

Population Dynamics of an Unexploited Rockfish, *Sebastes jordani*, in the California Current

J.C. Field and E.J. Dick

National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, California

M. Key

California Department of Fish and Game, Santa Cruz, California

M. Lowry

National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, California

Y. Lucero

University of California Santa Cruz, Center for Stock Assessment Research, Jack Baskin School of Engineering, Santa Cruz, California

A. MacCall, D. Pearson, and S. Ralston

National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, California

W. Sydeman and J. Thayer

PRBO Conservation Science, Marine Ecology Division, Petaluma, California

Abstract

The shortbelly rockfish, *Sebastes jordani*, is one of the most abundant rockfish species in the California Current, and is a key forage species for many fish, birds, and marine mammals. This species has not been the target of commercial fisheries, and consequently catch data are limited. Nevertheless, available evidence suggests that the population has undergone significant fluctuations in abundance over the last several decades, presumably in response to variable environmental conditions.

We present a population model, using standard methods and a variety of both traditional and untraditional data, to investigate population changes for this ecologically important species. The results from this analysis provide an opportunity to consider the dynamic nature of an unexploited rockfish population, and should ultimately provide insight into the potential causes and consequences of natural population variability on both exploited and non-exploited populations throughout the California Current.

Introduction

The shortbelly rockfish (*Sebastes jordani*) is best characterized by small size (individuals are rarely longer than 30 cm), rapid growth and maturity (in our data, 50% of females are mature by age 2, 99% by age 3), and high natural mortality rate (Pearson et al. 1991, Love et al. 2002). Shortbelly rockfish range from Punta Baja in Baja California as far north as La Perouse Bank off of British Columbia. However, they are most abundant along the continental shelf break between the northern end of Monterey Bay and Point Reyes, California, and around the Channel Islands in the Southern California Bight. Although stock structure is poorly understood, genetic analysis of fish collected between San Diego and Cape Mendocino (California) suggest a single, coastwide stock, with slight differences in allele frequencies across Point Conception (Constable 2006). Our paper considers only the shortbelly rockfish population in this region, which is shown in Fig. 1 along with the approximate spatial coverage and duration of the principal data time series used in the model.

Shortbelly rockfish feed primarily on juvenile and adult euphausiids, and are an important prey item to a wide range of piscivorous fishes, seabirds, and marine mammals (Chess et al. 1988, Sydeman et al. 2001). Merkel (1957) reported that juvenile rockfish were important prey of chinook salmon along the central California coast in late spring and summer, with shortbelly accounting for more than 60% of those identified to species. Although both juvenile and adult rockfish have rarely been identified to the species level in the diets of many California Current marine mammals (Antonelis and Fiscus 1980, Stroud et al. 1981), shortbelly rockfish were among the five most significant prey items for California sea lion (*Zalophus californianus*) in the Channel Islands (Lowry and Carretta 1999). Consequently, shortbelly rockfish have a trophic position and life history traits more similar to forage fishes than most other *Sebastes*.

Large catches of shortbelly rockfish were made during foreign fisheries of the 1960s and 1970s, although these were presumably incidental to the targeting of other rockfish and Pacific hake (*Merluccius productus*) (Rogers 2003). The expectation of eventual development

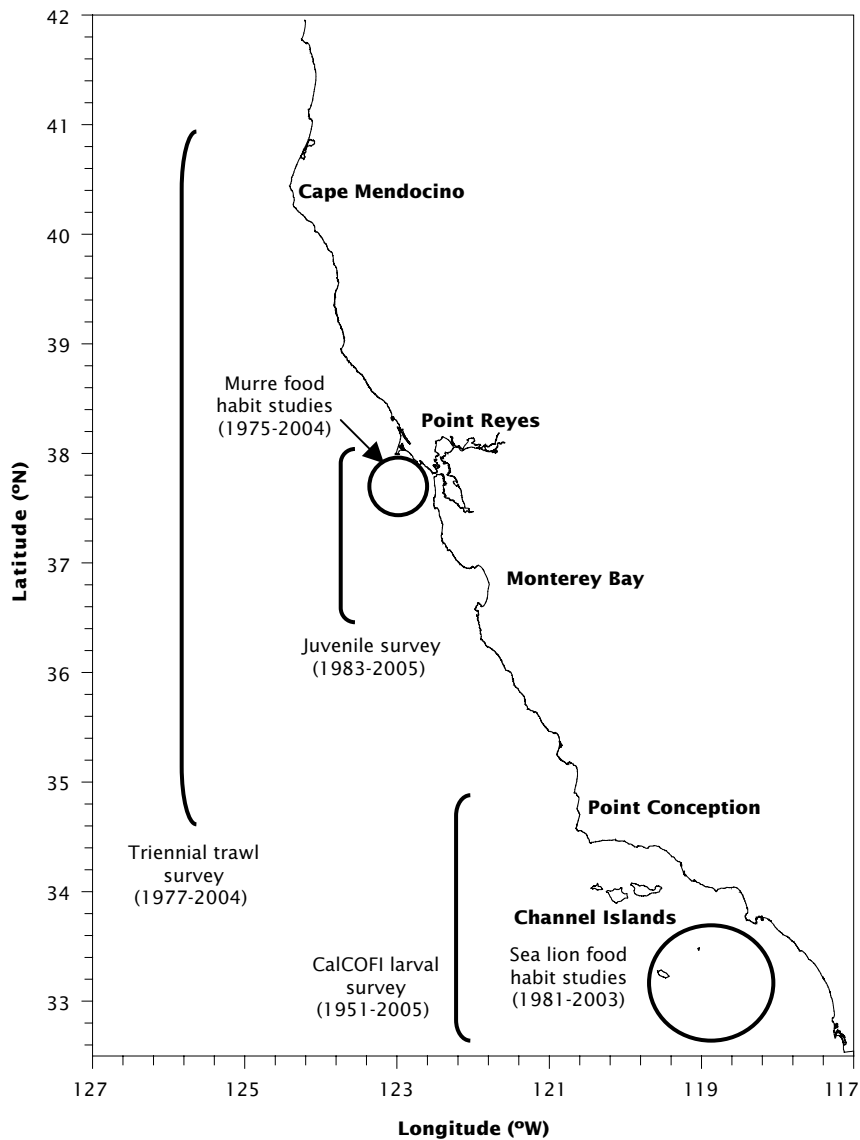


Figure 1. Approximate spatial coverage of major data sources used in this study. Note that actual coverage varied among years for many surveys; areas shown approximate the core areas sampled with consistency throughout the duration of the time series.

of a domestic commercial fishery led to past efforts to estimate stock abundance and productivity (Lenarz 1980) as well as evaluations of commercial potential (Kato 1981). Pearson et al. (1989, 1991) estimated that allowable catches for shortbelly could range from 13,900 to 47,000 tons per year, based on life history data and hydroacoustic survey estimates of abundance. Subsequently, the Pacific Fishery Management Council established an acceptable biological catch (ABC) of 23,500 tons for shortbelly, which was reduced to 13,900 tons in 2001 based on observations of poor recruitment throughout the 1990s. Only modest landings (10 to 70 tons per year) have been reported in California over the last 20 years. Discards may be somewhat greater, as shortbelly can be caught incidentally by trawl gear when targeting other semi-pelagic rockfish. A very modest amount of early data on bycatch rates off of Central California suggests that shortbelly rockfish were often encountered in intermediate depth tows (100 to 200 meters), and comprised approximately 7.8% of the rockfish catch by volume at this depth range (Heimann 1963). However, the desire and ability of fishermen to avoid shortbelly suggest that more recent bycatch rates are likely to be considerably less (T. Ghio, pers. comm.). Recent estimates of discards from the West Coast groundfish observer program have been on the order of five tons per year (or less) for 2002 and 2003, although these may not represent historical rates.

As the overall impacts of fisheries can be considered to be modest to inconsequential, the objectives of this paper and model are focused on an evaluation of the variability and change exhibited by this population over time, including the potential to infer such changes using non-traditional data. Fisheries management typically presumes that we understand population behavior even in unexploited systems. Consequently, understanding changes in unexploited populations could be insightful with respect to appreciating the dynamic nature of productivity and abundance for a wide range of species throughout the California Current ecosystem.

Materials and methods

The population was modeled using an age and size structured statistical model, Stock Synthesis 2, a modeling framework used for most recent California Current groundfish assessments. A full description of the population dynamics, selectivity and catch equations, and associated likelihood functions are given in Methot 2005. In our application, parameters for growth, fecundity, and maturity were estimated externally from the model and input as fixed values. Although shortbelly rockfish have been aged to 30 years, we found that 95% of all aged shortbelly available to us (~8,500) were 12 years of age or less, and 99% of the shortbelly available to us were less than 17 years of age or less,

consistent with estimates of natural mortality of 0.25 to 0.27 based on the Hoenig (1983) rule of thumb approach. We used a fixed natural mortality rate of 0.26, consistent with these observations, the range estimated by Pearson et al. (1991) and the point estimate by Ralston et al. (2003).

Ralston et al. (2003) used larval production methods to estimate that the spawning biomass in the Monterey to San Francisco area of approximately 65,000 tons in 1991, considerably less than the hydroacoustic estimates of 153,000 to 295,000 tons (in 1980 and 1977 respectively). The latter estimates are considered to be highly uncertain, since there is no estimate of target strength for shortbelly rockfish and the hydroacoustic estimates assumed a target strength equivalent to hake. MacGregor (1986) had earlier reported that 53% of shortbelly larvae occurred in the Monterey area, 35% occurred in the Channel Islands area, with the remaining ~12% occurring near the central coast. This suggests that a doubling of the Ralston et al. (2003) biomass estimate may be reasonable, giving a total biomass of 115,000 tons in 1991. This was incorporated as a point estimate of biomass with a coefficient of variation of 0.2 (based on Ralston et al. 2003), with a selectivity curve set identical to the maturity function. In order to evaluate the sensitivity of model behavior to potential bycatch, estimates of plausible bycatch streams were developed based on the Heimann (1963) data, extrapolated to what might have been caught based on historical shelf rockfish landings, and entered into the model as catches.

CalCOFI larval abundance data

Egg or larval abundance data from the California Cooperative Oceanic and Fisheries Investigations (CalCOFI) surveys have been used in stock assessments for a number of commercially important West Coast species, including bocaccio rockfish (MacCall 2003), sheephead (Alonzo et al. 2004), and several coastal pelagic species. Shortbelly larvae are the most frequently occurring of the rockfish larvae identifiable to species, accounting for approximately 15% of the total rockfish larvae in the survey (Moser et al. 2000). High levels of larvae abundance in CalCOFI surveys were observed throughout most of the 1950s, and the late 1980s through the early 1990s, while very low abundance levels occurred during the 1958-1959 El Niño, from the mid-1970s through the early 1980s, and in the late 1990s.

We used tow-specific information and a Delta-GLM approach, which combines a binomial model for presence/absence information with a model of catch per unit effort (CPUE) for positive tows (Stefansson 1996, Maunder and Punt 2004), to generate a relative index of spawning biomass. The data included over 11,200 observations during 1951-2005 for the regularly sampled survey grid, although from 1967 to 1984 this survey was limited to a triennial frequency. Presence/absence (π) was

modeled with a binomial GLM using a logit link (where the logit (π) = $\log[\pi/(1-\pi)]$), and the density (μ) of shortbelly rockfish larvae in positive tows was modeled with a Gaussian distribution of the log transformed data. Specification of the error distribution for the positive observation was determined based on Akaike Information Criteria, as in Dick (2004). Models included year, month, and station effects, and the product of the year effects of the two models ($\pi\mu$) was used as the final index of abundance.

Triennial Trawl Survey

A primary source of fishery independent information for many groundfish species in the California Current are area-swept estimates of abundance based on the Triennial Trawl Survey (Weinberg et al. 2002). However, for semi-pelagic species the patchiness of catches in the survey is particularly problematic, and area-swept estimates of abundance are highly uncertain. For example, out of nearly 1,500 tows made south of Cape Mendocino between 1977 and 2004, over half the total catch of shortbelly rockfish was made in only six tows, and over 95% of the catch was made in only fifty tows. Rather than use area-swept estimates, we developed a delta-GLM approach that estimated year, latitude (2° bins), and depth (50 meter bins) effects to estimate annual indices for each survey year, consistent with the approach of He et al. (2006) for another semi-pelagic species, widow rockfish (*S. entomelas*). We obtained haul-specific survey data from 1977 to 2004 (M. Wilkins, AFSC, pers. comm.; B. Horness, NWFSC, pers. comm.), and excluded bad performance tows based on Zimmermann et al. (2001). We included all tows south of Cape Mendocino (40°N) that occurred between depths of 55 to 366 meters for all years, with the exception of a small number of tows made south of $34^\circ30'$ in 1977 (as the survey did not cover this region in subsequent years). Catch per unit effort was estimated for each tow as in Weinberg et al. (2002). Length frequency data were also generated for each survey year, with the effective sample size based on the number of tows in which length samples were taken. Due to differences in the depth strata sampled in 1977, and low sample sizes in 1980-1986, only length data from 1989-2004 were used in the analysis. Length data demonstrate a movement to deeper water with size, as shown by Lenarz (1980).

Juvenile survey

Estimates of juvenile shortbelly rockfish abundance are available for 1983-2005 from the NMFS/SWFSC midwater trawl survey. Studies have shown that indices of year-class strength derived from the survey are effective at gauging impending recruitment (Ralston and Howard 1995), and consequently these indices have been used in forecasting year-class strength for a number of groundfish species, including widow rockfish (He et al. 2006), Pacific hake (Helser et al. 2006) and chilipepper rockfish

(Ralston et al. 1998). Similar to other surveys, we used a delta-GLM to remove spatial and seasonal effects. Shortbelly rockfish are by far the most abundant rockfish species in the juvenile survey data, and the results of the survey time series suggest a high degree of covariance among juveniles of different species (S. Ralston, unpubl. data). Although a power coefficient has been used in other assessments to transform juvenile indices, based on the assumed compensatory relationship between pelagic juvenile abundance and subsequent recruitment to the adult population (Adams and Howard 1996), the paucity of reliable age information necessary to estimate this parameter led to our decision to use the index as an absolute reflection of juvenile abundance. Consequently, the catchability of age-0 rockfish from this survey was treated as a nuisance parameter.

Seabird food habits data

The abundance, biology, and food habits of several species of seabirds have been monitored by the Point Reyes Bird Observatory on the southeast Farallon Islands (west of San Francisco, California) since the early 1970s, providing a thirty-year time series of food habits for some species (Sydeman et al. 2001). Juvenile rockfish have traditionally dominated the diets of common murre (*Uria aalge*) and many other seabird species during their breeding seasons. However, the proportion of rockfish in seabird diets declined severely through most of the 1990s, likely related to ocean conditions (Sydeman et al. 2001, Miller and Sydeman 2004). Although seabird food habits data can be informative in the evaluation of stock status or recruitment for some species (Cairns 1992, Montevecchi and Myers 1995), behavioral complications can also undermine the utility of such data in population models. Food habits data may reflect relative prey availability more than abundance, as predators tend to concentrate foraging effort on the most available prey. However, these are complications that similarly undermine the integrity of fisheries-dependent time series (Cairns 1992, Walters 2003).

Several factors make the utility of this data set as an indicator of year-class strength appealing. First, shortbelly are generally quite easy to distinguish in the sampling regime, and are the overwhelmingly dominant rockfish species found in murre diets (Ainley et al. 1996). Second, research has shown that common murrens prefer to forage locally for juvenile rockfish during their breeding season (May-June, when juvenile rockfish are most abundant), because the close proximity to the breeding grounds reduces foraging trip duration. In years when juvenile rockfish are less abundant, murrens forage in coastal waters for northern anchovy and other forage fishes (Ainley and Boekelheide 1990, Miller and Sydeman 2004). Third, the species composition of common murre prey has been at least partially validated by comparisons with rhinoceros auklet (*Cerorhinca monocerata*) food habits for 1987-2004,

in which prey are physically taken from the sampled birds and identified to species in a controlled setting (Sydeman et al. 2001). Finally, the proportion of juvenile rockfish in murre diets is highly correlated to the NMFS midwater trawl estimates of juvenile abundance, which indexes juvenile rockfish abundance over a larger spatial extent (Ainley et al. 1993, Mills et al. in press). Individual prey observations were treated with a binomial GLM to obtain annual indices and remove calendar date effects. Annual indices were arcsine transformed, as is appropriate for indices of proportionality (Zar 1996). The resulting index was included in the model as an index of age 0 abundance for the period from 1975 to 2004.

Sea lion food habits data

Another source of food habits data is based on ongoing monitoring of California sea lion (*Zalophus californianus*) food habits in the Channel Islands (Lowry et al. 1990, 1991; Lowry and Carretta 1999). Scat samples have been collected at regular (monthly to quarterly) intervals from 1981 to the present, from San Nicolas, San Clemente, and Santa Barbara islands. Prey species have been identified to the lowest possible taxon based on recovered hard parts (otoliths, cephalopod beaks, shark teeth, and invertebrate exoskeletal fragments). During 1981-2003, over 9,300 samples with identifiable prey remains were collected and enumerated. Shortbelly rockfish were among the most frequently occurring prey, generally present in 10 to 30% of samples (other *Sebastes* were relatively infrequent). The presence/absence sample data were treated with a binomial GLM (logit link) with year, island, and seasonal effects, and the arcsine transformed year effects were used as an index of relative abundance. Length frequency information was also available to assess the vulnerable portion of the shortbelly stock being predated upon, with lengths reconstructed from otolith lengths in specimens that were not eroded by digestion, based on the otolith to fish length regression reported in Wyllie Echeverria (1987). A total of over 4,500 reconstructed lengths were available, in which strong cohorts are clearly visible over time (Fig. 2). The rapid decline of fish larger than 20 cm suggests that sea lions are primarily foraging on younger, more shallowly distributed shortbelly rockfish, which may become less vulnerable as they move into deeper water with age and size. Although California sea lions usually forage between depths of 20 to 280 meters, Melin and DeLong (2002) found that most dives for female sea lions tended to be shallower than 80 meters, such that fish in deeper waters could be less vulnerable. Effective sample sizes were iteratively adjusted from the number of observations to the effective sample size estimated by the model.

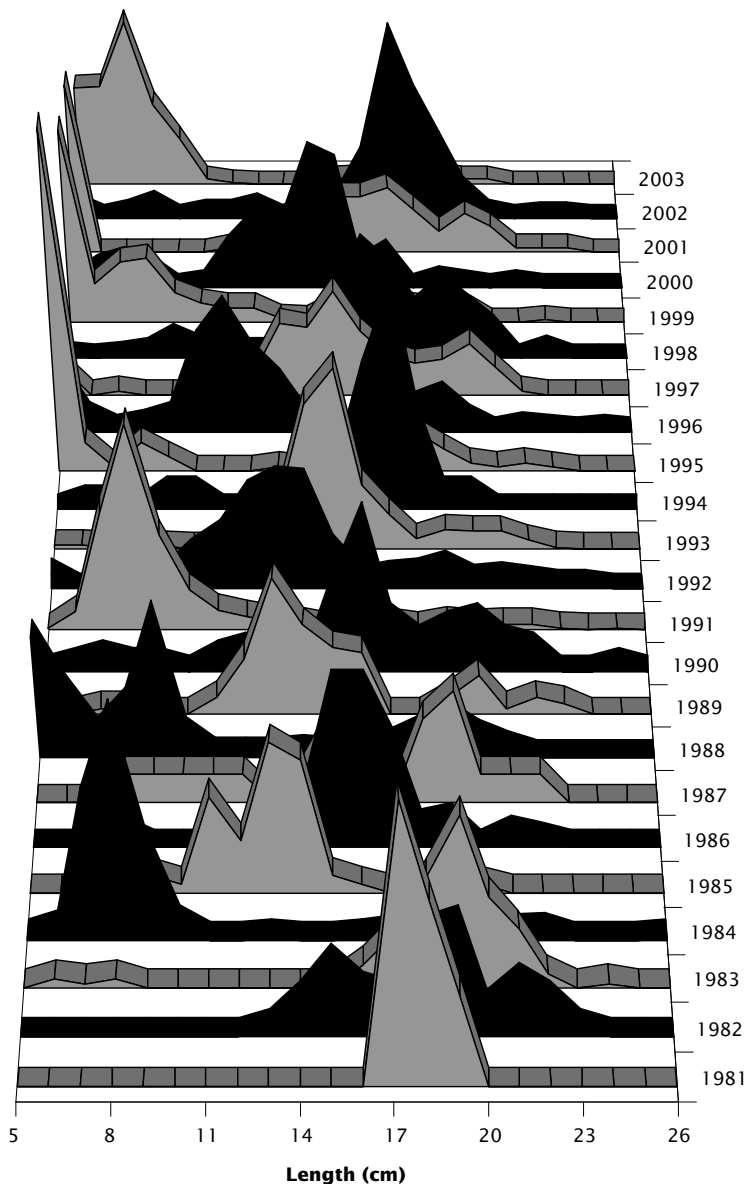


Figure 2. Length frequency composition derived from otoliths collected in sea lion scat samples from the Southern California Bight, 1981-2003, based on otolith length/fish length regressions.

Model configuration

We explored a wide range of model structures and trade-offs between model complexity and the informative limits of the data. Through the process of evaluating alternative model configurations, we developed a base model that had growth and the natural mortality rate estimated externally, and sigma-R (the standard deviation of the lognormally distributed recruitment deviations) fixed at 1. The model uses a Mace-Doonan (Mace and Doonan 1988) stock recruitment relationship, where R_0 , or equilibrium recruitment, represents the number of recruits that would be expected on average for an unfished stock, and steepness (h) refers to the amount of compensation in the spawner-recruit relationship. We estimated equilibrium recruitment (R_0), but found that the data were inadequate to provide a meaningful estimate of steepness. As steepness values close to 1 represent high compensation and those close to 0.2 represent little or no compensation, we fixed steepness at 0.65, consistent with Dorn (2002). Similar approaches are taken for most West Coast groundfish assessments of commercially exploited species.

An additional parameter estimated in this model was a scaling factor for the initial biomass, which allows the starting biomass value to deviate from the model estimated equilibrium biomass. As marine populations are typically not stationary, the equilibrium biomass is best described as the theoretical average level of biomass (or spawning biomass) around which the population would fluctuate in the absence of fishing. Allowing the starting biomass to be higher or lower than this value is typically not done in assessments for commercially exploited species, where historical catches are believed to have a greater impact on population trajectories than recruitment variability, but is a logical approach for this model. Other parameters that were freely estimated include recruitment deviations from 1960 to 2004 (which reflect relatively stronger or weaker year classes than would be expected from the spawner-recruit relationship), logistic selectivity curve parameters for fisheries catches (based on measurements of landed fish) and the Triennial Trawl Survey length data, and parameters for a double-logistic selectivity curve for the sea lion prey length composition data (in which only the descending limb of the double logistic was estimated; fish were assumed to be fully selected at 5 cm length). Selectivity curves for the CalCOFI data and the larval production point estimate were fixed at the maturity function. Selectivity for the pelagic juvenile (age-0) indices (the juvenile survey and the seabird data) were age-based; fish were assumed to be fully vulnerable at age 0, and fully invulnerable at all ages thereafter. The total number of freely estimated parameters in the model was 54; most were recruitment deviations (46) or selectivity parameters (6), and the remaining two were the mean unfished recruitment level and the ratio of starting biomass to the mean unfished biomass. We also evaluated the sensitivity of the model to a wide range

of different parameter values, including freeing up parameters such as natural mortality, the duration over which recruitment deviations were freed (e.g., to 1950, or beginning in 1975), the standard deviation of lognormal recruitment (σ -R), selectivity curve parameterization, and other factors. For brevity, only a summary of model sensitivities is provided here.

Results

The results demonstrate that the biomass of shortbelly rockfish has fluctuated substantially over time, with major declines apparent between the 1950s and 1960s, and from the early 1990s to the present (Fig. 3). The model estimated a mean “unfished” spawning biomass level of 48,000 tons, an initial (1950) spawning biomass of 187,000 tons, and a total spawning biomass in 2005 of 35,000 tons. By basing the equilibrium spawning biomass on the long-term average biomass level, the resulting “depletion” level of the stock in 2005 was 73% of the averaged unfished level, although it was less than 20% of the estimated 1950 abundance and 50% of the estimated 1991 abundance. Although recruitment was estimated from 1960 onward, only years after 1974 were meaningfully informed by data; prior to this the model was fitting to the trends inferred by CalCOFI data. The model clearly suggests a long period of poor recruitment through most of the 1990s, associated with a significant decline in biomass, a trend that is reflected in all of the recruitment and biomass indices used in the model. The consequence of fisheries was estimated to be negligible (an exploitation rate less than 0.01) in all years except the mid-1960s, suggesting that fishing mortality has probably not had a substantive impact on this stock since the days of the foreign fisheries, although very modest impacts may be plausible.

The fits to the survey data, particularly the CalCOFI data, demonstrated the challenge of interpreting a low frequency signal from highly variable time series (Fig. 4). For the fit to the CalCOFI data in particular, note that the recruitment deviations for the period between 1950 and 1960 were fixed at the equilibrium recruitment, in order to phase in a mean recruitment level for the early part of the time series. Relative abundance levels were highly sensitive to the time in which recruitment deviations were free, particularly given the very rapid decline in the CalCOFI index associated with the 1958-1959 El Niño event. Tuning to an equilibrium recruitment that captured both the high and the low index values throughout the early part of the time series is a reasonable balancing of model freedom and the limitations of the data. Furthermore, there is considerable high frequency variability in larval distribution and abundance inferred in the CalCOFI time series, that may be partially related to variability in ocean conditions and reproductive output (as

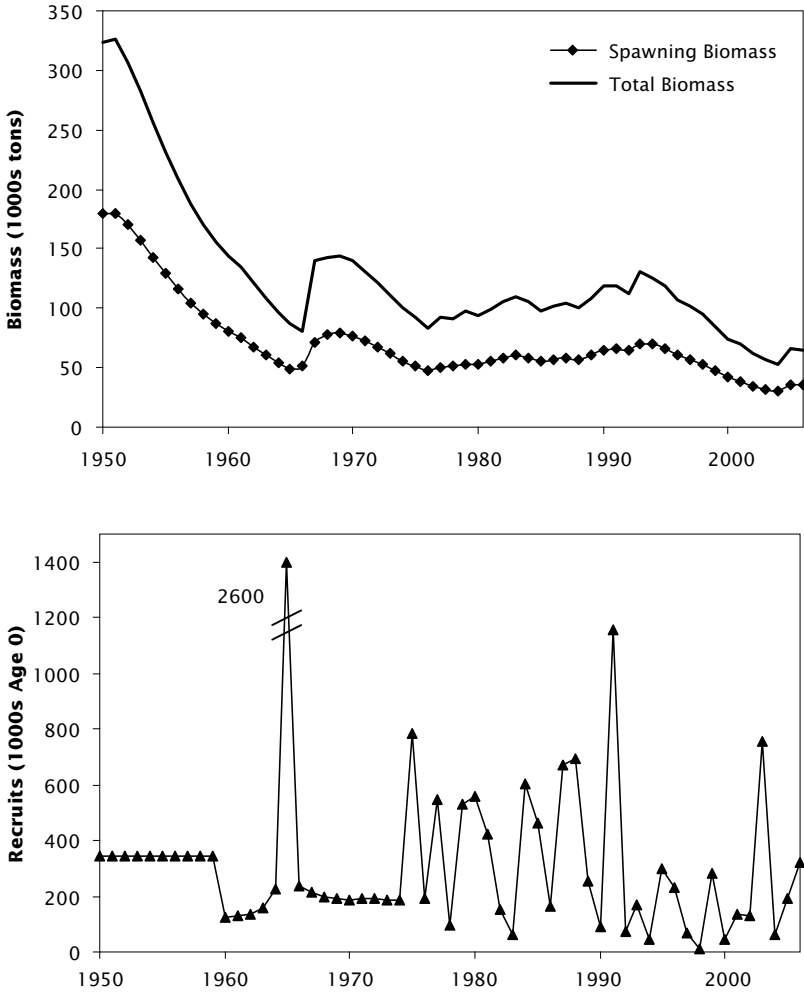


Figure 3. Results of the shortbelly rockfish base model. Total biomass and spawning stock biomass (SSB) estimates (top) and estimates of annual recruitment (bottom).

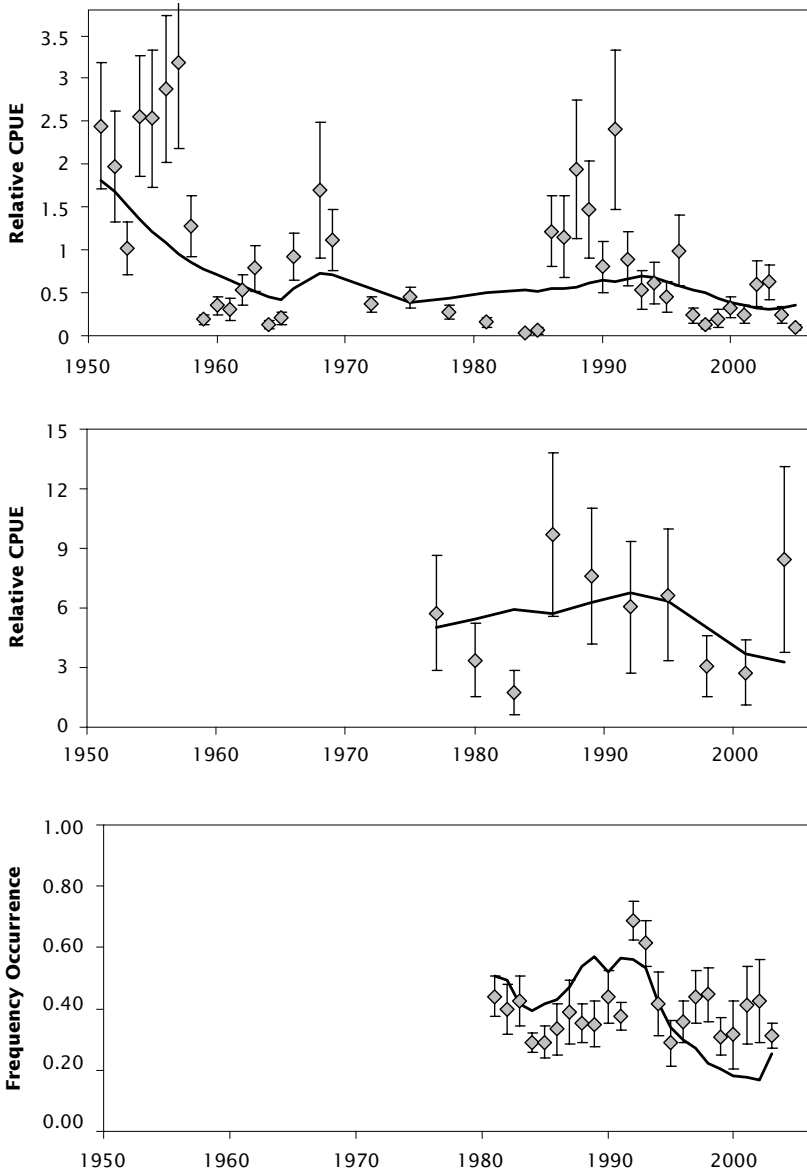


Figure 4. Model fits to relative abundance data: CalCOFI larval abundance (top), Triennial Trawl Survey (middle), and sea lion frequency of occurrence (bottom). Data are shown as points with standard error bars; model predicted fits are lines.

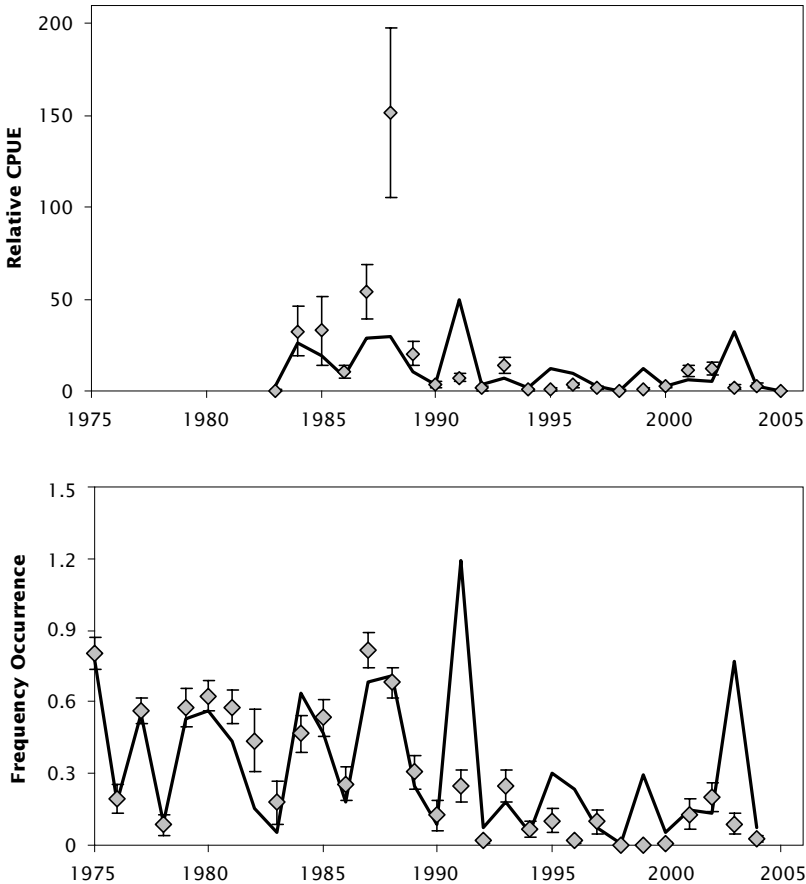


Figure 5. Model fits to Central California juvenile trawl survey (top) and arcsin transformed murre food habits data (bottom). Data are shown as points with standard error bars; model predicted fits are lines.

well as observation error), rather than actual interannual changes in abundance (MacGregor 1986, Moser et al. 2000; see also Lenarz and Wyllie Echeverria 1986). The fit to the Triennial Trawl Survey index is not remarkable, and the index itself is not very informative, which is not surprising for a patchily distributed, semi-pelagic species. Although the model does capture the declining trend from the late 1980s through 2001, the model estimates nearly identical trends in the absence of this data series. Finally, we note that although the relative abundance index generated from the sea lion food habits data seems to be somewhat

uninformative, the length composition data associated with this index are very informative, and clearly reflect strong cohorts moving through the fishery (Fig. 6). Although the model fit to the smallest size classes of the length frequency data is poor, reflecting a mismatch between the actual size of pelagic juveniles (age 3 to 6 months) and the growth model predictions of size at age 6 months, fits to the larger size classes in the length composition data are reasonable.

In general, the model estimated a higher natural mortality rate (0.35) and greater recruitment deviation (σ - R , 1.6) when these parameters were freely estimated. This was largely due to the improvement in model fit to the variability in the CalCOFI data; fits to other data were generally the same or eroded. Although it is possible that a higher natural mortality rate, or possibly a time or age-varying rate, could be reasonable for this species, we currently have inadequate information to justify such changes. As with any population model, the benefits and drawbacks of freely estimating parameters such as natural mortality are complex. We also considered the consequences of removing data sets sequentially on the model trend and behavior. Although different results were obtained when the CalCOFI index was excluded, due to the fact that no other indices extend further back in time than 1975, the trends from the late 1970s through 2005 were very similar even without these data. Similarly, the estimated recruitments changed significantly when the sea lion length composition data were removed, as these data tended to be more informative than either the juvenile survey or seabird data. This spoke to a key issue that arose often during the model development and evaluation, as data strongly suggest differences in recruitment north and south of Point Conception, suggesting that individual models for these two regions are likely to be appropriate. The lack of a consistent time series of age data with which to better validate the recruitment variability, and the problems inherent in using both proportional indices of abundance based on food habits data, are also noteworthy, as well as problems commonly faced in assessments of exploited species.

Discussion

Although there is considerable uncertainty surrounding the model results, and the lack of fishery-dependent data has led us to rely primarily on less traditional sources of information, the results of the model are consistent with both what is known about shortbelly life history and the available data regarding juvenile and adult abundance. Even without having a clear sense of the causes of such fluctuations, the most important result is the insight that substantive population variability has occurred for an (effectively) unexploited species in the California Current. Although fishery-independent drivers of popula-

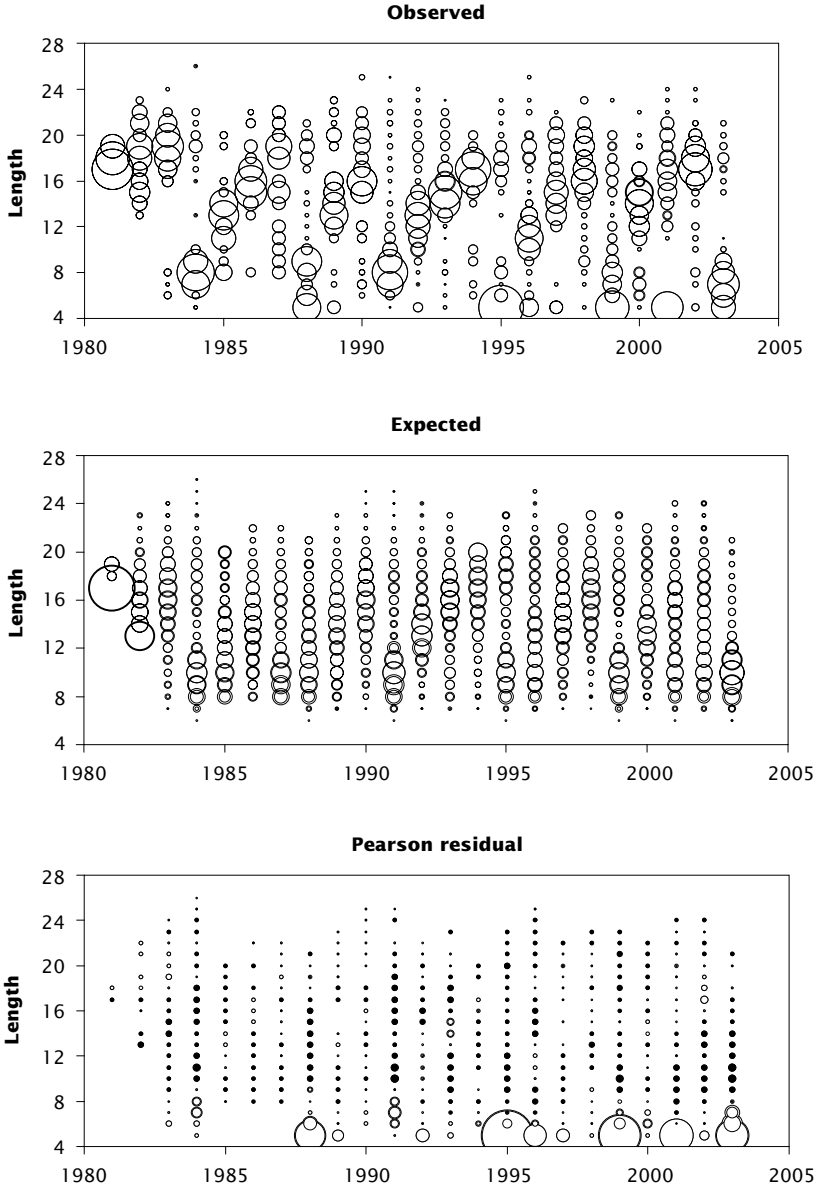


Figure 6. Plots of fits to the sea lion length frequency data, with observed data (top), predicted length composition (middle), and Pearson residuals (bottom). For the residuals, solid circles reflect negative values, open circles reflect positive values. Note that the poor fit to the smallest size classes of the length frequency data reflects the mismatch between the actual size of age zero juveniles and the growth model predictions of size at age zero.

tion variability have been described for many other California Current species (Baumgartner et al. 1992, MacCall 1996), comparable changes are less evident for groundfish, for which management tends to rely on equilibrium-based assessment methods and biological reference points. Such reference points have proven critical to implementing sustainable management measures, by portraying the consequences of exceeding biological limits to decision makers in terms of the risk to the resource (Mace 2001). Yet such reference points are unavoidably based on the assumption of stationarity, such that the biomass at the beginning of the exploitation history is assumed to represent a steady-state unfished equilibrium. However, it should be acknowledged that the life history traits of shortbelly rockfish, which is more similar to a forage fish than most longer-lived, slower growing and larger *Sebastes*, may impede the utility of considering this species as a "control" for commercially important stocks with different life history types.

As Hollowed et al. (2000) suggest, the role of all fisheries models, whether single or multispecies, is to understand and inform decision-makers of the consequences of fishing or other activities on living resources and the ecosystem in which they exist. They described three fundamental processes that structure populations: competition, predation (including fishing), and environmental variability. Any of these factors could plausibly account for the observed changes in the abundance of shortbelly rockfish in the California Current. For example, California sea lions, important predators of shortbelly rockfish, were severely depleted throughout the early part of the twentieth century as a result of hunting and culling (Cass 1985). Following increasing levels of protection from such impacts from the 1950s through 1970s, rapid population increases have been observed. Currently population growth rates regularly approach 9% per year, such that the population is thought to be well over 200,000 animals (Carretta et al. 2002). Models that account for changing natural mortality rates, by incorporating relative changes in the abundance of key predators, have been shown to be plausible for some species (Livingston and Methot 1998), and are worth exploring here. Environmental variability is also likely to be a factor. Large-scale changes in both physical and biological conditions throughout the California Current, including monotonic changes, have been well documented (McGowan et al. 1998, Francis et al. 1998, Mendelssohn et al. 2003), and climate information has the potential to inform population models under some circumstances (Maunder and Watters 2003, Schirripa and Colbert 2005). It has also been suggested that the observed long-term dynamics of many marine populations in the Northeast Pacific may not be a direct function of low frequency climate variation, but rather are responses to nonlinear amplification of physical forcing by ecological processes (Hsieh et al. 2005). Regardless of the mechanism, shortbelly rockfish have a potentially important role

as a species from which further exploration can be made of the linkages between population variability and environmental factors.

Acknowledgments

We thank Richard Charter (SWFSC) for providing CalCOFI data, Mark Wilkins (AFSC) and Beth Horness (NWFSC) for providing Triennial Trawl Survey data, Mark Maunder and Richard Methot for help with Stock Synthesis 2, Yvonne deReynier for help with the regulatory history, and Heather Constable for her insights from genetic analysis of stock structure. Xi He and Brian Wells provided helpful comments on earlier drafts of this manuscript, and the comments and suggestions of Jon Heifetz and two anonymous reviewers greatly improved the final manuscript. Finally, the authors are indebted to Chris Francis, Bill Lenarz, George Watters, and Tom Ghio for their constructive, thorough, and very helpful comments and guidance during a comprehensive review of the data and model presented in this manuscript.

References

- Adams, P.B., and D.F. Howard. 1996. Natural mortality of blue rockfish during their first year in nearshore benthic habitats. *Fish. Bull. U.S.* 94:156-162.
- Ainley, D.G., and R.J. Boekelheide (eds.). 1990. *Seabirds of the Farallon Islands: Structure and dynamics of an upwelling-system community*. Stanford University Press, Palo Alto.
- Ainley, D.G., W.J. Sydeman, R.H. Parrish, and W.H. Lenarz. 1993. Oceanic factors influencing distribution of young rockfish (*Sebastes*) in central California: A predator's perspective. *Calif. Coop. Ocean. Fish. Investig. Rep.* 34:133-139.
- Ainley, D.G., L.B. Spear, S.G. Allen, and C.A. Ribic. 1996. Temporal and spatial patterns in the diet of the common murre in California waters. *Condor* 98:691-705.
- Alonzo, S.H., M. Key, T. Ish, and A.D. MacCall. 2004. Status of the California sheephead (*Semicossyphus pulcher*) stock. California Department of Fish and Game Report.
- Antonelis, G.A., and C.H. Fiscus. 1980. The pinnipeds of the California Current. *Calif. Coop. Ocean. Fish. Investig. Rep.* 21:68-78.
- Baumgartner, T.R., A. Soutar, and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin. *Calif. Coop. Ocean. Fish. Investig. Rep.* 33:24-40.
- Cairns, D.K. 1992. Bridging the gap between ornithology and fisheries science: Use of seabird data in stock assessment models. *Condor* 94:811-824.

- Carretta, J.V., J. Barlow, K.A. Forney, M.M. Muto, and J. Baker. 2002. U.S. Pacific marine mammal stock assessments: 2002. NOAA Tech. Memo. NMFS-SWFSC-346.
- Cass, V.L. 1985. Exploitation of California sea lions, *Zalophus californianus*, prior to 1972. Mar. Fish. Rev. 47:36-38.
- Chess, J.R., S.E. Smith, and P.C. Fischer. 1988. Trophic relationships of the shortbelly rockfish, *Sebastes jordani*, off central California. Calif. Coop. Ocean. Fish. Investig. Rep. 29:129-136.
- Constable, H. 2006. Population genetics of juvenile *Sebastes jordani*, shortbelly rockfish, along the California coast. M.S. thesis, San Francisco State University. 68 pp.
- Dick, E.J. 2004. Beyond "lognormal versus gamma" discrimination among error distributions for generalized linear models. Fish. Res. 70:351-366.
- Dorn, M.W. 2002. Advice on West Coast rockfish harvest rates from Bayesian meta-analysis of stock-recruit relationships. N. Am. J. Fish. Manag. 22:280-300.
- Francis, R.C., S.R. Hare, A.B. Hollowed, and W.S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the Northeast Pacific. Fish. Oceanogr. 7:1-21.
- He, X., D. Pearson, E.J. Dick, J. Field, S. Ralston, and A.D. MacCall. 2006. Status of the widow rockfish resource in 2005. In: Status of the Pacific Coast groundfish fishery through 2005, stock assessment and fishery evaluation: Stock assessments and rebuilding analyses, vol. 3. Pacific Fishery Management Council, Portland, Oregon.
- Heimann, R.F.G. 1963. Trawling in the Monterey Bay area, with special reference to catch composition. California Department of Fish and Game 49:152-173.
- Helser, T., I.J. Stewart, G. Fleischer, and S. Martell. 2006. Stock assessment of Pacific hake (whiting) in U.S. and Canadian waters in 2006. In: Status of the Pacific Coast groundfish fishery through 2005: stock assessment and fishery evaluation, vol. 7. Pacific Fishery Management Council, Portland, Oregon.
- Hoening, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. U.S. 82:898-903.
- Hollowed, A.B., N. Bax, R. Beamish, J. Collie, M. Fogarty, P. Livingston, J. Pope, and J.C. Rice. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES J. Mar. Sci. 57:707-719.
- Hsieh, C., S.M. Glaser, A.J. Lucas, and G. Sugihara. 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature 435:336-340.
- Kato, S. 1981. Checking out shortbelly rockfish: Colinitino Rose II's mission accomplished. Pacific Fishing, Nov. 1981, pp. 96-100.
- Lenarz, W.H. 1980. Shortbelly rockfish, *Sebastes jordani*: A large unfished resource in waters off California. Mar. Fish. Rev. 42:34-40.

- Lenarz, W.H., and T. Wyllie Echeverria. 1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. *Fish. Bull. U.S.* 84:743-745.
- Livingston, P.A., and R.D. Methot. 1998. Incorporation of predation into a population assessment model of Eastern Bering Sea walleye pollock. In: F. Funk, T.J. Quinn II, J. Heifetz, J.N. Ianelli, J.E. Powers, J.F. Schweigert, P.J. Sullivan, and I.I. Zhang (eds.), *Fishery stock assessment models*. Alaska Sea Grant, University of Alaska Fairbanks, pp. 663-678.
- Love, M.S., M. Yoklavich, and L. Thorsteinson. 2002. *The rockfishes of the Northeast Pacific*. University of California Press, Berkeley.
- Lowry, M.S., and J.V. Carretta. 1999. Market squid (*Loligo opalescens*) in the diet of California sea lions (*Zalophus californianus*) in southern California (1981-1995). *Calif. Coop. Ocean. Fish. Investig. Rep.* 40:196-207.
- Lowry, M.S., C.W. Oliver, C. Macky, and J.B. Wexler. 1990. Food habits of California sea lions *Zalophus californianus* at San Clemente Island, California, 1981-86. *Fish. Bull. U.S.* 88:509-521.
- Lowry, M.S., B.S. Stewart, C.B. Heath, P.Y. Yochem, and J.M. Francis. 1991. Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981-86. *Fish. Bull. U.S.* 89:331-336.
- MacCall, A.D. 1996. Patterns of low-frequency variability in fish populations of the California Current. *Calif. Coop. Ocean. Fish. Investig. Rep.* 37:100-110.
- MacCall, A.D. 2003. Status of bocaccio off California in 2003. In: Appendix to the status of the Pacific coast groundfish fishery through 2003: Stock assessment and fishery evaluation. Pacific Fishery Management Council, Portland, Oregon. 61 pp.
- Mace, P.M. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. *Fish. Fish.* 2:2-32.
- Mace, P.M., and I.J. Doonan. 1988. A generalized bioeconomic simulation model for fish population dynamics. New Zealand Fishery Assessment Research Document 88/4. Wellington.
- MacGregor, J.S. 1986. Relative abundance of four species of *Sebastes* off California and Baja California. *Calif. Coop. Ocean. Fish. Investig. Rep.* 27:121-135.
- Maunder, M.N., and A.E. Punt. 2004. Standardizing catch and effort data: A review of recent approaches. *Fish. Res.* 70:141-159.
- Maunder, M.N., and G.M. Watters. 2003. A general framework for integrating environmental time series into stock assessment models: Model description, simulation testing, and example. *Fish. Bull. U.S.* 101:89-99.
- McGowan, J.A., D.R. Cayan, and L.M. Dorman. 1998. Climate, ocean variability and ecosystem response in the Northeast Pacific. *Science* 281:210-217.
- Melin, S.R., and R.L. DeLong. 2002. At-sea distribution and diving behavior of California sea lion females from San Miguel Island, California. In: D.R. Browne, K.L. Mitchell, and H.W. Chaney (eds.), *Proceedings of the Fifth California Islands Symposium*. Minerals Management Service, pp. 407-412.

- Mendelssohn, R., F.B. Schwing, and S. J. Bograd. 2003. Spatial structure of sub-surface temperature variability in the California Current, 1950-1993. *J. Geophys. Res.* 108:3093.
- Merkel, T.J. 1957. Food habits of the king salmon, *Oncorhynchus tshawytscha* (Walbaum), in the vicinity of San Francisco, California. *California Department of Fish and Game* 43:249-270.
- Methot, R. 2005. User manual for the assessment program Stock Synthesis 2 (SS2). Model Version 1.19. 47 pp.
- Miller, A.K., and W. Sydeman. 2004. Rockfish response to low-frequency ocean climate change as revealed by the diet of a marine bird over multiple time scales. *Mar. Ecol. Prog. Ser.* 281:207-216.
- Mills, K.L., S. Ralston, T. Laidig, and W.J. Sydeman. 2006. Diets of top predators indicate pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current system. *Fish. Oceanogr.* In press.
- Montevecchi, W.A., and R.A. Myers. 1995. Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. *Mar. Ecol. Prog. Ser.* 117:1-9.
- Moser, H.G., R.L. Charter, W. Watson, D.A. Ambrose, J.L. Butler, S.R. Charter, and E.M. Sandknop. 2000. Abundance and distribution of rockfish (*Sebastes*) larvae in the southern California Bight in relation to environmental conditions and fishery exploitation. *Calif. Coop. Ocean. Fish. Investig. Rep.* 41:132-147.
- Pearson, D.E., J.E. Hightower, and J.T.H. Chan. 1989. Age, growth, year class strength and potential yield for shortbelly rockfish. In: Status of the Pacific Coast groundfish fishery through 1989 and recommended acceptable biological catches for 1990. Pacific Fishery Management Council, Portland, Oregon.
- Pearson, D.E., J.E. Hightower, and J.T.H. Chan. 1991. Age, growth, and potential yield for shortbelly rockfish *Sebastes jordani*. *Fish. Bull. U.S.* 89:403-409.
- Ralston, S., and D.F. Howard. 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. *Fish. Bull. U.S.* 93:710-720.
- Ralston, S., D. Pearson, and J. Reynolds. 1998. Status of the chilipepper rockfish in 1998. In: Appendix to status of the Pacific Coast groundfish fishery through 1998 and recommended acceptable biological catches for 1999: Stock assessment and fishery evaluation. Pacific Fishery Management Council, Portland, Oregon. 81 pp.
- Ralston, S., J.R. Bence, M.B. Eldridge, and W.H. Lenarz. 2003. An approach to estimating rockfish biomass based on larval production, with application to *Sebastes jordani*. *Fish. Bull. U.S.* 101:129-146.
- Rogers, J.B. 2003. Species allocation of *Sebastes* and *Sebastolobus* sp. caught by foreign countries from 1965 through 1976 off Washington, Oregon, and California, USA. NOAA Tech. Memo. NMFS-NWFSC-57.

- Schirripa, M.J., and J.J. Colbert. 2005. Status of the sablefish resource off the continental U.S. Pacific coast in 2005. In: Status of the Pacific Coast groundfish fishery through 2005, stock assessment and fishery evaluation: Stock assessments and rebuilding analyses. Pacific Fishery Management Council, Portland, Oregon. 221 pp.
- Stefansson, G. 1996. Analysis of groundfish survey abundance data: Combining the GLM and delta approaches. ICES J. Mar. Sci. 53:577-588.
- Stroud, R.K., G.H. Fiscus, and H. Kajimura. 1981. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington. Fish. Bull. U.S. 78:951-959.
- Sydeman, W.J., M.M. Hester, J.A. Thayer, F. Gress, P. Martin, and J. Buffa. 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969-1997. Prog. Oceanogr. 49:309-329.
- Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. Can. J. Fish. Aquat. Sci. 60:1433-1436.
- Weinberg, K.L., M.E. Wilkins, F.R. Shaw, and M. Zimmerman. 2002. The 2001 Pacific West Coast bottom trawl survey of groundfish resources: Estimates of distribution, abundance and length and age composition. NOAA Tech. Memo. NMFS AFSC 128. 149 pp.
- Wyllie Echeverria, T. 1987. Relationship of otolith length to total length in rockfishes from northern and central California. Fish. Bull. U.S. 85:383-387.
- Zar, J.H. 1996. Biostatistical analysis. Prentice Hall, New Jersey.
- Zimmermann, M., M.E. Wilkins, K.L. Weinberg, R.R. Lauth, and F.R. Shaw. 2001. Retrospective analysis of suspiciously small catches in the National Marine Fisheries Service West Coast Triennial Bottom Trawl Survey. NOAA AFSC Proc. Rep. 2001-03. 109 pp.