution domain.

A significant change in larval distribution domain between the two periods corresponds to a small T . We randomize the data 1000 times and obtain the null ratios T^* . The change is deemed significant if T falls in the 5% lower tail.

We then consider whether shifting and non-shifting species have significantly different life history traits. Here, “shifting species” are defined as species showing a significant distributional (including mean latitude and boundaries) relationship with SST or a significant change in distribution domain from the cold to the warm period. We examine six life history traits: maximum length, length-at-maturation, age-at-maturation, fecundity, spawning duration, and trophic level (Chapter 3). For each trait, we compute the mean value and 95% bootstrapped (1000 times) confidence limits for shifting and non-shifting species, respectively, to perform our hypothesis test. A difference is deemed significant if the 95% confidence limits of shifting and non-shifting species do not overlap (Manly 1997). We refer to this analysis as the “bootstrapping test”. We then use a Monte Carlo two-way contingency table analysis (Romesburg and Marshall 1985) to test whether fish species showing a significant distributional response to climate have a particular phylogenetic relationship (based on fish taxonomic orders). In addition, logistic regression is applied to determine whether the shifting species are associated with specific ecological traits (geographic affinity, habitat, and spawning mode, Chapter 3) and exploitation (exploited or not). The Akaike Information Criterion (AIC) is used to select the best model.

Results

At the annual scale, seven of the 29 species significantly shift their mean latitude in relation to the SST (Table 4.1, see Fig. 4.3a for an example). In addition, one species, *Scorpaenichthys marmoratus* (cabezon), significantly shifts its southern boundaries in relation to the 1-year lagged SSTs among the cool water species, and five species significantly shift their northern boundaries in relation to SST among the warm water species (Table 4.1). All shifting species show a positive correlation with the SSTs, except for *Zaniolepis frenata* (shortspine combfish). For the shifting species, the rate of shift in mean latitude ranged from 17 to 37 km/°C (average = 25, upper limit = 30, and lower limit = 21 km km/°C, 7 species). The only shifting cool water species moved 49 km/°C in its southern boundary. The rate of shift in the northern boundary of warm water species ranged from 21 to 43 km/°C (average = 31 ± 7 km/°C, 5 species). (The 95% confidence limits are calculated using 1000 bootstraps.)

Significant distributional shifts of fishes at the bi-decadal scale were also observed (see Fig. 4.3b for an example). A total of 24 species (cool water species: 6/9; warm water species: 10/11; widely-distributed species: 8/9) move poleward from the cold period to the warm period (Fig. 4.4). This is highly significant as a meta-analysis (binomial test, $p < 0.001$), suggesting that most species move poleward in response to the warming in the southern California ocean ecosystem. The movements range from 1 to 86 km (average = 31, upper limit = 38, and lower limit = 25 km). However, upon investigating their distribution-centers closely, only 9 species significantly shift their distributional domain (Table 4.1). Thus, although most species show a tendency to move poleward in response

to the warming, the signal is clear in only 9 out of 29 species. The time series of distribution-centers for each species is provided in Appendix.

A particularly important finding is that the tendency for a species to exhibit a clear response to temperature is significantly associated with fishing (Table 4.2). Considering the annual and bi-decadal scales together, 12 species show a clear distributional shift in response to climate and among them, 9 are exploited species and only three are unexploited species (Table 4.1). Although, in theory, species with shorter generation time and associated life history traits should be more responsive to environmental variation (Perry et al. 2005), this is not the case in our study. We find no significant differences in life history traits between shifting and non-shifting species ($p > 0.05$, Fig. 4.5). Furthermore, whether or not a species exhibits a clear response to temperature changes is not associated with their phylogeny (Table 4.2), geographic affinity, habitat, or spawning mode (Table 4.3).

Discussion

Among the 29 species examined, only 10 species show a significant distributional shift (mean latitude or boundaries) in relation to the SST (Table 4.1). This might be due to the high noise associated with the CalCOFI larval data (Hsieh et al., 2005b). Nevertheless, given that the latitudinal range of the current study ($\sim 30 - 35^\circ\text{N}$, Fig. 4.1) is small and none of the studied species are bounded by this range, it is surprising to see these signals. Our results are consistent with other studies (Murawski 1993; Brander et al. 2003; Perry et al. 2005): poleward shifts of most fishes are found in response to

warmer average SST. The average shift rate (25 km/°C in mean latitude) of southern California fishes is smaller than that of the North Sea fishes (average 87 km/°C calculated from Perry et al. 2005) and North Atlantic fishes (ranges from 56 to 89 km/°C reported by Murawski 1993). The smaller shift rate may be due to the smaller latitudinal range of this study (less than 5 degrees) in comparison to the North Sea study (51 – 62 °N) and north Atlantic study (36 – 45 °N) because estimates of distribution-centers may be less reliable when the true population moves beyond the study boundary. Alternatively, species living at lower latitudes might be less sensitive to warming (Root et al., 2003), as our study area is located at lower latitude than the other two studies.

We find that 83% of species move poleward in response to warmer average SST, when comparing the fish distribution centroid in the cold period with that of the warm period (Fig. 4.4). However, only 9 species pass the randomization test for a shift in distribution centroid (Table 4.1), again, suggesting that the signal is not very strong. Given the geographic limit of our study area and noisiness of the data, our results indicate that most species have responded to temperature, but some species show a stronger response than others.

Which factor determines whether or not a species shows a clear (high signal/noise ratio) distributional shift? The most important finding is that more often than not the shifting species are exploited (Table 4.3); that is, exploited species exhibit a higher signal/noise ratio. Life history traits are not the main factor determining the sensitivity of fish's distributional response in this study (Fig. 4.5); nor is phylogeny (Table 4.2) or ecological traits (Table 4.3). In addition, one might suspect that high signal/noise is

statistically associated with high abundance; however, no significant difference in mean abundance exists between the shifting and non-shifting species (bootstrapping test, $p > 0.05$).

We suggest two hypotheses that fishing may increase the signal/noise ratio: 1) Fishing increases sensitivity (reduces the resilience) of fish populations to the environment by truncating their age-size structure. Fisheries tend to truncate the age-size structure of fish populations by removing large and old individuals through size (age)-selective fishing mortality (Conover and Munch 2002; Berkeley et al. 2004; Hutchings and Reynolds 2004). In fact, evidence of age (size) truncation has been found in several exploited species examined in this study (Chapter 3). Truncating the age-size structure of a fish population, and therefore, undermining their bet-hedging capabilities, may reduce their resilience to environmental variation (Murphy 1967; Marteinsdottir and Steinarsson 1998; Planque and Fredou 1999; Secor 2000a; Secor 2000b; Murawski et al. 2001; Berkeley et al. 2004). Thus, exploited populations may track environmental conditions more closely and show a stronger distributional response to climate (Ottersen et al. 2006). 2) Fishing increases the signal/noise ratio by causing constriction in spatial distribution of the exploited populations (“fishing as a noise filter”, as illustrated in Figure 4.6).

Consider an unexploited population that has a large distributional area and a large number of spawners. Because these spawners diffusively distribute to a larger area, the spawning locations might not be in the distribution-center of the population.

Accordingly, the larval locations produced by these aberrant spawners, along with effects caused by advection and diffusion, are less representative of the actual distribution of the

spawning population, i.e. they are noisy. Therefore, the distribution domain of an unexploited population might have changed from one environmental condition to another, but this signal might not be clearly found in larval distributions. In contrast, when a fish species is under strong fishing pressure, its distribution area may shrink (because peripheral individuals are removed) and the number of spawning individuals may decline (MacCall 1990). Thus, the distribution-center of an exploited population can be more precisely represented by the spawner locations inferred from the larval locations, since noise generated by peripheral spawners no longer exists. Because the signal/noise ratio is higher for an exploited species, a significant shift in larval distribution in response to climate is more likely to be observed.

If fisheries have caused constriction of a population, we predict the spatial distribution of their larvae to be more aggregated and less random. To test this hypothesis, we measure the degree of aggregation of the larvae for each species using Taylor's power law (Taylor 1984): $V = aM^b$, where V is the spatial variance of population density, M is the mean population density, a is the normalization coefficient, and the exponent, b , determines the degree of aggregation of the population (Taylor 1961; Taylor 1984). Empirically, b is between 1 and 2 (Anderson et al. 1982; Taylor 1984), with b equal to 1 indicating a random spatial distribution and b greater than 1 indicating an aggregated spatial distribution (Taylor, 1984). The greater the value of b , the more aggregated the population spatially (Taylor, 1984). Detailed procedures for calculating the aggregation index and the results are described in Appendix.

We use logistic regression to test if the shifting species are associated with a high aggregation index and fishing. The results indicate that either aggregation or fishing alone is a significant factor (Table 4.3). When both fishing and aggregation are included in the model, fishing is significant ($p = 0.023$) and aggregation is marginally significant ($p = 0.081$) (Table 4.3). If the interaction term is included, this interaction term becomes the only significant factor (Table 4.3). The best model (based on AIC) includes both fishing and aggregation. These results suggest both fishing and aggregation are important factors associated with the shifting species. The high degree of aggregation is likely caused by a fishing-induced constriction of population distribution (MacCall 1990). However, we cannot rule out the possibility that the aggregation is due to natural behaviors to form patches of certain species (Anderson et al. 1982).

Our results indicate that climate changes have had significant effects on fish distributions. More importantly, fishing might have reduced the resilience of fish populations by truncating their age-structure or causing constriction of their spatial distribution, and thus, makes exploited species more responsive to climate changes. This suggests that exploited species may be more vulnerable to the impacts of climate-induced trophic mismatch or reduction in suitable habitat. The effects of fishing, climate, and the interactions of these two factors on the dynamics of fish populations must be borne in mind for sound fisheries management. Protecting the age structure and spatial structure of fish populations will be useful in sustaining fish populations and should be taken into consideration for management.

Table 4.1. Results of regressions of the effects of interannual changes in temperature on mean latitude, southern and northern boundaries for 29 fish species off southern California. The final column indicates the results of a test of difference in spatial domain between the cold (1951-1976) and warm period (1977-1998). Only significant results ($p < 0.05$) are listed.

	Species	Common name	Mean latitude	Southern boundary	Northern boundary	Shift in domain
Exploited	<i>Engraulis mordax</i> ¹	Northern anchovy				0.021
	<i>Merluccius productus</i> ¹	Pacific hake or whiting	0.002*			0.001
	<i>Microstomus pacificus</i> ²	Dover sole				
	<i>Paralabrax clathratus</i> ³	Kelp bass	0.035*		0.011	0.009
	<i>Paralichthys californicus</i> ³	California halibut	0.007			0.043
	<i>Parophrys vetulus</i> ²	English sole				0.035
	<i>Sardinops sagax</i> ³	Pacific sardine	0.021		0.003*	0.005
	<i>Scomber japonicus</i> ³	Pacific chub mackerel			0.005*	0.020
	<i>Scorpaenichthys marmoratus</i> ²	Cabezon		0.028†		
	<i>Sebastes aurora</i> ²	Aurora rockfish				
	<i>Sebastes paucispinis</i> ²	Bocaccio				
	<i>Sphyræna argentea</i> ³	Pacific barracuda	0.008		0.008	0.003
	<i>Trachurus symmetricus</i> ¹	Jack mackerel				
	Unexploited	<i>Argentina sialis</i> ¹	Pacific argentine	0.044		
<i>Chromis punctipinnis</i> ³		Blacksmith			0.017	
<i>Cololabis saira</i> ¹		Pacific saury				
<i>Hippoglossina stomata</i> ²		Bigmouth sole				
<i>Hypsoblennius jenkins</i> ²		Mussel blenny				
<i>Ichthyosoma lockingtoni</i> ¹		Medusafish				
<i>Leuroglossus stilbius</i> ¹		California smoothtongue				
<i>Lyopsetta exilis</i> ²		Slender sole				
<i>Ophidion scrippsae</i> ³		Basketweave cusk-eel				
<i>Oxylebius pictus</i> ²		Painted greenling				
<i>Pleuronichthys verticalis</i> ³		Hornyhead turbot				
<i>Sebastes jordani</i> ²		Shortbelly rockfish				
<i>Symphurus atricaudus</i> ³		California tonguefish				
<i>Tetragonurus cuvieri</i> ²		Smalleye squaretail				
<i>Trachipterus altivelis</i> ²		King-of-the-salmon				
<i>Zaniolepis frenata</i> ²	Shortspine combfish	0.002 ⁻				

Geographic affinity of each fish species is determined based on its principal geographic distribution in the northeast Pacific (1. widely-distributed species; 2. cool water species; 3. warm water species) (Moser 1996, FishBase, Hsieh et al. in prep.).

*When abundance is significantly related to latitude, we factor out the abundance effect and present the results of partial correlation.

†The significant regression for cabezon is for temperature with 1-year lag.

⁻ *Zaniolepis frenata* shows a negative relationship with temperature. The reason for this negative relationship is unknown.

Table 4.2. Contingency table showing numbers of shifting and non-shifting species in each taxonomic order.

Order	Shifting	Non-shifting
Clupeiformes	2	0
Gadiformes	1	0
Perciformes	4	4
Beloniformes	0	1
Osmeriformes	1	1
Lampriformes	0	1
Pleuronectiformes	2	5
Scorpaeniformes	2	4
Ophidiiformes	1	0

Results of the Monte Carlo two-way contingency table analysis indicate that phylogeny does not determine whether or not a fish species shows a distributional response to temperature ($p = 0.529$).

Table 4.3. Results of logistic regressions showing effects of ecological traits and fishing on fish species' responsiveness to temperature. (AIC represents the Akaike Information Criterion.)

Model	Variable	P-value	R ²	AIC
shifting = fishing + region + bottom +spawning mode	fishing	0.011	0.576	37.151
	region	0.203		
	bottom	0.262		
	spawning mode	0.748		
shifting = fishing	fishing	0.010	0.319	34.491
shifting = aggregation	aggregation	0.041	0.251	37.344
shifting = fishing + aggregation	fishing	0.023	0.460	33.236
	aggregation	0.081		
shifting = fishing*aggregation	fishing*aggregation	0.008	0.332	35.141

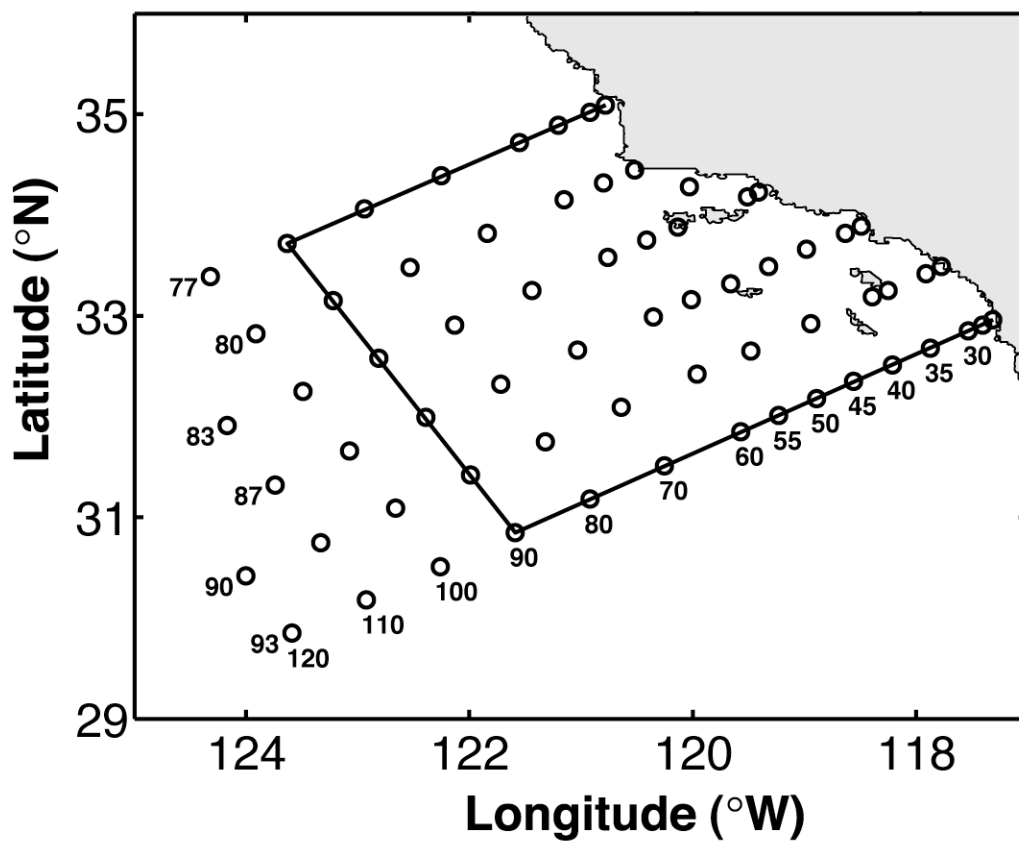


Figure 4.1. Map showing the spatial pattern of CalCOFI stations. Only stations within the solid lines (Station 90 and inshore) were used in this study because the stations outside the box were sampled with less consistency.

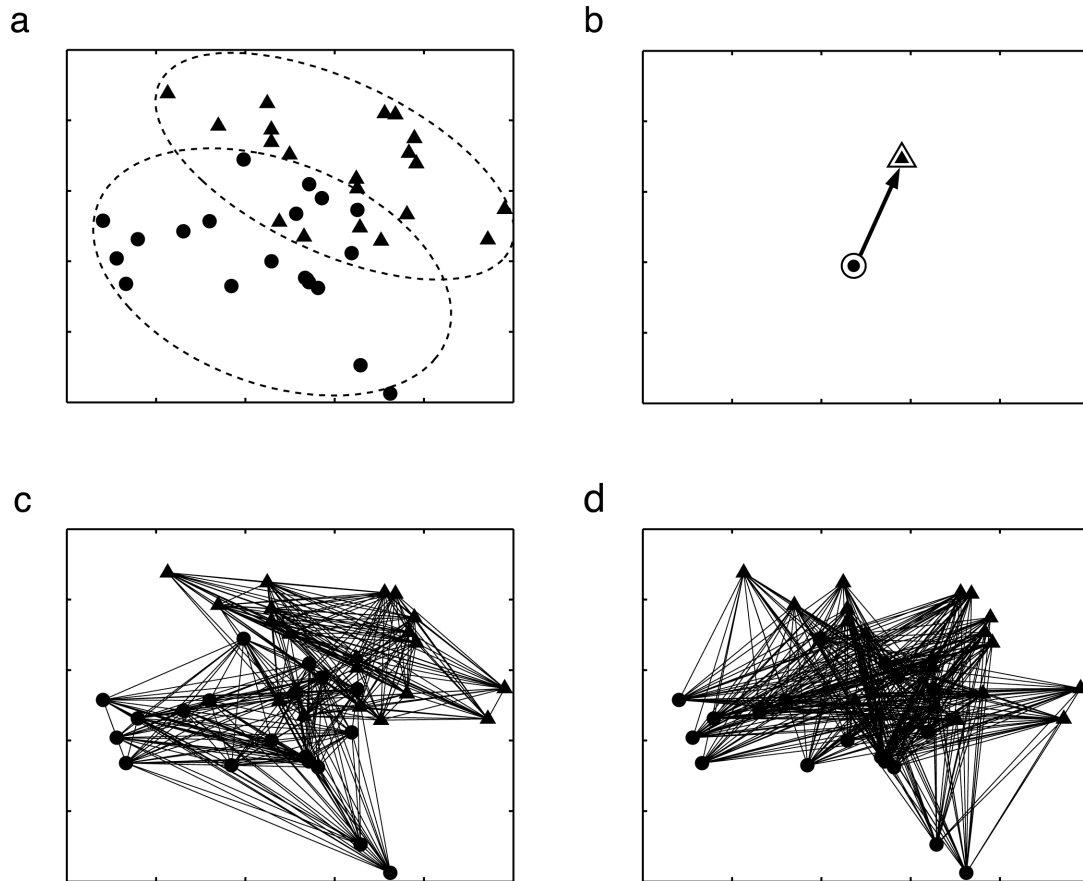


Figure 4.2. Schematic illustrating spatial analyses of change in distribution domain of fishes. (a) Circles and triangles represent hypothetical distribution-center in individual year in the cold and warm periods, respectively. (b) The double circle and triangle represent the centroid of the spatial distribution domain for the cold and warm period, respectively, and the arrow indicates the magnitude and direction of the change between the two periods. To test whether the change in distribution between the two periods is significant, we computed all pairwise distances of distribution-centers within (c) and between (d) the two periods. The change in distribution is significant if the ratio of the average pairwise distance within and average pairwise distance between is statistically smaller than the null ratio generated from a randomization procedure.

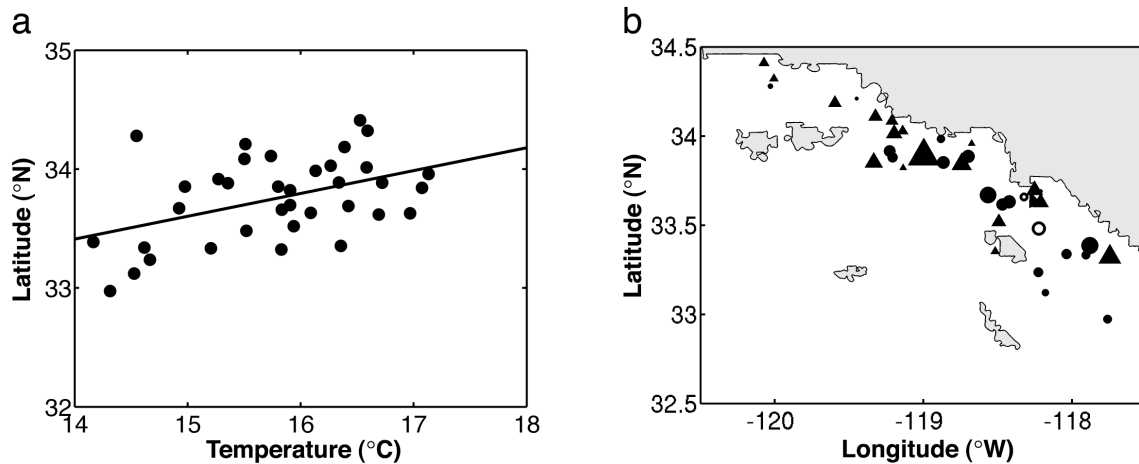


Figure 4.3. An example showing (a) the relationship between mean latitude and mean SST and (b) distribution-centers (1951-1976, solid circles; 1977-1998, solid triangles; 1999-2002, open circles) for California halibut. In (b), the size of the symbol is proportional to the mean abundance for a given year.

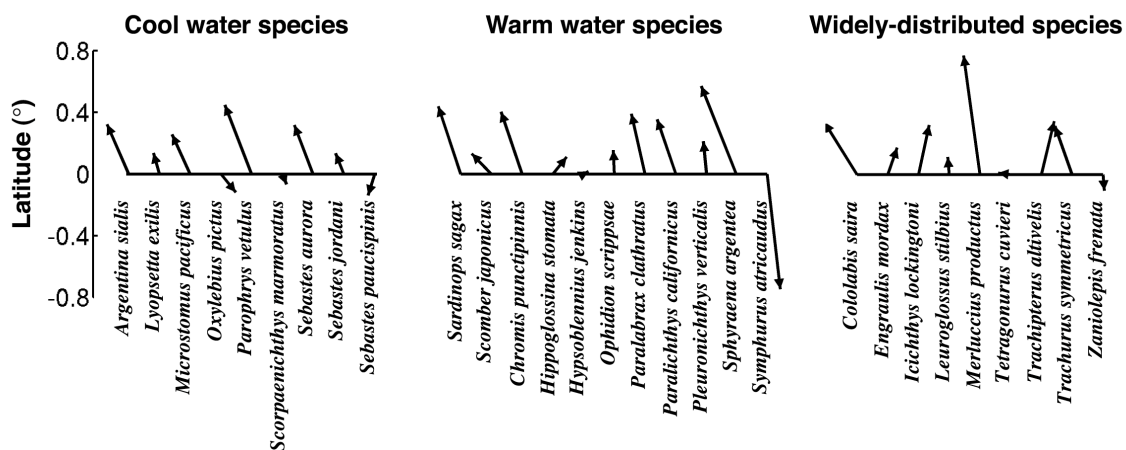


Figure 4.4. Magnitudes and direction of changes in distribution from the cold (1951-1976) to the warm (1977-1998) period for different fish species.

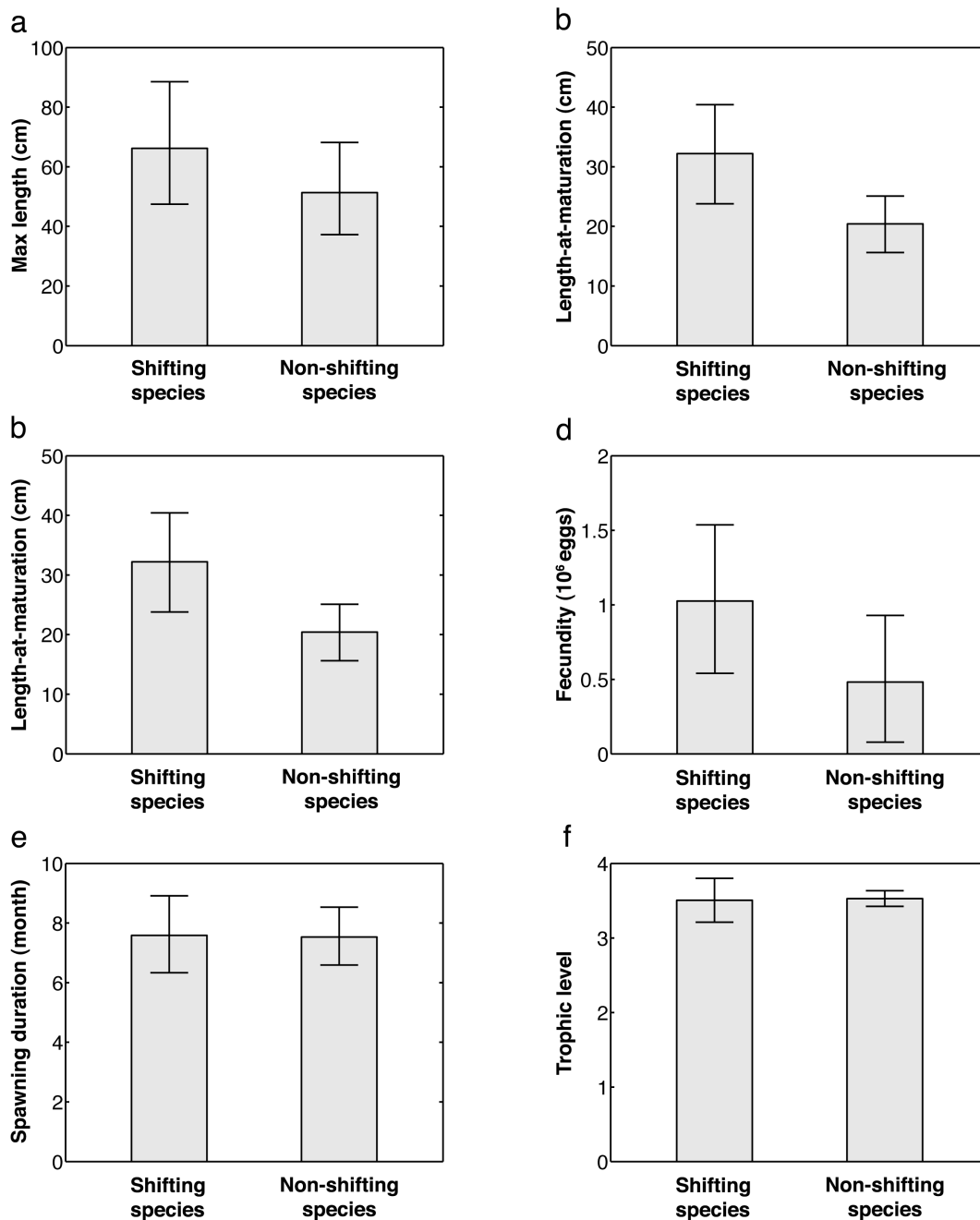


Figure 4.5. Comparison of life history traits of shifting and non-shifting species. Means are shown with 95% bootstrapped confidence limits. No significant difference is found between the shifting and non-shifting species ($p > 0.05$), although the shifting species have higher average maximum length, length-at-maturation, age-at-maturation, and fecundity.

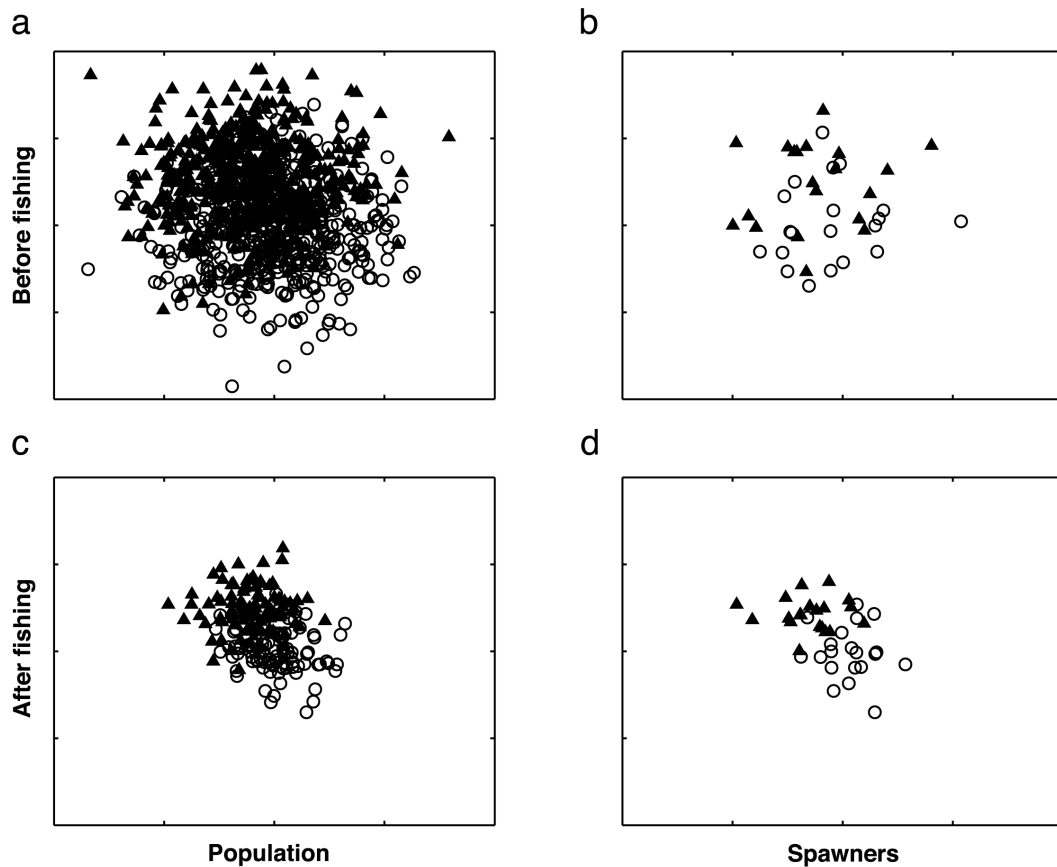


Figure 4.6. A model illustrating the “fishing as a noise filter” hypothesis. The spatial distribution of spawners before (a) and after (c) exploitation is simulated from a bivariate normal distribution with the same centroid. The exploited population (c) contains fewer spawners and shows lower variance in spatial distribution than the unexploited population (a), presumably due to fishery-induced constriction of their spatial distribution when peripheral individuals are removed. The solid triangles and open circles represent two different climatic conditions. In (b) and (d) are randomly sampled 20 points for each climatic condition from (a) and (c) respectively, which mimic spawner locations. A clear separation of fish distributions between two climatic conditions is observed in the exploited (d) but not in the unexploited (b) population. Assuming that each spawning individual will produce thousands of larvae, the signal/noise ratio of the exploited population (d) will be stronger than that of the unexploited population (b), because noise generated by peripheral spawners is removed.

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Appendix

Determining the aggregation index

We calculate the aggregation index for each species using the CalCOFI larval fish data. We use only the stations within a species' principal spawning habitat (i.e. the stations where most larvae are found), determined as follows. First, we select the stations containing at least five non-zero entries in all cruises from 1951 to 2002 (five data points are the minimum number required in order to maintain enough stations to calculate the aggregation index for each species). Second, we estimate the minimal polygon that encompasses these stations (as illustrated in Fig. A4.1) and define this polygon as the principal spawning habitat for the species. To estimate the aggregation index, b , we take the log of both sides of the equation $V = aM^b$: $\log(V) = \log(a) + b \cdot \log(M)$, and fit b using ordinary linear regression (see an example in Fig. A4.2). Note that cruises not within a species' principal spawning period (see text) are excluded in calculating b . The aggregation index of each species is shown in Table A4.1.

Table A4.1. Aggregation index for each species.

	Species	Aggregation index
Exploited	<i>Engraulis mordax</i>	1.823
	<i>Merluccius productus</i>	2.112
	<i>Microstomus pacificus</i>	1.524
	<i>Paralabrax clathratus</i>	1.558
	<i>Paralichthys californicus</i>	1.670
	<i>Parophrys vetulus</i>	1.597
	<i>Sardinops sagax</i>	1.801
	<i>Scomber japonicus</i>	1.771
	<i>Scorpaenichthys marmoratus</i>	1.710
	<i>Sebastes aurora</i>	1.499
	<i>Sebastes paucispinis</i>	1.577
	<i>Sphyraena argentea</i>	1.788
	<i>Trachurus symmetricus</i>	1.757
	Unexploited	<i>Argentina sialis</i>
<i>Chromis punctipinnis</i>		1.690
<i>Cololabis saira</i>		1.407
<i>Hippoglossina stomata</i>		1.665
<i>Hypsoblennius jenkins</i>		1.718
<i>Icichthys lockingtoni</i>		1.436
<i>Leuroglossus stilbius</i>		1.860
<i>Lyopsetta exilis</i>		1.458
<i>Ophidion scrippsae</i>		1.771
<i>Oxylebius pictus</i>		1.665
<i>Pleuronichthys verticalis</i>		1.676
<i>Sebastes jordani</i>		1.770
<i>Symphurus atricaudus</i>		1.646
<i>Tetragonurus cuvieri</i>		1.458
<i>Trachipterus altivelis</i>		1.383
<i>Zaniolepis frenata</i>		1.678

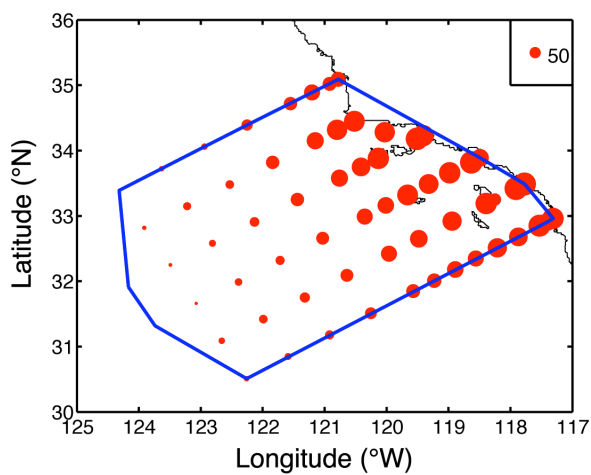


Figure A4.1. An example illustrating distribution of a species' habitat for *Sebastes jordani*. The filled circles represent the total number of samples, and the polygon defines the species' habitat.

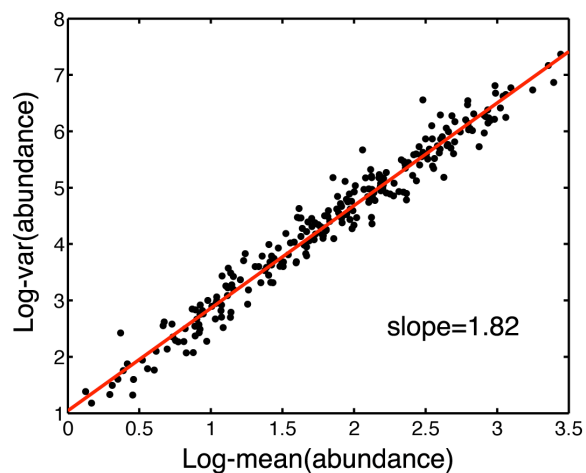


Figure A4.2. An example depicting the mean-variance relationship for *Sebastes jordani*.

The time series of distribution-centers for each coastal and neritic species

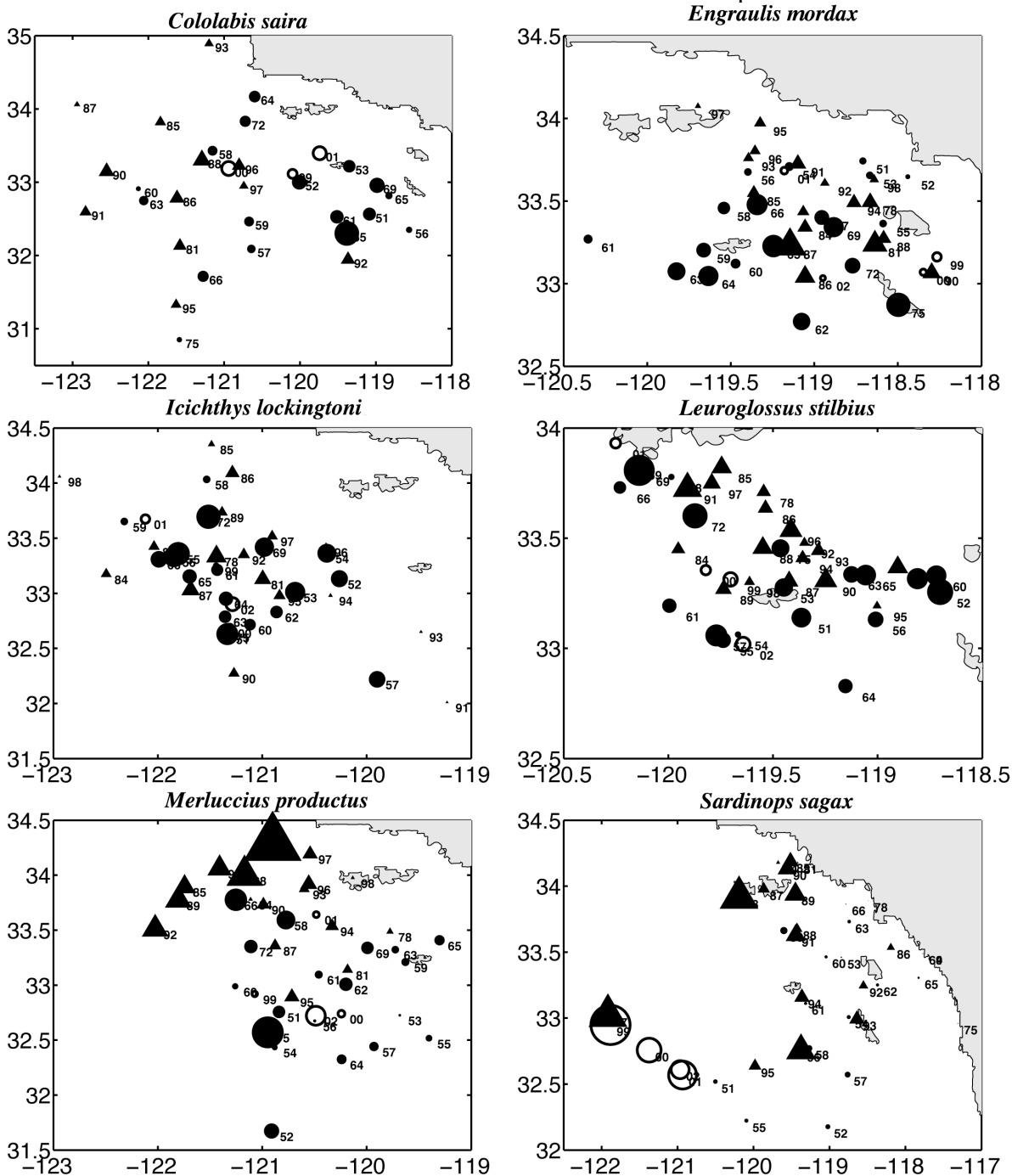


Figure A4.3. The time series of distribution-centers for each coastal and neritic species examined (1951-1976, solid circles; 1977-1998, solid triangles; 1999-2002, open circles). The size of the symbol is proportional to the mean abundance for a given year.

Figure A4.3 continued

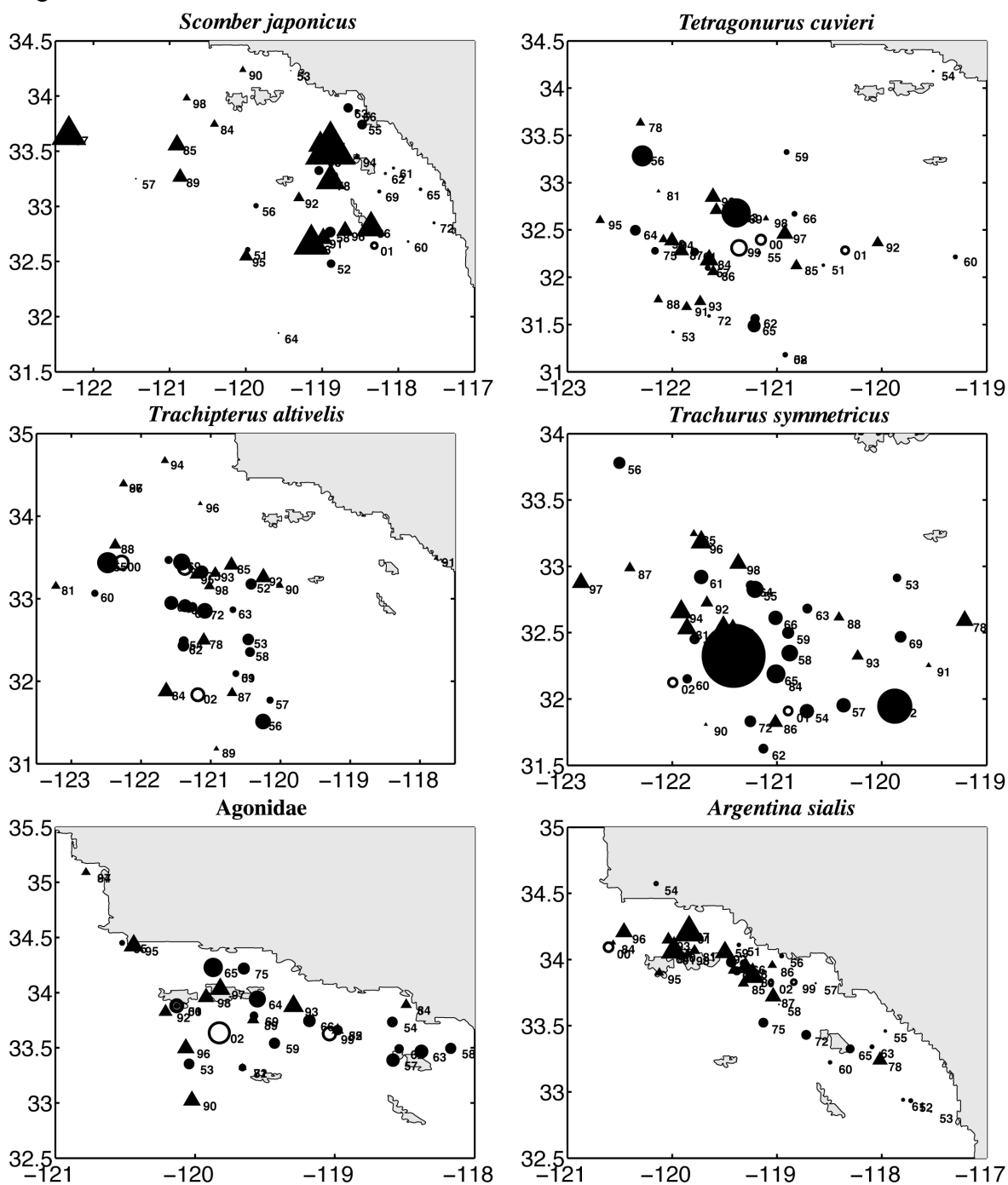


Figure A4.3 continued

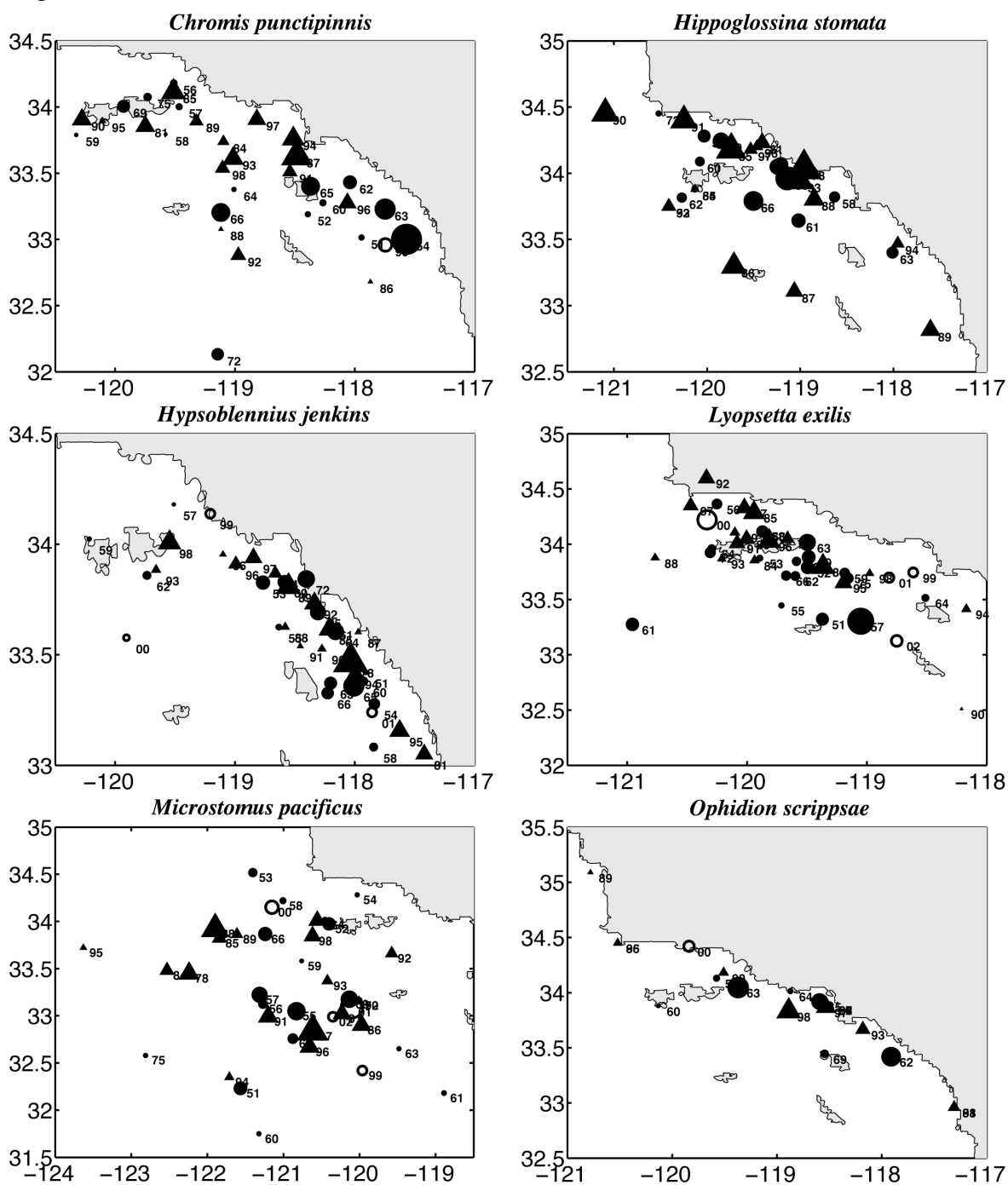


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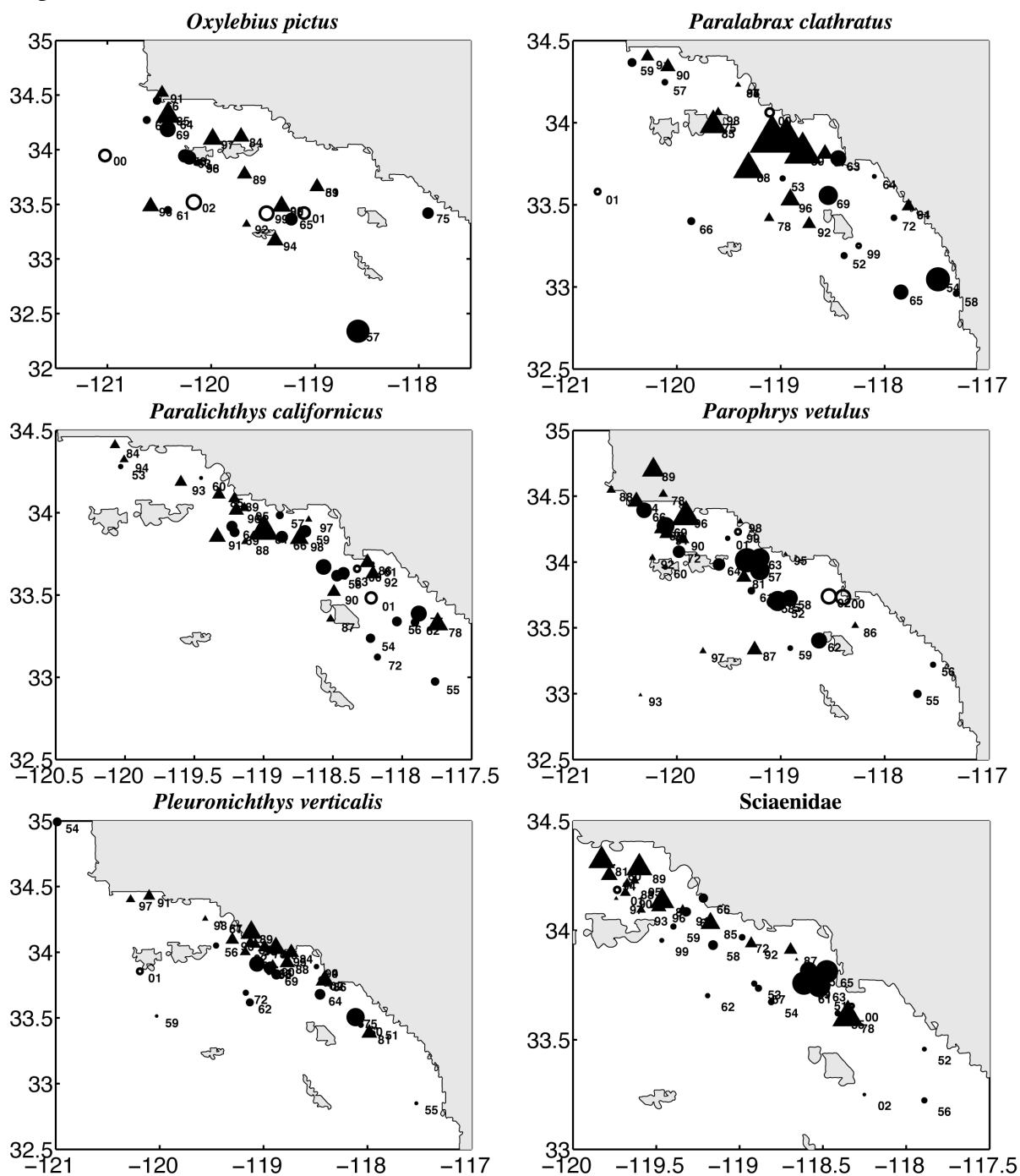


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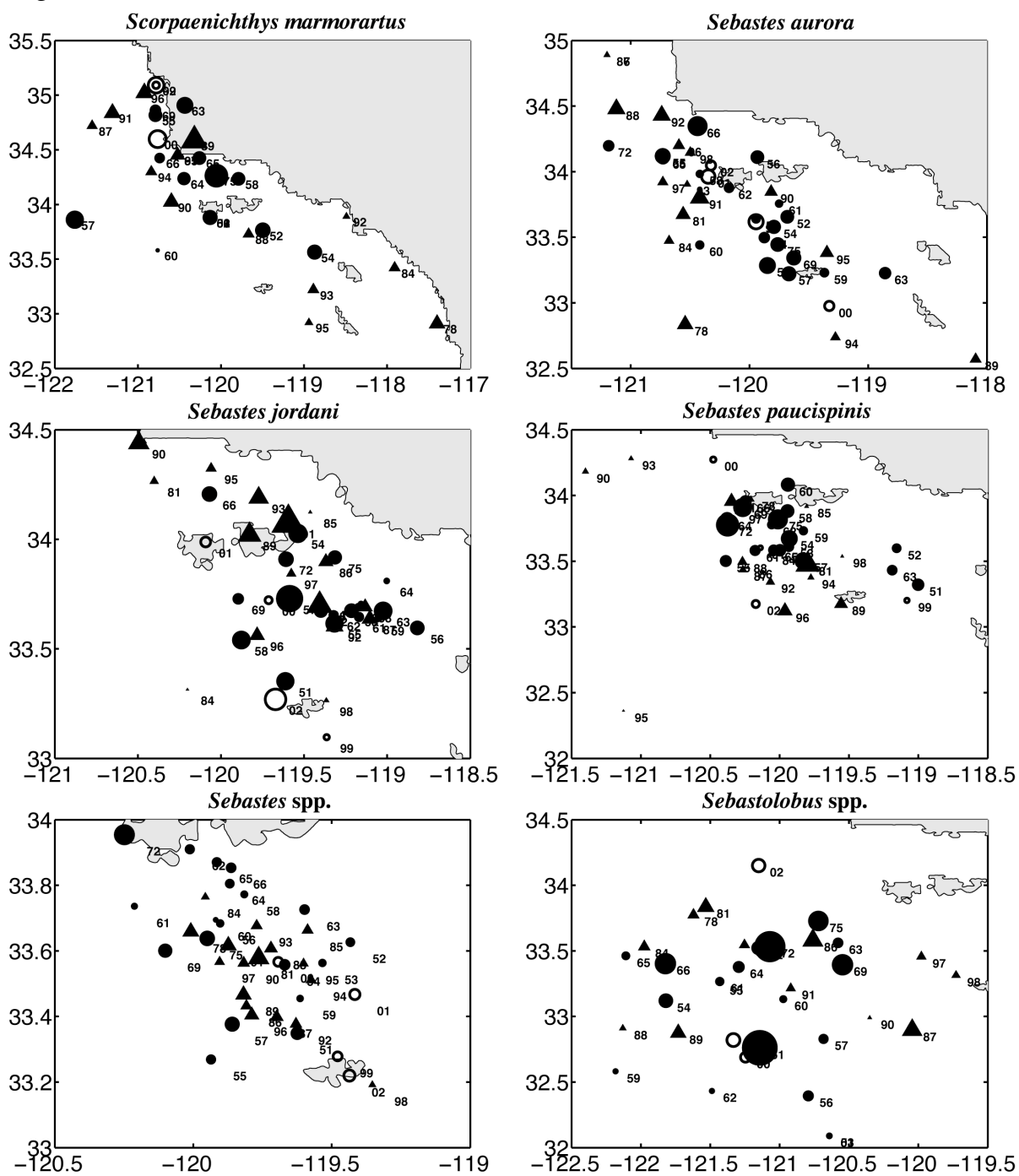
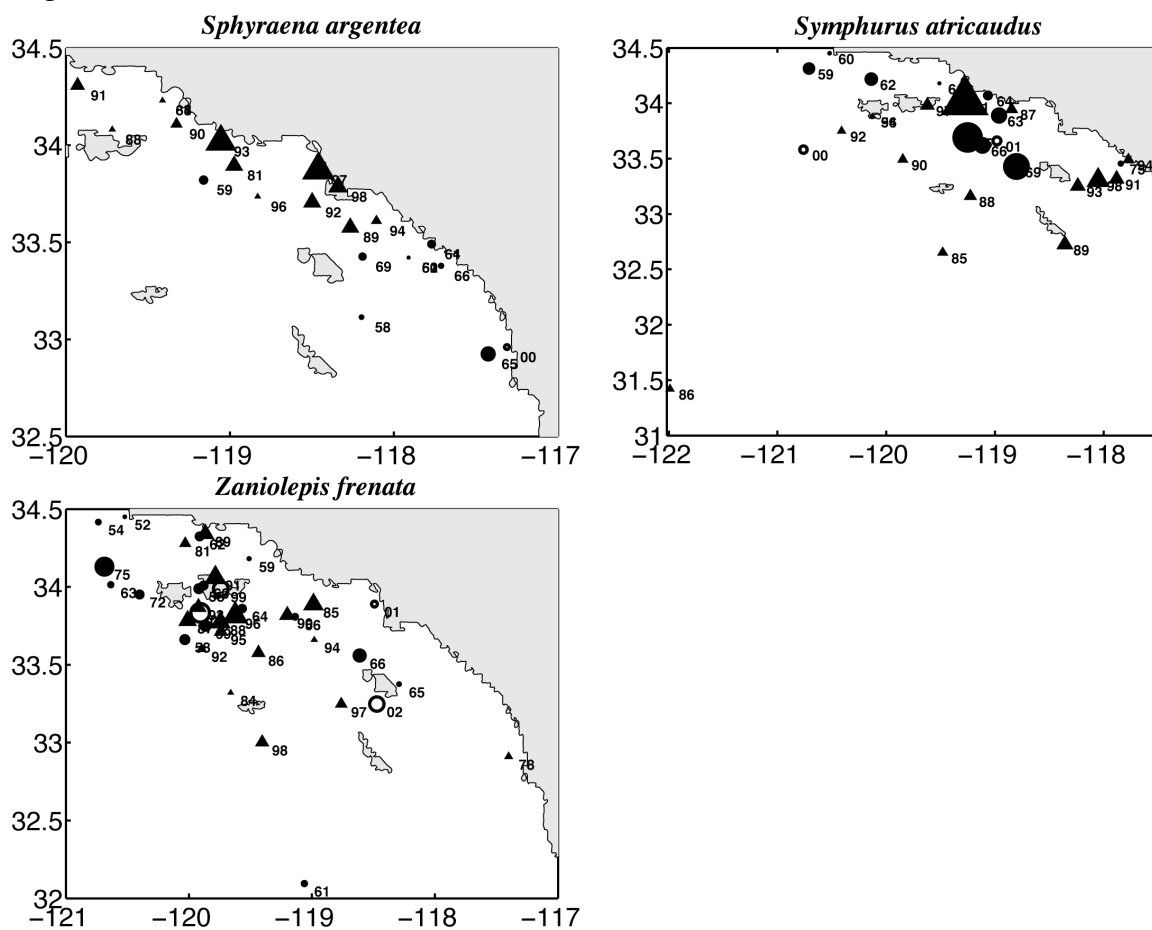


Figure A4.3 continued



Chapter 5. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean

LETTERS

Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean

Chih-hao Hsieh¹, Sarah M. Glaser¹, Andrew J. Lucas¹ & George Sugihara¹

The prospect of rapid dynamic changes in the environment is a pressing concern that has profound management and public policy implications^{1,2}. Worries over sudden climate change and irreversible changes in ecosystems are rooted in the potential that nonlinear systems have for complex and 'pathological' behaviours^{1,2}. Nonlinear behaviours have been shown in model systems³ and in some natural systems⁴⁻⁸, but their occurrence in large-scale marine environments remains controversial^{9,10}. Here we show that time series observations of key physical variables¹¹⁻¹⁴ for the North Pacific Ocean that seem to show these behaviours are not deterministically nonlinear, and are best described as linear stochastic. In contrast, we find that time series for biological variables^{5,15-17} having similar properties exhibit a low-dimensional nonlinear signature. To our knowledge, this is the first direct test for nonlinearity in large-scale physical and biological data for the marine environment. These results address a continuing debate over the origin of rapid shifts in certain key marine observations as coming from essentially stochastic processes or from dominant nonlinear mechanisms^{1,9,10,18-20}. Our measurements suggest that large-scale marine ecosystems are dynamically nonlinear, and as such have the capacity for dramatic change in response to stochastic fluctuations in basin-scale physical states.

Recent effort to characterize the decadal-scale behaviour of North Pacific physical and biological phenomena has centred on the concept of 'regime shifts'¹⁸⁻²¹. These regime shifts appear as quasi-stationary states in measured parameters, separated by periods of rapid transition²⁰. Although attention has been focused on the qualitative phenomenology of these shifts (that is, documenting the appearance of distinct regimes with rapid shifts between them), nowhere in the discussion has their dynamical origin been directly assessed. True regime shifts are not random features of the time series, but are formally associated with the ideas of nonlinear amplification⁷, alternative basins of attraction²², multiple stable states², hysteresis and fold catastrophe³, all of which require the underlying dynamics to be nonlinear in origin. For example, while it is quite clear that major changes occurred in the commonly measured North Pacific abiotic and biotic indices around 1976-77 (for example, patterns of sea surface temperature (SST), fisheries landings data, zooplankton abundance and community composition)^{8,21}, the nature of such changes remains elusive. Are such changes indicative of the operation of nonlinear dynamics or are they features of the data that might arise stochastically?

Some researchers (predominantly physical oceanographers) have suggested that apparent shifts observed in key physical variables are not singular (nonlinear transitional) events but instead represent the normal statistical deviation¹⁰. Insofar as similar features in marine physical observations can be reproduced stochastically as random

events³⁰, it is not necessary to invoke complicated nonlinear mechanisms. In contrast, others (predominantly biologists) have been inclined to see rapid environmental shifts as a fundamentally nonlinear phenomenon with important ecological implications^{8,19}. They view the changes in populations and community structure that occur across putative regimes as being more than passive linear tracking of environmental variability. Rather, they see the rapid shifts in biological variables as an amplified response to environmental change pushing the system into different local basins of attraction or alternative states^{8,20}. Fold catastrophes are a special case for achieving alternative states that raise the possibility of hysteresis or non-symmetrical reversibility of ecosystem states (for example, where population crashes are easier to attain than recoveries). Such instability and irreversibility have become a cautionary tale for environmental management and policy makers, bringing nonlinear phenomena to the fore.

A major weakness of the current debate is its focus on the statistical phenomenology of regime shifts. This approach examines the timing and magnitude of hypothesized shifts in the time series to see if they represent statistically distinct states separated by rapid transitions. Identifying these plateaus and transitions usually involves subjectivity at some level that is difficult to overcome (for example, specifying the timing of shifts). Techniques that promise solutions for this require too much data for the biological time series involved, and many of the approaches assume the existence of only two states of simple but arbitrary assertion. It seems curious that although the phenomenon being debated is a nonlinear one, nowhere in the qualitative phenomenology of these shifts (that is, documenting the appearance of distinct regimes with rapid shifts between them), examined. Insofar as it is the nonlinear basis of the putative shifts that give them their meaning, it should be illuminating to directly measure the observations to determine if they are in fact consistent with the necessary hypothesis of nonlinearity.

Here we test a suite of key physical and biological time series observations for the North Pacific basin. Our aim is not to examine particular events to see if they satisfy the statistical description of a regime; rather, we look at complete time series to see if the variations contained in the whole data series were nonlinear in origin.

We examine these data using established methods for nonlinear time series analysis that involve state space reconstruction with lagged coordinate embeddings (Takens' theorem²⁴). To determine whether a time series reflects linear or nonlinear processes, we compare the out-of-sample forecast skill of a linear model versus an equivalent nonlinear model. This involves a two-step procedure:

(1) we use simplex-projection to identify the best embedding dimension (the number of independent variables required to model the process) (Fig. 1), and (2) we use this embedding in the S-map procedure^{2,8,25,26} to assess the nonlinearity of the time series (Fig. 2). The method of S-maps relies on fitting a series of models

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(from linear to nonlinear) where the degree of nonlinearity is controlled by a local weighting parameter θ . Improved out-of-sample forecast skill with increasingly nonlinear models (larger θ) indicates that the underlying dynamics were themselves nonlinear. The forecast protocol, which involves a blind evaluation off orecast skill, is a rigorous standard that avoids model over-fitting or arbitrary fits to the data (see Methods and Supplementary Information).

We analyse the key time series commonly associated with the North Pacific regime shift debate that have sufficient length for the methods to apply. Physical measurements include indices that collapse North Pacific basin-wide phenomena into single time series (for example, via empirical orthogonal functions), and coastal SST time series (Table 1). The Southern Oscillation Index (SOI)¹³ is widely used for tracking the state of the El Niño/Southern Oscillation, which is the leading source of North Pacific interannual climate variations. The North Pacific Index (NPI)¹² and the Pacific Decadal Oscillation Index (PDO)¹¹ track the leading patterns of North Pacific sea-level pressure and SST variability, respectively. We chose the three longest daily coastal SST time series in the eastern North Pacific (Scripps Pier, Pacific Grove and Farallones Islands)⁴. These time series are highly correlated with basin scale indices while also reflecting strong local dynamics. This collection of data is broadly representative of the large-scale physical state of the North Pacific basin over the twentieth century (Table 1).

Biological data analysed include annual commercial landings for Pacific salmon and trout (1938–2000)⁷, the weekly Scripps Pier diatom record (1920–39)⁸ and the California Cooperative Oceanic Fisheries Investigation (CalCOFI) time series for copepod⁹ and larval fishes⁵ (Table 2). In order to generate time series of sufficient length, composite CalCOFI series were created and then analysed (see Methods). These data have been part of the regime-shift literature, and form a representative collection for this analysis.

All of the major physical indices in Table 1 possess characteristics consistent with high dimensional or stochastic processes (for example, Fig. 1c). This simple characterization is true from weekly to annual timescales. They are well modelled as linear autoregressive (AR) processes of high order, showing no significant forecast

improvement as the S-maps are tuned towards nonlinear solutions (for example, Fig. 2c).

In contrast, all of the biological data in Table 2 (both simple and composites) consistently exhibit nonlinear signatures. These series were best rendered in relatively low embedding dimensions (for example, Fig. 1d), and without exception showed improvement in out-of-sample forecast skill as the S-maps were tuned towards increasingly nonlinear solutions (for example, Fig. 2d). Although not all Δr (change in forecast skill measured as a difference in correlation coefficients) in Table 2 are significant, all show improvement, which is significant for the biological ensemble (binomial probability, 0.001).

The fundamentally different way that regime shifts in the North Pacific have been viewed by physical oceanographers and biological oceanographers coincides with the different character of their respective time series. The physical time series do not appear to arise from low dimensional nonlinear processes, and the irregular features that have been hypothesized to indicate nonlinear deterministic regimes are better characterized as stochastic. At first sight, they do not show the required nonlinearity to allow the interpretation that the shift-like features are more than random events.

It is perhaps not surprising that some of the physical indices appear to be linear-stochastic insofar as they are constructed from linear combinations of observations. As linear aggregates (that is, averages or linear orthogonal functions), these indices may mask possible nonlinearities in individual physical measurements. For example, although station-based barometric pressures in temperate latitudes are highly nonlinear, it has been shown that this nonlinearity can vanish in larger spatial aggregates¹⁴. The dynamics of measles in Great Britain also exhibit this behaviour: individual cities display highly nonlinear infection rates, but these deterministic nonlinear effects appear as noise when the individual cities are aggregated into a single time series for the country as a whole¹⁵. Thus, simply because the PDO, NPI and SOI do not show nonlinear characteristics does

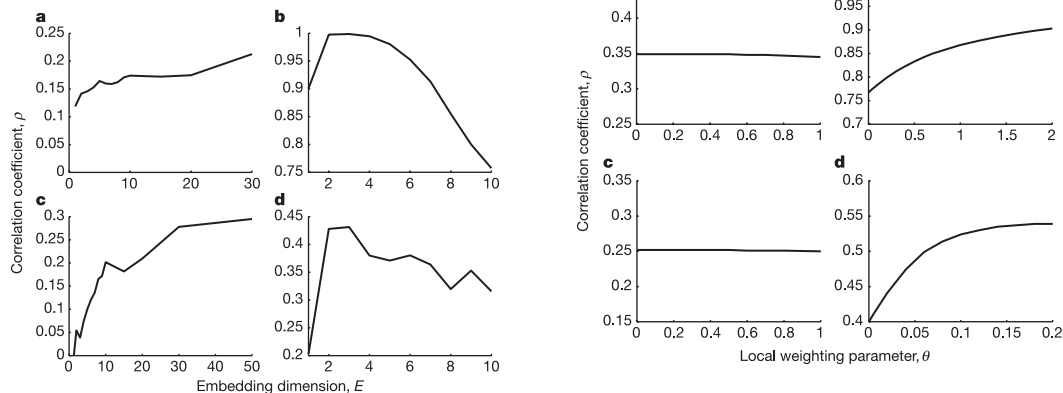


Figure 1 | Examples of the simplex projection method. a, b, Model time series; red noise⁶ (a) and the nonlinear tent map⁶ (b). c, d, Natural time series; Scripps Pier SST (c) and Scripps Pier diatoms (d). Panels b and c both show increasing skill (higher correlation coefficients) at higher embedding dimensions (E), which indicates that the underlying processes are high-dimensional (random for all practical purposes). In contrast, the chaotic tent map (b) and the Scripps Pier diatom time series (d) both show optimal skill (best r) with low-dimensional embeddings.

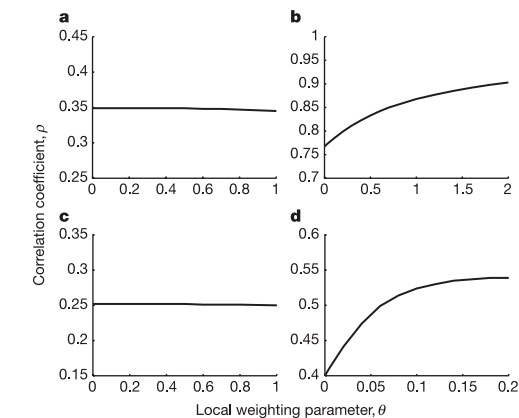


Figure 2 | Examples of the S-map method for the four time series from Fig. 1. The model generated red noise (a) and the Scripps Pier SST time series (c) show no improvement in forecast skill as S-maps are tuned towards increasingly local or nonlinear solutions (by increasing θ). Consequently, these time series do not show any indication of nonlinearity, and display all the hallmarks of a stochastic (high dimensional) linear generating mechanism. In contrast, the chaotic tent map (b) and the Scripps Pier diatom time series (d) both show increased skill as the S-map is tuned towards nonlinear solutions.

Table 1 | Analyses of key North Pacific physical time series

Timescale	Physical data	Best E	Best v	Best r	Dr	Nonlinear?	N	P-value
Weekly	SIO SST	20+	0	0.252	0	No	4,226	1
Monthly	SIO SST	20+	0	0.787	0	No	984	1
Monthly	Pacific Grove SST	20+	0	0.524	0	No	945	1
Monthly	Farallones SST	20+	0	0.486	0	No	764	1
Monthly	PDO	20+	0	0.255	0	No	1,248	1
Monthly	NPI	20+	0	0.636	0	No	1,260	1
Monthly	SOI	20+	0	0.380	0	No	852	1
Quarterly	SIO SST	20+	0	0.958	0	No	328	1
Quarterly	PDO	20+	0	0.376	0	No	416	1
Quarterly	NPI	20+	0	0.497	0	No	420	1
Quarterly	SOI	20+	0	0.328	0	No	284	1
Annual	SIO SST, composite	20	0	0.770	0	No	984	1
Annual	PDO, composite	10	0	0.547	0	No	1,248	1
Annual	NPI, composite	16	0	0.674	0	No	1,260	1
Annual	SOI, composite	13	0	0.640	0	No	852	1

E, embedding dimension; nonlinear tuning parameter. Best r (v_{best}) indicates forecast skill (correlation coefficient), obtained using $Dr \frac{1}{4}$ (r at v_{best}) 2 (r at v_0). A positive Dr measures the difference in forecasting skill of the best nonlinear model (that is, where $v = v_{best}$) as compared to the global linear model (that is, where $v = v_0$). Thus, $Dr \frac{1}{4} r_{best} > r_0$. Data were analysed at various decimations (resolution in time scale). The PDO, NPI and SOI indices have monthly resolution. Quarterly data are averages of those monthly values. Daily coastal SST anomalies (daily data minus the year-day average over the entire record) were averaged to form weekly, monthly and quarterly time series. Owing to the paucity of data at the annual scale, we constructed composite time series by concatenating monthly values (all Januaries, all Februaries, ... all Decembers). These data are best embedded in high dimensions and show no improvement in forecast skill as the S-maps are tuned towards nonlinear solutions. As such, on timescales relevant to the regime shift debate, these physical oceanographic time series are unanimous in showing the hallmarks of linear stochastic generating mechanisms.

not preclude the possibility of nonlinear dynamics operating on finer behaviour did not appear in the North Pacific physical oceanographic data that we tested, this obviously does not preclude the possibility of such behaviour having occurred further into the past or arising in the future. It simply did not occur in the last century, where the alleged shifts are indistinguishable from random events.

More significantly, the various SST records, which are primary (non-aggregated) measurements show the temperature shift phenomenon to be stochastic. That is, even simple SST measurements, which are emblematic of the physical regime shift phenomenon²¹, do not indicate that temperature shifts have low dimensional regime shifts. The relatively skilful out-of-sample forecasts at low nonlinear modes. Rather, they are high dimensional, and consequently they will be more difficult to model mechanistically in a way that replicates the phenomenological forecasting skill of a high degree AR model. This is a fundamental constraint on modelling efforts that we demonstrate empirically here. These findings resonate with the conception of the ocean as a linear red-noise integrator of atmospheric phenomena, a hypothesis first advanced in the 1970s. However, it is clear that not all physical environmental time series are defined by definition, high dimensional and stochastic; for example, analysis of meteorological observations shows strong low dimensional non-linearity in the atmosphere, indicative of the potential for catastrophic climate change²⁸. Furthermore, although true regime shift

Biological time series appear to have dynamics that are fundamentally different from those of the physical variables associated with regime shifts. The relatively skilful out-of-sample forecasts at low embedding dimensions (even in composites) are consistent with the full set of dynamics consists of a low dimensional, nonlinear, noise-free skeleton convolved with stochastic events acting on that skeleton to define the invariant measure²⁸. Thus, the biological populations are not simply tracking the environment. Rather, our results support the hypothesis that ecological dynamics in the oceans can be characterized by nonlinear amplification of stochastic physical forcing by biological processes²⁵. Regardless of interpretation, the biological time series for the North Pacific basin have the necessary signature for regimes to be actual nonlinear features of the data as opposed to randomly generated ones. This result for landings data and larval fish

Table 2 | Analyses of key North Pacific biological time series

Timescale	Biological data	Best E	Best v	Best r	Dr	Nonlinear?	N	P-value
Weekly	Scripps Pier diatom	3	0.3	0.539	0.139*	Yes	830	, 0.01
Monthly	Scripps Pier diatom	4	0.05	0.542	0.083	Yes	206	0.134
Quarterly	CalCOFI coastal larval fish	7	1.6	0.715	0.031*	Yes	3,220	, 0.01
Quarterly	CalCOFI coastal-oceanic larval fish	8	0.6	0.744	0.017	Yes	1,400	0.164
Quarterly	CalCOFI oceanic larval fish	8	1.4	0.678	0.020*	Yes	4,760	0.040
Biannual	CalCOFI copepod	6	1.2	0.677	0.027	Yes	1,736	0.078
Annual	CalCOFI copepod	5	0.4	0.566	0.015	Yes	868	0.322
Annual	CalCOFI coastal larval fish	5	0.6	0.603	0.060*	Yes	805	0.038
Annual	CalCOFI coastal-oceanic larval fish	4	0.2	0.502	0.092	Yes	350	0.063
Annual	CalCOFI oceanic larval fish	7	0.6	0.576	0.017	Yes	1,190	0.273
Annual	Chinook salmon	3	0.4	0.448	0.440*	Yes	63	, 0.01
Annual	Coho salmon	7	0.3	0.656	0.117	Yes	63	0.213
Annual	Chum salmon	4	0.18	0.634	0.767*	Yes	63	, 0.01
Annual	Steelhead trout	3	0.2	0.281	0.272	Yes	63	0.118
Annual	Sockeye salmon	4	0.7	0.484	0.168	Yes	63	0.168
Annual	Composite salmon and trout	4	0.3	0.464	0.078	Yes	315	0.148

Parameters as in Table 1. Monthly diatom data are averages of weekly samples. Quarterly larval fish data represent four cruises per year, and biannual copepod data represent two cruises per year. Annual larval fish data are averages of the quarterly samples, and annual copepod data are averages of biannual samples. Commercial fisheries landing data are annual totals. These population data (described in text) are best embedded in low dimensions, and show improvement in forecast skill as the S-maps are tuned towards increasingly nonlinear solutions. Even where Dr is not significant (asterisk indicates significant at the 0.05 level), the nonlinear model ($v = v_0$) still outperforms the global linear model ($v = v_0$). As such, these biological time series all show the hallmarks of nonlinear generating mechanisms.

abundance should call into question static conceptions of maximum sustainable yield and the use of fixed exploitation quotas for managing commercial fisheries. The potential for rapid and unpredictable shifts in response to environmental stochasticity and human impact supports a precautionary management approach for marine ecosystems.

METHODS

Forecasting techniques. To determine whether a time series reflects linear or nonlinear processes, we compare the out-of-sample forecast skill of a linear model versus an equivalent nonlinear model. This involves using lag coordinate embeddings in a two-step procedure: (1) we use simplex-projection to identify the best embedding dimension, and (2) we use this embedding in the S-map procedure^{8,25} to assess the nonlinearity of the time series. In both cases, model performance is evaluated out-of-sample with the time series divided into equal halves. The first half (library set) is used to build the model, while the second half (prediction set) is reserved to judge the out-of-sample performance of model forecasts.

Simplex projection is a nearest-neighbour forecasting algorithm that involves tracking the forward evolution of nearby points in a lag coordinate embedding. For this study, an exploratory series of embedding dimensions (ranging from 1 to 20 (or higher) are used to evaluate the prediction, and the best is chosen on the basis of prediction skill (Fig. 1). This embedding is then used in the S-map procedure. S-maps are an extension of standard linear autoregressive models in which the coefficients depend on the location of the predictee in an E-dimensional embedding^{7,8,25,26}. (The predictee is the current state of the system from which the prediction is being made.) New coefficients are recalculated by singular value decomposition for each new prediction. In this calculation, the weight given to each vector in the library depends on how close that vector is to the predictee. The extent of this weighting is determined by the parameter v . When $v = 1/4$ we obtain a global (single) linear map, and increasing values of v in the S-map give increasingly local or nonlinear mappings (Fig. 2). A detailed account of these methods is given in Supplementary Information.

All analyses were done both on raw values and on first differenced data to minimize the possibility of masking the nonlinear signal by trivial autocorrelation and to account for possible non-stationary trends in the data. As no qualitative difference was found between analyses, we report here only the more conservative first differenced results.

Composite technique. The CalCOFI data represent one of the most comprehensive oceanographic monitoring programmes in the Pacific. Although hundreds of individual species are sampled, each time series alone is too short to apply the forecasting methods directly, particularly on the annual scale. For example, each larval fish time series contained only 35 annual data points (140 quarterly observations from 1951–2002, with a gap in quarterly collection and identification between 1967 and 1983). To accommodate the individual paucity of points due to these gaps, we generate composite time series based on the known principal distributions of fish species^{5,29}: coastal (23 taxa), coastal-oceanic (10 taxa), and oceanic groups (34 taxa). To minimize the number of gaps in the copepod data, only time series from 1951–66 and 1985–99 were used (for a total of 31 annual data points). Thus, we could only use copepod time series for the 28 taxa that occurred most frequently during the sampling period (at least 20 of 31 years). The copepods are treated as a single equivalence class, given the lack of an unambiguous separation of species by region. However, the results are treated provisionally as separate groups.

Individual time series are normalized to have unit mean and variance, and combined by equivalence class to produce composite time series. This composite S-map procedure involves random combination of time series within each equivalence class (connecting individual time series end-to-end in different order to give different library/predictor combinations). The procedure is repeated 100 times or until all combinations are exhausted, and the average of these results for the CalCOFI data are reported in Table 2. The gaps and seams between time series are accounted for by discarding all vectors that traverse a gap²⁷ or seam²⁶. As a null test for the CalCOFI composites, we applied the procedure to null versions of each of the composite equivalence classes (composite time series with phases randomized) and as expected, obtained consistent linear signatures. By contrast, nonlinear signatures are obtained for the CalCOFI data even when the library and prediction halves are no longer randomly assigned, but are systematically chosen to be most different from each other (that is, with library and prediction sets each consisting of individual species whose time series covary most positively). This yields library sets of similar species that are most dissimilar to the prediction sets. In addition to the fact that all of the data in this study are

normalized and first differenced, this additional test eliminates the remote

possibility of producing a nonlinear artefact by combining heterogeneous data sets symmetrically into the library and prediction sets. Physical variables required compositing at the annual scale only. The library vector comprises all January values from the first half of the time series (here 1900–50) and so forth until December. The prediction vector is likewise constructed from the second half of the time series (here 1951–2000).

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Chapter 6: Synthesis and perspectives: Coping with uncertainty and nonlinearity in fisheries management

Introduction

Considerable evidence indicates that many marine commercially-important fish populations have declined in the past several decades due to overfishing (Hutchings 2000; Watson and Pauly 2001; Garcia et al. 2003; Myers and Worm 2003). Not only industrial fisheries but also recreational fisheries have had substantial impacts on fish populations (Coleman et al. 2004). Moreover, the over-fishing problem has extended from coastal to deep-sea fishes (Devine et al. 2006; Morato et al. 2006). However, another line of evidence suggests that the declines in some of the fish populations might be caused by climate change (Lluch-Belda et al. 1992; Mantua et al. 1997; Finney et al. 2002; Beaugrand et al. 2003; Chavez et al. 2003). Whether the declines of the fish populations are caused by fishing or climate is actively debated. Clearly, fishing and climate can act in concert to cause the declines of fish populations (Jacobson et al. 2001), and this was a fundamental lesson from the CalCOFI program (Ohman and Venrick 2003). Therefore, it is important to examine fishing effects on the dynamics of fish populations within the context of a changing environment; that is, to examine the interactive affects of fishing and climate. More importantly, we need to investigate how to manage fisheries in a changing climate.

Traditionally, fisheries management is largely based on the assumption of a stock-recruitment relationship (a production function relating recruits to spawners) (Hilborn and Walters 1992). This assumption forms the belief that fisheries are sustainable as long as fisheries removals do not exceed surplus production (excess of reproduction and growth over natural mortality) of a fish population (Graham 1935; Ricker 1954; Schaefer

1954; Beverton and Holt 1957). Unfortunately, the production function estimated from data is usually unreliable due to enormous error associated with the data (see Fig. 5.1 for examples presented in Myers 2002). In addition, since fish live in a changing environment, their production function might vary according to environmental conditions (Rothschild et al. 2005). Thus, the assumption of a single production function (assumption of an equilibrium state) might not reflect true fish population dynamics in nature.

This problem points to the importance of taking environmental conditions into consideration in fisheries management. Traditionally, fish population responses to environmental forcing are studied with linear statistical methods (e.g. correlation and regression analyses) (Beamish et al. 1997; Mantua et al. 1997; Klyashtorin 2001; Beamish et al. 2004; Erzini 2005; Harley et al. 2006). The underlying assumption is that the populations track environmental variables in a smooth and continuous way. However, this may be the exception rather than the rule (Hsieh and Ohman in press). Among the 33 coastal and coastal-oceanic fish species investigated in our analyses (Chapter 2), only 6 showed a significant linear correlation with the environmental variables examined (which included 2 local and 3 large-scale indices). These results are consistent with the recent finding that the underlying dynamics of marine biological populations is most likely nonlinear (Chapter 5). These marine fish populations have great potential to show abrupt shifts in response to environmental forcing (Hsieh et al. 2005). In addition to environmental variation, fishing might reduce resilience of fish populations, and therefore, make them more prone to abrupt shifts (Scheffer et al. 2001).

Below, I discuss two lines of investigation that may be useful for fisheries management in a changing environment: 1) avoid fishery-induced reduction in resilience of fish populations facing environmental variations, and 2) thinking nonlinearly in fisheries.

Avoid fishing-induced reduction in resilience of fish populations facing environmental variation

The problem that fishing may reduce resilience of exploited populations had been recognized almost four decades ago (Murphy 1967). Using a simple population model of Pacific sardine, Murphy (1967) showed that the fish population would be more sensitive to environmental variability if their spawning frequency were reduced, presumably due to fishery-induced age truncation. Recent studies suggest that truncating the age-structure may have strong impacts on exploited fish populations, including reduced ability to respond to environmental variability, increased sensitivity to environmental changes, and increased recruitment variability (Murawski et al. 2001; Berkeley et al. 2004; Hutchings and Reynolds 2004; Ottersen et al. 2006). These effects are inter-related but point to the same problem: reducing resilience of fish populations facing environmental variation (i.e., undermining their bet-hedging capability).

The results of my studies indicate that the aforementioned fishing effects may have happened in the southern California fish populations. By comparing exploited to unexploited species living in the same environment, I show that exploited species exhibit higher long-term variability in the abundance than unexploited species, after accounting for life history effects (Chapter 3). Evidence from the age (length) composition in catch

data suggests that the elevated variability is very likely caused by fishery-induced truncation of the age-structure. My results in Chapter 4 indicate that exploited species are more responsive to climate than unexploited species. In addition to truncated age-structure, the increased sensitivity of exploited species may be caused by a fishery-induced constriction of spatial distribution of fish populations (MacCall 1990). These results strongly support Murphy's (1967) foresight that fishing may reduce the resilience of fish populations.

These findings suggest the importance of maternal effects on the recruitment of larval fishes. To investigate how general maternal effects may influence early life history traits of fish, and thus future potential larval survival, I examined data compiled from the literature (Appendix). I examine studies that test the effects of female age and size on timing of spawning, egg quantity, egg quality, egg development, hatching rate, and larval survival. (Studies on paternal effects are sparse and are not included here). Only studies that include factors of both female age and size are considered. For a given species, if the conclusion is consistent in all studies, the results are reported only once, and if the conclusion is inconsistent in different studies, both positive and negative results are reported. These studies are from marine (25 species), freshwater (21 species), anadromous and amphidromous (5 species) iteroparous fishes. Semelparous fishes (e.g. salmon) are excluded because age effects cannot be examined.

Maternal age (size) has significant positive effects on fish early life history traits and potential larval survival for most marine (Fig. 5.2A) and freshwater (Fig. 5.2C) species. Maternal effects are not clear in anadromous and amphidromous species (Fig.

5.2B). For all species combined (Fig. 5.2D), maternal age (size) has significant positive effects on at least one of those traits for 46 out of 51 species (Binomial test, $p < 0.001$). These statistics indicate that maternal effects on larval survival are likely a general phenomenon in fishes. Thus, the impacts of fishery-induced age truncation of fish populations are likely widespread.

In order to sustain fish populations, fisheries management should conserve their age-structure in addition to viable spawning biomass. At least three strategies can be implemented to conserve the age-structure: first, regulate upper and lower limits of fish size in harvesting (Berkeley et al. 2004); second, using marine reserves to protect older and larger fish individuals (Roberts et al. 2001); and third, include an age-based biological reference point in the management plans (consider age-specific egg production, egg viability, and spawning duration in stock assessments). The third approach has been suggested in managing the stock of Atlantic cod (Murawski et al. 2001). Determining limits of fish size in harvesting and an age-based biological reference point require further studies of reproduction biology of targeted species.

In addition to age truncation, fishing may alter the spatial structure of fish populations (MacCall 1990; Berkeley et al. 2004), which also undermines the bet-hedging ability of fish populations. Therefore, it will be useful to monitor the spawning locations by observing spatial distribution of eggs. This can be achieved by a continuous underway fish egg sampler (CUFES) (Checkley et al. 1997). CUFES has been used effectively to study the egg distributions of Pacific sardine and northern anchovy in the central and southern California region (Checkley et al. 2000).

Think nonlinearly in fisheries

Nonlinear responses of fish populations to environmental forcing need to be considered in fisheries management. Consider two classic hypotheses that attempted to explain recruitment variability of marine fish populations: the larval retention hypothesis (Hjort 1914; Sinclair et al. 1984) and the match/mismatch hypothesis (Cushing 1969; Cushing 1990). The larval retention hypothesis states that fish recruitment variability may be determined by the loss of larvae through advective processes (e.g. strong upwelling and associated strong Ekman transport may reduce larval survival by sweeping them away from the suitable nursery ground), and emphasizes the importance of physical processes. The match/mismatch hypothesis states that high larval survival is determined by the phase relationship between the timing of spawning and plankton production, and emphasizes the importance of biological processes. Obviously, each of these hypotheses alone does not provide sound explanations to fish recruitment variability. Rather, it is highly possible that good recruitment can only happen when both conditions are met.

Fluctuations of fish populations are likely caused by nonlinear combination of several variables. For example, Dixon et al. (1999) found that episodic fluctuations in larval supply of a reef fish species are caused by multiplicative effects of physical-biological interactions: lunar phase of egg release, physical transport experienced by mature larvae, and turbulence levels on first-feeding larvae. Importantly, this was done in a forecast fashion rather than fitting data with models of any sort. Although their approach is data intensive and may not be applicable with normal fisheries data, their

idea provides a framework of using a nonlinear dynamic approach in fisheries management. For example, it is possible to identify combinations of biological and physical variables (certain conditions or thresholds) that lead to high or low fish population sizes. Thus, these variables may form indicators for management. This approach requires no assumption of any specific model or an equilibrium state. More importantly, this approach fulfills one of the most important goals in fisheries management, to predict the status of the fish stock.

Conclusions

Fishing may decrease the resilience of fish populations facing environmental variation and thus increase population variability. The reduced resilience is likely associated with fishery-induced changes in the age-size structure of fish populations. To sustain fish populations in an uncertain environment, a precautionary management approach is warranted not only because of normal uncertainties associated with estimates of stock size but also because fishing magnifies population variability. This is particularly important because fish populations are likely governed by nonlinear dynamics and thus have the potential for rapid shifts (Hsieh et al. 2005), and the reduced resilience due to fishing may cause the fish populations to be more vulnerable to shifts (Scheffer et al. 2001). To avoid collapse, fisheries management should not only pay attention to uncertainty in management but also implement strategies to prevent magnifying uncertainty, for example, extending from maintaining total viable biomass to conserving the age structure of fish populations. In addition, nonlinear phenomena

originating from biological populations themselves, or nonlinear combinations of physical factors, or interaction of biological and physical variables, need to be kept in mind in fisheries management. Nonlinear forecast methods may be a step forward to sound management.

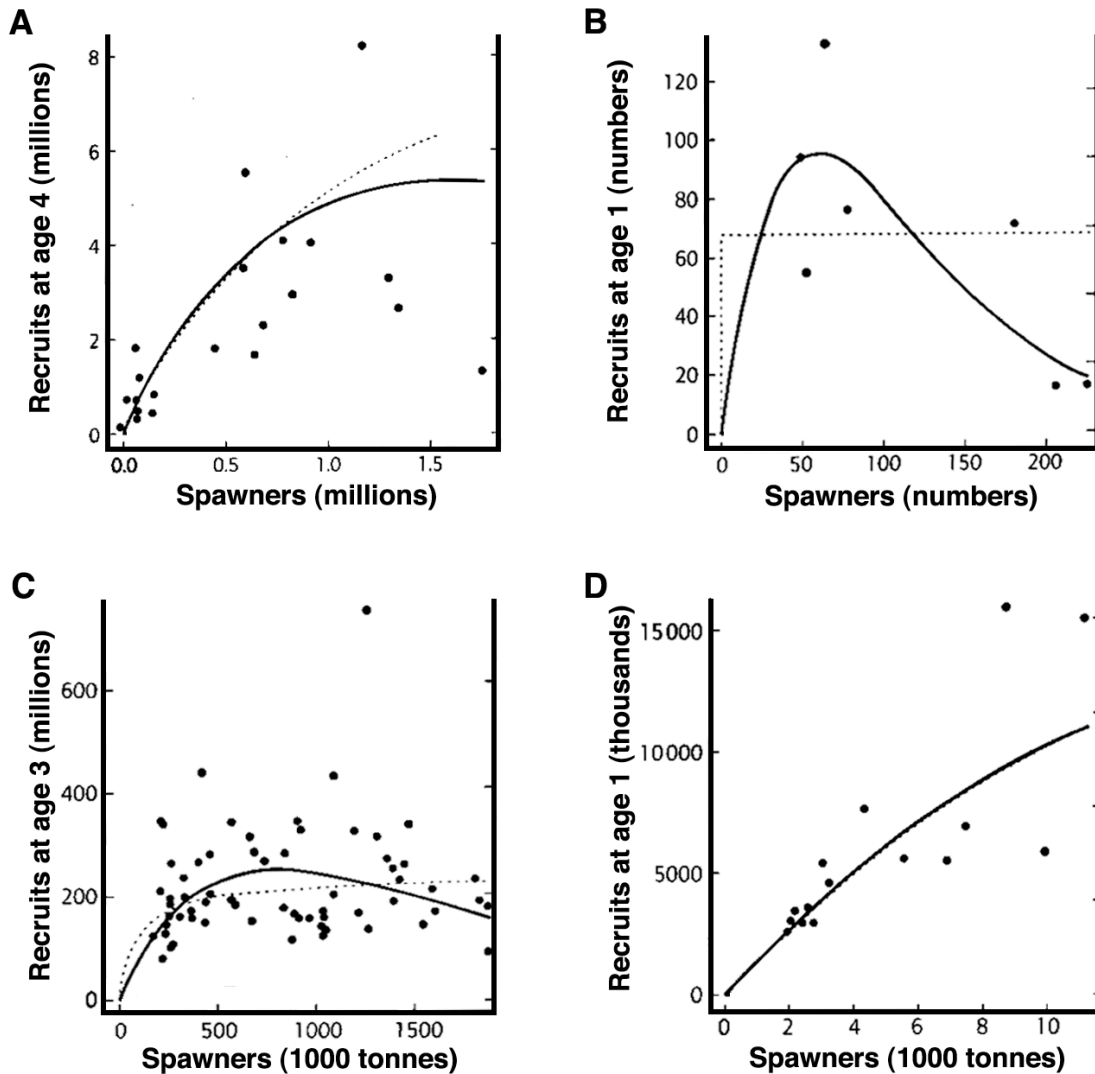


Figure 6.1. Spawner-recruitment data for (A) sockeye salmon from the Adams River, (B) brook trout from lakes in the Sierra Nevada Mountains, (C) cod from Iceland, and (D) striped bass from the east coast of North America (modified from Myers, 2002). The solid and dotted lines are the maximum likelihood fit for Ricker and Beverton-Holt models, respectively. In (D), both Ricker and Beverton-Holt models give similar estimates.

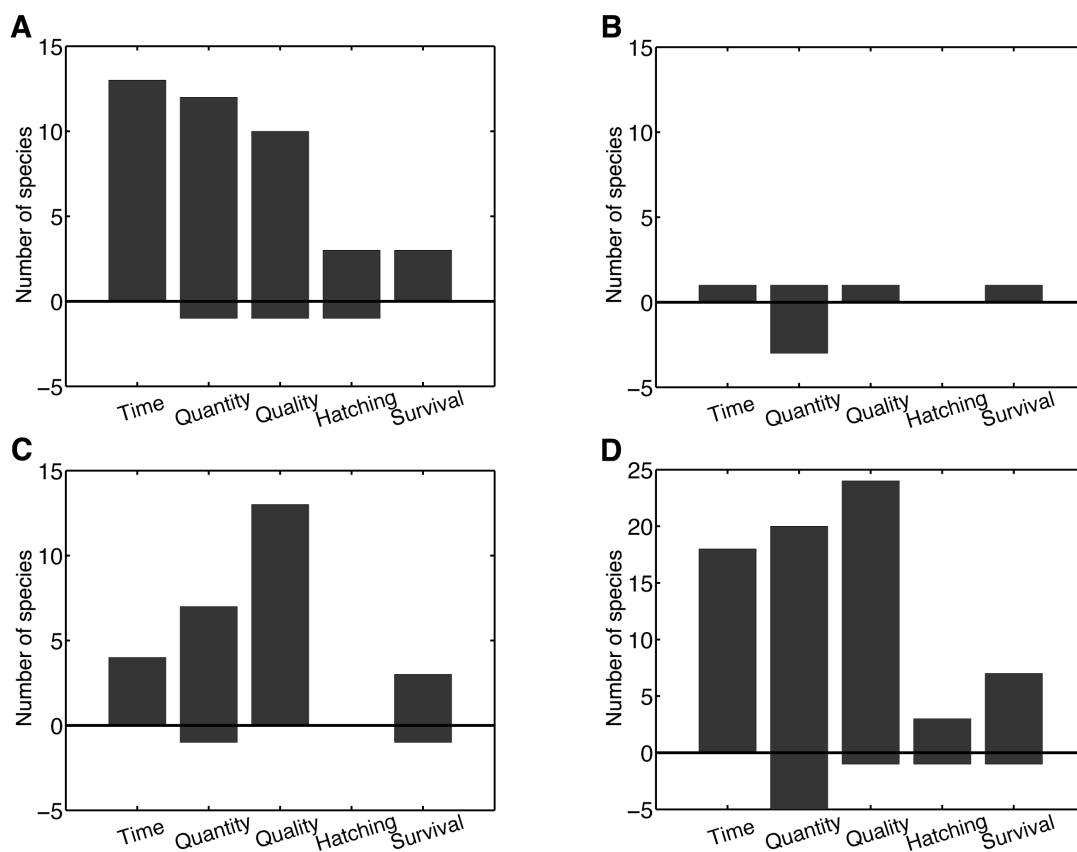


Figure 6.2. Frequency of maternal effects on fish early life history traits for (A) marine species, (B) anadromous and amphidromous species, (C) freshwater species, and (D) all species combined. Time, timing of spawning; Quantity, egg quantity; Quality, egg quality; Hatching, egg development or hatching rate; Survival, larval survival. Positive values indicate positive effects and negative values indicate negative or no effects.

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Appendix

Table A6.1. Literature used to examine maternal effects on larval recruitment. + indicates positive maternal influences, - indicates negative or no effects.

Species	Environment	Spawning time	Egg quantity	Egg quality	Egg development and hatching rate	Larval survivorship
<i>Acanthopagrus schlegeli</i> (black porgy)	Marine			-(Huang et al. 1999)		
<i>Clupea harengus</i> (Atlantic herring)	Marine	+(Lambert 1990)		+(Hempel and Blaxter 1967)		
<i>Cynoscion regalis</i> (weakfish)	Marine	+(Shepherd and Grimes 1984)				
<i>Engraulis mordax</i> (northern anchovy)	Marine	+(Parrish et al. 1986)	+(Parrish et al. 1986)			
<i>Gardus morhua</i> (Atlantic cod)	Marine	+(Trippel 1998)	+(Trippel 1998)	+(Trippel 1998)	+(Trippel 1998)	+(Marteinsdottir and Steinarsson 1998)
<i>Glyptocephalus cynoglossus</i> (witch flounder)	Marine		+(Bowering 1978)			
<i>Hemiramphus balao</i> (balao halfbeak)	Marine	+(Berkeley and Houde 1978)				
<i>Hemiramphus brasiliensis</i> (ballyhoo)	Marine	+(Berkeley and Houde 1978)				
<i>Hippoglossoides platessoides</i> (American plaice)	Marine	+(Morgan 2003)				
<i>Lutjanus synagris</i> (lan snapper)	Marine		+(Manickchand-Das 1987)			
<i>Mallotus villosus</i> (capelin)	Marine			+(Chambers et al. 1989)		
<i>Melanogrammus aeglefinus</i> (haddock)	Marine	+(Wright and Gibb 2005)		+(Hislop 1988)		

Table A6.1 continued

<i>Menidia menidia</i> (Atlantic silverside)	Marine						+(Bengston et al. 1987)
<i>Merluccius Merluccius</i> (hake)	Marine						+(Tsimenidis and Papaconstantinou 1985)
<i>Morone saxatilis</i> (striped bass)	Marine	+(Secor 2000)	+(Olsen and Rulifson 1992)	+(Montelone and Houde 1990)	+(Zastrow et al. 1989)		+(Montelone and Houde 1990)
<i>Pleuronectes ferrugineus</i> (yellowtail flounder)	Marine			+(Benoit and Pepin 1999)	+(Benoit and Pepin 1999)		
<i>Pseudopleuronectes americanus</i> (winter flounder)	Marine	+(Buckley et al. 1991)		+(Buckley et al. 1991)	-(Buckley et al. 1991)		
<i>Pleuronectes platessa</i> (plaice)	Marine	+(Simpson 1959)	-(Rijnsdorp 1991)				
<i>Sardinops sagax</i> (Pacific sardine)	Marine		+(Murphy 1967)				
<i>Scomber scombrus</i> (Atlantic mackerel)	Marine	+(Eltink 1987)	+(Morse 1980)	+(Dawson 1986)			
<i>Scophthalmus maximus</i> (turbot)	Marine						+(McEvoy and McEvoy 1991)
<i>Thunnus maccoyii</i> (southern bluefin tuna)	Marine		+(Thorogood 1986)				
<i>Sebastes entomelas</i> (widow rockfish)	Marine		+(Boehlert et al. 1982)				
<i>Sebastes melanops</i> (black rockfish)	Marine	+(Bobko and Berkeley 2004)	+(Bobko and Berkeley 2004)				+(Berkeley et al. 2004)
<i>Sprattus sprattus</i> (European sprat)	Marine		+(Avsar and Bingel 1994)				
<i>Alosa aestivalis</i> (blueback herring)	Anadromous		-(Jessop 1993)				

Table A6.1 continued

<i>Alosa pseudoharengus</i> (alewife)	Anadromous		-(Jessop 1993)		
<i>Atherina boyeri</i> (Big-scale sand smelt)	Amphidromous	+(Creech 1992)			
<i>Coregonus autumnalis</i> (arctic cisco)	Anadromous		-(Wilson and Pitcher 1984)		
<i>Rhinogobius</i> sp. (Rhinogobius goby)	Amphidromous		+(Tamada and Iwata 2005)	+(Tamada and Iwata 2005)	+(Tamada and Iwata 2005)
<i>Ambloplites rupestris</i> (rock bass)	Freshwater	+(Noltie and Keenleyside 1987)			
<i>Abramis brama</i> (Carp bream)	Freshwater			+(Kalmer 1992)	
<i>Brachymystax lenok</i> (Lenok)	Freshwater			+(Kalmer 1992)	
<i>Catostomus commersoni</i> (white sucker)	Freshwater	+(Green et al. 1966)		+(Johnson 1997)	
<i>Chondrostoma nasus</i> (Sneep)	Freshwater			+(Keckeis et al. 2000)	-(Keckeis et al. 2000)
<i>Coregonus albula</i> (vendace)	Freshwater			+(Kalmer 1992)	
<i>Cottus baird</i> (mottled sculpin)	Freshwater		+(Grossman et al. 2002)	+(Grossman et al. 2002)	
<i>Cyprinus carpio</i> (Common carp)	Freshwater			+(Kalmer 1992)	+(Kalmer 1992)
<i>Leuciscus cephalus</i> (European chub)	Freshwater		-(Libosvarsky 1979)		
<i>Morone chrysops</i> (white bass)	Freshwater		+(Baglin and Hill 1977)		
<i>Micropterus dolomieu</i> (Smallmouth bass)	Freshwater	+(Ridgway et al. 1991)	+(Vogele 1981)		

Table A6.1 continued

<i>Micropterus salmoides</i> (Largemouth bass)	Freshwater	+(Miranda and Muncy 1987)		
<i>Perca flavescens</i> (yellow perch)	Freshwater		+(Heyer et al. 2001)	+(Heyer et al. 2001)
<i>Pomoxis annularis</i> (white crappie)	Freshwater			+(Bunnell et al. 2005)
<i>Rutilus rubilio</i>	Freshwater		+(Daoulas and Kattoulas 1985)	
<i>Rutilus lemmingii</i> (pardilla)	Freshwater		+(Velasco et al. 1990)	+(Velasco et al. 1990)
<i>Rutilus rubilio</i>	Freshwater		+(Daoulas and Kattoulas 1985)	
<i>Rutilus rutilus</i> (roach)	Freshwater			+(Kalmer 1992)
<i>Salvelinus fontinalis</i> (brook trout)	Freshwater			+(Kalmer 1992) +(Hutchings 1991)
<i>Stizostedion vitreum</i> (walleye)	Freshwater			+(Thomas and Leggett 2002)
<i>Thymallus arcticus</i> (arctic grayling)	Freshwater			+(Kalmer 1992)

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