

Population Trends and Trophic Dynamics in Pacific OCS Ecosystems: What Can Monitoring Data Tell Us?

Final Technical Summary

Final Study Report



U.S. Department of the Interior Minerals Management Service Pacific OCS Region

Population Trends and Trophic Dynamics in Pacific OCS Ecosystems: What Can Monitoring Data Tell Us?

Final Technical Summary

Final Study Report

Authors

Russell J. Schmitt Andrew Brooks Sally J. Holbrook Principal Investigators

Prepared under MMS Cooperative Agreement No. 14-35-0001-30758 by Coastal Marine Institute Marine Science Institute University of California Santa Barbara, CA 93106-6150

U.S. Department of the Interior Minerals Management Service Pacific OCS Region

Camarillo October 2006

Disclaimer

This report has been reviewed by the Pacific Outer Continental Shelf Region, Minerals Management Service, U.S. Department of the Interior and approved for publication. The opinions, findings, conclusions, or recommendations in this report are those of the authors, and do not necessarily reflect the views and policies of the Minerals Management Service. Mention of trade names or commercial products does not constitute an endorsement or recommendation for use. This report has not been edited for conformity with Minerals Management Service editorial standards.

Availability of Report

Extra copies of the report may be obtained from:

U.S. Dept. of the Interior Minerals Management Service Pacific OCS Region 770 Paseo Camarillo Camarillo, CA 93010 Phone: 805-389-7621

A PDF file of this report is available at: http://www.coastalresearchcenter.ucsb.edu/CMI/

Suggested Citation

The suggested citation for this report is:

Schmitt, R.J., S.J. Holbrook, A. Brooks. Population Trends and Trophic Dynamics in Pacific OCS Ecosystems: What Can Monitoring Data Tell Us? MMS OCS Study 2006-055. Coastal Research Center, Marine Science Institute, University of California, Santa Barbara, California. MMS Cooperative Agreement Number 14-35-0001-30758. 65 pages.

Table of Contents

L TECHNICAL SUMMARY
L STUDY REPORT
Chapter 1
Abstract
Introduction
Methods
Results
Discussion
Acknowledgements
Chapter 2
Abstract
Introduction
Materials and Methods
Results
Discussion
Acknowledgements
Chapter 3
Abstract
Introduction
Materials and Methods
Results
Temporal Patterns at Santa Cruz Island
Temporal Patterns in the Southern California Bight
Evidence for response of trophic groups
Discussion
Acknowledgements
RENCES

List of Tables

CHAPTER 1

Table 1.	Criteria used to classify species and abundance	15
Table 2:	Values of the computed cross-correlation coefficients	17

CHAPTER 3

Table 1:	Mean proportional change in abundance	41
Table 2:	Mean proportional change among trophic groups	41

List of Figures

CHAPTER 1

Figure 1. Map of the Southern California Bight	9
Figure 2. Time series of standardized temperatures and zooplankton	10
Figure 3. Relationship between abundances	14
Figure 4. Time series of the average deviation in standardized abundance	16
Figure 5. Values of the cross-correlational coefficient	18
Figure 6. Values of the cross-correlational coefficient	19

CHAPTER 2

Figure 1.	The pattern of co-variation in magnitudes of temporal variability	28
Figure 2.	The relationships between the magnitudes of inter-annual variability	29
Figure 3.	The pattern of co-variation in magnitudes of inter-annual variability	30

CHAPTER 3

Figure 1. Density of kelp bass over time	. 37
Figure 2. Densities of surfperch at Santa Cruz Island	. 38
Figure 3. Abundance of the food base for surfperch at Santa Cruz Island	. 39
Figure 4. Trends in algal biomass and cover over time	. 40

FINAL TECHNICAL SUMMARY

STUDY TITLE: Population Trends and Trophic Dynamics in Pacific OCS Ecosystems: What Can Monitoring Data Tell Us?

REPORT TITLE: Population Trends and Trophic Dynamics in Pacific OCS Ecosystems: What Can Monitoring Data Tell Us?

CONTRACT NUMBER: 14-35-0001-30758

SPONSORING OCS REGION: Pacific

APPLICABLE PLANNING AREA(S): Southern California

FISCAL YEAR(S) OF PROJECT FUNDING: FY 97, FY 98, FY 99, FY 00, FY 01

COMPLETION DATE OF REPORT: October 2006

COSTS: FY 97-01 - \$195,000

CUMULATIVE PROJECT COST: \$195,000

PROJECT MANAGER: Russell J. Schmitt

AFFILIATION: Coastal Research Center, Marine Science Institute, University of California, Santa Barbara, CA 93106

ADDRESS: University of California, Santa Barbara, CA 93106

PRINCIPAL INVESTIGATORS: Russell J. Schmitt^{1,2} and Andrew J. Brooks^{1,3}

ADDRESSES: ¹Coastal Research Center, ² Department of Ecology, Evolution and Marine Biology, ³Marine Science Institute, University of California, Santa Barbara, CA 93106-6150

KEY WORDS: Trophic dynamics; climate change; food web ecology; PDO; Southern California bight

BACKGROUND: A number of entities (including MMS) have devoted considerable effort and resources to the long-term monitoring of various components of the coastal marine ecosystems in the Southern California outer-continental shelf (OCS) region. The primary goals of such monitoring programs are to estimate the current state of the biota and to identify long-term trends in population demographics. Data from such studies are vital to resource and regulatory agencies as they provide critical baseline information needed for accurate assessment of potential effects arising from such particular activities as offshore oil and gas production. The

fundamental need for such information is evidenced by the growing number of coastal marine monitoring programs that have been implemented in Southern California.

The vast amount of long-term data on nearshore biota collected by a large number of separate monitoring programs in the Southern California OCS region represents a relatively untapped "gold mine" of information for environmental managers. The occurrence of a regime shift in the ocean climate in the North Pacific (PDO) in the past two decades provides a unique opportunity to determine whether and how various components of the biota have responded to this natural perturbation. Data from long-term monitoring programs not only indicate the current state and recent history of the biota, they can reveal much about the ecological structure of various coastal ecosystems, including the dynamical behavior and regulation of different food webs. Such knowledge provides managers with better understanding and enhanced predictive ability regarding the potential impacts to these ecosystems from other potential sources of disturbance. Further, analyses of existing data sets can expose whether and how our ability to estimate or interpret responses of the biota may be constrained by present monitoring practices.

OBJECTIVES: Our MMS-UC CMI funded research encompassed two separate objectives: (1) the analysis and synthesis of existing monitoring data for long-term trends in the biota of the Southern California Bight and (2) the continued annual surveys of subtidal reef communities at Santa Cruz Island.

DESCRIPTION: We initially obtained data from 5 separate monitoring programs enumerating the flora and fauna of southern California nearshore marine communities in three different ecological systems, subtidal rocky reef, kelp bed, and open ocean/pelagic, between 1977 and 2006. These datasets included the CalCOFI monitoring program, King Harbor monitoring data collected by John Stephens Jr., Occidental College, Southern California Edison NPDES monitoring data for the San Onofre Nuclear Generating Station and the Huntington Beach, Redondo Beach and Ormond Beach Steam Electrical Generating Stations, National Park Service Kelp Forest Monitoring Program data for the northern Channel Islands, and data collected by Russell Schmitt and Sally Holbrook, University of California, Santa Barbara as part of their ongoing monitoring of subtidal communities around Santa Cruz Island. Subsequent to our initial analyses, we also obtained data collected by the National Marine Fisheries Services during their triennial surveys of west coast groundfishes. This last dataset covered roughly the same time period as our original datasets, 1977-2001, but concentrated on fish species inhabiting the deeper waters of the continental shelf (55-500m) along the west coast of the United States from Monterey Bay, California to Alaska.

Data were standardized between studies by re-expressing data on population densities as the percent change in initial population density over the time period 1977 through 1999-2000 and then again over the time period 1999-2000 through 2005-2006. Organisms within a given community were assigned to one of four trophic categories, primary producer, primary, secondary, or tertiary consumer, mode of reproduction, extent of geographic range, association with benthic or pelagic food webs, and habitat based on published life history information. Time-series analyses were performed on these data sets to describe temporal trends and explore the timing and magnitude of the observed changes.

STUDY RESULTS: (1) The analysis and synthesis of existing monitoring data for long-term trends in the biota of the Southern California Bight:

Trends in population abundances following the regime shift of the PDO to a warm water phase in 1977 show consistent declines in all three ecological systems, subtidal rocky reef, kelp bed, and open ocean/pelagic, between 1977 and 2001. Within each system examined, trends for each component trophic level showed approximately the same magnitude of decline. This pattern held across spatial scales ranging from a single island (Santa Cruz Island) within the northern Channel Islands group to the entire Southern California Bight suggesting genuine regional declines in abundances rather than a redistribution of individuals in response to changing environmental conditions. Also interesting is the fact that data collected using extremely different methodologies, e.g., coastal power plant impingement studies versus diver visual surveys, provide similar estimates of the magnitudes of these declines. Beginning in 2001 and following a reversal in the PDO to a cold water phase, some of these species, e.g., foliose algae, mesocrustaceans and surfperches, have begun to increase in abundance.

While observed declines in fishes inhabiting open ocean/pelagic communities occurred almost simultaneously with declines in pelagic zooplankton populations, declines in fishes associated with nearshore subtidal rocky reefs and kelp beds lagged one to two years and declines in fishes associated with soft bottom habitats lagged two to three years behind declining zooplankton populations. These patterns are consistent with an explanation that a regional decline in productivity was responsible for the regional declines observed in fish stocks within the southern California Bight. Differences in response times probably represent the effects of species being longer lived in rocky reef and kelp bed communities when compared with species in pelagic/open water communities, i.e., storage effects. Comparisons with changes in the population abundances of deeper water species indicated that even though many species, most notably several species of rockfishes, exhibited declines consistent with those observed in nearshore fish communities, certain species, particularly flatfishes, actually increased in abundance during the period 1977-2001.

(2) The continued annual surveys of subtidal reef communities at Santa Cruz Island:

Our detailed examinations of a simple food web indicated that for two species of viviparous surchperches examined (black surfperch *Embiotoca jacksoni*; striped surfperch *E. lateralis*), recruitment of new individuals varied comparatively little through time on some reefs while it fluctuated substantially on others. These fishes harvest invertebrate prey from specific benthic foraging microhabitats (algal turf for black surfperch; the red alga *Gelidium robustum* for striped surfperch), and these microhabitats showed a range in dynamics among the reefs examined over a 12 yr period. Interannual fluctuations in foraging microhabitat were a strong predictor of the extent to which the abundance of young-of-year surfperches fluctuated. However, the foraging microhabitat for black surfperch (algal turf) on a reef fluctuated independently of that for striped surfperch (*Gelidium*). As a consequence, the extent to which the abundance of young of one surfperch varied on a given reef was unrelated to that of its congener. These data show that the magnitude of temporal variation in year-class strength of reef-associated fishes was related to the magnitude of variation in the forage base, reefs in close proximity can show a range in resource

dynamics that can affect reproductive output, and the reproductive output of even closely-related species can fluctuate independently on the same reef.

SIGNIFICANT CONCLUSIONS: A primary goal of environmental assessments is to quantify trends in species responses following a perturbation. Evaluation or predictions of the effects of anthropogenic perturbations typically are made based upon the observed or hypothesized magnitude and direction of these trends. To be valid, however, trends observed to occur at small spatial scales, e.g., around an offshore oil production platform, must be placed within a larger regional context. In the case of predicted trends, these changes should reflect not only the hypothesized effects due to the perturbation, but also those effects likely to occur as a consequence of unrelated, natural changes in regional environmental conditions. Studies examining long-term or large scale spatial or temporal gradients in productivity provide both a regional context within which observed trends may be placed and an opportunity to explore responses of food webs to environmental perturbations.

STUDY PRODUCTS:

Published works:

- Brooks, A.J., R. J. Schmitt and S. J. Holbrook. 2002. Declines in regional fish populations: have different species responded similarly to environmental change? Marine and Freshwater Research 53(2):189-198.
- Schmitt, R.J. and S.J. Holbrook. 2006. Predicting the magnitude of temporal variation in youngof-year class strength of surfperch (Teleostei: Embiotocidae). Raffles Bulletin of Zoology. *In Press*.
- Holbrook, S.J., A.J. Brooks and R.J. Schmitt. Temporal variation in temperate reef assemblages: have trophic levels responded similarly to environmental change? To be submitted December, 2006.

Presentations:

- Brooks, A.J., R.J. Schmitt and S.J. Holbrook. "Population Trends and Trophic Dynamics, the Use of Long-term Datasets." 5th Temperate Reef Symposium, Capetown, S.A., January, 2000.
- Brooks, A.J., R.J. Schmitt and S.J. Holbrook. "Population Trends and Trophic Dynamics, the Use of Long-term Datasets." American Society for Ichthyology and Herpetology, La Paz, Mexico, June, 2000.
- Brooks, A.J. "Declines in Regional Fish Populations: Species Responses to Environmental Change and the Nature of Community Organization." Western Society of Naturalists, Ventura, CA, November 2001.
- Brooks, A.J. "Declines in Rocky Reef Fish Populations: Have Different Species Responded Similarly to Environmental Change." Southern California Academy of Sciences, Claremont, CA, June, 2002.

- Brooks, A.J., H.S. Lenihan and S. Lester. "Temporal Trends in Shallow Nearshore and Deeper Continental Shelf Fishes Since 1977: Do Similar Responses Suggest a Common Mechanism Behind Observed Declines?" Southern California Academy of Sciences, Northridge, CA, May 2003.
- Brooks, A.J., R.J. Schmitt and S.J. Holbrook. "Population Trends and Trophic Dynamics What Can Be Learned from Long-term Monitoring." The Nature Conservancy, Santa Barbara, CA, October, 2003.
- Schmitt, R.J. and S.J. Holbrook. "Predicting the magnitude of temporal variation in youngof-year class strength of surfperch (Teleostei: Embiotocidae)." 7th Indo-Pacific Fish Conference, Taipei, Taiwan, May, 2005.

FINAL STUDY REPORT

CHAPTER 1

This Chapter was published in Marine and Freshwater Research with the following citation:

Brooks¹, A.J., R. J. Schmitt^{1,2} and S. J. Holbrook². 2002. Declines in regional fish populations: have different species responded similarly to environmental change? *Marine and Freshwater Research* **53**(2):189-198.

¹Coastal Research Center, Marine Science Institute, and ²Department of Ecology, Evolution, and Marine Biology University of California, Santa Barbara, CA 93106, USA

Abstract

Abundances of many coastal species off southern California have undergone dramatic declines over the past two decades concurrent with a regional climate shift. This shift in climatic conditions represents a natural, large-scale perturbation and provides an opportunity to understand whether and how various components of coastal ecosystems respond. We conducted time-series analyses on long-term data sets of non-exploited fish populations from the Southern California Bight to describe their temporal trends and explore the timing and magnitude of change. The species examined were classified as to trophic level, mode of reproduction, extent of geographic range, association with benthic or pelagic food webs, and habitat. In general, the magnitude of decline was similar for all species, regardless of classification. Trends were similar at all locations examined within the Bight, suggesting regional declines in abundances rather than redistribution of individuals. These patterns are consistent with the explanation that a regional decline in productivity associated with the shift to an alternate climatic regime is responsible for regional decline in fish stocks.

Introduction

Understanding the processes that link and/or limit component populations within aquatic communities represents a significant ecological challenge. This understanding is essential, however, for predicting how perturbations to populations at one trophic level might be propagated throughout the rest of the community (Wootton 1994; Albritton *et al.* 2001). Current models predicting the responses of populations to "top down" or "bottom up" effects often differ widely in their estimates of the magnitude of change expected by species at other trophic levels (Hairston *et al.* 1960; Menge and Sutherland 1976; Fretwell 1977, 1987; Oksanen *et al.* 1981; Carpenter and Kitchell 1993; Estes and Duggins 1995; Hairston and Hairston 1997; see Sinclair *et al.* 2000 for a review). Attempts to experimentally test predictions of these models in temperate marine systems have been hindered by the logistical difficulties inherent in conducting long-term manipulative studies encompassing multiple levels of community organization at meaningful spatial scales.

Increasingly, marine ecologists are turning to observational studies of the responses of communities to environmental changes to gain insight into the mechanisms structuring marine communities (Carpenter 1990; Corten 1990; Aebischer et al. 1990; Barry et al. 1995; Holbrook and Schmitt 1996; Veit et al. 1996; Beamish et al. 2000). We use such an approach here. The behavior of the California Current system is one of the most important determinants of environmental conditions in the nearshore marine environment off Southern California (Brodeur et al. 1996). The typically high productivity of this system is attributed to coastal upwelling, which brings deeper, nutrient-rich waters to the surface near shore. This high supply rate of nutrients enhances primary productivity, which, in turn, drives the secondary productivity of nearshore benthic and pelagic food webs. Oceanographic conditions within the California Current system underwent a substantial shift in the late 1970s when there was a rapid, large, and persistent increase in seawater temperature (Miller et al. 1994; Minobe 1997; but see Mantua et al. 1997; Beamish et al. 1998). Between 1976 and 1977, recorded seawater temperatures within the Southern California Bight rose an average of $1-2^{\circ}$ C above the mean for the previous two decades (Roemmich 1992). Associated with this warming event was a decrease in upwelling intensity and productivity of nearshore surface waters (Roemmich and McGowan 1995; McGowan et al. 1996).

Numerous studies have documented decreases in the abundances of various nearshore species within the California Current region since the regime shift of the late 1970s. While these declines are often cited as evidence of a tight linkage between large scale changes in oceanographic circulation patterns and the productivity of nearshore marine ecosystems, few studies have attempted to compare observed trends in the magnitude and timing of these declines among species with differing life histories, geographical ranges, or trophic status (but see Barry *et al.* 1995; Veit *et al.* 1996; Holbrook *et al.* 1997). Such comparisons could provide useful insight into whether and how various components of the nearshore coastal ecosystem respond to the same disturbance.

We use data collected from fish impingement studies conducted at coastal electrical generating stations located throughout the Southern California Bight to describe trends over a 17 year period and establish the timing and magnitudes of change in the abundances of 37 species of nearshore fishes. These data thus provide a long-term estimate of fish abundances that is both integrated through time and spatially extensive. Specifically, we explore the extent to which responses (i.e., effect sizes and response times) were manifested similarly between pelagic and benthic ecosystems, among various habitat types (pelagic vs. reef associated vs. benthic), among different trophic levels, and among species that vary in life history attributes (e.g. reproductive mode and geographic range).

Methods

Coastal electrical generating stations entrain a wide variety of fishes in their cooling waters during the course of normal operating activities. We obtained data from the Southern California Edison Company's (SCE) Biological Monitoring Program on the numbers of fishes impinged at four coastal electrical generating stations located over a 200 km stretch of coastline throughout the Southern California Bight (Figure 1). Although the four plants differ somewhat in their designs (three are conventional fossil fuel fired and one is nuclear powered) all possess intake

structures that are surrounded by rock rubble and situated on sandy bottoms in depths ranging from 8-14m (Love *et al.* 1998). Temperature records for the southern and northern portions of the Southern California Bight indicate that an abrupt increase in surface water temperature occurred in 1977 concomitant with the 1976-1977 regime shift in the north Pacific (Figure 2a). We were able to obtain data from the beginning of this period in 1977 through the end of 1993. While impingement data have been collected through the present, data after 1993 were not available.



Figure 1. Map of the Southern California Bight showing the locations of the four coastal electrical generating stations providing impingement data used in this study. San Onofre is a nuclear powered plant. Huntington Beach, Redondo Beach, and Ormond Beach are all conventional fossil fuel fired.



Figure 2. (a) Time series of standardized surface water temperatures as recorded off San Diego, CA (closed bars) and Santa Barbara, CA (open bars). Temperature values were standardized to a mean of zero and a standard deviation of one by subtracting the 25 year mean (1972-1997) and dividing by the standard deviation of the 25 year mean for each location. Positive values represent years with surface water temperatures that were above the 25 year mean, while negative values indicate years that were colder than the long term mean. The arrow indicates the onset of the 1977 climate shift. (b) Time series of the standardized zooplankton anomaly within the Southern California Bight for the years 1972-1997 (data from the California Cooperative Oceanic Fisheries Investigations). Positive values represent years with zooplankton abundances that were above the long-term mean, while negative values indicate years. The arrow indicates the onset of the 1977 climate shift.

Raw data consisted of the counts of all fishes impinged within each generating station during a 24 hour period of normal power plant operations. Counts were made at least monthly at each plant and of the 112 species entrained during this period, 37 occurred with a great enough frequency, i.e. were present in samples collected from at least two of the four plants in at least half of the years sampled, to permit inclusion in this study (Appendix I). With few exceptions, notably *Sardinops sagax, Paralichthys californicus, Atractoscion nobilis, Paralabrax clathratus,* and the two species of *Sebastes*, none of these species are heavily targeted by either commercial or recreational fishers. Before being used in any analyses, raw data first were standardized by dividing the counts for each species averaged within a month if necessary by the appropriate average monthly flow rate (gallons*10⁶/day) to account for potential plant effects due to differences in the designs of the intake structures and in the amount of cooling water flowing through them from month to month.

Standardized impingement values calculated for most species demonstrated a high degree of both spatial (between generating stations) and temporal (between consecutive months) variability. To minimize the possibility that our estimate of the proportional change in the abundances of a species within the Southern California Bight was driven by extreme changes observed at only one or two of the four coastal generating stations included in this study, we first transformed the data series obtained from each station for a given species by calculating the natural logs (ln) of the standardized count data. The transformed values were averaged across the four power plants within a given month for each species to yield a single data series for that species. Because we primarily were interested in long-term changes in abundance, i.e. changes occurring over time spans of up to a decade or more rather than those occurring over a single year, data were smoothed using a three month moving average in an attempt to reduce the fine scale seasonal variability still present in each averaged series.

We estimated the magnitude of the long-term change in the average abundance for each species by calculating the proportional change in abundance using the equation $(N_{Final}-N_{Initial})/N_{Initial}$. Inspection of the standardized data series for each species indicated that the standardized number of individuals for most species sampled during impingement surveys increased slightly from 1977 until 1979 or 1980 when they began slowly decreasing to a minimum in 1991 before increasing again in 1992 and 1993. Given this pattern in the standardized data, we used the average of the maximum smoothed monthly ln (abundance) observed within each year during the period 1978-1980 as an estimate of $N_{Initial}$ and those observed during the years 1990-1992 as an estimate of N_{Final} . All statistical analyses were conducted using SAS (SAS v.8.1, SAS Institute 2001).

Implicit in all of our analyses was the assumption that changes in the number of fishes impinged by coastal electrical generating stations serve as a meaningful index of changes occurring in the abundances of these species within the Southern California Bight. To test this assumption, we correlated species specific values for the proportional change observed in the abundance of 17 species calculated using impingement data obtained from SCE's Redondo Beach plant with values calculated for the same species using a second, independently collected data set: a longterm study of the abundances of reef associated fishes within King Harbor, a small boat harbor and marina immediately adjacent to the cooling water intakes for the SCE Redondo Beach electrical generating station. In the King Harbor study, divers using SCUBA visually censused juvenile and adult fishes within a series of $50 \ge 2$ m band transects and hence, these data provided a different estimate of abundance for these species (see Terry and Stephens 1976; Stephens 1983; Holbrook *et al.* 1994; Holbrook *et al.* 1997 for details of the survey design).

To test for differences in the magnitude of the proportional response between species exhibiting different life history characteristics or habitat affinities, we used the criteria presented in Table 1 to establish several subcategories within the broader ecological categories of habitat, trophic level, geographic range, reproductive mode, and primary food web. Species were classified and placed within each sub-category based on dietary and life history information obtained from Cailliet *et al.* (2000) (see Appendix I for classifications). Values for the long-term proportional change in the ln (abundance) of each species were arcsine, squareroot transformed to meet the underlying assumptions of parametric statistics, and then comparisons between the various sub-categories present in each category were made using a one factor generalized linear model with species serving as replicates.

To explore possible links between the timing of aggregated species responses to long-term changes in secondary productivity (Figure 2b) associated with increased water temperatures and decreased levels of upwelling throughout the Southern California Bight (Roemmich and McGowen 1995; McGowen et al. 1996), we employed standard correlation analyses to compute cross-correlation coefficients between the California Cooperative Oceanic Fisheries Investigations (CalCOFI) bight-wide annual time series of mesozooplankton volumes (cubic centimeters per 1000 m³ of water sampled) and time series for the aggregated abundances of planktivores (those species feeding largely on zooplankton or small microinvertebrates), primary macrocarnivores (species feeding on polycheates, small crustacea and molluscs) and secondary macrocarnivores (species feeding on large crustaceans, molluscs, and other fishes) as estimated by the SCE impingement data. In order to meet the assumptions of stationarity required by this type of analysis (Chatfield 1984), time series of the standardized abundances for each fish species, as well as the CalCOFI zooplankton series, first were converted to an annual series of standard deviates (mean 0, standard deviation 1) by subtracting the 17 year mean (1977-1993) from each yearly averaged standardized abundance estimate and then dividing this result by the standard deviation of the 17 year series mean. Average annual standard deviates for each trophic level were calculated by averaging across all species assigned to a given trophic level category and cross-correlation coefficients then were computed between each of the three aggregated trophic level standard deviate series and the standard deviate time series for mesozooplankton volume. Similar analyses were performed to examine relationships between long-term changes in secondary productivity and the responses of fishes occupying positions within benthic versus pelagic food webs and between long-term changes in secondary productivity and the responses of fishes occupying benthic, pelagic, and reef habitats.

It is well known that the use of correlational analysis to explore relationships between time series of data that exhibit strong within series levels of autocorrelation is problematic. The presence of autocorrelation within the two data series violates the assumption of serial independence underpinning correlation analysis and results in an overestimation of the number of degrees of freedom that should be employed in statistically evaluating calculated cross-correlation coefficients. Consequently, failure to correctly account for significant autocorrelation present within each series can lead to an increase in the Type I error rate above that specified by α and

thus, the probability of erroneously concluding that a given correlation is statistically significant (Kope and Botsford 1988; Jassby and Powell 1990; Bence 1995; Pyper and Peterman 1998).

To account for the autocorrelation present in our data, we calculated an "effective" number of degrees of freedom, N^{*}, using the formula $1/N^* = 1/N + \{2/N*\Sigma\rho_{XX}j)*\rho_{YY}(j)\}$ over N/5 lags where N represents the sample size and $\rho_{XX}(j)$ and $\rho_{YY}(j)$ represent the autocorrelations present in the two series, X and Y, at lag j (Chelton 1984). This value of N^{*} was then used to calculate an adjusted critical value for the cross-correlation coefficient, r_{crit} , using the expression $r_{crit} =$ sqrt $(t^2_{\alpha, N^*-2}/(t^2_{\alpha, N^*-2} + N^*)$ (see Pyper and Peterman 1998 for a thorough review of methods).

Results

Thirty five of the 37 species examined in this study exhibited proportional declines in abundance between the initial period (1978-1980) and the final period (1990-1992) (Appendix I) as estimated using impingement data. Taken together, the abundances of the 37 species declined by an average (± 1 SE) of 41% ± 5 over an approximately 15 year period. Values for calculated declines ranged from 2% for the clinid, *Heterostichus rostratus*, to 89% for the elasmobranch, *Myliobatus californica*. Of the remaining two species, one species, *Sphyraena argentea*, was essentially unchanged (~ 1% increase) while the other, *Sardinops sagax*, increased by 37%.

Comparison of Impingement Data with Other Estimates of Population Abundances

We found a significant and positive relationship between calculated declines in standardized abundances for 17 species common to both the King Harbor diver surveys and the SCE impingement surveys (r=0.66, p=0.004) (Figure 3). Although the estimates of population declines obtained using data collected from diver surveys had a tendency to underpredict those calculated from impingement data (slope=0.59, intercept=0.02), estimates obtained using impingement data did appear to be relatively unbiased with nine of the 17 species representing underestimates and eight representing overestimates. In general, estimates of population declines based on diver survey data for schooling species such as the pomacentrid *Chromis punctipinnis* tended to exceed that estimated from impingement data, while those obtained for benthic or cryptic species such as the flatfish, *Hypsopsetta guttulata*, or the kelp associated *Heterostichus rostratus*, tended to be less.

Comparisons of Proportional Changes in Abundance



Figure 3. Relationship between the proportional decline in the abundance of 17 species of fishes as estimated by diver visual surveys conducted in King Harbor, Redondo Beach, CA and the proportional decline in the abundance of these same species as estimated using impingement data. Solid line represents the least squares fit to these data (p=0.004, $r^2=0.44$).

The magnitude of the proportional change in abundance displayed by the majority of species included in this study was extremely uniform regardless of classification. Although it appeared that primary macrocarnivores experienced larger declines than either planktivores or secondary macrocarnivores (Table 1), we found no statistically significant differences in the average proportional change in standardized abundance among species occupying different trophic levels ($F_{2,34}=1.01$, p=0.37), exhibiting different modes of reproduction ($F_{1,35}=2.00$, p=0.17), or associating within different food webs ($F_{1,35}=0.67$, p=0.42). Unlike results presented by Holbrook and Schmitt (1996) and Holbrook *et al.* (1997) who found that species with more northerly limits to their geographical ranges exhibited greater declines in abundance than more southern species, we found no difference between species with differing distributions ($F_{2,34}=2.26$, p=0.12). We did find that species occurring in benthic habitats experienced significantly larger declines ($F_{2,34}=5.52$, p=0.008) than species occupying either pelagic or reef associated habitats.

Comparisons of the Timing of Observed Changes

Table 1. Criteria used to classify species into functional groups and the mean change (± 1 SE) in proportional abundance exhibited by each group. N equals the number of species assigned to each group. (* indicates subcategories that differ significantly from one another within a category at the $\alpha = 0.05$ level).

Category		Mean Change	
Sub-category	Criteria	in Abundance	Ν
Habitat			
Pelagic	Found predominantly in water column	-0.32 (0.08)	13
Benthic	Found predominantly on benthos; not reef associated	-0.62 (0.08)*	11
Reef	Found in close association with rocky reefs or outcrops	-0.32 (0.06)	13
Trophic Level			
Planktivore	Feeds predominantly on zooplankton or other small invertebrates	-0.38 (0.08)	14
1 ⁰ Macro.	Feeds predominantly on small macroinvertebrates	-0.50 (0.07)	13
2 ⁰ Macro.	Feeds predominantly on large macroinvertebrates and fishes	-0.34 (0.09)	10
Geographic Range			
Southern	Northern range limit is approx. Pt. Conception, Calif.	-0.35 (0.07)	13
Central	Northern range limit is approx. Calif./Oregon border	-0.55 (0.08)	13
Northern	Northern range limit is approx. N. Canada or Alaska	-0.32 (0.08)	11
Reproductive Mode			
Eggs	Oviparous species	-0.38 (0.06)	29
Live	Ovoviviparous or viviparous species	-0.54 (0.07)	8
Food Web			
Pelagic	Feeds primarily in water column	-0.30 (0.10)	10
Benthic	Feeds primarily from benthos	-0.45 (0.05)	27

As with the magnitude of observed changes in the proportional abundances, we found a high degree of similarity in the timing of the responses exhibited by the various levels within each of our functional categories (Figure 4). All calculated cross-correlation coefficients between the average deviates of the standardized abundances showed significant correlations at a lag of zero (Table 2) indicating that each level of species aggregations responded simultaneously to changes in the environment. Within the habitat association category, the average abundance of reef associated species also showed significant correlations with the abundances of both benthic (r=0.73, p<0.05) and pelagic (r=0.68, p<0.05) species one year earlier suggesting that the timing of the response by reef associated species lagged slightly behind that of the other two groups.



Figure 4. Time series of the average deviation in standardized abundance for fish species by (**a**) habitat type: Benthic (closed circle), Pelagic (square), and Reef Associated (open circle); (**b**) trophic level: Planktivore (closed circle), Primary Macrocarnivore (square), and Secondary Macrocarnivore (closed circle); (**c**) geographic range: Southern (open circle), Central (closed circle), Northern (square); (**d**) reproductive mode: Egg bearers (circle) and Live bearers (square); and (**e**) food web: Benthic derived (circle) and Reef derived (square). Data were first standardized to a mean of zero and a standard deviation of one by subtracting the 17 year (1977-1993) mean and dividing by the overall standard deviation for each species. Data were then averaged across all species within a functional group by year.

Category	Category				
Sub-category	Sub-category				
Habitat	Benthic	Reef			
Pelagic	0.86	0.59			
Benthic		0.75			
Trophic Level Planktivore 1º Macrocarnivore	1 ⁰ Macrocarnivore 0.90	2 ⁰ Macrocarnivore 0.75 0.81			
Geographic Range Southern Central	Central 0.89	Northern 0.88 0.96			
Reproductive Mode Eggs	Live 0.92				
Food Web Pelagic	Benthic 0.77				

Table 2. Values of the computed cross-correlation coefficients between members of each functional group for a lag of 0 years. All values are statistically significant at the 0.05 level after adjustment for the within series autocorrelation.

Cross-correlations between the CalCOFI mesozooplankton time series and the abundances of species feeding within pelagic food webs showed a higher degree of synchrony as measured by the magnitude of the cross-correlation coefficient than did species feeding within benthic food webs (pelagic: $r_{max}=0.54$, benthic: $r_{max}=0.45$). Significant correlations at lags of two and three years indicated that the decline in the abundance of both pelagic and benthic feeding species occurred approximately two to three years following the observed decline in mesozooplankton abundance (Figure 5a and 5b). Species occupying different trophic levels differed slightly but systematically in the timing of their response to decreasing zooplankton abundance. While abundances of planktivores showed a significant correlation (r=0.49, p<0.05) with measured abundances of mesozooplankton only at a lag of two years (Figure 6a), secondary macrocarnivores showed significant correlations at lags of both two (r=0.50, p<0.05) and three (r=0.47, p<0.05) years (Figure 6c) suggesting that these species responded more slowly to changes in secondary productivity than did planktivores. Primary macrocarnivores, having a significant correlation at a lag of two years (r=0.54, p<0.05) and a marginally significant (r=0.54, $p\sim0.06$) correlation at a lag of three years (Figure 6b), appeared to have responded at a rate intermediate to that exhibited by planktivores and secondary macrocarnivores.



Figure 5. Values of the cross-correlational coefficient between the standardized zooplankton anomaly, expressed as deviations from the 25 year mean, and the average deviation in the standardized abundance of those species feeding (a) largely in the pelagic zone or (b) from the benthos for lags ranging from zero to eight years. Dashed horizontal line represents the value of the cross-correlation coefficient which is significant at p=0.05. Values lying on or above this line indicate a significant correlation between the standardized zooplankton anomaly and the average standardized abundance of fishes feeding in the pelagic zone or from the benthos at some time in the future.



Figure 6. Values of the cross-correlational coefficient between the standardized zooplankton anomaly and the average deviation in the standardized abundance of those species feeding largely on (a) zooplankton and other microcrustacea, (b) species feeding largely on mesocrustaceans and other small invertebrates, and (c) species feeding largely on macrocrustacea and fishes for lags ranging from zero to eight years. Dashed horizontal line represents the value of the cross-correlation coefficient which is significant at p=0.05. Values lying on or above this line indicate a significant correlation between the standardized zooplankton anomaly and the average standardized abundance of primary consumers at some time in the future.

Discussion

The ability to accurately predict whether and how rapidly changes manifested at one level of a biological community will be transmitted to other members of the community requires some mechanistic understanding of the linkages between the component species. Whether these predictions can be generalized from one system to the next will depend on the equivalency and consistency of the mechanisms operating within differing communities. One commonly held theory predicts that species ranges should shift poleward in response to increasing temperatures

(Lodge 1993; Lubchenco *et al.* 1993). As a result, community composition at a regional scale should become increasingly dominated by more warm-adapted species. This has been observed in several temperate marine communities over the last 30 years (intertidal invertebrates-Barry *et al.* 1995; subtidal fishes-Stephens *et al.* 1994). Our results contrast with these findings because with only two exceptions, *Sardinops sagax* and *Sphyraena argentea*, the abundances of all species included in our study declined regardless of their pre-1977 geographical distribution. We found no evidence that the magnitude of a species' decline was related to the extent of its geographical range.

These results do not appear to reflect inadequacies or systematic biases inherent in our use of impingement data to estimate abundances, as estimates derived from impingement surveys were significantly and positively correlated with those obtained directly using more traditional visual surveys. Holbrook *et al.* (1997) estimated that the average decline exhibited by populations of 75 species of fishes observed in King Harbor and the offshore waters near Palos Verdes, California between 1975 and 1993 was approximately 69%. Application of the fitted relationship we obtained from comparing diver survey estimates to those obtained from the impingement study to this value yields an estimate of the predicted average decline based on impingement data of approximately 43%. This value is statistically indistinguishable from our calculated average value of 41% based on the average declines observed among the 37 species included in the SCE impingement surveys.

The similarity in the population responses and their consistency among the sites we examined point to a regional decline in productivity as the underlying explanation. There are several lines of evidence for this. First, numerous authors have reported declines of similar magnitudes for a diverse array of species occupying a range of habitats and trophic levels (including primary producers) within both benthic and pelagic food webs throughout the Southern California Bight. The timing of these declines appears to be strongly correlated with the onset of a period of decreased upwelling and a lessening in the supply of nutrient-laden water to surface waters. Tegner et al. (1996) reported declines of 60% in stands of giant kelp, Macrocystis pyrifera, off of San Diego, while Holbrook et al. (1997) found that several species of foliose macroalgae off of Santa Cruz Island had decreased by approximately 80%. Roemmich and McGowan (1995) reported that the average biomass of macrozooplankton in surface waters throughout Southern California decreased by approximately 80% and a comparable decrease in the abundance of mesocrustaceans has occurred on understory algae at sites around Santa Cruz Island (Holbrook and Schmitt 1996). Veit et al. (1996) and Oedekoven et al. (2001) examined temporal patterns in the abundances of seabirds feeding on pelagic fishes and found that, on average, populations of species that fed over Southern California shelf and slope waters had declined by almost 40%. Finally, our finding of an average decline of approximately 41% in the abundance of nearshore fishes is comparable (when corrected for differences due to sampling methodologies) to reported declines of 70-90% for other populations of reef associated fishes throughout the Bight (Stephens 1983; Holbrook and Schmitt 1996; Holbrook et al. 1997; Love et al. 1998). As in previous studies, the magnitude of the declines observed in this study appeared to be independent of life history and we found no evidence of an effect that could be attributed to either trophic level or association with either benthic or pelagic food webs.

The second line of evidence that declining regional productivity underlies the observed changes is the similarity in the responses of species producing planktonic eggs and larvae relative to those giving birth to live, largely non-dispersing, young. It is well known that several large scale oceanographic features, e.g. fronts, jets, and eddies, acting on the dispersive larval phase of many marine species can introduce significant spatial and temporal variation in population abundances (Roughgarden et al. 1987; Kingsford 1990; Swearer et al. 1999; reviewed in Underwood and Keough 2001). The strength, timing, and magnitude of many of these oceanographic features are altered following a regime shift such as the one that occurred along the western coast of North America during 1977 (Chelton 1981; Chelton et al. 1982). As such, it is possible that the declines in the abundances of fishes possessing dispersive eggs and larvae may be due to the effects of altered current patterns or shifts in the locations of oceanic fronts leading to a redistribution or loss of eggs from the California Current region. This is not likely to be the case, however, for those species that lack a dispersive planktonic larval phase. The production of offspring by adult livebearing surfperches responds directly to changes in the amount of secondary productivity available to the adults on a reef and offspring rarely disperse from their natal reef (Holbrook and Schmitt 1996). Thus, it is unlikely that the declines we observed in live bearing species resulted directly from the redistribution of offspring, but rather resulted from a decrease in secondary productivity which led to lower birth rates and ultimately smaller population sizes (Holbrook et al. 1997). The similarity in the magnitudes of the response exhibited by species with dispersing larvae and those with non-dispersing young is suggestive of a common regional response by all species to decreased productivity.

We did find a significant difference in the magnitude of the decline exhibited by species that occupy benthic habitats versus those in pelagic or reef associated habitats. This might represent a simple shift in the distribution of benthic species into deeper, colder waters following the increase in seawater temperature. Such a behavioral response is less likely to be effective for pelagic species that are restricted to surface waters or even possible for reef associated species that are tied to areas possessing reef habitat. A perhaps more parsimonious explanation is that all three groups have responded to a regional decrease in productivity, but that benthic species, by virtue of their association with a lower productivity habitat, are more sensitive to this decrease.

Lastly, our data exhibited strong patterns of temporal coherency as measured by the crosscorrelation coefficients in the responses of the different levels of geographic range, habitat, reproductive mode, food web, and trophic level. All component levels of the fish assemblage showed significant correlations at a lag of zero indicating synchrony in the timing of changes in abundance. In addition, the abundances of reef associated species also were significantly correlated with the abundances of pelagic and benthic associated species in the previous year, suggesting that reef associated species may have experienced a slightly delayed response relative to the other two groups. This could be due to the large standing stocks of foliose macro-algae present on many Southern California reefs which could have partially buffered the initial decline in pelagic primary productivity associated with the regime shift. With regard to coherencies between the observed declines in fish abundance and those observed for zooplankton, the fact that we found no difference in the response times of species assigned to either benthic or pelagic food webs in relation to the onset of the decline in pelagic zooplankton abundance indicates that the productivity of both pelagic and benthic food webs may have declined synchronously throughout the Southern California Bight. Species in both food webs began declining two years following the initial decline in zooplankton abundance, suggesting some degree of inertia in the response of the higher trophic levels in both webs.

We also discovered lags in the response times of planktivores, and primary and secondary macrocarnivores to the decline in zooplankton abundance. While all three trophic levels displayed significant correlations between their abundances and the abundance of zooplankton two years earlier, there was a tendency for successively higher levels to display significant correlations at even longer lags. This is not the pattern expected if the declines were due strictly to climatic forcing, but it is consistent with a hypothesis involving the effects of decreased productivity and the propagation of those effects up the food chain (Aebischer *et al.* 1990).

That the declines in the abundances of nearshore fishes described here occurred simultaneously and were of approximately similar magnitudes across species groups possessing differing geographic ranges, reproductive modes, and habitat affinities as well as between species occupying different trophic levels within benthic and pelagic food webs suggests a common mechanism for the decline. Our results point to a concurrent decline in the regional productivity of the Southern California Bight as that mechanism. If this decrease in productivity is, in fact, the result of altered oceanographic conditions due to interdecadal fluctuations in atmospheric circulation patterns as has been suggested (Hayward 1996), then our results predict that abundances of nearshore fishes should increase when the current climate regime returns to one characterized by cooler surface waters and more pronounced upwelling leading to increased levels of productivity within the Bight. Several authors (Mantua et al. 1997; Beamish et al. 1998) have suggested that such a regime shift did take place toward the end of the 1980s and our data do indeed show a slight increase in the abundances of the nearshore species beginning in the early 1990s; a lag of approximately two to three years consistent with our earlier findings related to the timing of the initial declines. Recent data on global climate change (Smith and Lazo 2001) suggest, however, that sea surface temperatures may continue to increase well into the next century. If so, and if these changes are of sufficient magnitude to prevent or override the effects of the recent regime shift, our results predict continued declines in the abundances of most nearshore fishes regardless of their habitat, geographic range, or life history.

Acknowledgements

We thank K. Herbinson of the Southern California Edison Company for providing us with access to the data collected by the Southern California Edison's Biological Monitoring Program and J. S. Stephens Jr. of Occidental College for providing us with the King Harbor and Palos Verdes survey data. J. Lawyer and K. Seydel provided valuable logistical support and proved remarkably adapt at the collection of additional data. B. Williamson provided additional logistical support. This paper benefited from the comments of two anonymous reviewers. This research was supported by the UC-MMS Coastal Marine Institute Program, Minerals Management Service, U.S. Department of the Interior, under MMS Agreement No. 14-35-0001-30758 (Task No. 14181). The views and conclusions contained in this document are those of the authors and should not be interpreted as necessarily representing the official policies, either express or implied, of the U.S. Government.

CHAPTER 2

This Chapter is in press in Raffles Bulletin of Zoology with the following citation:

Schmitt^{1, 2}, R.J. and S.J. Holbrook^{1, 2}. 2006. Predicting the magnitude of temporal variation in young-of-year class strength of surfperch (Teleostei: Embiotocidae). *Raffles Bulletin of Zoology*. In Press.

¹Coastal Research Center, Marine Science Institute, and ²Department of Ecology, Evolution, and Marine Biology University of California, Santa Barbara, CA 93106, USA

Abstract

Members of the fish family Embiotocidae (surfperches) are viviparous and give birth to fully developed, non-dispersing juveniles. We explored (a) whether fluctuations in recruitment of young-of-year surfperches were similar among a series of shallow rocky reefs off southern California, USA, and (b) whether spatial variation in recruitment fluctuations mapped onto spatial differences in how much the local forage base on a reef fluctuated. For both surchperches examined (black surfperch Embiotoca jacksoni; striped surfperch E. lateralis), recruitment varied comparatively little through time on some reefs while it fluctuated substantially on others. These fishes harvest invertebrate prey from specific benthic foraging microhabitats (algal turf for black surfperch; the red alga Gelidium robustum for striped surfperch), and these microhabitats showed a range in dynamics among the reefs examined over a 12 yr period. Interannual fluctuations in foraging microhabitat were a strong predictor of the extent to which the abundance of young-ofvear surfperches fluctuated. However, the foraging microhabitat for black surfperch (algal turf) on a reef fluctuated independently of that for striped surfperch (Gelidium). As a consequence, the extent to which the abundance of young of one surfperch varied on a given reef was unrelated to that of its congener. These data show that (1) the magnitude of temporal variation in year-class strength of reef-associated fishes was related to the magnitude of variation in the forage base, (2) reefs in close proximity can show a range in resource dynamics that can affect reproductive output, and (3) the reproductive output of even closely-related species can fluctuate independently on the same reef.

Introduction

Subtidal marine reefs are subjected to considerable variation in environmental conditions that can influence the abundance and dynamics of such reef-associated organisms as benthic fishes, and there is growing interest in understanding how fishes will respond to disturbances and climate forcing (Holbrook et al., 1997; Jenkins, 2005). Many studies have explored spatial co-variation between attributes of reefs and of the associated fish assemblage (e.g., Sale & Dybdahl, 1975; Gladfelter et al., 1980; Anderson et al., 1981; Ogden & Ebersole, 1981; Choat & Ayling, 1987; Choat et al., 1988; Tolimieri, 1995; Caley & St John, 1996; Ault & Johnson, 1998; Holbrook et al., 1990, 1993, 1994, 2000, 2002; Holbrook & Schmitt, 2003; Schmitt & Holbrook,

2000). By contrast, there have been comparatively few explorations of whether or how the temporal dynamics of reef resources impinge on the structure or dynamics of associated fishes (e.g., Ault & Johnson, 1998; Schmitt & Holbrook, 1990a; Holbrook & Schmitt, 2003). When examined, the reef resource more often explored has involved structural attributes of the environment that might serve as refuge space from predators (e.g., Hixon & Beets, 1989, 1993; Holbrook & Schmitt, 2002). For example, Syms and Jones (2000) altered physical structure and habitat complexity of the reef to varying degrees, which was crossed with different levels of pulsed mortality on fish, to determine resilience of the fish community.

A critical reef resource that can fluctuate on a relatively fast time scale is the food supply of benthic fishes (e.g., Schmitt & Holbrook, 1986). With one exception, we know comparatively little about the demographic or population-level consequences of variation in the food supply of reef fishes. The exception concerns body growth - numerous studies have shown that the individual growth rate of fishes is plastic and can absorb some variation in per capita availability of prey (e.g., Doherty, 1982, 1983; Jones, 1984, 1987a, 1987b, 1988; Forrester, 1990; Anderson & Sabado, 1995; Booth, 1995, 2004). Fluctuations in food also should influence directly fecundity of individuals and thus subsequently their recruitment (e.g., McCauley et al., 1990), although this aspect is difficult to assess in reef fishes because most species produce dispersing larvae. Further, the dispersal of locally produced propagules decouples local variation in reproductive output from subsequent recruitment to that population (Shulman, 1985). Surfperches in the family Embiotocidae offer an unparalleled opportunity to explore the effect of fluctuations in the food supply on demographic and population-level attributes because these species are viviparous and give birth to fully-developed, non-dispersing juveniles (Baltz, 1984). Since adult surfperch convert food to young that are born into the parental population, it may be possible to determine the extent to which fluctuations in food affect reproductive output (here estimated as young-of-year class strength) and, for this type of life history, recruitment dynamics.

Here we explore the influence of temporal variation in the forage base of two species of surfperches, the black surfperch (Embiotoca jacksoni) and the striped surfperch (E. lateralis) that co-occur on shallow rocky reefs off the Pacific coast of North America. These species consume small invertebrates such as amphipods from benthic substrata (Schmitt & Coyer, 1982; Schmitt & Holbrook, 1984). The two species concentrate their foraging activities on different reef substrata: black surfperch primarily feed on crustaceans harbored in turf, a low-dimensional mixture of debris, colonial animals, turf algae and surfperch food, whereas striped surfperch harvest crustaceans on foliose algae, primarily from the red alga Gelidium robustum (Holbrook & Schmitt, 1989, 1996). While the density of surfperch prey contained on these foraging microhabitats can fluctuate substantially (Schmitt & Holbrook, 1986), observational and experimental evidence has shown that the abundance of black surfperch or striped surfperch on a reef is positively and strongly related to the amount of turf or *Gelidium* present (Holbrook et al., 1990, 1994). These foraging microhabitats are biogenic in nature and therefore have dynamics of their own (Schmitt & Holbrook, 1990a; Holbrook et al., 1994); much of the dynamics are caused by disturbances that range from local (e.g., sea urchin grazing, storm wave exposure; Schmitt & Holbrook, 1990a) to larger scales (e.g., climatic regime; Holbrook et al., 1997). Since the crustaceans that reside on turf and Gelidium are the food of these surfperches, these particular substrata represent a major component of the forage base of black surfperch and striped

surfperch respectively. This suggests that fluctuations in turf and *Gelidium* potentially could have substantial influences on local reproductive output and recruitment of young, thereby driving dynamics of local surfperch populations. Because surfperches do not consume their foraging substrata, there likely is no direct feedback between surfperches on the abundance of either turf or *Gelidium*.

The purposes of this study were: (1) to evaluate whether inter-annual variation in the abundance of young-of-year surfperch on a reef are correlated with fluctuations in the cover of turf and *Gelidium*, and (2) to determine the extent to which the dynamics of the forage base and young-of-year class strength of black surfperch and striped surfperch co-vary among reefs. Because all of the reefs examined occur within a 15 km stretch of shore, the study also indicated whether reef populations behave independently or coherently at this spatial scale.

Materials and Methods

Field work was conducted on a series of reefs along a 15 km stretch of Santa Cruz Island, $(34^{\circ}05'N:119^{\circ}45'W)$, which is located in the Santa Barbara Channel of southern California, USA. Reefs consisted of algae-covered bedrock that sloped from above the tide mark to sand at ~ 12 m depth. At each reef, permanent 40 x 2 m horizontal band transects were established at the 3, 6, and 9 m depth contours. The transects delineated a rectangular shaped study site on each reef that was similar in area among the reefs sampled. Study sites were established at 6 reefs in 1982, and sites at 5 additional reefs were established in 1986; data reported here were collected annually, except for 1984 and 1985, for a 12 year period beginning in 1982. Only reefs where young-of-year surfperch were observed were included in these analyses, which reduced the number of reefs to 9 for black surfperch and 8 for striped surfperch.

The number of young-of-year surfperch at each study site was estimated from visual counts along the permanent transects in August to September each year. Young-of-year surfperch are easily distinguished from older conspecifics by their size, morphology and behavior, and the newborn cohort was up to 3 months old at the time they were counted. Fish on transects were counted repeatedly over multiple days, and the number of counts ranged between 4 and 8 each year. For each survey date, the number of young-of-year for each species was summed across the transects to yield a site-wide estimate of young-of-year abundance, and the number of young seen per survey within a year was calculated.

For years when surfperch were counted, the percent cover of benthic substrata also was estimated within the study site of each reef using four 50 m lines per depth zone that were centered around the 3, 6 and 9 m fish transects. The substratum under 100 randomly selected points per line was identified (yielding N = 400 points per depth zone per reef per year). Previous work indicated that turf was the critical foraging microhabitat for black surfperch and the red alga *Gelidium robustum* was that for striped surfperch (Schmitt & Holbrook, 1986; Holbrook & Schmitt, 1989). To explore patterns of co-variation in the amount of variation in foraging habitats and young-of-year abundance, we calculated the temporal (inter-annual) variability in percent cover of these microhabitats separately for each reef sampled. Our main goal was to see if differences among reefs in the extent to which the forage microhabitat fluctuated were a good predictor of the spatial differences in the extent to which surfperch year-

class strength varied among years. A secondary goal was to explore whether the two species of surfperches showed spatial coherence (i.e., same patterns among reefs) in the amount of temporal variation in the abundance of young-of-year. The measure of temporal variability used was the Coefficient of Variation (CV), which is the (standard deviation x 100) / mean. Similarly, temporal variability in the number of young-of-year of each surfperch was estimated, again using the CV, for each reef. To determine how well temporal variation in the forage base (turf or *Gelidium*) predicted the pattern of temporal variation in abundance of young-of-year, we regressed the CV for black surfperch or striped surfperch young for each site against the CV for turf or *Gelidium* to explore spatial co-variation in the dynamical pattern of the foraging microhabitats. Finally, we calculated the correlation between CV in black surfperch young against that for striped surfperch young to explore whether there was spatial co-variation in the dynamical pattern of abundance of (locally produced) young-of-year among the reefs sampled.

Results

Turf and *Gelidium robustum*, the foraging microhabitats for black surfperch and striped surfperch respectively, did not remain constant over the 12 yrs of the study. The difference between the maximum and minimum availability of these microhabitats, averaged across the reefs examined, was ~ 2-fold for turf and ~ 4-fold for *Gelidium*. The amount of temporal variability in these foraging microhabitats differed among the reefs, with some showing relatively little variability in the cover of turf or *Gelidium* while other reefs showed substantially greater fluctuation (Figure 1). However, the degree to which turf fluctuated at a given site was independent of the magnitude of the temporal variability in *Gelidium* on that reef (Figure 1; r = -0.09; P > 0.8).



Figure 1. The pattern of co-variation in magnitudes of temporal variability (measured by the coefficient of variation CV), between turf and *Gelidium robustum*, the foraging microhabitats for black surfperch and striped surfperch respectively (correlation coefficient r = -0.09; P > 0.8). Each point represents a reef followed for either 8 or 12 yrs.

For both surfperches, there was considerable variation among reefs in the magnitude of interannual variation in recruitment of young-of-year (Figure 2). The extent to which the abundance of young-of-year varied from year to year on a reef was positively related to the dynamics of their foraging microhabitat (Figure 2). The degree of fluctuation in turf predicted almost two-thirds of the among-reef variance in the amount of temporal variability in the abundance of young-of-year black surfperch (Figure 2a; $r^2 = 0.64$; P < 0.01). The amount of temporal variability in *Gelidium* predicted even more of the among-reef difference in temporal variability in abundance of young-of-year striped surfperch (Figure 2b; $r^2 = 0.72$; P < 0.01). However, there was no relationship between the two species in the degree of temporal variation in the abundance of their young on a reef (Figure 3; r = + 0.30; P > 0.4). Thus, while microhabitat and young-of-year dynamics were tightly coupled for each surfperch species, there was no spatial co-variation between the species.



Figure 2. The relationships between the magnitudes of inter-annual variability in abundances of young-of-year surfperch and in the forage base for: (a) black surfperch young and turf ($r^2 = 0.64$; P < 0.01), and (b) striped surfperch young and *Gelidium robustum* ($r^2 = 0.72$; P < 0.01).



Figure 3. The pattern of co-variation in magnitudes of inter-annual variability in abundances of black surfperch and striped surfperch young-of-year (correlation coefficient r = 0.30; P > 0.4).

Discussion

Understanding processes that influence abundance and dynamics of marine reef fishes has been a central focus in marine ecological research. Much effort has been devoted to understanding whether and how local dynamics of reef fish are coupled to processes that occur in other locations, which reflects the fact that most species have dispersing larvae (Doherty, 1991). To the extent that the influence of variation in abundance of a reef resource on local dynamics of reef fishes has been explored, the main thrust has been to understand the nature of loss rates after larval recruitment (see reviews by Hixon & Webster, 2002; Osenberg et al., 2002), again reflecting the notion that variation in mortality is expressed locally while that for fecundity probably is not (Shulman, 1985). Because local populations typically are connected via exchange of reproductive output, local events that affect fecundity surely will be expressed 'downstream,' giving rise to the need to consider metapopulation dynamics and connectivity (e.g., Armsworth, 2002). However, there is growing evidence of relatively localized retention of larval fishes (e.g., Jones et al., 1999), suggesting that local fecundity and local recruitment may not be as decoupled as once believed. Despite the relevance, there has been little attention paid to whether and how fluctuations of reef resources affect reproductive output and recruitment of marine reef fish. Further, there have been extremely few long-term studies that have simultaneously estimated demographic rates and resources in assemblages of marine reef fish, adding to the difficulties in evaluating this important but under-studied issue (Holbrook & Schmitt, 1996).

The surfperch system provides an excellent model to explore the link between variability of reef resources and demographic and population-level responses because fecundity is expressed

locally and newborn fish do not disperse from the parental population (Baltz, 1984). Our longterm study revealed that the degree to which the forage base on a reef fluctuated predicted around two-thirds of the inter-annual variation in recruitment of young-of-year surfperch; the greater the variation in the forage base of a reef, the more the abundance of young varied from year to year. While previously published experiments confirmed the importance of turf and *Gelidium robustum* to the local abundance of adult black surfperch and striped surfperch respectively (Holbrook et al., 1990, 1994), the present findings strongly suggest that the availability of these foraging microhabitats influences the production of young-of-year surfperch on a reef. Further, there was considerable variation among the study sites in the dynamics of the forage base and hence in the production / recruitment of young surfperch. The spatial scale of this heterogeneity was highly localized as all reefs were situated along a 15 km stretch of the same shore.

The current study further revealed that the different forage bases of the two surfperch species varied independently among the sites. As a result, recruitment dynamics of the co-occurring surfperch also were independent. Given that these species of fish compete with one another (Hixon, 1980; Schmitt & Holbrook, 1986, 1990b), the independent responses to environmental fluctuations may be a mechanism that helps promote their coexistence (Chesson, 1994, 2000a, 2000b). At the very least, the results imply that the local dynamics of these surfperch species need not be similar.

The results reported here may shed insight into species of reef fishes that have the more typical life history where dispersing larvae are produced. In these cases the demographic or population-level consequences of a fluctuating food supply may not be easily discerned. Since mature fish convert food to reproductive products, fluctuations in the supply of food over an appropriate time scale should not only affect individual growth rates (Anderson & Sabado, 1995), but also should produce temporally varying size-specific fecundity relationships. Further, the surfperch system revealed considerable asynchrony in resource dynamics over relatively short distances. While connectivity and retention are now being included as potentially important aspects in metapopulation models of reef fishes (e.g., Armsworth, 2002), resource dynamics and its effect on fecundity also need to be incorporated if we are to fully understand effects of environmental fluctuations on reef fishes.

Acknowledgements

We thank D. Canestro, K. Seydel, W. Douros, K. Collins, M. Carr, M. Anghera, and M.M. Perez for assistance in the field. The work was funded by the U.S. National Science Foundation (OCE 99-10677, OCE 99-82105, OCE 04-17412 and earlier awards), the W.M. Keck Foundation and the Minerals Management Service, U.S. Department of the Interior (MMS agreement no.14-35-0001-30758). The views and conclusions contained in this paper are those of the authors and should not be interpreted as necessarily representing the official policies, either expressed or implied, of the U.S. government. This is a contribution of the Santa Barbara Coastal LTER Site.

CHAPTER 3

Temporal variation in temperate reef assemblages: have trophic levels responded similarly to environmental change?

Sally J. Holbrook^{1,2}, Andrew J. Brooks¹ and Russell J. Schmitt^{1,2}

¹Coastal Research Center, Marine Science Institute, and ²Department of Ecology, Evolution and Marine Biology University of California, Santa Barbara, CA 93106, USA

Abstract

Spatial or temporal gradients in productivity provide an opportunity to explore responses of food webs to environmental perturbations. Such variation is particularly marked in coastal marine environments, where climate-driven oceanographic processes drive the supply of nutrients and potentially can have profound effects on benthic and pelagic productivity. Oceanographic conditions in the California Current system underwent a substantial shift during the mid 1970s to the warm water, low productivity phase of the Pacific Decadal Oscillation (PDO) which persisted until the late 1990s. We assessed temporal patterns of abundance within two food pathways of the benthic food web at several locations in the Southern California Bight during the past two decades to explore responses to the bottom-up effects of lowered productivity during the warm phase, and assess evidence that the food chain is responding to the shift in the late 1990s to cooler, more productive ocean conditions. Abundances of all trophic levels of the two food pathways examined (kelp bass, surfperches, understory algae, mesocrustaceans; sheephead, urchins, edible algae) declined dramatically during the warm phase of the PDO. Within each pathway, the magnitude of the declines of the trophic levels was similar. In addition, the patterns of decline appeared consistent at several different locations within the Southern California Bight. By the final years of the warm phase, proportional declines from abundances documented earlier in the phase were on the order of 0.8 for one of the food pathways and 0.6 for the other. Since 2000, populations of kelp bass, surfperch, and foliose algae have increased modestly from the very low levels reached at the end of the warm phase of the PDO, consistent with predictions of bottom-up forcing of the effects of the rising nutrient supply associated with cooler oceanographic conditions.

Introduction

Ecologists have long sought to understand mechanisms that link trophic levels in order to predict whether effects of perturbations to populations in one portion of the food web will be propagated through the community. Models that predict reactions to variation in top-down or bottom-up forces differ greatly in their estimates of the magnitude of change of populations at different trophic levels (Hairston et al. 1960, Hairston and Hairston 1977, Menge and Sutherland 1976, Fretwell 1977, Oksanen et al. 1981, Carpenter and Kitchell 1993, Nisbet et al. 1997, Sinclair et al. 2000, Diehl et al. 2000, Shurin et al. 2002, Borer et al. 2005). Empirical studies have sought to resolve these differences by exploring the existence and strength of trophic cascades, which

involve indirect positive effects of predators on plant biomass, as well as potential effects of bottom-up forcing through alteration of primary production. Numerous investigations in both terrestrial and aquatic ecosystems have been conducted, and specific predictions of various trophic models have been tested (Menge 2000, Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002, Bell et al. 2003, Borer et al. 2005).

A recent meta-analysis of field experiments from several ecosystems revealed that trophic cascades were common but tended to be strongest in the lentic and marine benthos and weakest in the marine plankton and terrestrial systems (Shurin et al. 2002). Trophic responses often have been estimated during relatively short experimental manipulations, often at small spatial scales in the field or in laboratory mesocosms (Bell et al. 2003) and increasingly ecologists have turned to longer-term studies, sometimes carried out at relatively large spatial scales, to explore effects of food web perturbations (Menge 2000, Ripple and Beschta 2004, Findlay et al. 2005, Frank et al. 2005, Terborgh et al. 2006). Frequently these datasets involve cases where abundances of predators vary, following reduction in their previously-abundant populations (northwest Atlantic cod; Frank et al. 2005), reintroduction following a period of absence (wolves; Ripple and Beschta 2004), or introduction of a non-native predator species (northern pike; Findlay et al. 2005). In studies such as these evidence for trophic cascades is sought by examining the patterns of population sizes in low trophic levels, with high abundances of predators resulting in an indirect positive effect on primary producers.

Spatial or temporal gradients in productivity provide another context for exploring responses of food webs to perturbations (Holbrook et al. 1997, Menge 2000, Brooks et al. 2002, Chase 2003, Daskalov 2003, Hunt and McKinnell 2006). In studies of benthic food webs in ponds, Chase (2003) found that predator effects on prey biomass were strongest and cascaded to plants only under low productivity regimes; under conditions of moderate to high productivity predator effects on prey were weak and there was no trophic cascade. Similarly, the strength of top-down processes in marine rocky intertidal communities appears to be strongly impacted by oceanographic conditions that alter primary productivity (Menge 2000). These findings suggest that the magnitude and existence of trophic cascades could vary with productivity.

In coastal marine environments, productivity is heavily influenced by climate-driven oceanographic processes. For example, the behavior of the California Current system has a profound effect on nearshore conditions in Southern California (Brodeur et al. 1996, Hayward 1997, Peterson and Schwing 2003). Coastal upwelling, which brings deeper, nutrient-laden waters to the surface, enhances primary productivity, which in turn drives the secondary productivity of the benthic and pelagic food webs. Oceanographic conditions in the California Current system underwent a substantial shift in the late 1970s when there was a rapid, persistent increase in seawater temperature (Miller et al. 1994, Minobe 1997, Hayward 1997, Mantua and Hare 2002, Peterson and Schwing 2003, Chavez et al. 2003). Associated with this warming event was a decrease in upwelling intensity and productivity of nearshore surface waters (Roemmich and McGowan 1995, McGowan et al. 1996). By the middle 1990s, abundances of organisms representing several trophic levels in nearshore reef food webs in the Southern California Bight all had declined on the order of eighty percent, with no evidence of alternating control by trophic level (Holbrook and Schmitt 1996, Holbrook et al. 1997, Brooks et al. 2002). The warm, low productivity phase of the Pacific Decadal Oscillation (PDO) persisted until the

late 1990s, when a shift to the cool phase began (Peterson and Schwing 2003, Goericke et al. 2004, 2005). Both the declining productivity during the warm phase and the recent trend toward a higher productivity regime afford opportunities to explore the responses of the ecosystem to changes in bottom-up forcing.

Here we assess temporal patterns of abundance within two food pathways of the benthic food web in the Southern California Bight during the past two decades. Our goals are to explore the whether the two sets of linked trophic groups showed similar responses to the bottom-up effects of the warm phase of the Pacific Decadal Oscillation and if there was coherency in the regional scale of responses during that period. In addition, in light of predictions from trophic theory, we investigate the trophic responses to the recent apparent shift to the more productive cool oceanographic phase.

Materials and Methods

Temporal patterns in abundances of communities on shallow (<20 m depth) rocky reefs were established using three studies that assess long-term population trends in the Southern California Bight, USA. We focused on two sets of linked trophic groups that comprise different portions of the benthic food web: (1) kelp bass - surfperches - benthic crustaceans - understory algae and (2) California sheephead – urchins – edible understory algae. The three studies provided data on abundance of each trophic group during the recent warm phase of the Pacific Decadal Oscillation (i.e., from the onset of sampling in the 1970s or 1980s until the late 1990s). This enabled us to explore the magnitude of responses of species in different trophic levels to conditions during the warm phase at several different locations – a single island (Santa Cruz Island), the northern Channel Islands (situated in the northern region of the Southern California Bight), and a coastal reef near Los Angeles in the southern portion of the Southern California Bight. The consistency of trophic responses to declining productivity could thus be assessed over increasingly broad spatial scales. Recent data (since the late 1990s) from two of the datasets also provided insight into possible patterns of change in one of the food pathways in response to the shift to the cool, higher productivity phase of the Pacific Decadal Oscillation that now appears to be occurring (Goericke et al. 2004, 2005).

The first dataset is a long-term study of surfperches (Embiotocidae) and their associated reef resources at 11 reefs on Santa Cruz Island (35°5' N, 119°45' W) in the northern part of the Southern California Bight (see Schmitt and Holbrook 1986, 1990a, 1990b, in press; Holbrook and Schmitt 1989, 1996; Holbrook et al. 1994, 1997). At the beginning of the study in 1982, the study reefs were covered with foliose macroalgae and turf, a low-growing, debris-laden mixture of small animals and algae. Giant kelp, *Macrocystis pyrifera*, has occurred intermittently on some of the reefs during the past two decades but is generally absent. Estimates of abundances of three species of surfperch (black surfperch, *Embiotoca jacksoni*; striped surfperch, *Embiotoca lateralis*; and pile surfperch, *Damalichthys vacca*) are obtained from visual counts made by divers along 40 x 2 m isobathic transects ranging from 3 to 9 m bottom depth annually during September – November. Bottom cover on the reefs is characterized at the time fish are counted using a random point contact (RPC) method (see Schmitt and Holbrook 1986), to obtain estimates of the percent cover of turf and the common species of understory macroalgae. When present, the abundance of giant kelp is estimated in band transects (Schmitt and Holbrook

1990a). Abundance of crustaceans used by the surfperch as food is assessed during the fall months (a period of seasonally high crustacean abundance; see Schmitt and Holbrook 1986) by collecting prey in ten randomly placed 0.1 m^2 quadrats at three depths (3, 6 and 9 m). Preyladen substrates are collected, placed in plastic bags underwater; in the laboratory prey are removed, counted and identified. Substrates in each sample are sorted taxonomically and weighed damp to provide estimates of algal biomass. An estimate of the food base in a given year was computed from the product of the substrate cover used by fishes as foraging microhabitat in shallow reef zones (*Gelidium robustum*) and in deep reef zones (turf) as estimated by the RPC transects and respective prey densities estimated from 0.1 m^2 quadrats from each depth; these two values were averaged to yield the food base estimate for a site during a year.

The second dataset used in this study is the ongoing Kelp Forest Monitoring Program conducted by the Channel Islands National Park (Davis et al. 1997). In this effort, which was initiated in 1985 following a several year long design phase, population abundances of a wide variety of reef organisms are assessed annually during summer months at sites on 5 northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa, Santa Barbara) using a total of 12 sampling techniques. Visual transects (100 x 2 m until 1995; 50 x 2 m since 1996) by divers are used to assess abundances of 13 species of fish, several of which [kelp bass (*Paralabrax clathratus*), California sheephead (*Pimelometopon pulchrum*) and three species of surfperch (*E. jacksoni, E. lateralis*, and *D. vacca*)] are pertinent to this study. Abundance of benthic algae, red sea urchins (*Stronglyocentrotus franciscanus*) and purple sea urchins (*S. purpuratus*) are estimated in 1 m² quadrats placed along transect lines. Additional information on abundance of algae is obtained by random point contact sampling on the transect lines. Techniques are fully described in Davis et al. 1997. Here we present data from three islands (Santa Cruz, Anacapa and Santa Rosa).

The third dataset is the long term study conducted by J.S. Stephens and colleagues at King Harbor along the mainland coast off Los Angeles County in the southern part of the Bight (33°51' N, 118°24' W; see Terry and Stephens 1976, Stephens 1983, Stephens et al. 1984, 1994, Holbrook et al. 1997). Estimates of fish species occurrence and densities are obtained from visual counts made by divers along isobathic transects ranging from 3 to 20 m bottom depth. Multiple counts of different-staged fish (usually adult, sub-adult and young-of-year) were made four times each year starting in 1974. We include here analyses of data for the time period 1974 to 1993.

Abundances of all of trophic groups that we examined declined during the warm phase of the PDO. To quantify this change for each trophic group, we calculated the mean proportional decline between abundances during the initial two-year period in each dataset (1982-1983 for Santa Cruz Island, 1985-1986 for Channel Islands National Park, and 1974-1975 for King Harbor) and the last two years of the warm phase (1998-1999).

Results

Temporal Patterns during the Warm Phase of the PDO at Santa Cruz Island

Abundances of all four trophic levels of the Santa Cruz Island food chain – kelp bass, surfperches, mesocrustaceans and understory algae – declined during the warm phase of the PDO (Figs. 1-4, Table 1). By the final years of the warm phase, the proportional decline of all four trophic groups from abundances documented earlier in the phase (early 1980s) was on the order of 0.8. Abundances of kelp bass, surfperch, mesocrustaceans and algae fell steadily beginning in the middle of the 1980s, reaching their lowest points between 1995 and 2001. Species within a trophic level (e.g., the three species of surfperch) showed similar patterns of abundance over time (Figure 2). The decline in total biomass of understory algae at all depths was mirrored by the pattern in percent cover of the red alga that is the most productive feeding habitat for surfperch (*Gelidium robustum*). Taken together, the results indicate that all of the trophic levels displayed similar population responses to the declining productivity associated with the warm phase of the Pacific Decadal Oscillation.



Figure 1. Density of kelp bass (*Paralabrax clathratus*) over time at Santa Cruz Island. Given is the mean number of individuals seen on visual transects at 3-10 monitoring sites on the island per year.



Figure 2. Densities of black surfperch (*Embiotoca jacksoni*, top), striped surfperch (*E. lateralis*, middle) and pile surfperch *Damalichthys vacca*, bottom) at Santa Cruz Island. Given is the mean total number of individuals seen on visual transects per day per site (N = 6-11 sites monitored 2 to 8 times per year).



Figure 3. Abundance of the crustacean food base for surfperch at Santa Cruz Island. Given is the estimated food supply based on abundance of crustaceans in $0.1m^2$ quadrats (N = 30 per year) as well as the supply of the red alga *Gelidium robustum* and of algal turf, key foraging substrates for surfperch.



Figure 4. Trends in algal biomass (top) and in the cover of *Gelidium robustum* (bottom) over time at Santa Cruz Island. Algal biomass is estimated in $0.1m^2$ quadrats (N = 30 per year). Cover of *Gelidium* is estimated on RPC transects at 3m and 6m water depths.

Table 1. Mean proportional change (\pm 1 SE) in abundance during the warm phase of the Pacific Decadal Oscillation of four linked trophic groups at 3 different spatial scales: SCI = Santa Cruz Island; CINP = Channel Islands National Park; Redondo = King Harbor, Redondo Beach. See Methods for time frames of declines.

		SPATIAL SCALE	
	<u>SCI</u>	CINP	Redondo
TROPHIC GROUP			
Understory Algae	-0.78 (0.02)	-0.60(0.14)	
Meso-crustaceans	-0.80 (0.02)		
Surfperch	-0.79 (0.06)	-0.68 (0.06)	-0.75 (0.07)
Kelp bass	-0.78 (0.12)	-0.60 (0.15)	-0.62 (0.20)

Temporal patterns during the warm phase of the PDO in the Southern California Bight

The decline in abundance in the kelp bass–surfperch–algae–mesocrustacean trophic set that occurred on Santa Cruz Island starting in the 1980s also took place at other locations in the Southern California Bight (Table 1). On three northern islands, the mean proportional decline in abundances of these groups was about 0.6 from the mid 1980s until the late 1990s, and the magnitude of the change was similar among the trophic levels. A comparable decline occurred for kelp bass and surfperch populations at King Harbor (Table 1), consistent with a regional phenomenon of declining populations of reef organisms. In addition, on the northern Channel Islands, populations of species in the second reef-based trophic set we examined (California sheephead – urchins – edible algae) also experienced steep declines over the same time period (Table 2).

Table 2. Mean proportional change (± 1 SE) among three linked trophic groups within a benthic food web surveyed at the Channel Islands National Park from the mid 1980s to the late 1990s.

Trophic Group	Proportional Change
Edible Algae	-0.60 (0.14)
Urchins	-0.62 (0.05)
Sheephead	-0.45 (0.07)

Evidence for response of trophic groups to shift to cool phase of the PDO

Data on species abundances for the few years that have elapsed since the onset of cool oceanographic conditions indicate some modest increases in several trophic levels at Santa Cruz Island (Figs. 1-4). Only one group, pile surfperch, which reached their low in the mid-1990s, has regained abundances similar to those of the early 1980s (Figure 2). By contrast, kelp bass, striped surfperch and black surfperch show much smaller recent increases (Figs. 1 and 2), as do the biomass of algae and cover of *Gelidium robustum* (Figure 4). In addition, the data also suggest that most groups did not experience an immediate change in abundance at the end of the

warm phase of the PDO (1999). Rather, evidence for rising abundance does not become apparent for one to two years.

Discussion

Ecologists have long sought to understand the responses of ecosystems to trophic perturbations, and in recent decades, there has been increasing interest in determining how food webs are controlled. A large number of studies have explored top-down and bottom-up processes, and how various perturbations such as removal of top predators or increase in nutrient supply to the bottom of the food chain affects both structure (e.g., abundance, species diversity) and function (e.g., productivity, reproduction). Currently, there is abundant evidence that in many systems, both top-down and bottom-up processes operate; the challenge is to determine under what conditions one type of control predominates. This issue has been addressed in a few experimental studies where the relative importance of and potential interaction between top-down and bottom-up effects were explicitly tested. For example, top-down and bottom-up processes both contributed to control of the structure of stream communities studied by Nystrom et al. (2003), but the effects were largely independent. In contrast, the processes interacted to produce effects on plant growth in an old field food web. Stronger top-down forcing occurred under conditions of higher productivity (Moral and Schleider 2002), suggesting that the strength of top-down forcing can be mediated by the resource base.

Strong top-down forcing has been experimentally demonstrated in a variety of benthic marine communities, both in the rocky intertidal and the subtidal (Menge 2000, Shurin et al. 2002). However, marine populations are known to respond to large scale physical change in the environment that can greatly alter productivity. Temporal phenomena including short-term (e.g., El Nino events) and longer term decadal-scale processes (e.g., the Pacific Decadal Oscillation) drive changes in oceanic primary production and have been identified as important influences in fisheries production (Hunt and McKinnell 2006). Indeed, bottom-up forcing has been argued to be the predominant environmental force affecting commercially harvested fish stocks in the Northeast Pacific Ocean (Ware and Thompson 2005). In addition, spatial variation in physical processes such as currents and upwelling regimes can result in alterations in primary productivity at scales of tens to thousands of kilometers (Menge 2000). At these spatial scales, oceanographic influences help explain variation in the structure of rocky intertidal food webs, despite the fact that these communities have a rich history of studies demonstrating top-down effects operating at very small spatial scales (Menge 2000).

If it is true that bottom-up factors resulting from changing productivity regimes could reduce or even eliminate the potential for top-down control, evidence for declines (or increases) in productivity should be apparent at temporal and spatial scales that reflect the scale of ocean processes that influence nutrient availability. The results we report here are consistent with the idea that population abundances in the nearshore food webs of the Southern California Bight are driven by variation in oceanographic processes that influence productivity for several reasons. First, the magnitude of declines in abundance during the warm phase of PDO were similar for organisms on several different trophic levels within each food chain. Second, the patterns were consistent among the three data sets that represented sites in different portions of the Southern California Bight, indicating spatial coherence in the underlying mechanism. Third, the dramatic declines in population sizes that we report are concordant to those described previously for other organisms in the Southern California Bight during the two decades following the onset of the warm phase of the Pacific Decadal Oscillation in 1976, including giant kelp, *Macrocystis pyrifera*, off San Diego (Tegner et al. 1996), macrozooplankton in surface waters of the California Current (Roemmich and McGowan 1995), seabirds (Veit et al. 1996, Oedekoven et al. 2001), over 50 species of reef fishes sampled near Los Angeles (Holbrook et al. 1997), and a group of 37 species of fish from reef, pelagic and benthic habitats in the southern portion of the Bight (Brooks et al. 2002).

Earlier we documented declines for some of the groups in one of the Santa Cruz Island food webs described here that had taken place between the early 1980s and 1995 (Holbrook et al. 1997). If changing ocean productivity regimes and the associated bottom-up effects underlie the patterns of abundances in our dataset, we would predict continued low abundance until the next regime shift to the cool water, productive PDO phase. Indeed, the time series of data (Figs. 1-4) reveal low abundances for these groups on Santa Cruz Island persisted in most cases until 2000 or 2001. Although only a few years have elapsed since the reported end of the warm phase of the PDO in the late 1990s, the Santa Cruz Island data suggest that the food web there is perhaps responding to increasing supply of nutrients associated with cooler ocean conditions. Interestingly, most groups show a lag in response of approximately two years in that their populations remained low or declined further during the first years of the cool phase. Brooks et al. (2002) reported a two to three year lag in abundance responses of 37 species of fish in the Southern California Bight to declines in mesozooplankton abundances in the California Current. This result was argued to be consistent with the effects of decreased primary and secondary productivity in the pelagic nearshore ecosystem propagating (rapidly) up the benthic food chain.

The patterns that hint of increasing abundances of groups in our data set during the past several years are also consistent with reports regarding responses of the pelagic ecosystem on the West Coast to recent higher oceanic productivity. For example, beginning in 2000, zooplankton abundances in the California Current and biomass of cold-water species of copepods off Oregon both increased markedly, as did the number of adult Chinook salmon returning to the Columbia River system (Peterson and Schwing 2003).

Ecologists have long recognized impacts on populations and communities to short term climate events (ENSO), but in the past decade increasing attention has been paid to the effects of low-frequency climate change events like the Pacific Decadal Oscillation. Retrospective analyses have been hampered by a paucity of datasets of multidecadal length and longer for most organisms. Such datasets are more common for exploited species like marine fish, but interpretation of temporal patterns is confounded by exploitation pressure.

Acknowledgements

We thank the Channel Islands National Park and J.S. Stephens Jr. for providing us with access to the data collected in their monitoring programs. We are very grateful to K. Seydel and the many field and laboratory assistants who have worked with us over the years to collect the long time series of data at Santa Cruz Island. Research at Santa Cruz Island was supported by grants from the National Science Foundation (OCE 9503305, OCE 0620276 and earlier awards), and the UC-MMS Coastal Marine Institute Program, Minerals Management Service, US Department of the Interior, under MMS Agreement No. 14-35-0001-30758 (Task No. 14181). The views and conclusions contained in this document are those of the authors and should not be interpreted as necessarily representing the official policies, either expressed or implied, of the US Government.

REFERENCES

Chapter 1:

- Aebischer, N. J., Coulson, J. C., and Colebrook, J. M. (1990). Parallel long-term trends across four marine trophic levels and weather. *Nature* 347, 753-755.
- Barry, J. P., Baxter, C. H., Sagarin, R. D., and Gilman, S. E. (1995). Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* 267, 672-675.
- Beamish, R. J., King, J. R., Noakes, D., McFarlane, G. A., and Sweeting, R. (1998). Evidence of a new regime starting in 1996 and the relation to Pacific salmon catches. *North Pacific Anadromous Fish Commission Document 321*. pp.21. (Fisheries and Oceans Canada, Pacific Biological Station: Nanaimo).
- Beamish, R. J., McFarlane, G. A., and King, J. R. (2000). Fisheries climatology: understanding decadal scale processes that naturally regulate British Columbia fish populations. In 'Fisheries oceanography: an integrative approach to fisheries ecology and management'. (Eds. P. J. Harrison and T. R. Parsons) pp. 94-145. (Blackwell Science: Oxford).
- Bence, J. R. (1995). Analysis of short time series correction for autocorrelation. *Ecology76*, 628-639.
- Brodeur, R. D., Frost, B. W., Hare, S. R., Francis, R. C., and Ingraham, W. J. (1996). *California Cooperative Fisheries Investigations Reports*. 37, 80-99.
- Cailliet, G. M., Larson, R. J., Lea, R. N., VenTresca, D., and Knaggs, E. (2000). Final Report. Biological characteristics of nearshore fishes of California: A review of existing knowledge and proposed additional studies. Pacific Ocean Interjurisdictional Fisheries Management Plan Coordination and Development Project. (California State University: Moss Landing Marine Labs.)
- Carpenter, S. R. (1990). Large-scale perturbations: opportunities for innovation. *Ecology* 71, 2038-2043.
- Carpenter, S. R., and Kitchell, J. F. (1993). The trophic cascade in lakes. (Cambridge University Press, Cambridge).
- Chatfield, D. B. (1984). 'The analysis of time series; an introduction.' (Chapman and Hall, London.)
- Chelton, D. B. (1981). Interannual variability of the California Current physical factors. *California Cooperative Oceanic Fisheries Investigations Reports* 22, 34-48.

- Chelton, D. B. (1984). Commentary on short-term climatic variability in the Northeast Pacific Ocean. In 'The influence of ocean conditions on the production of salmonids in the North Pacific. (Ed. W. Percy). pp. 87-99. (Oregon State University Press: Corvallis).
- Chelton, D. B., Bernal, P. A., McGowan, J. A. (1982). Large-scale interannual physical and biological interaction in the California Current. *Journal of Marine Research* 40, 1095-1123.
- Corten, A. (1990). Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. *Netherlands Journal of Sea Research* 25, 227-235.
- Estes, J. A., and Duggins, D. O. (1995). Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* 65, 75-100.
- Fretwell, S. D. (1977). The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine* 20, 169-285.
- Fretwell, S. D. (1987). Food chain dynamics: the central theory of ecology? Oikos 50, 291-301.
- Hairston, N. G. Jr., and Hairston, N. G. (1997). Does food web complexity eliminate trophiclevel dynamics? *American Naturalist* 149, 1001-1007.
- Hairston, N. G., Smith, F. E., and Slobodkin, L. B. (1960). Community structure, population control and competition. *American Naturalist* 94, 421-425.
- Hayward, T. L. (1996). Long-term change in the North Pacific Ocean: a consideration of some important issues. *California Cooperative Oceanic Fisheries Investigations Reports* 37, 41-44.
- Holbrook, S. J., and Schmitt, R. J. (1996). On the structure and dynamics of temperate reef fish assemblages: are resources tracked? In 'Long-term studies of vertebrate communities'. (Eds. M. L. Cody and J. Smallwood) pp. 19-48. (Academic Press: San Diego).
- Holbrook, S. J., Kingsford, M. J., Schmitt, R. J., and Stephens, J. S. (1994). Spatial and temporal patterns in assemblages of temperate reef fish. *American Zoologist* 34, 463-475.
- Holbrook, S. J., Schmitt, R. J., and Stephens, J. S. (1997). Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications* 7, 1299-1310.
- Jassby, A. D., and Powell, T. M. (1990). Detecting change in ecological time series. *Ecology* 71, 2044-2052.

- Kingsford, M. J. (1990). Linear oceanographic features: a focus for research on recruitment processes. *Australian Journal of Ecology* 15, 391-401.
- Kope, R. G., and Botsford, L. W. (1988). Detection of environmental influence on recruitment using abundance data. *Canadian Journal of Fisheries and Aquatic Sciences* 45, 1448-1458.
- Lodge, D. M. (1993). Species invasions and deletions: Community effects and responses to climate and habitat change. In 'Biotic interactions and global change'. (Eds. P. M. Kareiva, J. G. Kingsolver, and R. B. Huey) pp. 367-387. (Sinauer Associates: Sunderland).
- Love, M. S., Caselle, J. E., and Herbinson, K. E. (1998). Declines in nearshore rockfish recruitment and populations in the southern California Bight as measured by impingement rates in coastal electrical power generating stations. *Fisheries Bulletin* 96, 492-501.
- Love, M. S., Caselle, J. E., and Van Buskirk, W. (1998). A severe decline in the commercial passenger fishing vessel rockfish (*Sebastes* spp.) catch in the Southern California Bight, 1980-1996. *California Cooperative Oceanic Fisheries Investigations Reports* 39, 180-195.
- Lubchenko, J. S., Navarrette, S. A., Tissot, B. N., and Castilla, J. C. (1993). Possible ecological responses to global climate change: Nearshore benthic biota of northeastern Pacific coastal ecosystems. In 'Earth System Responses to to Global Change'. (Eds. H. A. Mooney, E. R. Fuentes, and B. I. Kronberg) pp. 367-387. (Academic Press: San Diego).
- Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., and Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Journal of the American Meteorological Society* 78, 1069-1079.
- McGowan, J. A., Chelton, D. B., and Conversi, A. (1996). Plankton patterns, climate, and change in The California Current. *California Cooperative Oceanic Fisheries Investigations Reports* 37, 69-76.
- Menge, B. A., and Sutherland, J. P. (1976). Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* 110, 351-369.
- Miller, A. J., Cayan, D. R., Barnett, T. P., Graham, N. E., and Oberhuber, J. M. (1994). The 1976-77 climate shift of the Pacific Ocean. *Oceanography* 7, 21-26.
- Minobe, S. (1997). A 50-70 year climate oscillation over the North Pacific and North America. *Geophysical Research Letters* 24, 682-686.

- Oedekoven, C. S., Ainley, D. G., and Spear, L. B. (2001). Variable responses of seabirds to change in marine climate: California Current, 1985-1994. *Marine Ecology Progress Series* 212, 265-281.
- Oksanen, L., Fretwell, S. D., Arruda, J., and Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118, 240-261.
- Pyper, B. J., and Peterman, R. M. (1998). Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 2127-2140.
- Roemmich, D. (1992). Ocean warming and sea level rise along the southwest U. S. coast. *Science* 257, 373-375.
- Roemmich, D., and McGowan, J. (1995). Climatic warming and the decline of zooplankton in the California Current. *Science* 267, 1324-1326.
- Roughgarden, J., Gaines, S., and Pacala, S. (1987). Supply side ecology: the role of physical transport processes. In 'Organization of Communities Past and Present'. (Eds. J. H. R. Gee and P. S. Giller) 27, 491-518. (Blackwell Scientific Publications: Oxford).
- SAS (2001). SAS Software version 8.1. (SAS Institute: Cary).
- Sinclair, A. R. E., Krebs, C. J., Fryxell, J. M., Turkington, R., Boutin, S., Boonstra, R., Seccombe-Hett, P., Lundberg, P., and Oksanen, L. (2000). Testing hypotheses of trophic level interactions: a boreal forest ecosystem. *Oikos* 89, 313-328.
- Smith, J. B., and Lazo, J. K. (2001). A summary of climate change impact assessments from the US country studies program. *Climatic Change* 50, 1-29.
- Stephens, J. S. (1983). The fishes of King Harbor: A nine year study of fishes occupying the receiving waters of a coastal steam electric generating station. *Research and Development Series 83-RD-1*. Occidental College, Los Angeles, California.
- Stephens, J. S., Morris, P. A., Pondella, D. J., Koonce, T. A., and Jordan, G. A. (1994).
 Overview of the dynamics of an urban artificial reef fish assemblage at King Harbor, California. USA. 1974-1991: A recruitment-driven system. *Bulletin of Marine Science* 55, 1224-1239.
- Swearer, S. E., Caselle, J. E., Lea, D. W., and Warner, R. R. (1999). Larval retention and recruitment in an island population of a coral reef fish. *Nature* 402, 799-802.
- Tegner, M. J., Dayton, P. K., Edwards, P. B., and Riser, K. L. (1996). Is there evidence for long-term climatic change in Southern California kelp forests? *California Cooperative Oceanic Fisheries Investigations Reports* 37, 111-128.

- Terry, C. B., and Stephens, J. S. (1976). A study of the orientation of selected embiotocid fishes to depth and shifting seasonal vertical temperature gradients. *Bulletin of the Southern Academy of Sciences* 75, 170-183.
- Underwood, A. J., and Keough, M. J. (2001). Supply-side ecology: the nature and consequences of variations in recruitment of intertidal organisms. In 'Marine Community Ecology'. (Eds. S. D. Gaines and M. E. Hay) pp. 183-200. (Sinauer Associates: Sunderland)
- Veit, R. R., Pyle, P., and McGowan, J. A. (1996). Ocean warming and long-term climate change in pelagic bird abundance within the California current system. *Marine Ecology Progress Series* 139, 11-18.
- Wooton, J. T. (1994). Putting the pieces together: testing the independence of interactions among organisms. *Ecology* 75, 1544-1551.

Chapter 2:

- Anderson, G. R. V., A. H. Erlich, P. R. Erlich, J. R. Roughgarden, B. C. Russell & F. H. Talbot, 1981. The community structure of coral reef fishes. *American Naturalist*, **117**: 476-495.
- Anderson, T. W. & B. D. Sabado, 1995. Correspondence between food availability and growth of a planktivorous temperate reef fish. *Journal of Experimental Marine Biology and Ecology*, 189: 65-76.
- Armsworth, P. R., 2002. Recruitment limitation, population regulation, and larval connectivity in reef fish populations. *Ecology*, **83**: 1092-1104.
- Ault, T. R. & C. R. Johnson, 1998. Spatially and temporally predictable fish communities on coral reefs. *Ecological Monographs*, 68: 25-50.
- Baltz, D. M., 1984. Life history variation among female surfperches (Perciformes: Embiotocidae). *Environmental Biology of Fishes*, **10**: 159-171.
- Booth, D. J., 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology* **76**: 91-106.
- Booth, D. J., 2004. Synergistic effects of conspecifics and food on growth and energy allocation of a damselfish. *Ecology* **85**: 2881-2887.
- Caley, M. J. & J. St. John, 1996. Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology*, **65**: 414-428.
- Chesson, P., 1994. Multispecies competition in variable environments. *Theoretical Population Biology*, **45**: 227-276.

- Chesson, P., 2000a. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**: 343-366.
- Chesson, P., 2000b. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology*, **58**: 211-237.
- Choat, J. H. & A. M. Ayling, 1987. The relationship between habitat structure and fish faunas on New Zealand reefs. *Journal of Experimental Marine Biology and Ecology*, **110**: 257-284.
- Choat, J. H., A. M. Ayling & D. R. Schiel, 1988. Temporal and spatial variation in an island fish fauna. *Journal of Experimental Marine Biology and Ecology*, **121**: 91-111.
- Doherty, P. J., 1982. Some effects of density on the juveniles of two species of tropical territorial damselfishes. *Journal of Experimental Marine Biology and Ecology* **65**: 249-261.
- Doherty, P. J., 1983. Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* 64: 176-190.
- Doherty, P. J., 1991. Spatial and temporal patterns in recruitment. In: Sale, P.F. (ed.), *The Ecology of Fish on Coral Reefs*. San Diego, California, Academic Press, Pp. 261-292.
- Forrester, G. E., 1990. Factors influencing the juvenile demography of a coral reef fish. *Ecology* **71**: 1666-1681.
- Gladfelter, W. B., J. C. Ogden & E. H. Gladfelter, 1980. Similarity and diversity among coral reef fish communities: a comparison between tropical Western Atlantic (Virgin Islands) and Tropical Central Pacific (Marshall Islands) patch reefs. *Ecology*, **61**: 1156-1168.
- Hixon, M. A., 1980. Competitive interactions between California reef fishes of the genus *Embiotoca. Ecology*, **61**: 918-931.
- Hixon, M. A. & J. P. Beets, 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science*, **44**: 666-680.
- Hixon, M. A. & J. P. Beets, 1993. Predation, prey refuges, and the structure of coral reef fish assemblages. *Ecological Monographs*, **63**: 77-101.
- Hixon, M. A. & M. S. Webster, 2002. Density dependence in reef fishes: coral-reef populations as model systems. In: Sale, P. F. (ed.), *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. San Diego, California, Academic Press, Pp. 303-325.
- Holbrook, S. J. & R. J. Schmitt, 1989. Resource overlap, prey dynamics, and the strength of competition. *Ecology*, **70**: 1943-1953.

- Holbrook, S. J. & R. J. Schmitt, 1996. On the structure and dynamics of temperate reef fish assemblages: are resources tracked? In: Cody, M. L. & J. A. Smallwood (eds.), *Longterm Studies of Vertebrate Communities*. San Diego, California, Academic Press, Pp. 19-48.
- Holbrook, S. J. & R. J. Schmitt, 2002. Competition for shelter space causes density-dependent mortality in damselfishes. *Ecology*, 83: 2855-2868.
- Holbrook, S. J. & R. J. Schmitt, 2003. Spatial and temporal variation in mortality of newly settled damselfish: patterns, causes and covariation with settlement. *Oecologia*, **135**: 532-541.
- Holbrook, S. J., R. J. Schmitt & R. F. Ambrose, 1990. Biogenic habitat structure and characteristics of temperate reef fish assemblages. *Australian Journal of Ecology*, 15: 489-503.
- Holbrook, S. J., S. L. Swarbrick, R. J. Schmitt & R. F. Ambrose, 1993. Reef architecture and reef fish: correlates of population densities with attributes of subtidal rocky environments. In: Battershill, C. N. et al. (eds.), *Proceedings of the Second International Temperate Reef Symposium*. Wellington, NZ, NIWA Marine. Pp. 99-106.
- Holbrook, S. J., M. J. Kingsford, R. J. Schmitt & J. S. Stephens, Jr., 1994. Spatial and temporal patterns in assemblages of temperate reef fish. *American Zoologist* **34**: 463-475.
- Holbrook, S. J., R. J. Schmitt & J. S. Stephens Jr., 1997. Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications*, 7: 1299-1310.
- Holbrook, S. J., G. E. Forrester & R. J. Schmitt, 2000. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia*, **122**: 109-120.
- Holbrook, S. J., A. J. Brooks & R. J. Schmitt, 2002. Predictability of fish assemblages on coral patch reefs. *Marine and Freshwater Research*, **53**: 181-188.
- Jenkins, G. P., 2005. Influence of climate on the fishery recruitment of a temperate, seagrassassociated fish, the King George whiting *Sillaginodes puncata*. *Marine Ecology Progress Series*, **288**: 263-271.
- Jones, G. P., 1984. Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch & Schneider (Pisces, Labridae). I. Factors influencing recruitment. *Journal of Experimental Marine Biology and Ecology* **75**: 257-276.
- Jones, G. P., 1987a. Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* **68**: 1534-1547.

- Jones, G. P., 1987b. Some interactions between residents and recruits in two coral reef fishes. Journal of Experimental Marine Biology and Ecology **114**: 169-182.
- Jones, G. P., 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **123**: 115-126.
- Jones, G. P., M. J. Milicich, M. J. Emslie & C. Lunow, 1999. Self-recruitment in a coral reef fish population. *Nature*, 402: 802-804.
- McCauley, E., W. W. Murdoch & R. M. Nisbet, 1990. Growth, reproduction, and mortality of *Daphia pulex* Leydig: life at low food. *Functional Ecology*, **4**: 505-514.
- Ogden, J. C. & J. P. Ebersole, 1981. Scale and community structure of coral reef fishes: a long-term study of a large artificial reef. *Marine Ecology Progress Series*, **4**: 97-103.
- Osenberg, C. W., C. M. St. Mary, R. J. Schmitt, S. J. Holbrook, P. Chesson & B. Byrne, 2002. Rethinking ecological inference: density-dependence in reef fishes. *Ecology Letters*, **5**: 715-721.
- Sale, P. F. & R. Dybdahl, 1975. Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology*, **56**: 1343-1355.
- Schmitt, R. J. & J. A. Coyer, 1982. The foraging ecology of sympatric marine fish in the genus *Embiotoca* (Embiotocidae): importance of foraging behavior in prey size selection. *Oecologia*, 55: 369-378.
- Schmitt, R. J. & S. J. Holbrook, 1984. Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. *Oecologia*, **63**: 6-12.
- Schmitt, R. J. & S. J. Holbrook, 1986. Seasonally fluctuating resources and temporal variability of interspecific competition. *Oecologia*, **69**: 1-11.
- Schmitt, R. J. & S. J. Holbrook, 1990a. Contrasting effects of giant kelp on dynamics of surfperch populations. *Oecologia*, **84**: 419-429.
- Schmitt, R. J. & S. J. Holbrook, 1990b. Population responses of surfperch released from competition. *Ecology*, **71**: 1653-1665.
- Schmitt, R. J. & S. J. Holbrook, 2000. Habitat-limited recruitment of coral reef damselfish. *Ecology*, **81**: 3479-3494.
- Shulman, M. J., 1985. Variability in recruitment of coral reef fishes. *Journal of Experimental Marine Biology and Ecology*, **89**: 205-219.

- Syms, C. & G. P. Jones, 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology*, **81**: 2714-2729.
- Tolimieri, N., 1995. Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. *Oecologia*, **102**: 52-63.

Chapter 3:

- Bailey DM, Ruhl HA, Smith KL Jr (2006) Long-term change in benthopelagic fish abundance in the abyssal northeast Pacific Ocean. Ecology 87:549-555
- Bell T, Neill WE, Schluter D (2003) The effect of temporal scale on the outcome of trophic cascade experiments. Oecologia 134:578-586
- Borer ET, Seabloom EW, Shurin JB, Anderson KE, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2005) What determines the strength of a trophic cascade? Ecology 86:528-537
- Brodeur RD, Frost BW, Hare SR, Francis RC, Ingraham WJ (1996) Interannual variation in zooplankton biomass in the Gulf of Alaska, and covariation with California Current zooplankton biomass. CalCOFI Rep 37:80-99
- Brooks AJ, Schmitt RJ, Holbrook SJ (2002) Declines in regional fish populations: have species responded similarly to environmental change? Mar Freshwat Res 53:189-198
- Carpenter SR, Kitchell JF (1993) The Trophic Cascade in Lakes. Cambridge University Press, Cambridge
- Chase JM (2003) Strong and weak trophic cascades along a productivity gradient. Oikos 101:187-195
- Chavez FP, Ryan J, Lluch-Cota SE, Niquen MC (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299:217-221
- Daskalov GM (2003) Long-term changes in fish abundance and environmental indices in the Black Sea. Mar Ecol Prog Ser 255:259-270
- Diehl S, Cooper SD, Kratz KW, Nisbet RM, Roll SK, Wiseman SW, Jenkins TM Jr (2000) Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. Am Nat 156:293-313
- Findley DL, Vanni MJ, Paterson M, Mills KH, Kasian SEM, Findlay WJ, Salki AG (2005) Dynamics of a boreal lake ecosystem during a long-term manipulation of top predators. Ecosystems 8:603-618

- Frank KT, Petrie B, Choi JS, Leggett WC (2003) Trophic cascades in a formerly cod dominated ecosystem. Science 308:1621-1623
- Fretwell SD (1977) Food chain dynamics: the central theory of ecology? Oikos 50:291-301
- Goericke R, Venrick E, Mantyla A, Bograd SJ, Schwing FB, Huyer A et al (2004) The state of the California Current, 2003-2004: A rare "normal" year. CalCOFI Rep 45:27-59
- Goericke R, Venrick E, Mantyla A, Bograd SJ, Schwing FB, Huyer A et al (2005) The state of the California Current, 2004-2005: Still cool? CalCOFI Rep 46:32-71
- Hairston NG JR, Smith FE, Slobodkin LB (1960) Community structure, population control and competition. Am Nat 94:421-425
- Hairston NG Jr, Hairston NG (1977) Does food web complexity eliminate trophic-level dynamics? Am Nat 149:1001-1007
- Halaj J, Wise DH (2001) Terrestrial trophic cascades: how much do they trickle? Am Nat 157:262-281
- Hayward TL (1997) Pacific Ocean climate change: atmospheric forcing, ocean circulation and ecosystem response. TREE 12:150-154
- Holbrook SJ, Schmitt RJ (1989) Resource overlap, prey dynamics, and the strength of competition. Ecology 70:1943-1953
- Holbrook SJ, Schmitt RJ (1996) On the structure and dynamics of temperate reef fish assemblages: are resources tracked? In: Cody ML, Smallwood JA (eds) Long-term Studies of Vertebrate Communities. Academic Press, San Diego CA, pp 19-48
- Holbrook SJ, Kingsford MJ, Schmitt RJ, Stephens JS (1994). Spatial and temporal patterns in assemblages of temperate reef fish. Am Zool 34:463-475
- Holbrook SJ, Schmitt RJ, Stephens JS (1997) Changes in an assemblage of temperate reef fishes associated with a climate shift. Ecol App 7:1299-1310
- Hunt GL Jr, McKinnell S (2006) Interplay between top-down, bottom-up and wasp-waist control in marine ecosystems. Progr Oceanography 68:115-124
- Mantua NJ, Hare SR (2002) The Pacific Decadal oscillation. J Oceanogr 58:35-44
- McGowan JA, Chelton DB, Conversi A (1996) Plankton patterns, climate, and change in the California Current. CalCOFI Rep 37:69-76
- Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. J Exp Mar Biol Ecol 250:257-289

- Menge BA, Sutherland JP (1976) Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am Nat 110:351-369
- Miller AJ, Cayan DR, Barnett TP, Graham NE, Oberhuber JM (1994) The 1976-77 climate shift of the Pacific Ocean. Oceanography 7:21-26
- Minobe S (1997) A 50-70 year climate oscillation over the North Pacific and North America. Geophys Res Lett 24:682-686
- Moran MD, Scheidler AR (2002) Effects of nutrients and predators on an old-field food chain: interactions of top-down and bottom-up processes. Oikos 98:116-124
- Nystrom P, McIntosh AR, Winterbourn MJ (2003) Top-down and bottom-up processes in grassland and forested streams. Oecologia 136:596-608
- Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. Am Nat 118:240-261
- Peterson WT, Schwing FB (2003) A new climate regime in northeast pacific ecosystems. Geophys Res Lett 30(17): Art No 1896
- Ripple WJ, Beschta RL (2004) Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of southwestern Montana, USA. Forest Ecol Management 200:161-181
- Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California Current. Science 267:1324-1326
- Schmitt RJ, Holbrook SJ (1986) Seasonally fluctuating resources and temporal variability of interspecific competition. Oecologia 69:1-11
- Schmitt RJ, Holbrook SJ (1990a) Contrasting effects of giant kelp on dynamics of surfperch populations. Oecologia 84:419-429
- Schmitt RJ, Holbrook SJ (1990b) Population responses of surfperch released from competition. Ecology 71:1653-1665
- Schmitz OJ, Hambaeck PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. Am Nat 155:141-153
- Schneider N, Cornuelle BD (2005) The forcing of the Pacific Decadal Oscillation. J Climate 18:4355-4373
- Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2002) A cross-ecosystem comparison of the strength of trophic cascades. Ecol Lett 5:785-791

- Sinclair ARE, Krebs CJ, Fryxell JM, Turkington R, Boutin S, Boonstra R, Seccombe-Hett P, Lundberg P, Oksanen L (2000) Testing hypotheses of trophic level interactions: a boreal forest ecosystem. Oikos 89:313-328
- Stephens JS (1983) The fishes of King Harbor: A nine year study of fishes occupying the receiving waters of a coastal steam electric generating station. Research and Development Series 83-RD-1. Occidental College, Los Angeles, California
- Stephens JS, Zerba KE (1981) Factors affecting fish diversity on a temperate reef. Environ Biol Fish 6:111-121
- Stephens JS, Morris PA, Zerba K, Love M (1984) Factors affecting fish diversity on a temperate reef: the fish assemblage of Palos Verdes Point, 1974-1981. Environ Biol Fish 11:259-275
- Stephens JS, Jordan GA, Morris PA, Singer MM, McGowen GE (1986) Can we relate larval fish abundance to recruitment or population stability? A preliminary analysis of recruitment to a temperate rocky reef. CalCOFI Rep 27:65-83
- Stephens JS, Morris PA, Pondella DJ, Koonce TA, Jordan GA (1994) Overview of the dynamics of an urban artificial reef fish assemblage at King Harbor, California, USA, 1974-1991. Bull Mar Sci 55:1224-1239
- Tegner MJ, Dayton PK, Edwards PB, Riser KL (1996) Is there evidence for long-term climatic change in Southern California kelp forests? CalCOFI Rep 37:111-128
- Terborgh J, Feeley K, Silman M, Nunez P, Balukjian B (2006) Vegetation dynamics of predator-free land bridge islands. J Ecol 94:253-263
- Terry CB, Stephens JS (1976) A study of the orientation of selected embiotocid fishes to depth and shifting seasonal vertical temperature gradients. Bull S Calif Acad Sci 75:170-183
- Veit RR, Pyle P, McGowan JA (1996) Ocean warming and long-term climate change in pelagic bird abundance within the California Current system. Mar Ecol Prog Ser 139:11-18
- Vucetich JA, Peterson RO (2004) The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. Proc Royal Soc London Series B Biological Sciences 271:183-189
- Ware DM, Thompson RE (2005) Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science 308:1280-1284

APPENDIX I

Species and classifications (after Cailliet *et al.* 2000, Table 1) used in the analysis of the proportional change in population abundance from 1977 to 1993 as estimated from monthly fish impingement surveys conducted by the Southern California Edison Company. Species marked with a ^{*} were used in the comparison of the proportional changes in abundance estimated from impingement data with that from diver visual surveys. (P = Planktivore, 1^0 M = Primary Macrocarnivore, 2^0 M = Secondary Macrocarnivore

Family Species	Habitat	Trophic Level	Geographic Range	Reproductive Mode	Food Web	Proportional Change
Atherinidae	monut	20101	1.41150	111040		chunge
Atherinops affinis	Pelagic	р	Northern	Faas	Pelagic	-0.69
Atherinopsis californiensis	Pelagic	P	Northern	Eggs	Pelagic	-0.39
I aurosthos tonuis	Pelagic	D I	Central	Eggs	Pelagic	-0.42
Carangidae	relagie	1	Central	Lgg5	I clagic	-0.42
Trachurus symmetricus	Pelagic	D	Northern	Faas	Benthic	-0.43
Clinidae	I clagic	1	Normenn	Lggs	Dentine	-0.45
Heterostichus rostratus [*]	Reef	$1^0 M$	Central	Foos	Benthic	-0.02
Clupeidae	Reel	1 101	Central	Lggs	Dentine	-0.02
Sardinons sagar	Pelagic	D	Northern	Faas	Pelagic	0.37
Cottidae	I clagic	1	Normenn	Lggs	I clagic	0.57
Scorpaniehthus marmoratus [*]	Deef	$2^0 M$	Northern	Faas	Bonthia	0.24
Desvetididee	Reel	2 101	Normenn	Lggs	Denunc	-0.24
Unolophus hallori	Donthio	1 ⁰ M	Control	Livo	Donthia	0.47
Embiotogidag	Denunc	1 101	Central	LIVE	Denune	-0.47
Prochujstius fromatus [*]	Doof	D	Northorn	Livo	Donthia	0.45
Damalishthys yasaa [*]	Reel	г 1 ⁰ М	Northern	Live	Denthia	-0.43
Embiotoog igeksoni [*]	Reel	$1^{0} M$	Control	Live	Denthia	-0.39
Emotoloca jacksoni	Reel	1 101	Central	Live	Denunc	-0.32
Anghag ageneration	Dalagia	р	Couthorn	Eaga	Dalagia	0.21
Anchoù compressa En angulia mandau	Delegie	Г	Control	Eggs	Delegie	-0.31
Engrauits moraax	relagic	Г	Central	Eggs	relagic	-0.85
Anigotromus devideouii*	Dalagia	1 ⁰ M	Couthorn	Eaga	Donthio	0.22
Anisoiremus adviasonii Vanistius aslifamiansis*	Pelagic	I MI D	Southern	Eggs	Delunic	-0.23
Aenisius caujorniensis	Pelagic	ľ	Soutien	Eggs	Pelagic	-0.29
Circlla nioniogna [*]	Deef	р	Couthorn	Eaga	Donthio	0.29
Giretta nigricans	Reel	ľ	Soutien	Eggs	Benunc	-0.58
Convicting a gliformia g*	Deef	D	Control	Egga	Donthio	0.12
Oxyjuus caujornica	Reel	ľ	Central	Eggs	Benunc	-0.12
Muliahatia aglifamiag	Donthio	1 ⁰ M	Control	Lina	Donthio	0.80
Mylloballs callfornica	Dentific	I IVI	Central	Live	Benunc	-0.89
Ophidian agrinnage	Donthio	D	Couthorn	Eaga	Donthio	0.95
Develophiaton scrippsae	Dentific	ľ	Southern	Eggs	Benunc	-0.83
	Dauthia	$2^0 M$	Control	Ease	Danthia	0.92
Paralichtnys californicus	Benthic	2 M	Central	Eggs	Benthic	-0.82
	Dauthia	1 ⁰ M	Control	Ease	Danthia	0.95
Hypsopsetta guttulata	Denthic	1 IVI 1 ⁰ M	Central	Eggs	Denthic	-0.85
r ieuronichinys verticalis	Dentnic	1 111	Central	Eggs	Dentnic	-0.70
Chaomia munotinimin*	Deef	п	Coult and	Ecco	Dalari	0.22
Chromis punctipinnis	Reel	r	Southern	Eggs	relagic	-0.22
	Dout	10 N.C	Control	т :	Dar 41	0.47
riatyrninoiais triseriata	Benthic	1 M	Central	Live	Benthic	-0.4 /

Saiaanidaa						
Atractoscion nobilis	Dologio	$2^0 M$	Northarn	Eggs	Dalagia	0.26
Alracioscion nobilis	Pelagic		Northern	Eggs	Pelagic	-0.20
Cheilotrema saturnum	Reef	1° M	Southern	Eggs	Benthic	-0.50
Genyonemus lineatus	Benthic	$1^0 M$	Central	Eggs	Benthic	-0.80
Menticirrhus undulatus	Benthic	$1^0 M$	Southern	Eggs	Benthic	-0.55
Seriphus politus	Pelagic	Р	Central	Eggs	Benthic	-0.36
Umbrina roncador	Benthic	$1^0 M$	Southern	Eggs	Benthic	-0.24
Scorpaenidae						
Sebastes paucispinis *	Pelagic	$2^0 M$	Northern	Eggs	Benthic	-0.38
Sebastes serranoides *	Reef	$2^0 M$	Central	Live	Benthic	-0.82
Serranidae						
$Paralabrax\ clathratus^{*}$	Reef	$2^0 M$	Southern	Eggs	Benthic	-0.15
$Paralabrax nebulifer^{*}$	Reef	$2^0 M$	Southern	Eggs	Benthic	-0.11
Sphyraenidae						
Sphyraena argentea	Pelagic	$2^0 M$	Southern	Eggs	Pelagic	0.01
Synodontidae						
Synodus lucioceps	Benthic	$2^0 M$	Northern	Eggs	Benthic	-0.18
Torpedinidae						
Torpedo californica	Reef	$2^0 M$	Northern	Live	Benthic	-0.51



The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.



The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Royalty Management Program** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.