Fishing-induced shifts in a Pacific ocean fish assemblage

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Abstract

The US Pacific Coast has been largely free of fishery collapses that have occurred elsewhere, but the situation appears to be changing. Here, we show results from the first systematic study of demersal fishes along the US Pacific Coast. Using data from a quarter-century long, fishery-independent, coast-wide trawl survey, we document fundamental shifts in the demersal fish assemblage along the US west coast. Average fish size, across a diversity of species, has declined 45% in 21 years There have been major shifts in the constituent species of the assemblage, with some species achieving annual population growth rates (i.e. λ) of > 1.1, while others have declined with λ's of < 0.90. λ appears to be function of life history and habitat interacting with historical fishing pressure. The results of our analyses are disquieting as they raise the possibility that fishing-induced phase shifts in fish communities may affect the recovery of fishes, even after the implementation of severe fishing restrictions.

Introduction

With the exception of the collapse of the sardine fishery in 1950's, the West Coast of the United States has been largely free of the spectacular collapses of marine fishes that have occurred elsewhere. However, this envious position appears to be changing (Parker *et al.*2000) . Indeed, concern over a number of rockfishes (*Sebastes* spp.) along the US Pacific coast has resulted in the implementation of large-scale fishery closures along the U.S. Pacific continental shelf, with an expected annual cost to coastal communities of about $60 million (PFMC 2003). Although it is clear that many groundfish species along the US Pacific Coast are in trouble, there is generally a lack of information on the status of west coast fishes--the National Marine Fisheries Service (NMFS) has formally assessed the status of only 20% of the 82 groundfishes it manages (NMFS 2003).

For the majority of groundfish species, gathering the data required to evaluate the status of unassessed populations using traditional methodology is a daunting task that is unlikely to be accomplished in the foreseeable future. Even so, the demise of fisheries around the globe (Baum *et al.*2003; Myers & Worm 2003; Christensen *et al.*2003) demands that we evaluate the status of all exploited fishes—not just those few for which detailed data are available. Here, we present an analysis of the status of the demersal fish assemblage along the US Pacific coast. We used simple count data from fishery-independent trawls to examine general trends in numbers and weight of a 31 fish species along the continental shelf. While not as detailed as traditional stock assessments, our approach allows us to move beyond the few species that have been formally assessed to provide the first synthetic study of the status of the groundfish assemblage of the US west coast.

Methods

Trawl surveys of Pacific Northwest groundfish were performed triennially on the continental shelf by NMFS from 1977-2001. We focused on 16 species of rockfish, 8 species of flatfish, and 7 species of elasmobranchs (sharks, ratfish and rays) that appear regularly within the survey. Sampling has occurred during summer at depths of 55-366 m and from 34ºN to the US-Canada border with tow locations assigned using a stratified design (latitude and depth). For each 30 minute trawl, the distance traveled as well as the total weight and count for each species is recorded. By dividing the total weight by the count, we estimated the average weight of individuals for each species.

Because the latitudes and depths surveyed differed somewhat from year to year, we subsampled the available trawls for each year to create a sample with a standardized distribution of latitudes/depths across all years. We randomly selected 188 trawls that were stratified into 25 latitude and depth combinations from the total available trawls for each year (Table 1). The number of fish caught in this subset represents a standardized index of population size for each year. The index is weighted towards some depths and latitudes that have been well surveyed over the 27 years. When more samples were available for a given latitude/depth combination, the available trawls within a latitude/depth category were repeatedly subsampled using monte carlo and the mean count used. The amount of sampling error in the standardized count for each species and year was estimated by bootstrapping the data.

From the time series of standardized counts, a long-term population growth rate (λ) was estimated. In this case, the point estimate of $\ln(\lambda)$ was

$$\frac{1}{18}\ln\left(\frac{N(1995)+N(1998)+N(2001)}{N(1977)+N(1980)+N(1983)}\right).$$

Using the running sum of counts gives more robust estimates when there is significant sampling error or cycles within the data (Holmes 2001). Confidence intervals on λ were estimated using the estimate of sampling error in each count and the amount of process error in the times series data:

$$\sigma^2_{\ln(\lambda)} = \frac{1}{18} pe^2 + \frac{1}{18^2}\frac{1}{3}\left(\frac{se^2(1995)+se^2(1998)+se^2(2001)}{3} + \frac{se^2(1977)+se^2(1980)+se^2(1983)}{3}\right)$$

where $se(t)$ is the sampling error estimate for the log mean count at year t from the trawl data (2) and pe is the estimate of the process error:

$$pe^2 = \frac{1}{3}\mathrm{var}(N_{t+3} / N_t) - 2\,\mathrm{average}(se^2)$$

where N_t is the mean log count in year t. The procedure for estimating confidence intervals on λ from stochastic population trajectories is given by Holmes and Fagan (2002).

We then examined how λ differed among species in different taxa, with different size of maturities, habitat preferences and histories of exploitation. To examine the association of λ with size of maturity (cf., Jennings *et al.* 1998)we performed an ANCOVA in which taxa was the main effect and the length of maturity (Love *et al.* 2002; Froese & Pauly 2002) was a covariate. To determine if species using different macrohabitats varied in their average population growth rates, we focused on rockfishes (flatfish and elasmobranches examined here exhibit little variability in macrohabitat use, McCain 1998). Some rockfishes tend to associate with hard substrate while others show a relationship to soft substrate (Love *et al.* 2002; McCain 1998). We thus performed an ANOVA with posthoc contrasts using A matrices (Wilkinson *et al.* 1996) to test the hypothesis of that λ did not differ between rockfish with different habitat associations or between soft-sediment rockfish and flatfish or elasmobranches.

To investigate the association of λ with harvest, we used an ANCOVA in which taxa (flatfish or rockfish) was the main effect and the total catch from 1981-2001 (log transformed) was a covariate. Elasmobranches were excluded from the analysis because catch data were not available. We performed an additional analysis in which we used a standardized measure of catch as a covariate in our model. To standardize catch, we divided the mean catch from 1980-2001 by the average catch-per-unit-effort estimated from the NMFS trawl surveys. Prior to calculating this ratio, catch-per-unit-effort was adjusted by multiplying the mean catch by the catchability of species. For flatfishes, catchabilities were available for petrale sole (0.30) and dover sole (0.26) from stock assessments. For other flatfishes we used 0.28, the average of the two available catchabilities. For rockfishes, we used catchabilities estimated by Millar and Methot (2002) for bocaccio (0.25), canary (0.28), chilipepper (0.15), widow (0.05) and yellowtail rockfishes (0.25). For other rockfishes associated with hard substrate, we used 0.22, the average of the preceding species excluding widow rockfish (which have a low catchability because of their unusual behavior). For rockfishes associated with soft substrate we used 0.28, the same value we used for flatfishes.

Results

Trends in population size differed dramatically among the taxa we examined. The average λ for flatfishes and elasmobranchs was 1.09 and 1.05, respectively (Fig. 1). This corresponds to an average 8-fold increase in flatfish numbers between 1977 and 2001 and an average 3-fold increase in elasmobranchs. Although there was variability in population growth rates among species, the increasing trend was consistent across these two taxa: none of the 8 flatfish showed a declining trend and only 1 of the 7 elasmobranchs had a declining trend (Fig. 1). While numbers of flatfishes and elasmobranchs are increasing, the average weight of individual fish has been declining since 1980 (Fig 2.; we used 1980 for comparison because not all fish were weighed in 1977). The average flatfish caught in 2001 weighed 57% of average flatfish caught in 1980. Similarly, the average elasmobranch was 67% of average 1980 weight.

In contrast to the numbers of flatfish and elasmobranchs, we observed an average decline of 22% in rockfishes from 1977-2001, yielding a λ of 0.99. However, there was tremendous variability among the rockfish species (Fig. 1). Many of the smaller rockfishes such as greenstriped (*Sebastes elongatus*), splitnose (*S. diploproa*), and chilipepper (*S. goodei*) showed increases of > 6% per year while most of the larger species showed significant declines averaging from 5 to even 17% per year. Two rockfish species in particular, canary (*S. pinniger*) and boccacio (*S. paucispinis*), experienced 85% and 96% declines, respectively, from 1977. Overall, 9 of the 16 rockfishes we investigated had an estimated λ of < 1.0. Additionally, like the other taxa we examined, the average weight of rockfish has declined--average rockfish weight in 2001 was 35% lower than in 1980 (Fig. 2).

We observed the expected negative relationship between fishing pressure and growth rates: species that experienced heavier fishing pressure showed generally lower growth rates relative to species within the same taxa that experienced less fishing pressure ($\lambda = 1.162 + \log(\text{total catch})*(-0.015)$; $p = 0.028$). The nature of this relationship was similar for flatfish and rockfish; however, the amount of variance in λ explained by catch varied between taxa. In flatfishes, more than 65% of the variation in population growth was explained by the total catch, while in rockfish < 7% of the variation was explained. When we standardized catches by expressing catch as a proportion of the standing biomass, the results were qualitatively the same—λ was negatively related to standardized catch ($P = 0.023$). As with the total catch, this amount of variation in λ explained by standardized catches was much more in flatfish (60%) than in rockfish (13%).

In flatfishes and rockfishes there was an inverse relationship between the rate of population growth and length of maturity ($F_{1,23} = 8.45, P = 0.008$), and the slopes of the regression lines were similar for the two taxa ($P = 0.41$; Fig. 3). In flatfishes, 52.8% of the variance in λ was explained by length at maturity, and in rockfishes 31.5% of the variance in λ was explained by length at maturity. In contrast, no association between population growth and length at maturity was evident in elasmobranches (Figure 3).

Population growth rates were also related to the primary habitat used by rockfish species. Population growth rates of populations of rockfish that typically occur on hard substrates averaged 0.96 with a minimum of 0.83 and a maximum of 1.06. In contrast, λ for rockfishes associated with soft substrates were significantly greater, averaging 1.028 with a range from 0.98 to 1.08 ($P = 0.03$, posthoc contrasts using A matrices (Wilkinson *et al.* 1996)). The average λ of soft-substrate rockfish was not different than the λ we observed in elasmobranches ($P = 0.52$), but was significantly lower than the λ we report for flatfishes ($P = 0.02$).

Discussion

Our analyses suggest that over the last 25 years there have been fundamental changes in the fish assemblage on the continental shelf of the US Pacific coast. Flatfish and elasmobranch abundances have increased dramatically. Similarly, populations of small rockfishes associated with soft substrate have expanded at rapid rates. In contrast, populations of large rockfishes associated with hard-substrate habitats have fallen at alarming rates. Indeed, in 1977, rockfish comprised more than 60% of the fish captured in the survey, while flatfishes were 34% of the catch. However, by 2001 rockfish declined to 17% of the catch and flatfish had increased to nearly 80%. Historically, overfishing has been viewed as declines of single species (Rosenberg 2003), and it would be a simple matter to summarize our results as the sum of all the changes we report. However, such an approach to fisheries problems ignores that communities are more than just a group of populations. Fishing affects more than the trends of individual species; it influences the state of the entire community (Steneck *et al.* 2002). In this paper we have not only shown changes in populations, we have also documented a shift in the fish assemblage from hard-substrate to soft-substrate rockfishes and from rockfish to flatfish domination. Fishing has clearly affected not only individual populations, but it has also disturbed the entire community.

While we might expect the reduction of fishing effort either through traditional fisheries management or marine protected areas to restore dwindling rockfish populations, such expectations ignore potential interactions among members of the fish community (Zabel *et al.* 2003). Because even smaller species of rockfish may be able to consume or outcompete recruiting juveniles of larger species (e.g.,Shulman *et al.* 1983)) and since many rockfishes overlap greatly in their patterns of resource use (Love *et al.* 2002), it is possible that fishing is a disturbance that has shifted the rockfish assemblage to an alternate stable state. As a result, even severe reductions in fishing may not result in recovery of overfished larger species. Similarly, in the Northeastern Atlantic, Dulvy and colleages (2000) showed a shift in skate assemblages harvested over a 40 year period. Large-bodied species with long generation times have declined while smaller species have increased in abundance. Dulvy et al. argued that larger skates historically outcompeted smaller species for food, and that overfishing of larger species released the small skates from competition. Fogarty and Murawski (1998) also suggested that competitive release resulted in a phase-shift from teleost-dominated to elasmobranch-dominated communities in the Northwestern Atlantic.

Fishing certainly does have effects on fish populations –in terms of population growth rates, life history and size (Jennings & Kaiser 1998). Such population-level effects, however, may just be the beginning of broader systemic changes induced by fishing (Mangel & Levin. 2004). Whether community-level interactions ultimately prevent the recovery of imperiled rockfish populations remains to be seen, but it is clear that the demersal fish community of US west coast is now very different than it was only 25 years ago.

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Table 1. For each year of the trawl survey we selected 188 trawls that were stratified into 25 latitude/depth combinations. Numbers below represent the number of trawl samples used each year from a given latitude and depth.

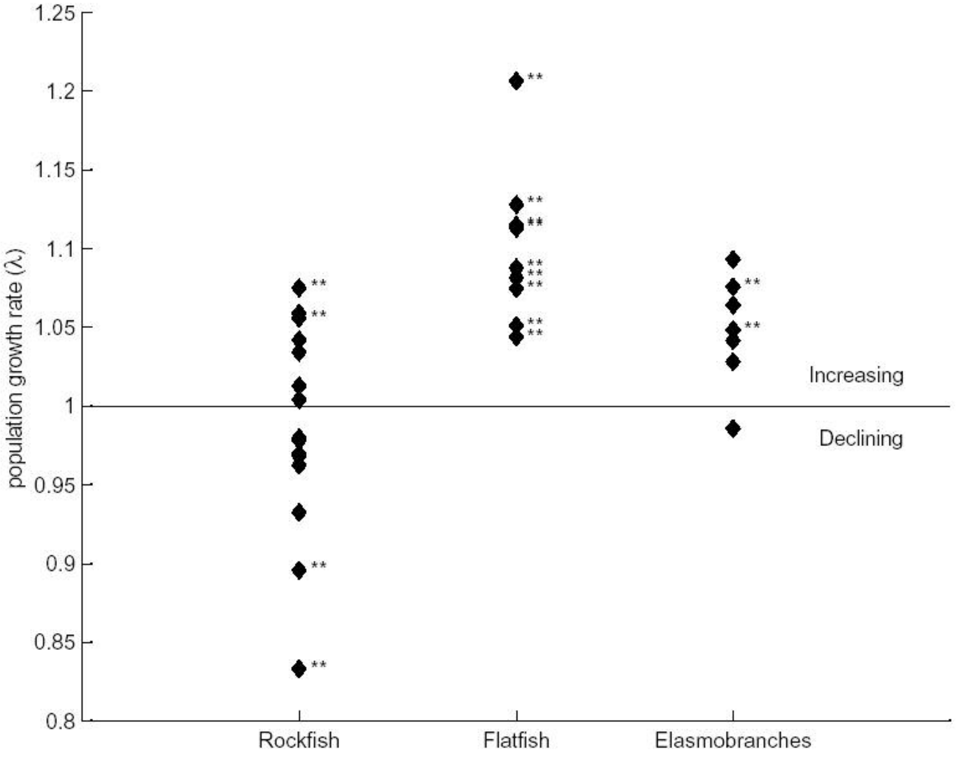
Latitude/Depth	55-117.2m	117.2-179.4m	179.4-241.6m	241.6-303.8m	303.8-366m
36-38.5ºN	19	4	2	0	1
38.5-41ºN	5	10	1	2	1
41-43.4ºN	4	7	3	1	0
43.4-45.9ºN	17	30	9	3	4
45.9-48.3ºN	19	35	10	1	0

Figure legends

Figure 1. Estimated long-term yearly population growth rate (λ) for Pacific northwest rockfish, flatfish, and elasmobranches. λ greater than 1.0 indicates an increasing population while a λ less than 1.0 indicates a declining population. Estimates that are significantly different than 1.0 ($p < 0.05$) are indicated by **. Species-specific λ's are provided in the supplementary information.

Figure 2. Mean annual weight of individual rockfish, flatfish and elasmobranches relative to 1980. Each species within a taxonomic group were considered a datum. Error bars are 1 SE. Species-specific patterns are provided in the supplementary information.

Figure 3. The relationship between length (cm) of maturity with long-term population growth rate (λ) for Pacific northwest rockfish, flatfish and elasmobranches. In flatfishes, 52.8% of the variance in λ was explained by length at maturity, and in rockfishes 31.5% of the variance in λ was explained by length at maturity. In contrast, no association between population growth and length at maturity was evident in elasmobranches.


1.25
1.2
1.15
1.1
1.05
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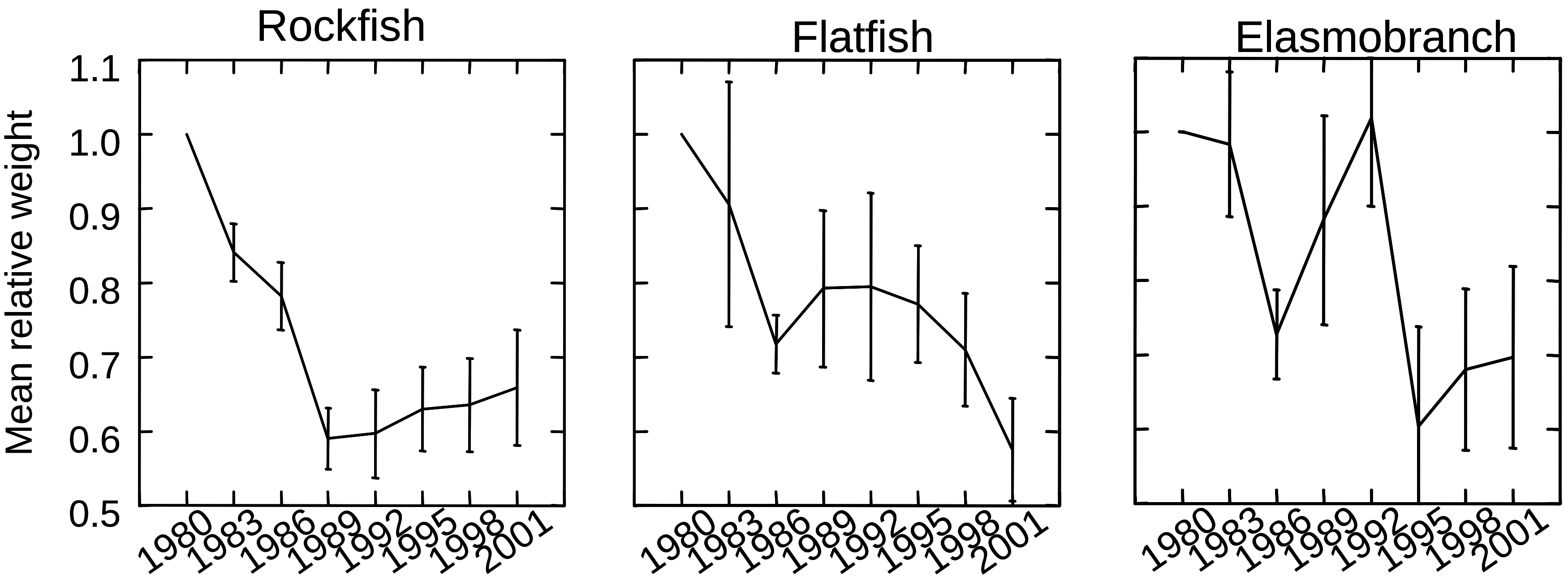
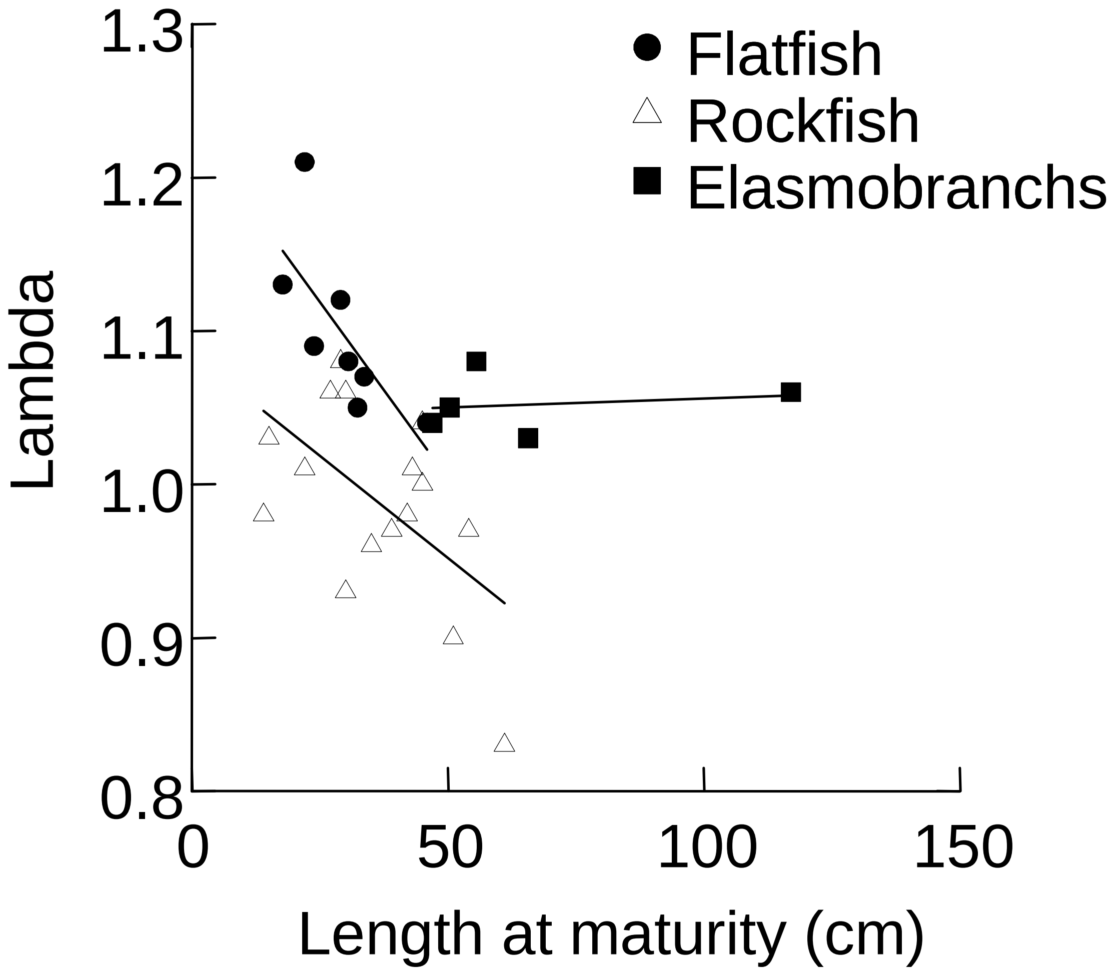
0.8
population growth rate (λ)
Increasing
Declining
Rockfish
Flatfish
Elasmobranches
**


Rockfish
Flatfish
Elasmobranch
Mean relative weight
1.1
1.0
0.9
0.8
0.7
0.6
0.5
1980
1983
1986
1989
1992
1995
1998
2001


● Flatfish
△ Rockfish
■ Elasmobranchs
Lambda
1.3
1.2
1.1
1.0
0.9
0.8
0
50
100
150
Length at maturity (cm)

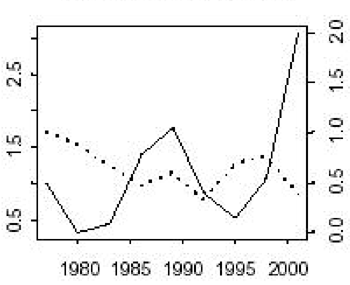
Supplemental Information

Table S1. The population growth rates (λ) with 95% confidence intervals for each of the 31 focal species in the study.

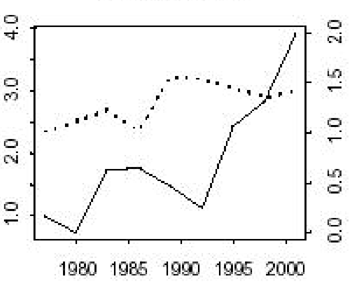
Taxonomic group	Common Name	Scientific Name	λ	Lower 95% CI	Upper 95% CI
Flatfish					
	Arrowtooth Flounder	*Atheresthes stomias*	1.04	1.01	1.08
	Petrale Sole	*Eopsetta jordani*	1.05	1.02	1.08
	Rex Sole	*Glyptocephalus zachirus*	1.07	1.06	1.09
	Rock Sole	*Pleuronectes bilineatus*	1.08	0.92	1.27
	English Sole	*Pleuronectes vetulus*	1.09	1.06	1.12
	Flathead Sole	*Hippoglossoides elassodon*	1.12	1.07	1.17
	Pacific Sandab	*Citharichths sordidus*	1.13	1.09	1.16
	Curlfin Sole	*Pleuronectes decurrens*	1.21	1.11	1.31
Rockfish	Bocaccio	*Sebastes paucispinis*	0.83	0.79	0.88
	Canary rockfish	*Sebastes pinniger*	0.9	0.84	0.96
	Sharpchin rockfish	*Sebastes zacentrus*	0.93	0.84	1.03
	Pacific Ocean Perch	*Sebastes alutus*	0.96	0.9	1.03
	Darkblotched rockfish	*Sebastes crameri*	0.97	0.93	1.01
	Yelloweye rockfish	*Sebastes ruberrimus*	0.97	0.89	1.06
	Redbanded rockfish	*Sebastes babcocki*	0.98	0.94	1.02
	Shortbelly rockfish	*Sebastes jordani*	0.98	0.88	1.09
	Yellowtail rockfish	*Sebastes flavidus*	1	0.93	1.08
	Rosethorn rockfish	*Sebastes helvomaculatus*	1.01	0.95	1.08
	Widow rockfish	*Sebastes entomelas*	1.01	0.94	1.1
	Stripetail rockfish	*Sebastes saxicola*	1.03	0.96	1.11
	Rougheye rockfish	*Sebastes aleutianus*	1.04	0.96	1.14
	Chilipepper rockfish	*Sebastes goodei*	1.06	0.98	1.14
	Splitnose rockfish	*Sebastes diploproa*	1.06	1	1.11
	Greenstriped rockfish	*Sebastes elongatus*	1.08	1.02	1.13
Elasmobranch	Pacific Electric Ray	*Torpedo californica*	0.99	0.93	1.04
	Spiny Dogfish	*Squalus acanthias*	1.03	0.96	1.1
	Bering Skate	*Bathyraja interrupta*	1.04	1	1.09
	Spotted Ratfish	*Hydrolagus colliei*	1.05	1	1.1
	Big Skate	*Raja binoculata*	1.06	0.98	1.15
	Longnose Skate	*Raja rhina*	1.08	1.04	1.11
	Brown Catshark	*Apristurus brunneus*	1.09	0.98	1.22

Figure Legend

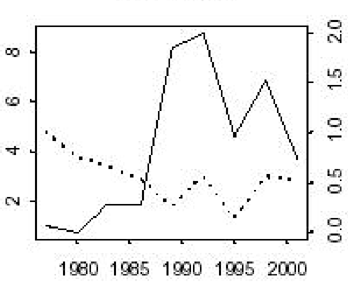
Figure S1. The standardized index counts (solid line) and weight relative to 1980 (dashed line) for each of the focal species in the study.



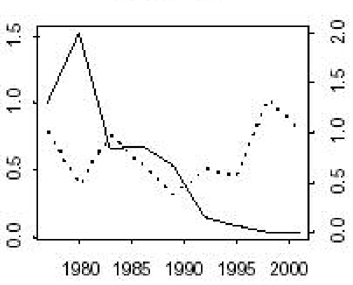
Arrowtooth Flounder



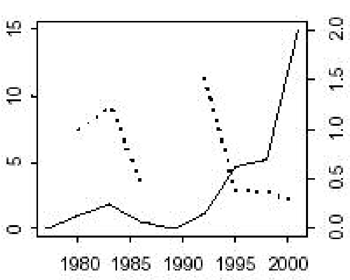
Bering Skate



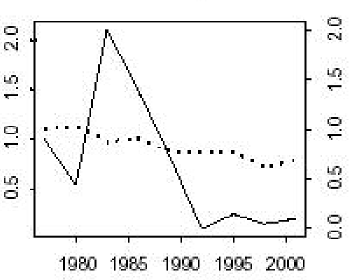
Big Skate



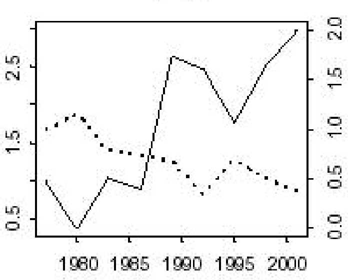
Bocaccio



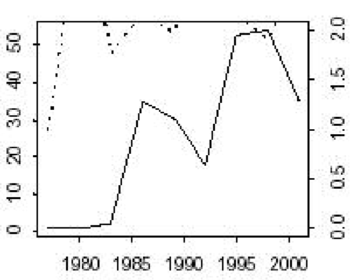
Brown Catshark



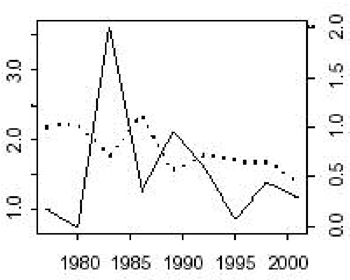
Canary



Chilipepper



Curlfin Sole



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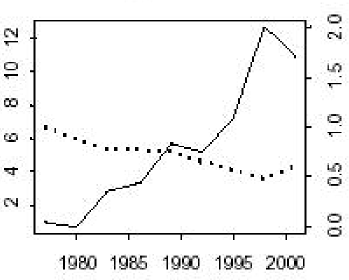
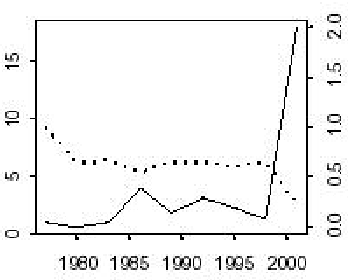
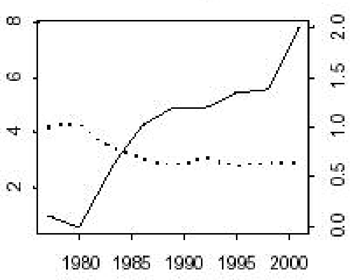


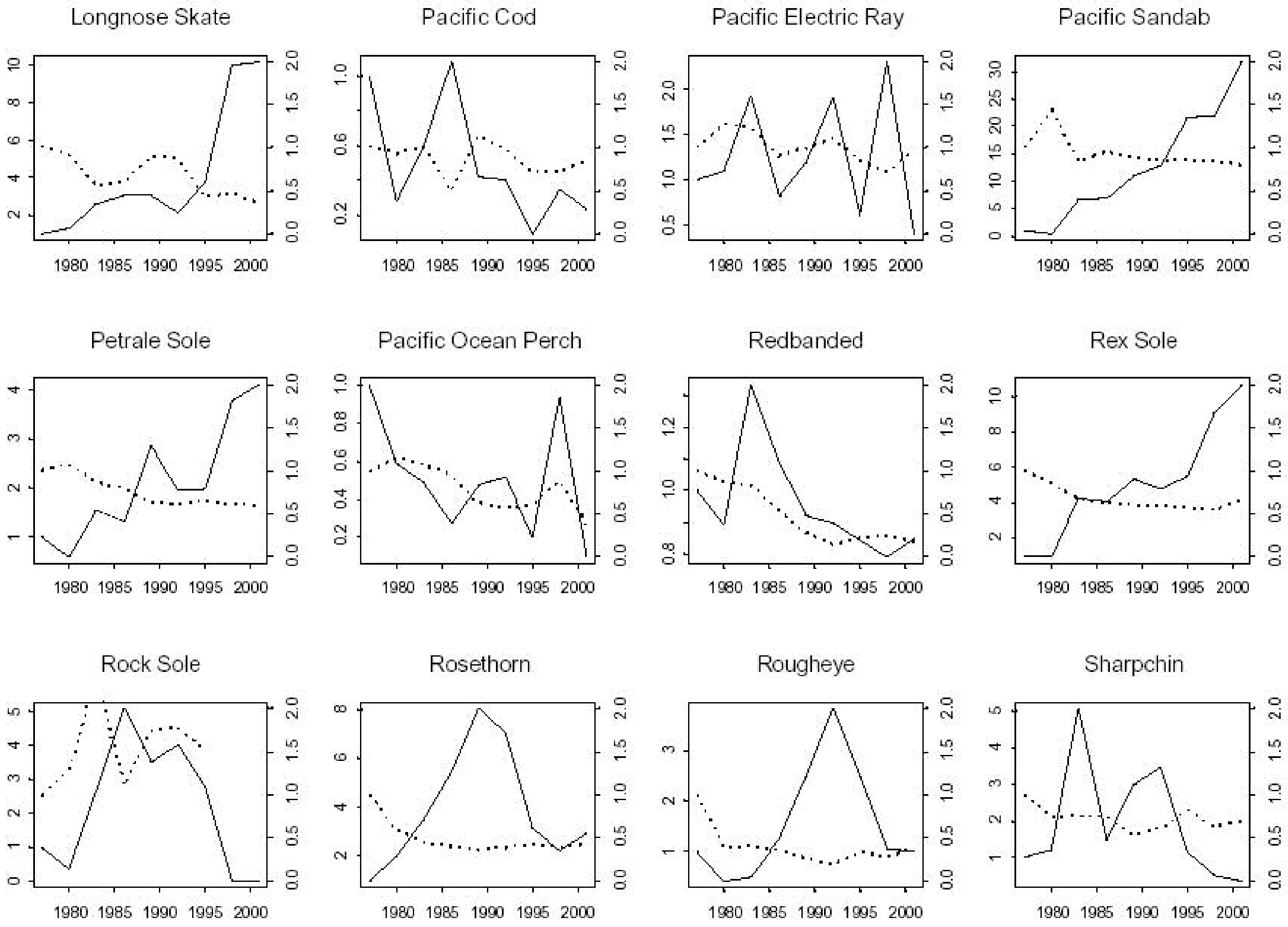
English Sole

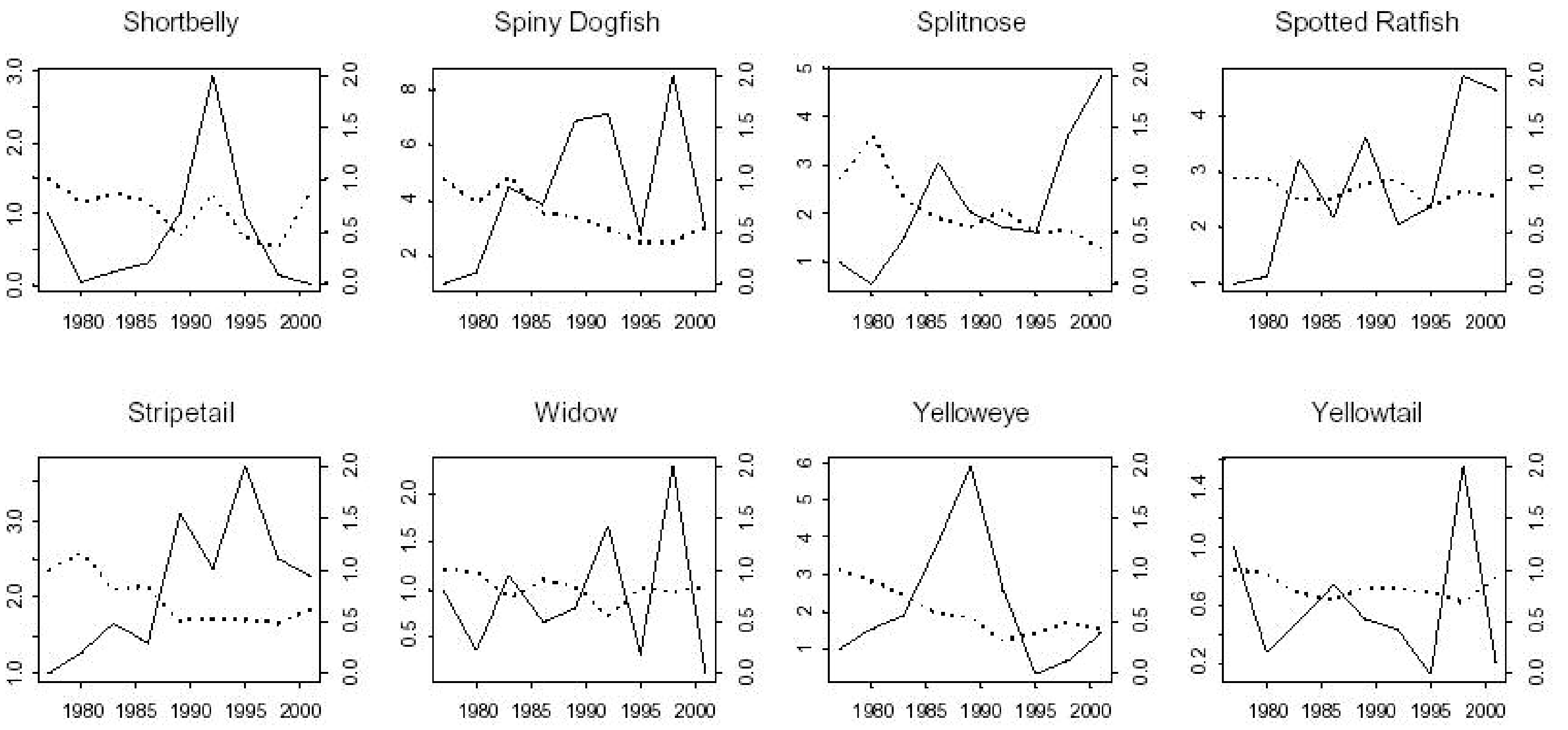


Flathead Sole



Greenstriped


Longnose Skate
Pacific Cod
Pacific Electric Ray
Pacific Sandab
Petrale Sole
Pacific Ocean Perch
Redbanded
Rex Sole
Rock Sole
Rosethorn
Rougheye
Sharpchin
1980 1985 1990 1995 2000
0.0 0.5 1.0 1.5 2.0


Shortbelly
Spiny Dogfish
Splitnose
Spotted Ratfish
Stripetail
Widow
Yelloweye
Yellowtail
0.0
1.0
2.0
3.0
0.0
0.5
1.0
1.5
2.0
1980
1985
1990
1995
2000