
Shifts in a Pacific Ocean Fish Assemblage: the Potential Influence of Exploitation

PHILLIP S. LEVIN,* ELIZABETH E. HOLMES, KEVIN R. PINER, AND CHRIS J. HARVEY
NOAA Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Boulevard E, Seattle, WA 98112, U.S.A.

Abstract: *As in many regions of the world, marine fishes and invertebrates along the Pacific coast of the United States have long been subjected to overexploitation. Despite this history, however, we lack basic information on the current status of many fishes along this coastline. We used data from a quarter century of fishery-independent, coast-wide trawl surveys to study systematically the demersal fish assemblages along the U.S. Pacific coast. We documented fundamental shifts in this fish assemblage. 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 of >10% and others declining in excess of 10% per year. Annual rate of change in population size appeared to be a function of life history interacting with fishing pressure. Negative trends in population size were particularly apparent in rockfish (*Sebastes* spp.). However, across all taxa examined, trends in population size were associated with size of maturity, maximum size, and growth rate. Trends in population size were associated inversely with harvest levels, but stocks that mature late tended to decline faster than would be predicted by catch rates alone. Our results are disquieting because 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.*

Keywords: body size spectrum, fisheries, marine conservation, overfishing, phase shift, rockfish, *Sebastes*

Cambios en un Ensemble de Peces del Océano Pacífico: la Influencia Potencial de la Explotación

Resumen: *Como en muchas regiones del mundo, los peces e invertebrados marinos a lo largo de la Costa del Pacífico de los Estados Unidos han sido sujetos a la sobreexplotación. Sin embargo, a pesar de esta historia carecemos de información básica sobre el estado actual de muchos peces a lo largo de esta costa. Utilizamos datos de un cuarto de siglo de muestreos con redes de arrastre, independientes de pesquerías, para estudiar a los ensambles de peces demersales a lo largo de la Costa del Pacífico de E.U.A. Documentamos cambios fundamentales en este ensamble de peces. La talla corporal promedio, de una diversidad de especies, ha declinado 45% en 21 años. Ha habido cambios mayores en las especies que componen el ensamble, con algunas especies alcanzando tasas de crecimiento poblacional de >10% y otras declinando más de 10% por año. La tasa anual de cambio en el tamaño poblacional pareció ser una función de la historia de vida interactuando con la presión de pesca. Las tendencias negativas del tamaño poblacional fueron particularmente aparentes en los peces piedra (*Sebastes* spp.). Sin embargo, en todos los taxa examinados, las tendencias en el tamaño poblacional se asociaron con la talla a la madurez, la talla máxima y el crecimiento poblacional. Las tendencias en el tamaño poblacional se asociaron inversamente con los niveles de explotación, pero las existencias que maduran tardíamente tendieron a declinar más rápidamente que lo predicho sólo por las tasas de captura. Nuestros resultados son inquietantes porque aumentan la posibilidad de que los cambios de fase inducidos por la pesca en las comunidades de peces pueden afectar a la recuperación de los peces, aun después de la implementación de severas restricciones de pesca.*

Palabras Clave: Cambio de fase, conservación marina, espectro de tamaño corporal, pesquerías, pez piedra, *Sebastes*, sobrepesca

*email pbil.levin@noaa.gov

Paper submitted March 9, 2005; revised manuscript accepted September 12, 2005.

Introduction

As in many regions of the world, marine fishes and invertebrates along the West coast of the United States have long been subjected to overexploitation. The collapse of the California sardine fishery is infamous and foreshadowed the nature of fisheries crises for much of the twentieth century (Wolf 1992; Rodriguez-Sanchez et al. 2002). Perhaps less well known are substantial historic declines in a variety of fish populations along the U.S. Pacific coast. For example, black and white seabass (*Stereolepis gigas* and *Atractoscion nobilis*, respectively) and perhaps yellowtail (*Seriola lalandi*), were heavily fished and considerably depleted in southern California waters in the 1920s and 1930s (MacCall 1996; Dayton et al. 1998); soupfin (*Galeorhinus galeus*), basking (*Cetorhinus maximus*), and dogfish (*Squalus acanthias*) sharks were severely depleted during World War II (Ripley 1946; Ketchen 1986; Holts 1988) and northern anchovy (*Engraulis mordax*) stocks declined dramatically under high rates of exploitation in combination with a reduction of ocean productivity (Rodriguez-Sanchez et al. 2002). In recent years, concern over a number of rockfishes (*Sebastes* spp.; Parker et al. 2000) has resulted in the implementation of large-scale fishery closures along the continental shelf, with an expected annual cost to coastal communities of about \$60 million (PFMC 2003a). Although it is clear that many fish species along the U.S. Pacific coast are in trouble, there is generally a lack of information on the current status of west coast fishes. The federal agency charged with managing fish stocks, National Oceanic and Atmospheric Administration (NOAA) Fisheries, has formally assessed the status of only 20% of the nearly 90 demersal fishes it manages along this coast (NMFS 2003).

Gathering the data required to use traditional assessment methodologies to evaluate the status of unassessed populations of groundfish species 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; Christensen et al. 2003; Myers & Worm 2003) demands that we should evaluate the status of all exploited fishes—not just those few for which detailed data are available. Additionally, as the tenets of ecosystem-based management begin to be adopted, it is clear that the entire fish community, not just species targeted by fisheries, will need to be assessed. Here, we present an analysis of the status of the demersal fish assemblage along the U.S. Pacific coast. We used simple count data from fishery-independent trawls to examine general trends in numbers and weights of 31 fish species along the continental shelf. Although not as detailed as traditional stock assessments, our approach allows us to move beyond the few species that have been assessed formally to provide the first synthetic study of the status of the groundfish assemblage of the U.S. West coast.

Fishery and Ecology Overview

The federally managed “groundfish” (i.e., fish species typically associated with the sea floor) fishery occurs on the continental shelf and slope off the states of California, Oregon, and Washington. The fishery is managed according to the Pacific Coast Groundfish Fishery Management Plan by the Pacific Fishery Management Council and NOAA Fisheries (PFMC 2004). Eighty-nine fish species are included in the plan, including 62 scorpaenids (59 of which are rockfish, genus *Sebastes*), 12 species of flatfish, 6 cartilaginous fishes, 1 chimaerid, 1 morid, 1 grenadier, and 6 roundfish (notably Pacific hake [*Merluccius productus*]) and sablefish (*Anoplopoma fimbria*). The dominant taxa retained are hake, rockfish, sablefish, and flatfish.

Annual commercial landings in the fishery have averaged approximately 233,000 tonnes since 1981 (Pacific Coast Fisheries Information Network, <http://www.psmfc.org/pacfin/pfmc.html>, accessed February 2005), the majority of which comes from the limited-entry trawl fleet. Several management tools are in place to regulate harvest, minimize bycatch, and decrease the probability of overfishing. For example, time/space closures are enacted when certain species reach defined quotas in a season or year. Recently, there have been several large-scale closures in areas throughout the continental shelf. The primary purpose of these closures has been to limit bycatch of several species of overfished rockfish. Managers have also restricted the size of footropes on shelf trawls to prevent trawling in rocky habitats (Hannah 2003). Additionally, a buyback of trawl permits and vessels in the limited entry fishery began in 2003 with the goal of reducing fishing effort on groundfish by roughly one-third (and also to increase financial stability among the fishing community).

A species is considered “overfished” when the spawning stock biomass declines below 25% of the estimated unfished biomass (PFMC 2004), and under this criterion, bocaccio (*Sebastes paucispinis*), canary rockfish (*S. pinniger*), cowcod (*S. levis*), darkblotched rockfish (*S. cramerii*), Pacific ocean perch (*S. alutus*), widow rockfish (*S. entomelas*), and yelloweye rockfish (*S. ruberrimus*) are considered overfished (PFMC 2003b).

Rockfish occupy a broad range of habitats and trophic roles. They are most often associated with some type of substrate, including rocks, kelp, and soft sediments, but they may be found in midwater habitats. Their prey range from gelatinous zooplankton to fish; in turn, rockfish are preyed upon by other groundfish, pelagic piscivorous fishes, marine mammals, and birds (Love et al. 2002). In general, rockfish have long life spans, often exceeding 50 years. Rockfish are slow to mature and have very low first-year survival, resulting in long generation times. For example, generation times of some assessed species range from 14 years (bocaccio) to 44 years (yelloweye) (PFMC 2003b). Juvenile and adult flatfishes mostly eat

benthic invertebrates and some fish, and are preyed upon by sharks, marine mammals, sablefish, and other flatfish. The flatfishes we investigated reach maturity at 2–4 years of age and have lifespans ranging from 15 years to 25 years. The cartilaginous fishes we studied are an eclectic group with diverse life histories and ecologies. Most of these cartilaginous fishes are benthic and feed on invertebrates and benthic fish.

Methods

Trawl surveys of Pacific Northwest groundfish were performed triennially on the continental shelf by NOAA Fisheries from 1977 to 2001 (Weinberg et al. 2002). During the surveys, trawl samples were taken from 55 to 366 m and from 34°N to the U.S.–Canada border. Tow locations have typically been assigned using a stratified design (latitude and depth). These surveys were operated during summer (June–August) with a NOAA research vessel in the early part of the time series and chartered commercial trawl vessels in more recent years. Vessels were equipped

with a Nor'easter bottom trawl with a 27.2-m headrope, 37.4-m footrope, and 567-kg steel V-doors. Hauls were approximately 30 minutes in duration. Tows in which the net was not reliably on the bottom (Zimmermann et al. 2003) were excluded from the analysis. The survey history and potential shortcomings of the survey are detailed by Weinberg et al. (2002), and Zimmermann (2003) and Zimmermann et al. (2003). For each trawl, the distance traveled and the total weight and count for each species were recorded. By dividing the total weight by the count, we estimated the average weight of individuals for each species.

We focused on 16 species of rockfish, 8 species of flatfish, and 7 species of cartilaginous fishes that appear regularly within the groundfish survey on the continental shelf (Table 1). Although many species were sampled during the survey, we focused on those species that were effectively sampled by the gear and whose depth and latitudinal distribution substantially overlapped that of the trawl survey. We calculated the sample mean density of individuals in the West coast survey region (by species) with stratified means (Gunderson 1993) within

Table 1. The average annual change in population abundance (trend) for each of the 31 focal species in the study.

Taxonomic group and common name	Scientific name	Trend	Trend 95% CI	Trend SD
Flatfish				
arrowtooth flounder	<i>Atheresthes stomias</i>	0.018924	0.021627	0.010792
Pacific sandbar	<i>Citharichthys sordidus</i>	0.170964	0.021321	0.011065
petrale sole	<i>Eopsetta jordani</i>	0.054887	0.011886	0.005937
rex sole	<i>Glyptocephalus zachirus</i>	0.084377	0.009583	0.004729
flathead sole	<i>Hippoglossoides elassodon</i>	0.096504	0.030489	0.014964
rock sole	<i>Pleuronectes bilineatus</i>	0.075822	0.060711	0.031578
curlfin sole	<i>Pleuronectes decurrens</i>	0.118919	0.031162	0.016141
English sole	<i>Pleuronectes vetulus</i>	0.112866	0.017007	0.008775
Rockfish				
rougheye rockfish	<i>Sebastes aleutianus</i>	0.050788	0.031813	0.016951
Pacific ocean Perch	<i>Sebastes alutus</i>	−0.03534	0.038925	0.020426
redbanded rockfish	<i>Sebastes babcocki</i>	−0.01913	0.017365	0.008643
darkblotched rockfish	<i>Sebastes crameri</i>	−0.00360	0.016683	0.009273
splitnose rockfish	<i>Sebastes diploproa</i>	0.047421	0.030464	0.016246
greenstriped rockfish	<i>Sebastes elongatus</i>	0.079216	0.015452	0.008427
widow rockfish	<i>Sebastes entomelas</i>	0.005409	0.045298	0.023318
yellowtail rockfish	<i>Sebastes flavidus</i>	0.005899	0.054768	0.027395
chilipepper rockfish	<i>Sebastes goodei</i>	0.049808	0.047625	0.024123
rosethorn rockfish	<i>Sebastes helvomaculatus</i>	0.016333	0.031446	0.015005
shortbelly rockfish	<i>Sebastes jordani</i>	0.086525	0.070355	0.036701
bocaccio	<i>Sebastes paucispinis</i>	−0.16940	0.025994	0.013034
canary rockfish	<i>Sebastes pinniger</i>	−0.10901	0.028202	0.016463
yelloweye rockfish	<i>Sebastes ruberrimus</i>	−0.01309	0.037454	0.019561
stripetail rockfish	<i>Sebastes saxicola</i>	0.029298	0.046559	0.025501
sharpchin rockfish	<i>Sebastes zacentrus</i>	0.01178	0.043794	0.021474
Cartilaginous fish				
brown catshark	<i>Apristurus brunneus</i>	0.141425	0.057333	0.028017
Bering skate	<i>Bathyraja interrupta</i>	0.047625	0.01332	0.00664
spotted ratfish	<i>Hydrolagus colliei</i>	0.056807	0.013107	0.006893
big skate	<i>Raja binoculata</i>	0.023585	0.030974	0.015663
longnose skate	<i>Raja rhina</i>	0.072149	0.008876	0.005117
spiny dogfish	<i>Squalus acanthias</i>	0.051628	0.025186	0.013635
Pacific electric ray	<i>Torpedo californica</i>	0.01507	0.023372	0.012111

five latitude regions and three depth strata (Weinberg et al. 2002). Catch data from trawl surveys are typically delta distributed (similar to a lognormal distribution but with zeros) (Pennington 1996). Pennington (1996) used the sample mean, \bar{y} , and variance, s^2 , of the logged nonzero trawl samples to determine minimum variance estimates for the mean and variance from a delta distribution. We used Eq. 1 in Pennington (1996) to calculate the mean density, c , and Eq. 4 in Pennington (1996) to calculate the variance of the mean, $\text{var}_{\text{est}}(c)$.

We first examined each species' trend in density (c) from 1977 to 2001 with a weighted linear regression of log of c against year, where the $\log(c)$ at year t was weighted by $\text{var}_{\text{est}}(c)$ at year t . The confidence intervals of the estimated trend were calculated by parametric bootstrapping. We then examined how trends in the log mean density differed among species in different taxa with different sizes of maturity and histories of exploitation.

Density Changes as a Function of Taxonomy and Life History

To examine the association of trends in density with life-history traits we performed two analyses. Because size at maturity is a metric available for all the species we examined, and is a correlate of a number of life-history traits in fishes (Jennings et al. 1998), we first performed an analysis of covariance (ANCOVA) in which taxon was the main effect and the length of 50% maturity (Froese & Pauly 2002) was a covariate. We obtained lengths at maturity from Love et al. (2002) and Froese and Pauly (2002). To augment this analysis, we performed a principal components analysis (PCA) with a number of life-history parameters that were available for several of the rockfish and flatfish we examined. Specifically, maximum age, age at maturity, maximum size, size at maturity, average life-time fecundity, and the growth coefficient (k) from the von Bertalanffy growth function were available for 4 flatfish and 15 rockfish species (Love et al. 2002). We ran these six life-history variables through a PCA. We used the resulting PC score as a covariate in an ANCOVA in which taxon was the main effect. This approach allowed us to reduce the number of independent variables while recognizing that there were high levels of correlation among our life-history variables.

Density Changes as a Function of Harvest Level

To investigate the association of trends in density with harvest, we used an ANCOVA in which taxon (flatfish or rockfish) was the main effect and commercial landings from 1980 to 2001 (log transformed) was a covariate. We did not include bycatch in this analysis. We selected 1980 as a starting point because this is the first year for which catch data are available. Cartilaginous fishes were excluded from the analysis because catch data were not available for this group. We used a standardized measure of catch as a covariate in our model. To standardize catch, we multi-

plied the mean annual commercial landing for each species by the catchability of species and then divided by the catch-per-unit effort estimated from the NOAA trawl surveys. 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 appear to have unusually low catchability). For rockfishes associated with soft substrate we used 0.28; the same value we used for flatfishes.

We next asked whether trends in abundance of fishes with specific life-history attributes tended to decline more than expected from their historic catch rates. To accomplish this we first determined the residuals from the regression between the trends in abundance and standardized catch rates. These residuals were then regressed against female length at maturity. A significant negative relationship between residuals from the trend-catch curve and length at maturity indicates fish that mature at larger sizes decline faster than would be predicted by historic catch rates alone. In this analysis, we used only length at maturity as a response variable (i.e., not the PC score) because this metric was available for all the species we used in the analysis.

Results

Density and Size Changes by Taxonomic Group

Trends in population density differed dramatically among the taxa we examined (Table 1). The average annual change in abundance for flatfishes and cartilaginous fishes was 9.2% (SD 4.5%) and 5.8% (SD 4.2%), respectively (Table 1). This corresponds to an average circa eightfold increase in flatfish numbers between 1977 and 2001 and an average twofold increase in cartilaginous fishes. Although there was variability in population growth rates among species, the increasing trend was consistent across these two taxa: none of the eight flatfishes or seven cartilaginous fishes showed a declining trend (Table 1). Although numbers of flatfishes and cartilaginous fishes increased, the average weight of individual fish declined since 1980 (Fig. 1). (We used 1980 for comparison because not all fish were weighed in 1977.) However, there was a great deal of variability in this pattern among species (Fig. 1). The average flatfish caught in 2001 weighed 57% of average flatfish caught in 1980. Similarly, the average cartilaginous fish weighed 67% of average 1980 weight.

In contrast to the population trends of flatfishes and cartilaginous fishes, the average annual decline of rockfishes was 8.7% (SD 6.6%) from 1977 to 2001 (Table 1).

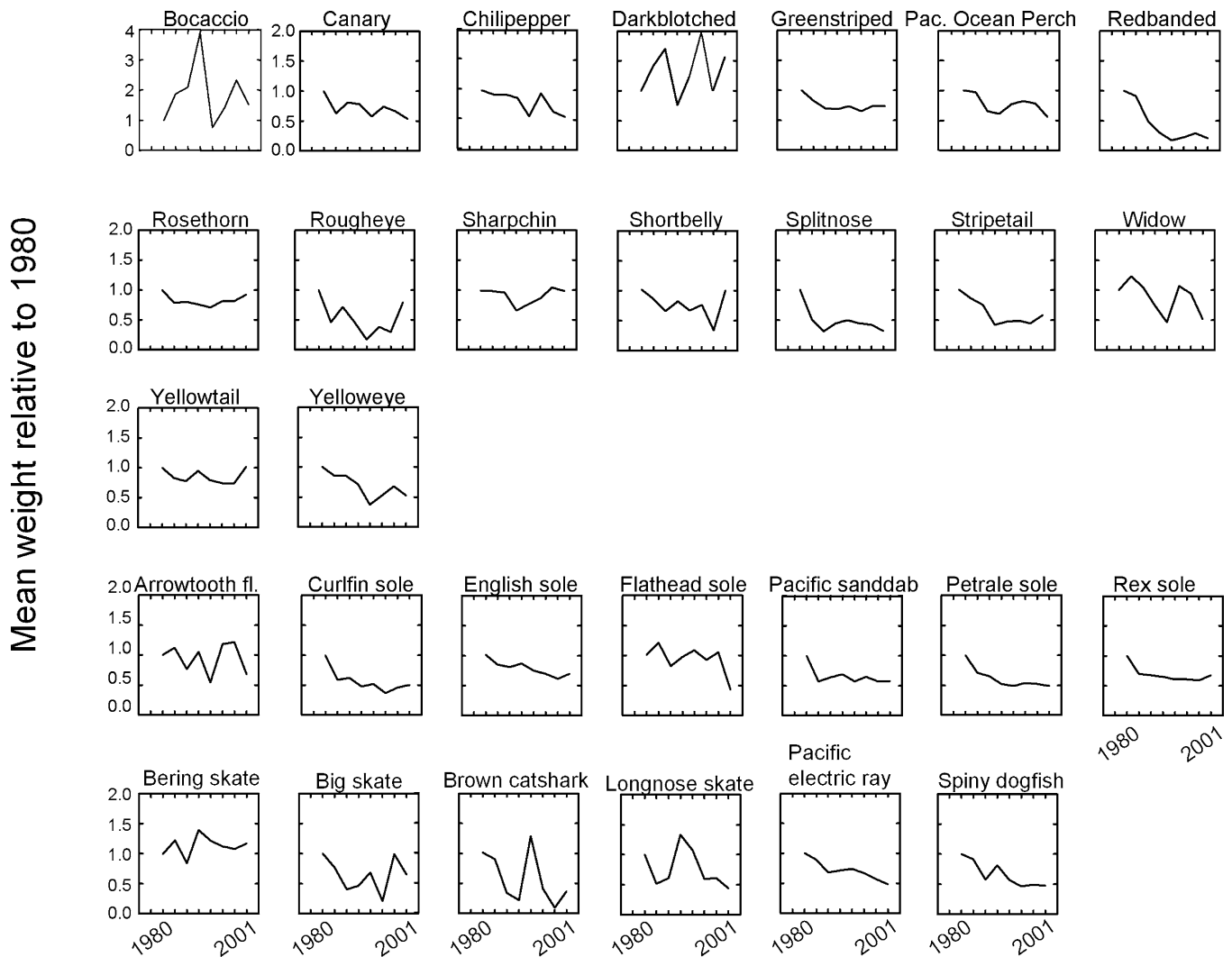


Figure 1. Species-specific changes in mean weight of rockfishes, flatfishes, and cartilaginous fishes relative to 1980. Spotted ratfish and rock sole are not included because data were not available for all years. The y-axis scale for the bocaccio differs from other species.

However, there was tremendous variability among rockfish species (Table 1). Many of the smaller rockfishes, such as the greenstriped, splitnose, and chilipepper, increased annually by $>6\%$ /year, whereas most of the larger species showed significant declines averaging from 5% to even 17% per year. Two rockfish species in particular, the canary and bocaccio, experienced 85% and 96% declines, respectively, since 1977. Additionally, like the other taxa we examined, the average weight of rockfish declined. Average rockfish weight in 2001 was 35% lower than in 1980 (Fig. 1), but again the magnitude of this pattern varied among species (Fig. 1).

Life-History Influences

In flatfishes and rockfishes there was an inverse relationship of trends in population density and length at maturity ($F_{1,23} = 8.45, p < 0.001$), and the slopes of the regression

lines were similar for the two taxa ($p = 0.41$; Fig. 2). In flatfishes, 90% of the variance in population trend was explained by length at maturity, and in rockfishes 54% of the variance in trend was explained by length at maturity. In contrast, no association between population trends and length at maturity was evident in cartilaginous fishes (Fig. 2).

Our PCA provided two principal components from the six variables we examined (Fig. 3), and these two PCs explained $>70\%$ of the variance in the variables. The ANCOVA revealed an association between PC 1 and average trend in abundance (Fig. 4), but this relationship was weakened by an outlier (rougheye rockfish, studentized residual = 2.697). When this outlier was removed from the analysis, the relationship between the PC and average trend in abundance was highly significant ($p = 0.004$) and similar for both taxa (taxon \times PC interaction, $p = 0.88$).

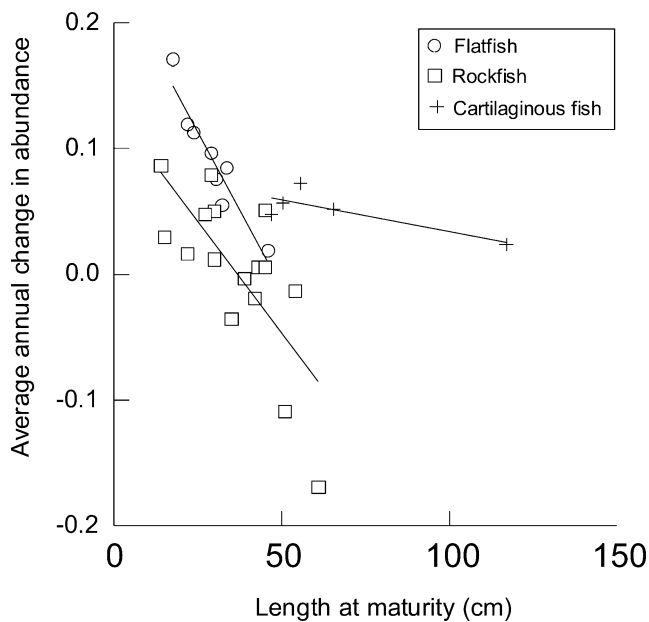


Figure 2. The relationship between length (cm) at maturity and annual changes in population size for Pacific rockfish, flatfishes, and elasmobranchs.

Influences of Harvest Pressure

We observed the expected negative relationship between fishing level and trends in population density ($p = 0.007$). The nature of this relationship was similar for flatfishes and rockfishes (taxon \times total catch interaction $p = 0.82$);

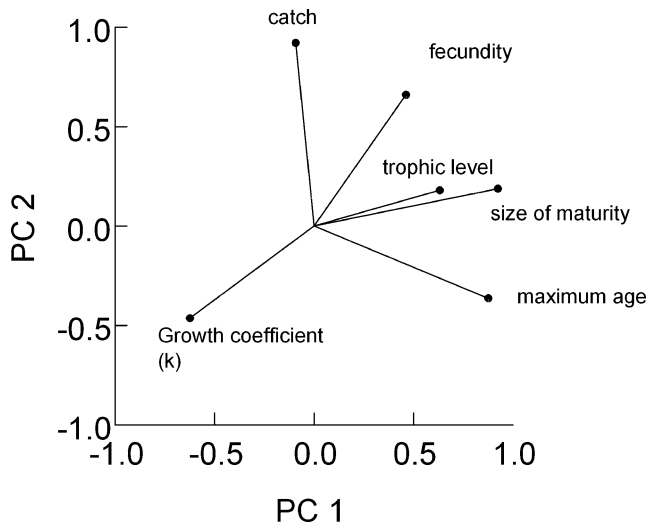


Figure 3. Component loadings for the two principal components generated from a principal component analysis of six life-history variables: maximum age, age at maturity, maximum size, size at maturity, average life-time fecundity, and the growth coefficient (k) from the von Bertalanffy growth function for 4 flatfish and 15 rockfish species.

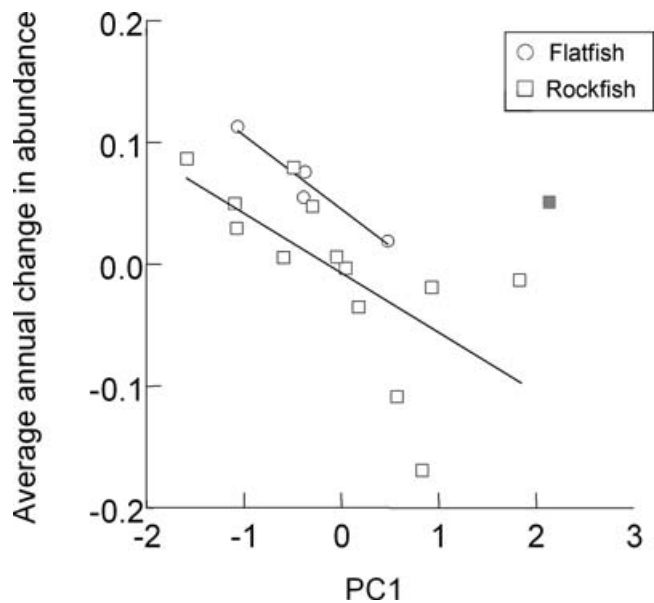


Figure 4. The relationship between annual changes in population size for Pacific rockfish and flatfish with the principal component from a principal component analysis of the following life-history variables: maximum age, age at maturity, maximum size, size at maturity, average life-time fecundity, and the growth coefficient (k) from the von Bertalanffy growth function. The shaded square is rough eye rockfish that was identified as an outlier in the analysis.

however, the amount of variance in abundance trends explained by catch varied between taxa. In flatfishes, 59% of the variation in average trends was explained by the catch, whereas in rockfishes 36% of the variation was explained.

In some cases, stocks that mature at larger sizes decline faster than would be predicted by catch rates alone. We observed a nonsignificant relationship between residuals and length at maturity in rockfishes ($p = 0.09$) when we included all species in our analysis (Fig. 5). However, when we analyzed those species with negative residuals separately from those with positive residuals, the potential interactive effects of life history and fishing became clearer. For those rockfish species with trends in abundance that were below that predicted by the trend-catch relationship (i.e., residuals < 0), there was a strong ($r^2 = 0.90$) and significant ($p = 0.004$) negative relationship between residuals and length at maturity (Fig. 5). However, for those rockfishes with positive residuals, there was no association between the residuals and length at maturity ($r^2 = 0.04$; $p = 0.62$; Fig. 5).

A negative relationship between residuals from the trend-catch curve and length at maturity also existed for flatfish (Fig 5). The relationship between residuals and length at maturity was significant ($p = 0.02$), and length at maturity explained 61% of the variance of the residuals.

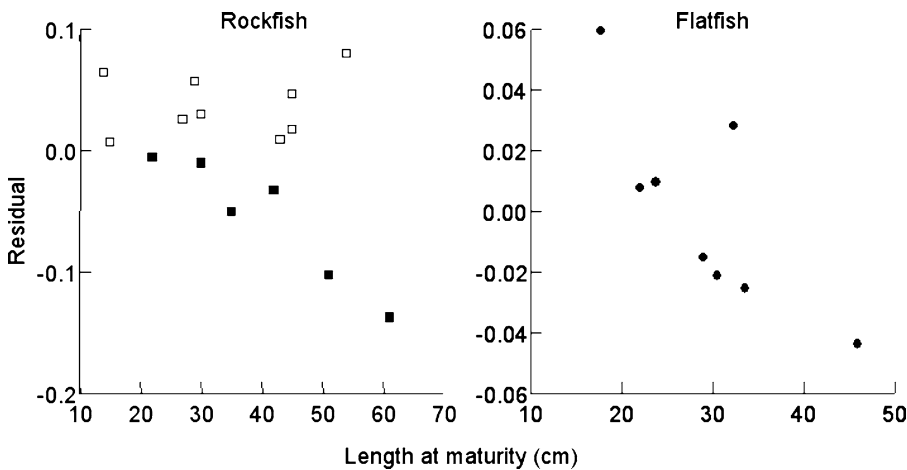


Figure 5. Association of residuals from the regression between the average annual change in abundance and standardized catch rates and length at maturity (cm) in Pacific rockfishes and flatfishes. In the rockfish panel, open squares indicate residuals > 0 , whereas filled squares identify residuals < 0 .

The petrale sole was an outlier in this relationship (studentized residual = 2.392), and when this species was removed from the analysis the r^2 increased to 0.79 ($p = 0.007$).

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 U.S. Pacific coast. Flatfish and cartilaginous fish abundances have increased, in some cases 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, rockfishes were more than 60% of the fish captured in the survey, whereas flatfishes were 34% of the catch. However, by 2001 rockfishes declined to 17% of the catch and flatfishes had increased to nearly 80%. Our analysis of the residuals from the trend-catch curve (Fig. 5) implicates fishing as a cause for some of the changes in the fish assemblages we report. Thus, we propose that fishing has played a large role in the changes we documented, that the changes are related to the size and life histories of the taxa involved, and that the community ecology of the system has been profoundly altered as a result.

Recent declines (and extinctions) of species are clearly not phylogenetically random (Purvis et al. 2000; Levin & Levin 2002). In a number of taxa, large-bodied species have lower reproductive rates than do smaller members of the taxon (Fisher & Owens 2004), and this may make them more susceptible to human exploitation and/or less able to compensate for the increased mortality imposed by harvest (e.g., Owens & Bennett 2000; Johnson 2002; Cardillo 2003). For instance, Johnson (2002) demonstrated that the risk of extinction of mammals dur-

ing the Late Quaternary was related to reproductive rates and suggested that those slow-reproducing species that survived this extinction bottleneck occurred in habitats inaccessible to human hunters. Similarly, fish species with "slow" life histories are also less resilient to exploitation (Jennings et al. 1998, 1999; Denney et al. 2002). For instance, Jennings et al. (1999) demonstrated that those fish stocks in the North sea that have declined due to fishing tended to be larger and mature later than phylogenetically related species that did not decline. Intrinsic rates of increase of some of the rockfish species we examined may be so low that even modest rates of fishing mortality may lead to severe declines in abundance (Parker et al. 2000). For example, Tolimieri and Levin (2005) showed that the bocaccio would have had an annual population growth rate of 1.009 over the last 25 years in the absence of fishing. Thus, even the slight levels of fishing mortality that bocaccio experience could produce the large declines in abundance that we documented here.

Although fishing likely played a significant role in the patterns we documented, climatic forcing is an additional plausible mechanism for some of the species we investigated (Francis et al. 1998; Hare & Mantua 2000). For instance, temporal trends in flatfish production in the Eastern Bering sea are consistent with decadal-scale climate influences on survival during early life history (Wilderbuer et al. 2002). Similarly, the El Niño Southern Oscillation has a large influence on the early life history of some rockfish populations (Tolimieri & Levin 2005). Thus, although fishing is a likely suspect for some, if not all, of the changes we report, a correlative study such as this cannot rule out environmental causes for some of the observed changes.

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 trends for each species separately. 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, but we have also documented a shift in the fish assemblage from large to small species of rockfishes and from rockfish to flatfish domination. To the extent that fishing caused these shifts, it has clearly affected not only individual populations, but has also disturbed the entire community. The species that have come to dominate this assemblage have vastly different trophic roles and life-history strategies than the species they replaced. Whether changes in relative fish abundances will result in change throughout the community is a matter of speculation; however, community-level changes as a consequence of overfishing have been observed in other systems. For example, Worm and Myers (2003) demonstrated that the demise of cod stocks in the North Atlantic ocean led to increases in their prey, the northern shrimp (*Pandalus borealis*). Similarly, Zabel et al. (2003) suggest that even moderate levels of fishing of cod in the Baltic sea resulted in major shifts in the relative abundance of species at lower trophic levels. At present we lack the data necessary to parameterize detailed food-web models that would allow us to determine whether a shift from large- to small-bodied rockfish would alter the benthic invertebrate community; however, this possibility exists.

Although one 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; Mangel & Levin 2005). Because even smaller species of rockfish may be able to consume or outcompete recruiting juveniles of larger species (e.g., Shulman et al. 1983; Yoklavich et al. 2000) and because 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 state (Mangel & Levin 2005). As a result, even large reductions in fishing may not result in recovery of overfished larger species. Similarly, in the northeastern Atlantic, Dulvy et al. (2000) showed a shift in skate assemblages harvested over a 40-year period. Large-bodied species with long generation times have declined and smaller species have increased in abundance. Dulvy et al. (2000) 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 suggest that competitive release results in a phase shift from teleost-dominated to elasmobranch-dominated communities in the northwestern Atlantic.

Many researchers agree that natural shifts in the composition of marine communities can be heightened by fisheries that sequentially discover and then deplete the most valuable fish species. However, the appropriate response to such serial depletion is a matter of much debate (e.g.,

compare Pauly et al. 2002; Hilborn et al. 2004). Hilborn et al. (2004) clearly illustrate the crux of the problem for the mixed-stock groundfish fishery on the U.S. West coast. If one maximizes yield from the ecosystem by maximizing the sum of single-species benefits, then overfishing will always occur. In contrast, if one manages an assemblage of fishes to prevent some stocks from becoming overexploited, then fishers will clearly have to forgo harvest of strong stocks. Lessening the tradeoff between overfishing and lost fishing opportunities requires movement beyond single species thinking and development of approaches for exploiting productive stocks while protecting species that are less productive. Edwards et al. (2004) proposed one solution to this dilemma based on the management of portfolios of fish stocks. Portfolios of fish species interact ecologically and are captured jointly. Managers then manage a portfolio to balance the expected combined return of the fishery portfolio against risks associated with life-history attributes or other uncertainties. The objectives of such an approach could be economic or ecological. In either case the goal of such an approach would be to achieve multispecies objectives within clearly defined ecological safeguards.

Implementing a portfolio approach to fisheries depends critically on understanding ecological interactions among species within the portfolio, knowledge of covariance in the response of species to environmental variability, and the dynamics of key components of the ecosystem. Although the data demands of a portfolio approach seem formidable, emerging analytical techniques, such as first-order multivariate autoregressive models, make it possible to understand which species within portfolios have relatively large impacts on other species or which species are most sensitive to particular environmental factors (Ives et al. 2003). Importantly, such techniques require only basic data of the sort already collected by fisheries agencies; thus, implementing a portfolio approach may be scientifically achievable. However, to be successful, this approach must be combined with management approaches that assess value of assets in the ecosystem, manage conflicting uses, and reconcile economic objectives of an ecosystem with constraints inherent in the environment (Edwards et al. 2004; Hilborn et al. 2004). Exactly how to respond to the drastic changes in fish abundance and size that we have documented here has been a matter of much debate; however, our results make a strong case for the value of a holistic, ecosystem approach to fisheries.

Acknowledgments

We are greatly indebted to dozens of researchers from the National Marine Fisheries Service who conducted the thousands of trawl tows upon which this paper is based. We appreciate discussions with or comments by

R. Methot, T. Helser, R. Zabel, N. Tolimieri, J. Field, and M. Mangel, which improved the manuscript. P. S.L. gratefully acknowledges G. Hincapie for leading the way and the support of a Nature Conservancy David H. Smith Senior Scholarship.

Literature Cited

- Baum J. K., R. A. Myers, D. G. Kehler, B. Worm, S. J. Harley, and P. A. Doherty. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**:389–392.
- Cardillo M. 2003. Biological determinants of extinction risk: why are smaller species less vulnerable? *Animal Conservation* **6**:63–69.
- Christensen V., S. Guenette, J. J. Heymans, C. J. Walters, R. Watson, D. Zeller, and D. Pauly. 2003. Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries* **4**:1–24.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications* **8**:309–322.
- Denney N. H., S. Jennings, and J. D. Reynolds. 2002. Life-history correlates of maximum population growth rates in marine fishes. *Proceedings of the Royal Society of London Series B-Biological Sciences* **269**:2229–2237.
- Dulvy N. K., J. D. Metcalfe, J. Glanville, M. G. Pawson, and J. D. Reynolds. 2000. Fishery stability, local extinctions, and shifts in community structure in skates. *Conservation Biology* **14**:283–293.
- Edwards S. E., J. S. Link, and B. P. Rountree. 2004. Portfolio management of wild fish stocks. *Ecological Economics* **49**:317–329.
- Fisher D. O., and I. P. F. Owens. 2004. The comparative method in conservation biology. *Trends in Ecology & Evolution* **19**:391–398.
- Fogarty M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecological Applications* **8**:S6–S22.
- Francis, R. C., S. R. Hare, A. B. Hollowed, W. S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the northeast Pacific. *Fisheries Oceanography* **7**:1–21.
- Froese, R., and D. Pauly. FishBase. International Center for Living Aquatic Resources Management (ICLARM), Los Baños, Laguna, Philippines. Available from <http://www.fishbase.org> (accessed July 2005)
- Hannah, R. W. 2003. Spatial changes in trawl fishing effort in response to footrope diameter restrictions in the U.S. west coast bottom trawl fishery. *North American Journal of Fisheries Management* **23**:693–702.
- Hare S. R., and N. J. Mantua. 2000. Empirical indicators of climate variability and ecosystem response since 1965. *Progress in Oceanography* **47**:103–145.
- Hilborn R., A. E. Punt, and J. Orensanz. 2004. Beyond band-aids in fisheries management: fixing world fisheries. *Bulletin of Marine Science* **74**:493–507.
- Holts, D. B. 1988. Review of U. S. West Coast commercial shark fisheries. *Marine Fisheries Review* **50**:1–8.
- Ives A. R., B. Dennis, K. L. Cottingham, and S. R. Carpenter. 2003. Estimating community stability and ecological interactions from time-series data. *Ecological Monographs* **73**:301–330.
- Jennings S., J. D. Reynolds, and S. C. Mills. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London, Series B* **265**:333–339.
- Jennings S., J. D. Reynolds, and N. V. C. Polunin. 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conservation Biology* **13**:1466–1475.
- Johnson C. N. 2002. Determinants of loss of mammal species during the late quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society of London Series B-Biological Sciences* **269**:2221–2227.
- Ketchen, K. S. 1986. The spiny dogfish (*Squalus acanthias*) in the Northeast Pacific and a history of its utilization. Canadian Special Publications of Fisheries and Aquatic Sciences 88.
- Levin P. S., and D. A. Levin. 2002. The real biodiversity crisis. *American Scientist* **90**:6–8.
- Love M. S., Yoklavich, M., and Thorsteinson L. 2002. The rockfishes of the Northeast Pacific. University of California Press, Berkeley.
- MacCall, A. D. 1996. Patterns of low-frequency variability in fish populations of the California current. *California Cooperative Oceanic Fisheries Investigations Reports* **37**:100–110.
- Mangel M., and P. S. Levin. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. *Philosophical Transactions Royal Society of London* **360**:95–105.
- Millar R. B., and R. D. Methot. 2002. Age-structured meta-analysis of U.S. West Coast rockfish (Scorpaenidae) populations and hierarchical modeling of trawl survey catchabilities. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:383–392.
- Myers R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423**:280–283.
- NMFS (National Marine Fisheries Service). 2003. Annual report to Congress on the Status of U.S. Fisheries—2002. NMFS, Silver Spring, Maryland.
- Owens I. P. F., and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences* **97**:12144–12148.
- Parker S. J., S. A. Berkeley, J. T. Golden, D. R. Gunderson, J. Heifetz, M. A. Hixon, R. Larson, B. M. Leaman, M. S. Love, J. A. Musick et al. 2000. Management of Pacific Rockfish. *Fisheries* **25**:22–29.
- Pauly D., V. Christensen, S. Guenette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. *Nature* **418**:689–695.
- Pennington, M. 1996. Estimating the mean and variance of highly skewed marine data. *Fishery Bulletin* **94**:498–505.
- PFMC (Pacific Fishery Management Council). 2003a. Final environmental impacts statement for the proposed groundfish acceptable biological catch and optimum yield specifications and management measures: 2003 Pacific coast groundfish fishery. PFMC, Portland, Oregon.
- PFMC (Pacific Fishery Management Council). 2003b. Proposed acceptable biological catch and optimum yield specifications and management measures for the 2004 Pacific coast groundfish fishery. PFMC, Portland, Oregon.
- PFMC (Pacific Fishery Management Council). 2004. Pacific coast groundfish fishery management plan for the California, Oregon, and Washington groundfish fishery, as amended through Amendment 17. PFMC, Portland, Oregon.
- Purvis A., P.-M. Agapow, J. L. Gittleman, and G. M. Mace. 2000. Non-random extinction and the loss of evolutionary history. *Science* **288**:328–330.
- Ripley, W. E. 1946. The soupfin shark and the fishery. *California Fish and Game Fish Bulletin* **64**:7–37.
- Rodriguez-Sanchez R., D. Lluch-Belda, H. Villalobos, and S. Ortega-Garcia. 2002. Dynamic geography of small pelagic fish populations in the California current system on the regime time scale (1931–1997). *Canadian Journal of Fisheries and Aquatic Sciences* **59**:1980–1988.
- Rosenberg A. A. 2003. Managing to the margins: the overexploitation of fisheries. *Frontiers in Ecology and the Environment* **1**:102–106.
- Shulman M. J., J. C. Ogden, J. P. Ebersole, W. N. McFarland, S. L. Miller, and C. G. Wolf. 1983. Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* **64**:1508–1513.
- Steneck R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* **29**:436–459.
- Tolimieri N., and P. S. Levin. 2005. The roles of fishing and climate in the population dynamics of bocaccio rockfish. *Ecological Applications* **15**:458–468.

- Weinberg K. L., M. E. Wilkins, F. R. Shaw, and M. Zimmermann. 2002. The 2001 Pacific west coast bottom survey of groundfish resources: estimates of distribution, abundance, and length and age composition. Technical memorandum NMFS-AFSC-128. National Oceanic and Atmospheric Administration, Washington, D.C.
- Wilkinson L., Blank G., and Gruber C. 1996. Desktop data analysis with SYSTAT. Prentice Hall, Upper Saddle River, New Jersey.
- Wolf P. 1992. Recovery of the Pacific sardine and the California sardine fishery. California Cooperative Oceanic Fisheries Investigations Reports **33**:76-86.
- Worm, B., and R. A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* **84**: 162-173.
- Yoklavich M. M., H. G. Greene, G. M. Cailliet, D. E. Sullivan, R. N. Lea, and M. S. Love. 2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. *Fishery Bulletin* **98**:625-641.
- Zabel R. W., C. J. Harvey, S. L. Katz, T. P. Good, and P. S. Levin. 2003. Ecologically sustainable yield. *American Scientist* **91**:150-157.
- Zimmerman, M. 2003. Calculation of untrawlable areas within the boundaries of a bottom trawl survey. *Canadian Journal of Fisheries and Aquatic Sciences* **60**:657-669.
- Zimmermann M., M. E. Wilkins, K. L. Weinberg, R. R. Lauth, and F. R. Shaw. 2003. Influence of improved performance monitoring on the consistency of a bottom trawl survey. *ICES Journal of Marine Science* **60**:818-826.

