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Authors

Graves, Michelle R.

Larson, Ralph J.

Alevizon, William S.

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TEMPORAL VARIATION IN FISH COMMUNITIES
OFF SANTA CRUZ ISLAND, CALIFORNIA

California Sea Grant Project R/MLPA-01

Technical Narrative, December 31, 2006

Michelle R. Graves,
Ralph J. Larson
William S. Alevizon

Department of Biology
San Francisco State University

Abstract

The assemblage of fishes inhabiting subtidal rocky reefs off Santa Cruz Island, California has changed noticeably since the 1970s. Subtidal surveys were conducted annually in 1971-74, in 1996, 2004 and 2005, using the “cinetransect” method. The period 1971-74 fell during the last cool “regime” of the Pacific Decadal Oscillation, while 1996 was near the end of the recent warm phase. Some of the changes observed between the 1970s and 1996 were consistent with ocean warming, while others seemed associated with a large-scale decline in kelp. Several southern species increased in abundance, while a number of northern species either declined in abundance or disappeared altogether. Current oceanographic data indicate cooler ocean conditions from 1999 through early 2005. Although kelp has returned to the south side of Santa Cruz Island, there appears to be little recovery of kelp at the original survey sites on the north side of Santa Cruz Island. However, analysis of data collected in 2004-05 suggests some interesting changes since 1996, including a slight increase in more northerly-distributed species.

These results, along with other similar work in the southern California Bight, demonstrate the important role of climate change in the distribution and abundance of fishes in California. Such changes influence both exploited and non-exploited species, so monitoring the abundance of both categories of species can help to distinguish the effects of fishing vs. climatic and other effects. In addition, monitoring of unfished reserves can help to refine these comparisons. The prevalence of climatic shifts and their effects on all fish populations means that long-term fishery management plans must be placed into the context of inevitable changes in the distribution and abundance of fish populations.

INTRODUCTION

Widespread change has occurred in the marine biota off southern California since the mid-1970s, including changes in the distribution and abundance of fishes, invertebrates, and kelp (Holbrook et al., 1997; Barry et al., 1995; Stephens et al., 1994; Love et al., 1998). An ecosystem-wide decline in primary productivity, and a late 20th-century increase in abundances of tropical and subtropical foraminifera have also been reported (Roemmich and McGowan, 1995; Field et al., 2006).

Recent work indicates that fluctuations in atmospheric and ocean climate, acting over several spatial and temporal scales, have had strong effects on marine ecosystems (Francis & Hare, 1994; Mantua et al., 1997; McGowan et al., 1998; Bond et al., 2003; Chavez et al., 2003;). Regionally, and on a scale of days to months, seasonal and sub-seasonal shifts in coastal winds lead to variation in coastal upwelling, with subsequent effects on marine food webs. Throughout the Pacific, larger-scale variability occurs on a scale of 3 to 7 years, in the form of El Niño and La Niña events. Although initiated in the tropical Pacific, these events drive basin-wide changes in sea surface temperature, coastal currents and thermocline depth, and have a marked effect on nutrient availability and larval transport (McGowan et al., 1998). Further, the Pacific Decadal Oscillation (PDO), a basin-wide pattern of climate variability at decadal time scales, has been identified in the northern Pacific (Mantua et al., 1997). Like the El Niño and La Niña events, the PDO is described as having “warm” and “cool” phases. The cool “regime” has been characterized as a period of higher primary productivity, stronger upwelling, shallower thermocline and cooler than average sea surface temperatures (SSTs) off the California coast, while essentially the opposite conditions prevail during the warm regime (McGowan et al., 1998; Chavez et al., 2003; Horn and Stephens, 2006). It is widely

acknowledged that the California Current region was affected by a cool phase of the Pacific Decadal Oscillation from 1947-1976, followed by a warm phase from 1977 to approximately 1998 (Mantua et al., 1997; Chavez et al., 2003; Horn and Stephens, 2006). The “regime shift” that occurred in 1976-77 was rapid and had profound effects on California’s marine ecosystems (Stephens et al., 1994; Holbrook et al., 1997; Hayward, 1997; McGowan et al., 1998; Hare and Mantua, 2000), although it was more than a decade before these effects were described in the scientific literature.

The well-documented El Niño event of 1997-98 preceded a strong La Niña in 1999, and heralded another possible regime shift, ostensibly back to the “cool” phase of the PDO that dominated the Pacific from 1947-1976 (Goericke et al., 2005; Horn & Stephens, 2006). While there is considerable debate regarding the nature and duration of this shift (Bond et al., 2003; Goericke et al., 2004 and 2005), the California Current region appears to have been dominated by cooler than normal ocean temperatures from 1999 through 2002 (Goericke et al., 2004; Bond et al., 2003). A moderate El Niño event occurred in late 2002 and peaked in early 2003 (Venrick et al., 2003), prompting speculation that the California Current was no longer in the cool phase of the PDO. Despite the fact that current climatological data do not support the assertion that the Pacific is in exactly the same state as during the 1947-1976 cool phase, and not all biological parameters have responded in a manner consistent with continued cool conditions, the pattern of sea surface temperatures in the California Current through early 2005 indicates that a cool phase continues (Goericke et al., 2005). Regardless, documenting the biological effects of this return to cooler ocean conditions is of vital importance.

Long-term studies are essential for understanding the effects of climate change on marine ecosystems. Although it may be impossible to completely separate anthropogenic

effects such as fishing and habitat alteration from climate effects, understanding natural change in marine populations is critical for management of marine resources. Within the Southern California Bight, there exist a few long-term data sets on kelp forest and rocky reef fishes. Stephens and colleagues have monitored the fish assemblage at King Harbor and Palos Verdes, near Los Angeles, since 1974, conducting subtidal surveys up to four times each year (Stephens et al., 1994; Holbrook et al., 1997). This work documents a substantial change in species composition over time, including a decrease in cool-temperate “northern” species and an increase in warm-temperate “southern” species since 1977. However, Holbrook et al. (1997) also reported an overall decline in abundance of all species in this assemblage after 1990. These changes were attributed to biogeographically related range shifts with increased sea temperatures after 1977, as well as to a regional decline in productivity within the Southern California Bight.

Another long-term fish abundance data set is based on impingement rates in the water intake structures at coastal power plants. Studies by both Love et al. (1998) and Brooks et al. (2002) describe region-wide declines in abundances of both exploited and unexploited fish populations, attributable to documented declines in ocean productivity (Roemmich and McGowan, 1995). While this data set represents both a broader spatial scale and finer temporal scale than that of Stephens et al., data collection did not begin until 1977, so there is no information prior to the regime shift of 1976-77.

The entire Southern California Bight (SCB) is situated within the broad transition zone between the warm-temperate San Diegan Province to the south and the cool-temperate Oregonian Province to the north (Horn et al., 2006) (Figure 1). Further, the islands within the Bight can be classified into a northern (along the Santa Barbara Channel) and a southern

(principally Santa Catalina and San Clemente Islands) group (Ebeling et al., 1980b, Pondella et al., 2005). Finer scale classifications have been made, based on similarities of marine algae and fauna, as well as on distribution of sea surface temperatures throughout the Bight. Murray et al. (1980) described three distinct groups based on marine algal assemblages, identifying Anacapa, San Clemente and Santa Catalina as Group I, Santa Barbara and Santa Cruz as Group II and San Miguel, San Nicolas and Santa Rosa as Group III. Within Ebeling et al.'s "northern" group, or Channel Islands, there exists a finer-scale transition zone, between the cool-temperate biota of San Miguel Island and the mainland California coast north of Pt. Conception, and the warm-temperate biota to the southeast (Ebeling et al., 1980b). The north shore of Santa Cruz Island is virtually at the center of this transition zone, with both warm- and cool-temperate fish assemblages inhabiting its kelp forests and subtidal rocky reefs.

This study is an extension of a long-term study of nearshore fish communities off Santa Cruz Island, California, initiated by Drs. Alfred Ebeling, Ralph Larson and Bill Alevizon in the early 1970s to evaluate temporal variability in kelp forest / rocky reef fish assemblages (Ebeling et al. 1980b). The original study involved annual subtidal surveys of several sites on the north side of Santa Cruz Island from 1971 to 1974. These data sets are the only samples of kelp forest / rocky reef fish species composition and abundance from the northern portion of the Southern California Bight gathered before the 1976-77 regime shift. Since the original study sites are located within the transition zone from the cooler water at the west end of the Santa Barbara Channel to the warmer water of the Southern California Bight, this study may be uniquely sensitive to slight changes in species composition over time.

In 1996, two of the participants in the original surveys, Drs. Ralph Larson and William Alevizon, returned to the original island sites to evaluate the effects of climate change on the

abundance and species composition of kelp forest / rocky reef fishes by re-sampling the sites their group had visited in the early 1970s. They found a considerable decline in the abundance of kelp at these sites from the early 1970s, and established two additional survey sites with canopy-forming kelp forests. This later work showed the effects of ocean warming and loss of kelp, but data were only collected in one year, making it difficult to assess interannual variation. In addition, the short-term climatic changes discussed above occurred after the 1996 survey. A strong El Niño affected the eastern Pacific in 1997-98, followed by a La Niña in 1999. Another weak El Niño occurred during the winter of 2002-03. Current oceanographic and climate data indicate an extended period of cooler ocean conditions from 1999 through 2002 (Bond et al., 2003), and it has been suggested that another “regime shift” of the Pacific Decadal Oscillation occurred in the late 1990s (Horn and Stephens, 2006; Chavez et al., 2003), returning the Pacific to its “cool” phase. Data for the study described here were collected in 2004-05, approximately 5 years after the purported regime shift, and within the period of continued cool conditions in the California Current region. Although there was little recovery of kelp at the original Ebeling et al. (1980a) Santa Cruz Island sites, kelp density has been extremely high since 2000 at other sites nearby, especially San Miguel Island and the south shore of Santa Cruz Island (Jenn Caselle, pers. comm.).

With samples from both cool (1970s and 2004-05) and warm (1996) periods, that include a broad range of species, this study attempts to address the question of how climate change affects marine populations. Furthermore, by sampling at sites with kelp in some years, and no kelp in others, as well as at sites with and without kelp in the same years, this study addresses the effects of kelp on this fish assemblage. Some studies have suggested that the effects of climate change may be direct, causing biogeographic range shifts in response to

warming, or cooling, ocean temperatures (Stephens et al., 1994; Holbrook et al., 1997; Sagarin et al., 1999), while others have suggested the effects may be more indirect, related to a regional decline in productivity (Brooks et al., 2002; Love et al., 1998). In addition, Stephens et al. (2006) noted that few studies to date have examined the effects of kelp on the abundance and species composition of fishes on high-relief rocky bottom in southern California, since kelp has usually been present over this substrate. The situation at Santa Cruz Island offers an opportunity to address this problem.

Objectives

The goals of this study are to (1) evaluate the continued effects of climate change on fish communities at Santa Cruz Island; (2) attempt to separate the effects of kelp loss from the effects of climate change by sampling sites with and without kelp in the same years, as well as by comparing fish counts from the same sites over time; (3) assess within year and within season variation in fish counts by comparing early and late season samples.

METHODS

Study sites

Sampling was conducted at five sites on the north side of Santa Cruz Island, in the California Channel Islands (Figure 1). From west to east, the sites were as follows (abbreviations in parentheses): Cueva Valdaze (CV), 34°03.23'N, 119°49.11'W; "Monitor Cove" (M), noted on some charts as "Fern Cove", 34°03.10'N, 119°44.84'W; "B.S. Rock" (B), 34°02.58'N, 119°42.66'W; Pelican Bay (P), 34°02.06'N, 119°42.10'W; "Prisoner's to Pelican" (PP) (two adjacent areas of kelp bed), PP2 = 34°01.79'N, 119°41.74'W and PP1 = 34°01.75'N, 119°41.55'W. All sites were sampled in 2004 and 2005 (by Graves and Larson), and in 1996 (by Larson and Alevizon). Pelican Bay and Monitor Cove were sampled annually from 1971-1974, and B.S. Rock was sampled in 1972 and 1974. Additional sites sampled in the 1970s include: Dick's Cove (D), which was mistaken for the B.S. Rock site in 1973, and several sites along the north shore of Santa Cruz Island (collectively referred to as SCI) that were sampled in 1970 only (Ebeling et al., 1980a). Sampling in 1971-74 was described in Ebeling et al. (1980b).

Pelican Bay and Monitor Cove were the initial sites chosen by Ebeling et al. (1980a), and both are semi-enclosed coves. B.S. Rock, an exposed headland, was added in 1972 to represent habitat outside of a protected cove. All three of these sites supported canopy-forming kelp forests at that time. The Prisoner's to Pelican and Cueva Valdaze sites were added in 1996, when Larson and Alevizon returned to Santa Cruz Island to continue the long-term sampling. They found the kelp at the initial study sites much diminished from the 1970s, and added these two sites to minimize the confounding effect of kelp loss. Both sites were

sampled again in 2004-05. Collectively, the study sites represent the diversity of nearshore rocky habitat on the north side of Santa Cruz Island.

Field methods

Data for this study were collected using the “cinetransect” sampling method of Ebeling et al. (1980a,b). In this method, a diver-observer swims parallel to shore, maintaining a constant depth within each transect. Each transect is conducted as though it were a visual survey, with the diver-observer actively searching for fish and recording with an underwater movie or video camera all those sighted that are within the range of the camera. When schools of fish are encountered, the diver-observer pans the camera slowly across the school then points the camera away, to minimize redundant sampling. The movies or videotapes are then reviewed in the laboratory, where all fish are counted and identified to species. Fish that are beyond the focal distance of the camera (approximately 3 m), or obscured by turbidity, are deemed unidentifiable and are not counted (Larson and DeMartini, 1984). In addition to fish counts, a qualitative score was assigned to each transect for abundance of kelp (*Macrocystis pyrifera*) and benthic algae as well as bottom relief. Scores ranged from 1 (no kelp or algae, or low relief) to 5 (dense kelp, complete coverage by benthic algae or very high bottom relief). All data collected from 1970 through 1996 were tabulated and entered into a database by Larson. Video collected by Graves and Larson in 2004 and 2005 was viewed on an Apple laptop computer using iMovie digital video editing software. Each transect was downloaded to the computer so it could be viewed frame by frame for complete and accurate species identification and counts.

During each sampling period, approximately 15-20 bottom transects and 8-12 canopy transects were surveyed at every site. The bottom transects represented a variety of depths and distances from shore, generally from 5 m depth at the inshore edge of the site to the rock-sand interface at a depth of 10-20 m, depending on the site. The steep bottom contour on the north side of Santa Cruz Island is primarily high-relief rocky bottom from shore to the deeper sandy bottom. Canopy transects were made at depths of 2-3 m, from the inshore edge of the site to the outer margin of the kelp canopy. At sites with no kelp, canopy transects were made in the same manner, as though kelp were present. In 2004-05, mid-water transects were made at some of the sites. Approximately five transects per site per sampling period were made, at a depth of approximately 5-7m. The exact number of transects completed at each site was determined by site area, in order to ensure complete coverage of the site. Ebeling et al. (1980a) estimated the average length of 11 bottom transects at 47.8 m (SE=1.25 m) and Larson and DeMartini (1984) estimated the length of 12 canopy transects as 75.6 m (SE=1.5 m). Sampling for this study was conducted in the same manner as the aforementioned studies, and is assumed to yield similar transect lengths. The use of video in 1996 and 2004-05 allowed for large sample sizes, so typical sampling covered a large fraction of the habitat at each site. For example, at Monitor Cove, two bottom transects generally covered the distance along one side of the cove (we sampled both sides of the cove). If each transect covered about 48 m, the depth range sampled covered 10 m (3 to 13 m), and the slope of the substrate was approximately 30°, the substrate on one side of the cove covers approximately 1900 m². Ten transects on that side of the cove covered 1440 m² (48m x 3m x 10), or approximately 75% of the substrate. In the initial 1970s surveys, transect length was determined by the amount of film carried in the underwater movie camera. The Super-8 movie camera was loaded with a

single 50 ft. film cartridge that ran for 2.5 minutes, so the diver had to return to the surface and reload film after every transect. When Larson and Alevizon returned to Santa Cruz Island in 1996, they used a video camera mounted in an underwater housing, and were not constrained by film length; however, the 2.5 minute transect length was retained. This was achieved by having a second diver follow the observer and time each transect with a stopwatch. The second diver also recorded depth of filming, depth of bottom, underwater visibility and temperature. When Graves and Larson sampled in 2004-05 they used a digital video camera, loaded with 60-minute mini DV tapes, and maintained the 2.5 minute transect length, with two divers per transect. The use of video beginning in 1996 allowed for a greater number of samples to be collected each day, and larger sample sizes overall.

Field sampling was carried out by Ebeling, Larson, Alevizon, and Bray in 1971-74. Larson and Alevizon sampled in 1996, and Larson and Graves in 2004-5. Graves was trained in the cinetransect technique by Larson before she began conducting transects herself, and was observed by Larson during about half of her samples. This ensured a consistent sampling effort.

Primary sampling for this study was conducted in approximately 1 week intervals in August or September by Ebeling et al. (1980a) in 1971-74, by Larson and Alevizon in 1996 and by Graves and Larson in 2004-05. This period offered the greatest likelihood of favorable sampling conditions, and allows for between-year comparisons of data. In addition to the week of sampling in August of 2004 and 2005, Graves and Larson conducted a second sub-sample in early October 2004 and late September 2005. Only the B.S. Rock and Prisoner's to Pelican sites were sampled during this later period. Data from this later sample were used to assess intra-annual and within season variation in fish abundances.

Analytical methods

The principal mode of data analysis was ordination of $\log(x+1)$ -transformed fish counts using Nonmetric Multidimensional Scaling (McCune and Mefford, 1999) for bottom and canopy separately. The results of Principal Components Analyses of the same data sets were used as starting points for each ordination, and the ordination was constrained to a two-dimensional solution. From the results of the NMS ordination, centroids were computed for decadal sample sets (1970s, 1996 and 2000s), as well as for each site-year sample. Mean site-year sample scores were then compared statistically using the General Linear Model of SPSS. Since both bottom and canopy data showed statistically significant differences among both decade and site-year samples, these means were then compared in post-hoc analyses employing Tamhane, Dunnett's T3 and Games-Howell tests. The minimum significance level of the three tests was reported.

Pearson product moment correlation coefficients were calculated to compare $\log(x+1)$ transformed individual species counts with kelp score, for all transects in each of the three decadal sample sets.

Correlation analysis of data from 2004-05 was used to assess intra-annual variation in fish counts. Pearson product moment correlation coefficients were calculated to compare mean $\log(x+1)$ transformed species counts from the early (August 2004 and 2005) and late (October 2004 and September 2005) season sampling periods in both years.

RESULTS

A total of 1078 transects, representing nearly 45 hours of sampling, were completed for this study. This total includes 629 bottom, 391 canopy and 58 mid-water transects surveyed at seven sites in 8 years (Tables 1 and 1a). In both 2004 and 2005 there was a second sampling period approximately 6 weeks after the first. Samples from August and October 2004 were pooled, as were samples from August and September 2005, for all analyses of the entire data set; however, these samples were separated for analysis of intra-annual variation. The benthic habitat was surveyed for 34 site-year samples, with a mean of 18.5 (± 6.6 SD) bottom transects per sample. Canopy habitat was surveyed for 33 site-year samples, with a mean of 11.85 (± 3.4 SD) canopy transects per sample. The mid-water region was surveyed for nine site-year samples, with a mean of 6.44 (± 2.3 SD) transects per sample. Although 42 fish species from 18 families were recorded throughout the sampling, only 20 species from seven families were common enough to be included in these analyses (Table 2). Counts for black and yellow and gopher rockfishes (*Sebastes chrysomelas* and *S. carnatus*) were combined because of the difficulty in distinguishing them on film and videotape. Eighteen taxa were included in the analyses of bottom transect data, while 13 species were included in the canopy analyses.

Bottom samples

Average scores of environmental variables and of $\log(x+1)$ transformed fish counts for each of 30 site-year bottom samples (combining the two sample sets per year at two sites in 2004-5) are shown in Table 3. All sites that were sampled extensively in the 1970s showed a marked decline in kelp abundance between 1974 and 1996 that persisted into the 2004-05 surveys. Kelp scores for bottom transects fell from a mean of 2.5 in the 1970s to 1.05 in 1996

and 1.2 in 2004-05 at both Monitor Cove and Pelican Bay. B.S. Rock had a mean kelp score of 2.15 in the 1970s that decreased to 1.56 in 1996 and 1.01 in 2004-05. The Prisoner's to Pelican (PP) and Cueva Valdaze sites that were added to the study by Larson and Alevizon in 1996 maintained an average kelp score of 3.32 from 1996 through 2005.

Bottom algae scores declined markedly at Monitor Cove and Pelican Bay, from a mean of 3.85 and 3.02 respectively in the 1970s to 2.04 and 1.23 in 2004-05. Although giant kelp disappeared from the B.S. Rock site between the 1970s and 2004-05, coverage by benthic algae declined only slightly, from a mean score of 2.91 in the 1970s to 2.08 in 2004-05. Interestingly, coverage by benthic algae was highest at B.S. Rock in 1996, with a mean score of 3.89. Mean coverage by benthic algae remained relatively constant at Cueva Valdaze and Prisoner's to Pelican. Mean bottom depth of transects surveyed was similar over all sampling periods at each of the sites (Table 3).

A Nonmetric Multidimensional Scaling (NMS) ordination of the bottom transect data showed a clear change in species composition over the decades (Figure 2). Although there was a high degree of overlap in the sample scores, samples from the 1970s tended to occur in the lower right of the ordination space, while samples from 2004-05 tended to occur in the upper left. Samples from 1996 occurred in the upper center of the ordination space, indicating a high score on Axis 2, and a more neutral score on Axis 1. Scores of samples on Axis 2 were strongly correlated with decade ($r = 0.512$). Additional correlations of note were kelp abundance, benthic algae and bottom depth. Benthic algae showed a positive correlation with Axis 1 ($r=0.209$) and a negative correlation with Axis 2 ($r = -0.248$), while kelp showed a weak negative correlation with Axis 2 ($r = -0.188$). These values suggest that samples scoring in the lower right portion of the ordination space (high on Axis 1 and low on Axis 2) were

associated with higher benthic algal coverage, and that samples scoring low on Axis 2 were associated with higher kelp density. Bottom depth had a weak positive correlation with Axis 2 ($r=0.136$).

NMS ordination results showed that several species differed in relative abundance over decades (Figure 2). Blacksmith, señorita, rock wrasse, and, to a lesser degree, halfmoon and painted greenling, all scored high on Axis 2, indicating relatively higher abundance in samples from 1996 and 2004-05. Species that scored low on Axis 2, especially blue rockfish, striped perch, and black & yellow/gopher rockfish, were relatively more abundant in samples from the 1970s. Blacksmith, the species scoring highest on Axis 2, occurred in the greatest numbers at two of the deepest sites (B.S. Rock and Monitor Cove). The painted greenling tends to be associated with cooler ocean temperatures, unlike the other four species scoring highest on Axis 2; this cryptic, benthic species was more frequently observed at sites with little kelp and less benthic algae.

The centroids (mean scores on Axes 1 and 2) of the data sets from each decade further illustrate the changes in species composition over time (Figure 3). The 1970s centroid was highest on Axis 1 and by far the lowest on Axis 2, suggesting that the greatest change in species composition occurred between the 1970s and the later sample sets. The 2004 centroid was the lowest on Axis 1 and lower on Axis 2 than either the 1996 or 2005 centroids, indicating samples that were slightly more similar to those from the 1970s.

Centroids for the site-year samples also showed change over time at each of the seven sites (Figure 4). All of the sites except B.S. Rock and Monitor Cove in 2005 showed samples from 2004-05 scoring lower on Axis 2 than the 1996 samples. The high Axis 2 scores at B.S. Rock may be related to the complete absence of kelp in 2004-05. Although the kelp coverage

had diminished from the 1970s, some kelp was present when Larson and Alevizon sampled there in 1996. The 2004-05 samples at all sites except B.S. Rock also scored lower on Axis 1 than the samples from 1996. In fact, at all sites except B.S. Rock, the 1996 centroid is the upper rightmost of all the centroids. These results suggest that the 2004-05 samples (with the exception of Monitor Cove in 2005) may represent a slight return to early 1970s conditions.

Axis 2 of the NMS ordination primarily revealed interdecadal changes in fish species composition, and mean scores of the site-year samples on NMS Axis 2 differed significantly (GLM, one-way ANOVA, $P < 0.001$), further demonstrating the changes in species composition over time. Mean scores from the 1970s were generally low, and most did not differ significantly from one another in post-hoc comparisons (Table 4). Samples from Monitor Cove in 1972 and 1973 scored the lowest, indicating that they were the most distinct of the 1970s samples. Of the five samples from 1996, three were significantly different from virtually all of the 1970s samples. A fourth 1996 sample (B.S. Rock) was significantly different from more than half of the 1970s samples. In 1996, only Cueva Valdaze did not differ significantly from most of the 1970s samples. Although few of the 2004-05 samples differed significantly from the 1996 samples, three of the 2004 and two of the 2005 site-year samples were also not significantly different from most of the 1970s samples. Of all the samples from 1996 on, the 2004 Cueva Valdaze sample was the most similar to the 1970s. Cueva Valdaze is the westernmost (i.e. coolest water), and had the most dense kelp coverage of the study sites.

Three of the samples from 2005, and two from 2004, differed significantly from most of the 1970s samples, with the 2005 Monitor Cove sample being the most distinctive. Some interesting changes in species abundances at Monitor Cove between 2004 and 2005 may have led to this distinctness. Mean numbers per transect of four warm-temperate species

(blacksmith, señorita, rock wrasse and halfmoon), increased from 2004 to 2005 (Figure 5b). Additionally, mean number of blue rockfish (a species typically associated with cooler water) decreased from 0.6 per transect in 2004 to 0.03 in 2005 (Table 3).

Although only a weak negative correlation ($r = -0.188$) between kelp and NMS Axis 2 was detected, there was an interesting relationship between the mean kelp score of a site-year sample and its mean score on Axis 2 of the NMS ordination (Figure 6). Samples from the 1970s formed a loose cluster in the middle lower portion of the graph, while samples from the later decades formed two distinct clusters, one in the upper right and one in the upper left. This clustering indicates both a decadal effect and an effect of kelp on species composition. Contrasting low Axis 2 scores of the 1970s samples with higher Axis 2 scores for all samples from the later decades clearly demonstrates a kelp-independent interdecadal effect. However, the effect of kelp is apparent in the separation of kelp-rich and kelp-poor sites in the later decades. The 1996 and 2004-05 samples from Cueva Valdaze and Prisoner's to Pelican had the highest kelp scores, and generally scored lower on Axis 2 than the kelp-poor 1996 and 2004-05 samples from Pelican, Monitor and B.S. Rock. The difference in kelp scores between the 1970s samples and the Cueva Valdaze and Prisoner's to Pelican samples from later years may be attributable to maturity of the kelp bed. In the early 1970s, all the sites supported mature kelp forests, with fewer individual plants with larger stipe bundles. Conversely, younger kelp forests, with more individual plants with few stipes, were present at CV and PP in later years.

Changes in abundance over time of representative taxa in bottom samples are depicted graphically (Figures 5a,b,c). General trends include an increase in species with southerly distributions, a decrease in species associated with cooler water north of Pt. Conception and

minimal change in two mid-water secondary carnivores. Blacksmith, señorita and rock wrasse, all southern species, scored highest on Axis 2 and showed a marked increase from the 1970s to 1996, followed by a slight decline at most sites in 2004-05. The halfmoon, another species that is characteristic of southern California and scored relatively high on NMS Axis 2, also showed higher counts in later decades. Painted greenling scored on the upper left of the NMS ordination, and generally increased from the 1970s through 1996 to the 2004-05 sampling period, although their abundance was higher at sites with little kelp and benthic algae. This may have been a genuine increase, or individuals may simply have been more visible to the diver-observer without the algal cover. The two most northerly distributed of all the species included in this study were blue rockfish and striped surfperch. Both scored lowest on NMS Axis 2 and declined dramatically from the 1970s to 1996, but increased slightly in 2004-05. The black and yellow-gopher rockfish complex also appeared to decline in abundance since the 1970s. Some species that are rare north of Pt. Conception did not increase in abundance over time, however. These include the kelp bass, garibaldi (which was most abundant in the most easterly sites), opaleye, and California sheephead. The decline in California sheephead may be more strongly related to their capture for the live fish fishery than anything related to climate. Olive rockfish, kelp rockfish and kelp bass all scored near the center left of the NMS ordination, and showed little change in abundance over time. However, the kelp rockfish appeared to be more abundant in the sites with kelp present, including BS Rock in 1996.

Canopy samples

Table 5 shows mean log (x+1) transformed counts of the 13 most commonly observed species at each of the 29 site-year samples. Environmental variables included in the analysis of

canopy transects were decade, kelp abundance (ranked score from 1-5) and visibility, measured in feet (Table 5).

Canopy samples at all three sites that were sampled in the 1970s showed substantial declines in kelp density for canopy transects over the period of the study. Both Pelican Bay and Monitor Cove declined from a mean kelp score of 3.47 in the 1970s to 1.14 in 1996 and 2004-05. B.S. Rock maintained much of its kelp coverage through 1996, with a mean score of 3.78 in the 1970s, and 2.89 in 1996. However, this kelp was not present in 2004-05, and the mean kelp score was just 1.08. The two sites added by Larson and Alevizon in 1996 both maintained dense kelp coverage and high kelp scores, with means of 3.24 and 3.88 at Prisoner's to Pelican and Cueva Valdaze respectively. Visibility averaged approximately 20 feet over all sites and years, with the exception of very poor visibility in 1973 (average 11 ft.).

As with the bottom transects, a NMS ordination of the canopy transect data also showed a very clear decadal effect (Figure 7). Samples from the 1970s scored lower on Axis 1 and higher on Axis 2, tending to occur in the upper left portion of the ordination space. Conversely, samples from 2004-05 tended to occur in the lower right, while the 1996 samples tended toward the center right of the ordination space. This pattern is most clearly exemplified with the plot of centroids (mean sample scores) calculated for each decade (Figure 8). Correlation analysis of environmental variables and NMS axes also showed a strong positive correlation between decade and Axis 1 ($r = 0.490$), as well as a fairly strong negative correlation between decade and Axis 2 ($r = -0.310$). These values corroborate the general pattern shown by figures 7 and 8. In addition, kelp density was strongly correlated with Axis 1 of the NMS ordination ($r = -0.585$), indicating that samples occurring to the left of the ordination space had higher kelp density than samples occurring to the right. This strong

correlation suggests that kelp abundance may have exerted a stronger influence on species composition in canopy samples than in bottom samples.

A plot of species scores on Axes 1 and 2 of the NMS ordination shows more variation on Axis 1 than Axis 2 (Figure 7). Species that scored lowest on Axis 1 were striped surfperch, kelp perch and kelp rockfish, suggesting these species decreased in abundance since the 1970s, and were more strongly associated with kelp than blacksmith and halfmoon. These last two species scored highest on Axis 1 and appear to have increased in abundance since the 1970s. Olive and blue rockfish were also more closely associated with 1970s canopy samples, and California sheephead may be more closely associated with samples from the later decades.

Axis 1 of the NMS ordination primarily revealed interdecadal changes in fish species composition in the canopy samples, and mean scores of site-year samples on NMS Axis 1 differed significantly (GLM, one-way ANOVA, $P < 0.001$). Post-hoc analyses revealed a clear effect of both kelp and decade on species composition for canopy transects (Table 6). As with the bottom transects, most of the 1970s samples did not differ significantly from one another. Furthermore, samples from Cueva Valdaze (CV) and Prisoner's to Pelican (PP) in both 2004 and 2005 did not differ significantly from virtually all of the 1970s samples. While B.S. Rock maintained some of its kelp through 1996, CV and PP were the only two sites with canopy-forming kelp from 1996 through the 2004-05 sampling period. Although the 1996 samples from CV and PP were significantly different from many of the 1970s samples, they were more similar to the 1970s than any other 1996 samples. In fact, close examination of the species counts from 1996 (Table 5), reveals that three of the four species scoring lowest on NMS Axis 1 (i.e., most strongly associated with the 1970s and high kelp abundance) were represented at Cueva Valdaze and Prisoner's to Pelican, but poorly represented at, or absent from, the other

three sites. Kelp perch were relatively abundant at CV and PP, but absent from all three other sites, while kelp and olive rockfish were present at CV, PP and B.S. Rock, but absent from Monitor Cove and Pelican Bay. The 1996 samples from CV, PP and, to a lesser extent, B.S. Rock were also more similar to the 1970s samples than any of the 2004-05 samples from the three sites with no kelp (Monitor Cove, B.S. Rock and Pelican Bay).

Figure 9 clearly depicts both the effects of kelp on species composition at a site and a kelp-independent decadal effect for the canopy samples. The tight cluster in the upper left corner (high Axis 1 score, low kelp score) represents all the sites with little or no kelp in 1996 and 2004-05. This includes Monitor Cove and Pelican Bay in all the later years, as well as B.S. Rock in 2004-05, when all the kelp at that site had disappeared. The remaining points represent all of the 1970s samples, and the 1996 and 2004-05 samples from sites with kelp. Although there is a range of scores on Axis 1, it is interesting to note that the 2004-05 samples from Cueva Valdaze and Prisoner's to Pelican are virtually indistinguishable from the 1970s samples. The high Axis 1 scores of the 1996 Cueva Valdaze and PP samples clearly show a decadal effect, independent of kelp. The lower Axis 1 score of the 1996 B.S. Rock sample sets it apart on this graph and suggests the effect of kelp on the fish assemblage.

Plots of the centroids (mean sample score) for each of the site-year samples further highlight the effect of kelp on community composition at these sites (Figure 10). Virtually all of the 1970s centroids occur to the left of the ordination space, while all of the 1996 centroids occur to the right. Centroids of the 2004-05 Cueva Valdaze and Prisoner's to Pelican samples all occurred on the left of the ordination space, indicating a high degree of similarity to samples from the 1970s. Conversely, centroids of the 2004-05 samples from B.S. Rock, Monitor Cove and Pelican Bay all occurred on the far right of the ordination space. As stated

previously, Cueva Valdaze and Prisoner's to Pelican were the only two sites with canopy-forming kelp in 1996, 2004 and 2005.

Plots of individual species' abundance over the time of this study graphically depict slight increases in some "southern" species and dramatic declines in most "northern" species (Figure 11a,b). As in the bottom transects, blue rockfish and striped surfperch declined most dramatically from the 1970s to 1996, and both were slightly more abundant in the 2004-05 samples. Other species showing this pattern were kelp and olive rockfish, and, more dramatically, kelp perch. Three abundant southern kelp bed species, blacksmith, señorita and halfmoon all showed a slight increase in abundance from the 1970s to 1996, followed by a slight decline from 1996 to 2004-05. Some species, such as kelp perch, kelp rockfish, and, to a lesser extent, kelp bass and señorita, appeared to be more abundant at sites with kelp in 1996, 2004, and 2005. There was some indication that the opposite applied to blacksmith and halfmoon.

Intra-annual variation

Within-year variation in counts was assessed by correlating mean $\log(x+1)$ transformed species counts from the "early season" (August 2004 and 2005) samples with those from the "late season" (October 2004 and September 2005) samples. Pearson product moment correlation coefficients were calculated for B.S. Rock and Prisoner's to Pelican in both 2004 and 2005 (Table 7). All values showed strong correlation between the two sampling periods, indicating little variation in counts within the same season in a given year. Although the early and late season counts were strongly correlated at both sites, the weakest correlations were at B.S. Rock, for bottom transects in 2004 and mid-water transects in 2005. A large

difference in numbers of blacksmith explains the higher variability in both. In 2004, there were far more blacksmith counted in bottom transects in August (early) than in October (late), while in the 2005 mid-water transects, the opposite was true.

DISCUSSION

This study adds to the growing body of work on the effects of climate change on marine populations. Although sampling was conducted in just eight of the 35 years covered by this study, data are from key time periods. The original Ebeling et al. (1980a) surveys give a clear picture of rocky-reef / kelp-forest fish community composition in the northern portion of the Southern California Bight prior to the 1976-77 regime shift. Larson and Alevizon sampled nearly 20 years after the regime shift, and approximately 3 years prior to the apparent return of cooler ocean conditions. Although these 1996 data are from a single year, analysis of data from the Channel Islands National Park's Kelp Forest Monitoring program indicate that they were typical of conditions from approximately 1985-1996 (Larson and Kushner, unpublished). Finally, sampling by Graves and Larson in 2004-05 was conducted after 5 consecutive years of cool conditions in the California Current region (Goericke et al., 2005). Our findings suggest that, in this sensitive indicator region of the Southern California Bight, there is a direct effect of changing ocean climate on some species. Specifically, this study documents the decline of several species with northerly affinities, and increase of several "southern" species from the 1970s to 1996. Of perhaps greater interest, though, is the slight increase of the "northern," and slight decline of species with more southerly affinities from 1996 to 2004-05.

Additionally, our findings address one of the indirect effects of changing ocean climate on rocky-reef fish communities: loss of kelp. The large-scale decline of giant kelp at the original study sites on the north side of Santa Cruz Island from the early 1970s to 1996 led to sampling of sites with and without kelp in 1996 and 2004-05. Although the effect of kelp density on the abundance of most California reef fishes on high-relief rocky bottom has not yet been clearly documented (Stephens et al. 2006), our results suggest that presence or absence of

kelp strongly affects community composition, and the presence of kelp may have moderated, and the absence of kelp may have exacerbated, the effects of increased ocean temperatures.

Role of climate and ocean productivity

With samples from both cool (1970s and 2004-05) and warm (1996) periods, which include a broad range of species, this study addressed the question of how climate change affects marine populations. These findings may support previous work showing that changes in ocean climate lead to biogeographically-related range shifts (Stephens et al., 1994; Barry et al., 1995; Holbrook et al., 1997; Sagarin et al., 1999). Ordination of the entire data set revealed a clear effect of decade on the fish assemblage on the north side of Santa Cruz Island. For both bottom and canopy transects, decade was strongly correlated with one of the ordination axes, indicating that samples from each of the three decades were relatively distinct. This pattern was largely associated with a substantial change in species composition, especially from the early 1970s to 1996, but also between 1996 and 2004-05.

Although classified as “northern” species (Allen and Pondella, 2006), blue rockfish were common off southern California during the cool conditions of the early 1970s (Ebeling et al., 1980a; Stephens et al., 1994). Where Ebeling et al. (1980a) recorded numerous blue rockfish at Santa Cruz Island between 1970-74, Larson and Alevizon didn’t see a single blue rockfish in 1996; not only on sampling dives, but on all dives of that trip. One of the strongest indicators of a possible return of cool conditions in 2004-05 was the presence of blue rockfish. Although certainly not abundant, Graves and Larson counted more than 100 blue rockfish in 2004-05. Gundelfinger (2005) noted the near absence of blue rockfish born before 1999 at

Santa Cruz Island, and Larson's dive notes from 2004 samples indicate many 1 year olds observed.

Striped perch, black and yellow rockfish and olive rockfish are additional "northern" species showing a similar pattern: decreased abundance from the early 1970s to 1996, followed by a slight increase from 1996 to 2004. Ordination of data from the Channel Islands National Park Kelp Monitoring Program revealed a west to east biogeographic gradient within the Santa Barbara Channel (Larson and Kushner, unpublished). Their analysis indicates that blue and olive rockfish and striped perch are most strongly associated with the islands at the cooler west end of the channel (San Miguel and Santa Rosa). The increased abundance of these species from 1996 to 2004 may be indicative of cooler conditions farther east in the channel.

Further suggesting a biogeographically related range shift in response to warming, and then cooling, ocean conditions, several "southern" species increased in abundance from the early 1970s to 1996, then decreased from 1996 to 2004. Señorita, blacksmith and rock wrasse are respectively characterized as "southern kelp reef", "abundant southern kelp bed" and "Baja kelp reef" species (Allen and Pondella, 2006). Although not the species most strongly associated with the warmer eastern Channel Islands (Larson and Kushner, unpublished), blacksmith and señorita were relatively more common at Anacapa and Santa Barbara islands in the CINP surveys of 1985-1999 (Davis et al., 1999). Rock wrasse primarily occur on southernmost Baja reefs, but can be abundant as far north as the southern portion of the Southern California Bight (Allen and Pondella, 2006). The increase of these three species from the early 1970s to 1996 suggests a northward range shift, while their decline from 1996 to 2004 may indicate a southward contraction of their ranges, both attributable to ocean

temperatures. Furthermore, most of the rock wrasse counted by Graves and Larson were 1 year olds seen in 2005, not a stable adult population.

Although several studies have reported declining fish populations attributable to an overall decline of secondary productivity in the California Current region (Roemmich and McGowan, 1995; Holbrook et al., 1997; Love et al., 1998; Brooks et al., 2002), we found no such general trend in abundances. Some species did decline dramatically, others increased in abundance and some species showed no real change in abundance over the period of this study. Holbrook et al. (1997) reported an overall decline of >80% in abundances of three surfperch species (black, striped and pile) at Santa Cruz Island from 1982-1995. This decline was highly correlated with both regional productivity and local abundance of benthic crustaceans and algae. Here, we report a decline in abundance of striped perch, but abundances of both black and pile perch changed little. Furthermore, several species representing different trophic categories all maintained relatively constant abundances. Horn and Ferry-Graham (2006) characterize kelp bass as mid-water secondary carnivores, sheephead, garibaldi, pile perch and black perch as benthic macro- and micro-carnivores and opaleye and halfmoon as herbivores or omnivores. All showed little change in abundance over the period of this study.

Role of kelp

Kelp is an important component of California's nearshore marine habitat. It adds three-dimensional structure to primarily rocky reef habitats, providing cover and a visual reference for midwater fishes some distance from the reef itself. Although few fish taxa appear to require kelp *per se*, some species do seem to require a threshold density of kelp to be present (Holbrook et al., 1990). Further, species such as kelp perch, giant kelpfish and possibly kelp

rockfish do exhibit a high degree of dependence on kelp, even though they may occur in other habitats (Stephens et al., 2006). By sampling at sites with kelp in some years, and no kelp in others, as well as at sites with and without kelp in the same years, this study addressed the effects of kelp on this fish assemblage.

This study documents the large-scale decline of kelp on the north side of Santa Cruz Island from the early 1970s to 1996, and its subsequent failure to re-establish with the return of cooler ocean conditions. Reed et al. (2000) speculated that the recovery of kelp on the south side, and failure of kelp to return to the north side of Santa Cruz Island are related both to bottom topography and differential dispersal ability of kelp and benthic invertebrates. They suggest that the steep bottom contour on the north side of the island restricted kelp beds to a narrow band, while larger stands of kelp existed on the gradual slope on the south side of the island and at nearby Santa Rosa. Further, they found that recovery of sedentary marine organisms is related to dispersal ability, with short-range dispersers, such as giant kelp, recovering more slowly than long-range dispersers, such as urchins, on the north side of Santa Cruz Island. The ENSO event of 1982-83 removed most of the kelp on the north side of Santa Cruz Island, so the pool of propagules that could reach the area within the 1 day that giant kelp propagules are viable was much smaller than in the remnant kelp beds on the south side of the island. Additionally, urchins arrived and established first, inhibiting the re-establishment of giant kelp.

Significant correlations between individual species' abundance and kelp score for each of the three decades are shown in Table 8. The 1996 and 2004-05 correlations are of greatest interest, since sites with and without kelp were sampled. Kelp bass, kelp perch and kelp rockfish are all more, or less, positively correlated with kelp abundance, for both bottom and

canopy transects. Not surprisingly, more species are positively correlated with kelp in canopy transects than on the bottom. Interestingly, nearly twice as many species are significantly correlated with kelp abundance in the 2004-05 samples than in either 1996, or the early 1970s. This suggests that kelp may affect community composition more during the early stages of a cool phase than at other times. At these study sites, kelp was abundant and well established in the early 1970s, and was either absent or poorly established in 1996. Kelp was generally abundant and well-established in the 1970s, so only a narrow range of variation in kelp density was present. In 1996, the kelp forest at Cueva Valdaze was clearly young, consisting of individuals with few stipes, and the kelp at BS Rock was sparse. A more mature forest was present at PP. However, even at PP, densities of such kelp-related species as kelp perch were low. We wonder whether the kelp forest there was also established relatively recently, and that the populations of kelp-related species had not yet recovered completely. In 2004-5, the wide range of kelp densities among sites, and the longer period of time for kelp reestablishment and maturation, may have allowed for better contrasts among sites. These results demonstrate that kelp can affect species composition over high-relief rocky bottom.

Several species were negatively correlated with kelp, especially in bottom samples from 2004-5. Sheephead, blacksmith, señorita and halfmoon were generally most abundant at B.S. Rock. Benthic cover at this site was largely echinoderms (purple urchins and small sea cucumbers), preferred prey for sheephead. Additionally, as the deepest of the five study sites, situated on a rocky headland, we noted more current here than at the other sites, perhaps providing ample zooplankton prey for the blacksmith and señorita. Furthermore, this high-relief site has numerous small caves and crevices that likely provide nocturnal shelter for blacksmith. This may also explain the negative correlation between blacksmith and kelp for

canopy transects. Garibaldi were most common at Pelican Bay, another site with no kelp and abundant echinoderms.

Another interesting possibility is that presence or absence of kelp may exert a behavioral effect on fish, especially blacksmith. Bray (1981) investigated the effects of currents, and found that blacksmith, a planktivorous reef fish, foraged preferentially on the upcurrent edge of a kelp bed. In the absence of kelp, currents comparable to those on the edge of the kelp bed may exist nearer to shore and to the bottom. This may mean that blacksmith are more abundant nearer to the shore and the bottom, foraging in this current and orienting visually to the rocky bottom, instead of to the edge of the kelp canopy.

Finally, perhaps the clearest evidence for the effect of kelp on the fish assemblage at Santa Cruz Island is the post-hoc analysis for the canopy site-year samples and the relationship shown in Figure 9. Although community composition was largely related to decade and climate effects, the presence or absence of kelp clearly affected which species were present. Generally, samples from sites with kelp in the later decades were more similar to 1970s samples than those from sites without kelp.

Interannual variability

Both on the bottom and in the canopy, the 2004 samples were more similar to those from the 1970s than either the 1996 or 2005 samples, and appeared to represent a return to cooler ocean conditions. Unexpectedly, the 2005 samples were somewhat different, and appeared to be slightly more similar to 1996 samples. There are several possible explanations for this difference, primarily related to abundances of species in the assemblage and to

recruitment variation. Although this study did not explicitly investigate recruitment patterns, it is worth noting that variation in recruitment appeared to play a role in these results.

In both bottom and canopy samples, there was a general increase in species with southerly affinities and a definite decrease in some of the northerly species between 2004 and 2005. In bottom samples, much of the increase in southerly species was attributable to strong recruitment of kelp bass, rock wrasse and sheephead in 2004. In fact, at the Prisoner's to Pelican site, actual numbers of kelp bass per bottom transect increased from a mean of 4.5 in 2004 to 17.2 in 2005, nearly all of which were 1 year olds. PISCO (Partnership for Interdisciplinary Studies of Coastal Oceans) sampling in the region showed that kelp bass recruitment failed in 2002 and 2003, but was relatively high in 2004, with the greatest number of recruits since 2000 (Jenn Caselle, pers. comm.). Other differences between 2004 and 2005 bottom samples include a notable increase in blacksmith at three, and an increase in señorita at four, of the five sites. Additionally, numbers of blue rockfish declined at four sites, and they remained absent from the fifth site. This increase in "southern" and decrease in "northern" species certainly contributed to the 2005 samples being more similar to those from 1996. Interestingly, data from subtidal surveys conducted at Santa Cruz Island by PISCO show blue rockfish abundance declining from an approximate mean of 0.7 per transect in 2000 to zero in 2005 (<http://www.piscoweb.org>). Although the difference between the 2004 and 2005 canopy samples was less than the bottom samples, a similar pattern was observed. Blacksmith increased at two sites and señorita increased at three sites, while blue rockfish and striped surfperch each declined at two sites.

Conclusions

As tools for monitoring both atmospheric and ocean climate become more sophisticated, we are more readily able to detect long-term climate patterns, including shifts in the Pacific Decadal Oscillation regime. However, we can only understand their effects by investigating natural populations. Indeed, Hare and Mantua (2000) suggest that monitoring marine organisms may be a better way to detect these regime shifts than monitoring climate alone. Ultimately, understanding the effects of these climate changes on marine populations is vital for effective conservation and management. Long-term monitoring is one of the most effective means for documenting changes in these populations. Furthermore, long-term monitoring may be the only means of separating the effects of climate variability on multiple scales from the effects of human-induced changes in nearshore fish populations.

The data presented here include the only samples of the rocky reef fish assemblage at Santa Cruz Island collected prior to the 1977 PDO shift; therefore, they may be of use to ongoing monitoring programs such as the Channel Islands National Park Kelp Monitoring Program and PISCO. Additionally, since both cool- and warm-temperate fish assemblages inhabit the rocky reefs on the north shore of Santa Cruz Island, we believe we will find that this sensitive indicator region may be a bellwether for the rest of the Southern California Bight, with the effects of changing ocean climate apparent here first.

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REFERENCES

- Allen LG, Pondella DJ II. 2006. Ecological Classification. In: Allen LG, Pondella DJ II, Horn MH editors. *The Ecology of Marine Fishes: California and Adjacent Waters*. Berkeley (CA): University of California Press. p 81-113.
- Barry JP, Baxter CH, Sagarin RD, Gilman SE. 1995. Climate-related long-term faunal changes in a California rocky intertidal community. *Science* 267:672-675.
- Beamish RJ, Mahnken C, Neville CM. 1997. Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. *J Mar Sci* 54:1200-1215.
- Blanchette CA, Broitman BR, Gaines SD. 2006. Intertidal community structure and oceanographic patterns around Santa Cruz Island, CA, USA. *Mar Biol* (2006), doi: 10.1007/s00227-005-0239-3.
- Bond NA, Overland JE, Spillane M, Stabeno P. 2003. Recent shifts in the state of the North Pacific. *Geophys Res Lett* 30 (23), doi: 10.1029/2003GL018597, 2003.
- Bray RN. 1981. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. *U.S. Fish Bull* 78:829-41.
- Brooks AJ, Schmitt RJ, Holbrook SJ. 2002. Declines in regional fish populations: have species responded similarly to environmental change? *Mar Freshwater Res* 53:189-198.
- Browne DR. 1994. Understanding the oceanic circulation in and around the Santa Barbara Channel. In: Halvorson WL, Maender GJ, editors. *The Fourth California Islands Symposium: Update on the Status of Resources*. Santa Barbara (CA): Santa Barbara Museum of Natural History. p 27-34.
- Chavez FP, Ryan J, Lluch-Cota SE, Ñiquen CM. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299:217-221.
- Davis GE, Kushner DJ, Mondragon JM, Morgan JE, Lerma D, Richards D. 1999. *Kelp Forest Monitoring Handbook, Volume 1: Sampling Protocol*. Ventura (CA): Channel Islands National Park. 55 p.
- Dayton PK, Tegner MJ. 1984. Catastrophic storms, El Niño and patch stability in a southern California kelp community. *Science* 224:283-285.
- Dayton PK, Tegner MJ, Edwards PB, Riser KL. 1999. Temporal and spatial scales of kelp demography: The role of oceanographic climate. *Ecol Monog* 69(2):219-250.
- Ebeling AW, Larson RJ, Alevizon WS, Bray RN. 1980a. Annual variability of reef fish

assemblages in kelp forests off Santa Barbara, California. *Fish Bull* 78:361-377.

Ebeling AW, Larson RJ, Alevizon WS. 1980b. Habitat groups and island-mainland distribution of kelp-bed fishes off Santa Barbara, California. In: Power DM, editor. *The California Islands: Proceedings of a Multidisciplinary Symposium*. Santa Barbara (CA): Santa Barbara Museum of Natural History. p. 403-431.

Engle JM. 1994. Perspectives on the structure and dynamics of nearshore marine assemblages of the California Channel Islands. In: Halvorson WL, Maender GJ, editors. *The Fourth California Islands Symposium: Update on the Status of Resources*. Santa Barbara (CA): Santa Barbara Museum of Natural History. p 13-26.

Field DB, Baumgartner TR, Charles CD, Ferreira-Bartrina V, Ohman MD. 2006. Planktonic foraminifera of the California Current reflect 20th-century warming. *Science* 311:63-66.

Finney BP, Gregory-Eaves I, Douglas MSV, Smol JP. 2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. *Nature* 416:729-733.

Francis RC, Hare SR. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. *FishOceanogr* 3(4):279-291.

Goericke R, Venrick E, Mantyla A, Bograd SJ, Schwing FB, Huyler A, Smith RL, Wheeler PA, Hoof R, Peterson WT, Gaxiola-Castro G, Gomez-Valdes J, Lavaniegos BE, Hyrenbach KD, Sydeman WJ. 2004. The state of the California Current, 2003-2004: a rare "normal" year. *CalCOFI Rep.* 45:27-59.

Goericke R, Venrick E, Mantyla A, Hoof R, Collins C, Gaxiola-Castro G, Bograd SJ, Schwing FB, Peterson WT, Marinovic B, Durazo R, Huyler A, Smith RL, Wheeler PA, Chavez F, Lo N, Hyrenbach KD, Sydeman WJ. 2005. The state of the California Current, 2004-05: still cool? *CalCOFI Rep.* 46:32-71.

Gundelfinger P. 2005. Regional variation in year-class structure of blue rockfish (*Sebastes mystinus*). M.S. Thesis, San Francisco State University, San Francisco, CA. 86 pp.

Hare SR, Mantua NJ. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog Oceanog* 47:103-45.

Hayward TL. 1997. Pacific Ocean climate change: atmospheric forcing, ocean circulation and ecosystem response. *TREE* 12(4):150-154.

Holbrook SJ, Carr MH, Schmitt RJ, Coyer JA. 1990. Effect of giant kelp on local abundance of reef fishes: The importance of ontogenetic resource requirements. *Bull Mar Sci* 47:104-114.

Holbrook SJ, Schmitt RJ, Stephens JS Jr. 1997. Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecol Appl* 7:1299-1310.

Horn MH, Allen LG, Lea RN. 2006. Biogeography. In: Allen LG, Pondella DJ II, Horn MH editors. *The Ecology of Marine Fishes: California and Adjacent Waters*. Berkeley (CA): University of California Press. p 3-25.

Horn MH, Ferry-Graham LA. 2006. Feeding mechanisms and trophic interactions. In: Allen LG, Pondella DJ II, Horn MH editors. *The Ecology of Marine Fishes: California and Adjacent Waters*. Berkeley (CA): University of California Press. p 387-410.

Horn MH, Stephens JS Jr. 2006. Climate change and overexploitation. In: Allen LG, Pondella DJ II, Horn MH editors. *The Ecology of Marine Fishes: California and Adjacent Waters*. Berkeley (CA): University of California Press. p 621-635.

Larson RJ, DeMartini EE. 1984. Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. *Fish Bull* 82(1):37-53.

Love MS, Caselle JE, Herbinson K. 1998. Declines in nearshore rockfish recruitment and populations in the southern California Bight as measured by impingement rates in coastal electrical power generating stations. *Fish Bull* 96:492-501.

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull Am Met Soc* 78(6):1069-1079.

McCune B, Grace JB. 2002. *Analysis of ecological communities*. Gleneden Beach (OR): MjM Software Design. 300 pp.

McGowan JA, Cayan DR, Dorman LM. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281:210-217.

Moser HG, Charter RL, Watson W, Ambrose DA, Butler JL, Charter SR, Sandknop EM. 2000. Abundance and distribution of rockfish (*Sebastes*) larvae in the southern California Bight in relation to environmental conditions and fishery exploitation. *CalCOFI Rep.* 41:132-147.

Murray SN, Littler MM, Abbott IA. 1980. Biogeography of the California marine algae with emphasis on the southern California islands. In: Power DM, editor. *The California Islands: Proceedings of a Multidisciplinary Symposium*. Santa Barbara (CA): Santa Barbara Museum of Natural History. p.325-339.

Pondella DJ II, Gintert BE, Cobb JA, and Allen LG. 2005. Biogeography of the nearshore rocky-reef fishes at the southern and Baja California islands. *J. Biogeogr.* 32:187-201.

Reed DC, Raimondi PT, Carr MH, Goldwasser L. 2000. The role of dispersal and disturbance in determining spatial heterogeneity in sedentary organisms. *Ecology* 81(7):2011-2026.

Roemmich D, McGowan J. 1995. Climatic warming and the decline of zooplankton in the

California Current. *Science* 267(5202):1324-1326.

Schiel DR, Steinbeck JR, Foster MS. 2004. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology* 85(7):1833-1839.

Stephens JS JR., 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: A recruitment driven system. *Bull Mar Sci* 55:1224-1239.

Stephens JS Jr., Larson RJ, Pondella DJ III. 2006. Rocky reefs and kelp beds. In: Allen LG, Pondella DJ II, Horn MH editors. *The Ecology of Marine Fishes: California and Adjacent Waters*. Berkeley (CA): University of California Press. p. 227-252.

Venrick E, Durazo R, Huyer A, Mantyla A, Bograd SJ, Gaxiola-Castro G, Hyrenbach KD, Schwing FB, Checkley D, Hunter J, Laveniegos BE, Smith RL, Sydeman WJ, Wheeler PA. 2003. The state of the California Current, 2002-2003: tropical and subarctic influences vie for dominance. *CalCOFI Rep.* 44:28-60.

Table 1. Sample sizes for bottom and canopy transects at Santa Cruz Island. Sites are listed from west to east and are abbreviated as follows: **CV**=Cueva Valdaze, **M**=Monitor Cove, **D**=Dick's Cove, **B**=B.S. Rock, **P**=Pelican Bay, **PP**=Prisoner's to Pelican, **SCI**=various sites on the north side of Santa Cruz Island.

Year	CV		M		D		B		P		PP		SCI	
	<i>Btm</i>	<i>Can</i>	<i>Btm</i>	<i>Can</i>	<i>Btm</i>	<i>Can</i>	<i>Btm</i>	<i>Can</i>	<i>Btm</i>	<i>Can</i>	<i>Btm</i>	<i>Can</i>	<i>Btm</i>	<i>Can</i>
1970	4	2							6	4	2		20	16
1971			32	15					5	7				
1972			12	12			20	16	13	11				
1973			16	16	19	15			20	15				
1974			15	13			17	15	16	12				
1996	19	12	25	11			18	9	18	10	17	13		
8/2004	21	11	24	13			26	10	23	13	22	15		
10/2004							18	8			19	11		
8/2005	22	17	24	12			24	10	21	13	23	14		
9/2005							24	8			24	12		
Total	66	42	148	92	19	15	147	76	122	85	107	65	20	16

Table 1a. Sample sizes for mid-water transects at Santa Cruz Island. Sites are abbreviated as above.

Year	B <i>MW</i>	P <i>MW</i>	PP <i>MW</i>
8/2004	5	4	9
10/2004	5		8
8/2005	5		10
9/2005	4		8
Total	19	4	35

Table 2. Taxa of fish included in this study at Santa Cruz Island, California. Sample set indicates whether species was used in analysis of bottom (B) or canopy (C) transects.

Scientific name	Common name	Abbreviation	Sample set
<u>Embiotocidae</u>			
<i>Brachyistius frenatus</i>	kelp perch	kprch	C
<i>Embiotoca jacksoni</i>	black surfperch	bprch	B
<i>E. lateralis</i>	striped surfperch	sprch	B, C
<i>Rhacochilus vacca</i>	pile perch	pile	B, C
<i>R. toxotes</i>	rubberlip surfperch	rub	B, C
<u>Scorpaenidae</u>			
<i>Sebastes atrovirens</i>	kelp rockfish	krock	B, C
<i>S. mystinus</i>	blue rockfish	blue	B, C
<i>S. serranoides</i>	olive rockfish	olive	B, C
<i>S. serriceps</i>	treefish	tree	B
<i>S. chrysomelas</i>	black and yellow rockfish	by	B
<i>S. carnatus</i>	gopher rockfish	gopher	B
<u>Labridae</u>			
<i>Semicossyphus pulcher</i>	California sheephead	sheep	B, C
<i>Oxyjulis californica</i>	señorita	sen	B, C
<i>Halichoeres semicinctus</i>	rock wrasse	rwras	B
<u>Pomacentridae</u>			
<i>Chromis punctipinnis</i>	blacksmith	bsmth	B, C
<i>Hypsypops rubicundus</i>	garibaldi	gar	B
<u>Kyphosidae</u>			
<i>Girella nigricans</i>	opaleye	opal	B, C
<i>Medialuna californiensis</i>	halfmoon	half	B, C
<u>Serranidae</u>			
<i>Paralabrax clathratus</i>	kelp bass	kbass	B, C
<u>Hexagrammidae</u>			
<i>Oxylebius pictus</i>	painted greenling	pgrn	B

Table 3. Bottom transects: Mean and standard deviation of environmental variables and log (x+1) transformed species counts by site and year. See Table 2 for species abbreviations. Kelp (kelp density) and Algae (density of bottom algae) were scored from 1 (low or absent) to 5 (highest, or most dense). Depth is the mean transect depth of the site, in feet. Vis represents horizontal underwater visibility, in feet.

Location	Year	Environmental Variables				Fish species																		
		N	Kelp	Algae	Depth	Vis	kbass	sheep	sen	bsmth	gar	half	opal	bprch	sprch	pile	rub	krock	blue	olive	pgrn	rwras	tree	gopher
Pelican Bay	1970 Mean	3.67	3.00	22.00	25.8	0.941	0.489	0.141	0.080	0.400	0.130	0.342	0.151	0.289	0.283	0.080	0.558	0.368	0.050	0.000	0.060	0.030	0.000	
	6 SD	0.52	0.63	4.47	2.0	0.290	0.430	0.345	0.195	0.453	0.208	0.385	0.369	0.234	0.343	0.195	0.537	0.493	0.123	0.000	0.123	0.093	0.000	
	1971 Mean	2.00	3.40	17.00	20.0	0.651	0.361	0.120	0.598	1.041	0.120	0.698	0.675	0.140	0.276	0.000	0.276	0.000	0.060	0.000	0.000	0.000	0.000	
	5 SD	0.00	1.14	4.47	0.0	0.200	0.135	0.165	0.461	0.028	0.165	0.398	0.289	0.313	0.172	0.000	0.172	0.000	0.135	0.000	0.000	0.000	0.165	
	1972 Mean	2.92	3.15	21.92	37.7	0.910	0.518	0.129	0.614	0.837	0.046	0.333	0.537	0.289	0.295	0.322	0.542	0.366	0.106	0.162	0.000	0.023	0.143	
	13 SD	1.12	1.07	2.53	10.1	0.454	0.341	0.176	0.552	0.221	0.113	0.337	0.302	0.202	0.230	0.258	0.289	0.254	0.211	0.199	0.000	0.083	0.231	
	1973 Mean	1.90	2.55	19.35	8.1	0.731	0.346	0.184	0.000	0.525	0.000	0.203	0.359	0.235	0.129	0.090	0.223	0.237	0.000	0.075	0.000	0.000	0.060	
	20 SD	0.91	1.15	4.33	1.8	0.365	0.328	0.360	0.000	0.341	0.000	0.286	0.243	0.222	0.193	0.172	0.323	0.339	0.000	0.134	0.000	0.000	0.124	
	1974 Mean	2.44	3.00	21.25	13.8	0.743	0.324	0.234	0.456	0.672	0.097	0.345	0.543	0.165	0.143	0.078	0.392	0.264	0.067	0.019	0.000	0.049	0.056	
	16 SD	0.96	1.15	6.50	3.2	0.325	0.331	0.419	0.674	0.336	0.180	0.341	0.266	0.202	0.172	0.173	0.378	0.310	0.150	0.075	0.000	0.137	0.121	
	1996 Mean	1.11	2.11	36.00	21.9	0.860	0.290	0.350	1.576	0.770	0.307	0.226	0.668	0.033	0.159	0.110	0.060	0.000	0.043	0.127	0.160	0.017	0.000	
	18 SD	0.32	0.47	8.29	2.5	0.195	0.360	0.353	0.756	0.175	0.282	0.304	0.287	0.097	0.224	0.165	0.142	0.000	0.129	0.168	0.224	0.071	0.000	
	2004 Mean	0.59	1.35	23.39	19.2	0.591	0.039	0.013	0.698	0.670	0.021	0.065	0.411	0.071	0.275	0.000	0.047	0.000	0.026	0.231	0.013	0.034	0.000	
	23 SD	0.29	0.57	8.28	4.1	0.266	0.104	0.063	0.695	0.325	0.099	0.156	0.302	0.228	0.270	0.000	0.128	0.000	0.087	0.212	0.063	0.115	0.000	
2005 Mean	1.10	1.10	21.71	17.4	0.799	0.143	0.146	0.668	0.667	0.109	0.125	0.654	0.014	0.339	0.043	0.000	0.000	0.014	0.051	0.014	0.014	0.000		
21 SD	0.30	0.30	7.44	2.6	0.272	0.181	0.203	0.600	0.249	0.188	0.243	0.378	0.066	0.302	0.108	0.000	0.000	0.066	0.133	0.066	0.066	0.000		
Monitor Cove	1971 Mean	2.41	3.81	25.84	27.0	0.436	0.693	0.150	0.457	0.539	0.092	0.703	0.448	0.169	0.205	0.028	0.373	0.056	0.109	0.158	0.038	0.028	0.056	
	32 SD	0.56	0.93	8.51	2.8	0.390	0.290	0.207	0.505	0.347	0.184	0.362	0.328	0.227	0.227	0.089	0.349	0.161	0.156	0.177	0.101	0.089	0.119	
	1972 Mean	2.50	3.58	31.58	31.7	0.230	0.786	0.105	0.040	0.545	0.000	0.251	0.313	0.295	0.318	0.090	0.232	0.321	0.115	0.115	0.000	0.000	0.115	
	12 SD	0.90	1.31	10.68	7.8	0.223	0.376	0.194	0.138	0.243	0.000	0.174	0.263	0.226	0.329	0.168	0.319	0.274	0.176	0.176	0.000	0.000	0.176	
	1973 Mean	2.00	4.00	32.69	10.0	0.205	0.519	0.086	0.000	0.254	0.075	0.479	0.379	0.341	0.254	0.075	0.190	0.362	0.124	0.049	0.038	0.000	0.146	
	16 SD	1.10	1.15	7.81	2.8	0.263	0.258	0.159	0.000	0.258	0.135	0.448	0.288	0.225	0.272	0.135	0.241	0.467	0.170	0.137	0.103	0.000	0.202	
	1974 Mean	3.13	4.00	20.93	38.7	0.267	0.520	0.040	0.473	0.417	0.040	0.619	0.303	0.164	0.161	0.020	0.207	0.104	0.084	0.040	0.072	0.000	0.072	
	15 SD	1.06	1.07	4.64	9.5	0.320	0.300	0.106	0.502	0.354	0.106	0.341	0.233	0.190	0.193	0.078	0.232	0.184	0.177	0.106	0.154	0.000	0.154	
	1996 Mean	1.00	2.84	29.12	23.0	0.267	0.497	0.599	0.965	0.340	0.059	0.330	0.131	0.024	0.147	0.000	0.060	0.000	0.024	0.209	0.086	0.012	0.000	
	25 SD	0.00	0.90	8.15	2.5	0.271	0.284	0.363	0.730	0.343	0.173	0.364	0.196	0.083	0.239	0.000	0.123	0.000	0.083	0.233	0.162	0.060	0.000	
	2004 Mean	1.13	1.79	35.29	16.5	0.277	0.227	0.215	0.701	0.334	0.025	0.133	0.088	0.000	0.320	0.077	0.025	0.203	0.000	0.382	0.000	0.063	0.013	
	24 SD	0.34	0.93	10.29	0.9	0.232	0.237	0.312	0.660	0.257	0.085	0.268	0.140	0.000	0.259	0.159	0.085	0.354	0.000	0.258	0.000	0.125	0.061	
	2005 Mean	1.42	2.29	29.21	20.0	0.491	0.239	0.870	1.201	0.281	0.169	0.145	0.478	0.013	0.640	0.045	0.083	0.013	0.025	0.246	0.040	0.050	0.025	
	24 SD	0.65	0.75	10.32	0.0	0.319	0.265	0.369	0.669	0.276	0.258	0.259	0.316	0.061	0.307	0.153	0.150	0.061	0.085	0.204	0.135	0.115	0.085	
BS Rock	1972 Mean	2.30	3.00	28.00	21.3	0.365	0.494	0.264	0.045	0.841	0.057	0.508	0.496	0.261	0.282	0.072	0.547	0.275	0.104	0.069	0.000	0.024	0.105	
	20 SD	0.73	0.86	4.15	7.4	0.333	0.229	0.276	0.110	0.213	0.197	0.415	0.256	0.231	0.277	0.175	0.314	0.363	0.202	0.146	0.000	0.107	0.202	
	1974 Mean	2.00	2.82	32.24	22.3	0.371	0.404	0.180	0.215	0.557	0.137	0.092	0.315	0.081	0.284	0.152	0.257	0.282	0.018	0.089	0.000	0.078	0.089	
	17 SD	0.71	1.13	7.05	5.3	0.340	0.285	0.394	0.507	0.296	0.240	0.176	0.273	0.156	0.278	0.202	0.250	0.261	0.073	0.141	0.000	0.013	0.141	
	1996 Mean	1.56	3.89	34.22	24.7	0.854	0.512	0.959	0.499	0.577	0.170	0.324	0.569	0.000	0.279	0.127	0.325	0.000	0.060	0.259	0.170	0.137	0.043	
	18 SD	0.62	0.83	8.50	1.2	0.260	0.271	0.412	0.609	0.295	0.287	0.323	0.296	0.000	0.273	0.236	0.277	0.000	0.142	0.220	0.183	0.183	0.129	
	2004 Mean	1.00	2.36	34.07	16.3	0.493	0.429	0.564	0.869	0.532	0.181	0.370	0.545	0.045	0.373	0.081	0.062	0.169	0.119	0.125	0.007	0.007	0.021	
	44 SD	0.00	1.04	11.46	3.9	0.295	0.303	0.399	0.636	0.274	0.260	0.404	0.321	0.162	0.292	0.212	0.123	0.238	0.185	0.207	0.045	0.045	0.077	
	2005 Mean	1.02	1.81	35.42	17.5	0.656	0.419	0.800	1.379	0.460	0.337	0.348	0.533	0.035	0.400	0.075	0.086	0.069	0.083	0.200	0.091	0.108	0.048	
	48 SD	0.14	0.89	11.52	2.5	0.302	0.251	0.474	0.781	0.295	0.348	0.335	0.359	0.123	0.293	0.158	0.179	0.167	0.179	0.203	0.192	0.206	0.119	
	Dick's Cove	1973 Mean	1.89	2.68	39.84		0.729	0.445	0.114	0.095	0.366	0.057	0.434	0.319	0.170	0.252	0.079	0.498	0.510	0.129	0.057	0.000	0.016	0.111
		19 SD	0.57	0.89	9.23		0.445	0.252	0.178	0.175	0.336	0.171	0.358	0.290	0.218	0.289	0.136	0.304	0.334	0.207	0.139	0.000	0.069	0.206
	Prisoner's to Pelican	1970 Mean	3.50	4.00	15.00	20.0	1.021	0.477	0.557	0.000	0.540	0.000	0.000	0.845	0.000	0.651	0.151	0.452	0.000	0.000	0.000	0.000	0.000	0.000
		2 SD	0.71	0.00	0.00	0.0	0.029	0.000	0.788	0.000	0.337	0.000	0.000	0.000	0.000	0.069	0.213	0.213	0.000	0.000	0.000	0.000	0.000	0.000
1996 Mean		3.35	3.00	32.12	32.6	1.080	0.330	0.783	1.209	0.554	0.035	0.507	0.563	0.099	0.081	0.183	0.513	0.000	0.053	0.089	0.180	0.018	0.000	
17 SD		0.49	0.50	5.18	2.6	0.232	0.301	0.275	0.498	0.357	0.100	0.396	0.357	0.163	0.156	0.271	0.395	0.000	0.118	0.141	0.183	0.073	0.000	
2004 Mean		3.05	2.85	26.76	20.4	0.867	0.247	0.429	0.323	0.565	0.152	0.348	0.632	0.044	0.338	0.041	0.229							

Table 4. Bottom transects: Post-hoc comparisons of mean year-site sample scores on Axis 2 of the NMS ordination of bottom transects. Comparisons were made with Tamhane, Dunnett T3, and Games-Howell post-hoc tests for samples with unequal variances. Double asterisks indicate $P < 0.01$ on all three tests, single asterisks indicate $0.01 < P < 0.05$, and question marks indicate $0.05 < P < 0.10$. Sample sets: M = Monitor Cove, B = B.S. Rock, P = Pelican Bay, PP = Prisoner's to Pelican, CV = Dick's Cove, and SCI = various sites on the north side of Santa Cruz Island.

	M73	M72	B72	P73	D73	B74	M74	M71	P74	P72	CV04	P71	SCI70	PP04	CV05	B96	P05	M04	P04	CV96	B04	PP05	PP96	P96	B05	M96	M05	
Mean	-1.08	-0.97	-0.68	-0.64	-0.57	-0.51	-0.42	-0.35	-0.35	-0.35	-0.14	-0.11	-0.10	-0.07	0.03	0.10	0.19	0.22	0.23	0.24	0.25	0.28	0.37	0.42	0.47	0.52	0.70	
M73																												
M72																												
B72																												
P73																												
D73																												
B74																												
M74																												
M71	**	**																										
P74																												
P72	**	*																										
CV04	*	*																										
P71																												
SCI70	**	**																										
PP04	**	**	**	*																								
CV05	**	**	**	*																								
B96	**	**	**	**	*			*																				
P05	**	**	**		*			*																				
M04	**	**	?																									
P04	**	**	**	**	*			*																				
CV96	**	**	*																									
B04	**	**	**	**	**	?	?	**		**																		
PP05	**	**	**	**	**	*	*	**		**														*				
PP96	**	**	**	**	**	*	*	**		**														?				
P96	**	**	**	**	*	**	**	**	?	**														*				
B05	**	**	**	**	**	**	**	**	*	**			*	**		*												
M96	**	**	**	**	**	**	**	**	*	**														?				
M05	**	**	**	**	**	**	**	**	**	**	*	**	**	**	**	**						**	**					

Table 5. Canopy transects: Mean and standard deviation of environmental variables and log (x+1) transformed species counts by site and year. See Table 2 for species abbreviations. Kelp (kelp density) was scored from 1 (absent) to 5 (most dense). Vis represents horizontal underwater visibility, in feet.

Location	Year	Env. Var.		Fish Species													
		N	Vis	kbas	sheep	sen	bsmth	half	opal	sprch	pile	rub	kprch	krock	blue	olive	
Pelican Bay	1970	MEAN	4.00	27.50	0.758	0.000	0.239	0.983	0.239	0.075	0.151	0.175	0.000	0.907	0.530	0.151	0.075
	4	SD	0.00	2.89	0.343	0.000	0.275	1.208	0.477	0.151	0.174	0.349	0.000	0.357	0.576	0.174	0.151
	1971	MEAN	3.43	21.43	0.179	0.000	0.288	1.514	0.043	0.086	0.000	0.000	0.043	1.563	0.554	0.000	0.186
	7	SD	0.53	2.44	0.231	0.000	0.394	0.833	0.114	0.147	0.000	0.000	0.114	0.708	0.421	0.000	0.267
	1972	MEAN	3.36	35.45	0.460	0.027	0.391	0.629	0.077	0.055	0.000	0.027	0.000	0.831	0.282	0.253	0.091
	11	SD	1.12	9.34	0.538	0.091	0.411	0.680	0.255	0.122	0.000	0.091	0.000	0.478	0.311	0.363	0.221
	1973	MEAN	3.40	11.07	0.535	0.000	0.144	0.133	0.098	0.020	0.272	0.020	0.000	0.944	0.258	0.180	0.144
	15	SD	0.63	2.27	0.437	0.000	0.222	0.302	0.217	0.078	0.269	0.078	0.000	0.683	0.406	0.337	0.222
	1974	MEAN	3.17	14.92	0.295	0.000	0.185	0.770	0.025	0.025	0.050	0.025	0.000	0.392	0.516	0.205	0.176
	12	SD	0.58	1.73	0.241	0.000	0.382	0.862	0.087	0.087	0.117	0.087	0.000	0.362	0.318	0.282	0.239
	1996	MEAN	1.30	20.50	0.168	0.048	0.000	1.379	0.168	0.030	0.000	0.030	0.000	0.000	0.000	0.000	0.000
	10	SD	0.48	1.58	0.356	0.151	0.000	0.645	0.233	0.095	0.000	0.095	0.000	0.000	0.000	0.000	0.000
2004	MEAN	1.08	19.92	0.298	0.023	0.000	1.474	0.046	0.023	0.000	0.023	0.000	0.000	0.000	0.000	0.023	
13	SD	0.28	4.05	0.325	0.083	0.000	0.329	0.113	0.083	0.000	0.083	0.000	0.000	0.000	0.000	0.083	
2005	MEAN	1.15	18.46	0.023	0.000	0.046	1.905	0.037	0.077	0.000	0.000	0.000	0.000	0.000	0.000	0.023	
13	SD	0.38	2.40	0.083	0.000	0.113	0.377	0.132	0.205	0.000	0.000	0.000	0.000	0.000	0.000	0.083	
Monitor Cove	1971	MEAN	3.33	27.67	0.373	0.000	0.120	0.982	0.020	0.308	0.020	0.060	0.000	1.467	0.092	0.020	0.394
	15	SD	0.49	4.17	0.286	0.000	0.274	0.772	0.078	0.338	0.078	0.125	0.000	0.633	0.163	0.078	0.343
	1972	MEAN	3.75	39.17	0.368	0.000	0.506	1.441	0.000	0.462	0.140	0.050	0.000	1.470	0.310	0.638	0.401
	12	SD	0.62	2.89	0.213	0.000	0.280	0.684	0.000	0.547	0.221	0.117	0.000	0.288	0.265	0.432	0.426
	1973	MEAN	2.94	10.00	0.000	0.000	0.406	0.019	0.000	0.044	0.116	0.019	0.000	0.471	0.038	0.038	0.000
	16	SD	0.77	0.00	0.000	0.000	0.521	0.075	0.000	0.175	0.215	0.075	0.000	0.247	0.103	0.151	0.000
	1974	MEAN	3.85	36.54	0.342	0.000	0.701	1.283	0.093	0.498	0.123	0.000	0.000	0.476	0.645	0.758	0.342
	13	SD	0.55	9.87	0.372	0.000	0.467	0.535	0.190	0.456	0.217	0.000	0.000	0.338	0.376	0.333	0.272
	1996	MEAN	1.00	20.00	0.027	0.000	0.082	1.846	0.298	0.125	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	11	SD	0.00	0.00	0.091	0.000	0.195	0.335	0.355	0.225	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	2004	MEAN	1.15	15.00	0.000	0.000	0.023	0.521	0.000	0.046	0.000	0.000	0.000	0.000	0.000	0.046	0.000
	13	SD	0.38	0.00	0.000	0.000	0.083	0.469	0.000	0.167	0.000	0.000	0.000	0.000	0.000	0.113	0.000
2005	MEAN	1.17	20.00	0.155	0.025	0.154	1.509	0.100	0.273	0.000	0.098	0.000	0.050	0.000	0.000	0.000	
12	SD	0.65	0.00	0.200	0.087	0.303	0.770	0.196	0.407	0.000	0.234	0.000	0.117	0.000	0.000	0.000	
BS Rock	1972	MEAN	3.88	22.50	0.406	0.019	0.679	1.227	0.067	0.418	0.078	0.000	0.000	1.508	0.581	1.190	0.419
	16	SD	0.81	4.47	0.336	0.075	0.413	0.593	0.150	0.544	0.173	0.000	0.000	0.604	0.377	0.451	0.305
	1974	MEAN	3.67	16.40	0.419	0.020	0.269	0.040	0.040	0.060	0.052	0.000	0.000	0.821	0.508	0.592	0.080
	15	SD	0.72	4.98	0.335	0.078	0.516	0.155	0.106	0.125	0.141	0.000	0.000	0.425	0.273	0.451	0.179
	1996	MEAN	2.89	20.00	0.211	0.000	1.221	2.027	0.348	0.439	0.000	0.000	0.000	0.000	0.033	0.000	0.100
	9	SD	0.60	5.00	0.237	0.000	0.500	0.339	0.343	0.408	0.000	0.000	0.000	0.000	0.100	0.000	0.151
	2004	MEAN	1.06	15.000	0.149	0.017	0.067	1.165	0.230	0.151	0.017	0.033	0.043	0.000	0.000	0.033	0.077
18	SD	0.24	0.000	0.278	0.071	0.165	0.665	0.285	0.390	0.071	0.142	0.183	0.000	0.000	0.097	0.152	
2005	MEAN	1.11	20.56	0.093	0.033	0.325	1.679	0.130	0.135	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
18	SD	0.32	5.11	0.160	0.097	0.458	0.858	0.221	0.333	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Dick's Cove	1973	MEAN	3.27	13.13	0.194	0.000	0.266	0.032	0.000	0.060	0.089	0.000	0.000	0.553	0.261	0.136	0.222
	15	SD	0.88	2.26	0.324	0.000	0.520	0.123	0.000	0.169	0.275	0.000	0.000	0.425	0.328	0.412	0.305
Prisoner Pelican	1996	MEAN	3.23	32.69	0.390	0.000	0.431	1.671	0.060	0.318	0.000	0.000	0.000	0.342	0.093	0.000	0.023
	13	SD	0.44	2.59	0.328	0.000	0.371	0.405	0.150	0.359	0.000	0.000	0.000	0.409	0.190	0.000	0.083
	2004	MEAN	2.92	18.65	0.259	0.000	0.136	0.912	0.060	0.127	0.012	0.053	0.012	1.098	0.046	0.000	0.023
	26	SD	0.63	2.26	0.309	0.000	0.202	0.623	0.147	0.321	0.059	0.131	0.059	0.471	0.111	0.000	0.082
2005	MEAN	3.58	15.00	0.480	0.000	0.267	0.910	0.121	0.269	0.046	0.069	0.000	1.171	0.012	0.000	0.000	
26	SD	0.76	0.00	0.456	0.000	0.440	0.790	0.201	0.354	0.111	0.129	0.000	0.336	0.059	0.000	0.000	
Cueva Valdaze	1970	MEAN	4.00	35.00	0.903	0.000	0.389	2.055	0.151	0.301	0.239	0.000	0.239	1.060	1.331	0.588	0.423
	2	SD	0.00	0.00	0.000	0.000	0.125	0.102	0.213	0.000	0.337	0.000	0.337	0.648	0.533	0.832	0.598
	1996	MEAN	3.92	15.00	0.280	0.000	0.732	0.937	0.025	0.205	0.050	0.050	0.000	0.105	0.065	0.000	0.075
	12	SD	0.29	0.00	0.147	0.000	0.686	0.684	0.087	0.192	0.117	0.117	0.000	0.253	0.156	0.000	0.136
	2004	MEAN	3.91	18.00	0.000	0.000	0.098	0.292	0.027	0.192	0.055	0.055	0.055	0.939	0.137	0.000	0.244
	11	SD	0.54	0.00	0.000	0.000	0.174	0.394	0.091	0.309	0.122	0.122	0.182	0.426	0.157	0.000	0.264
2005	MEAN	3.77	13.00	0.430	0.000	0.183	0.502	0.089	0.000	0.000	0.067	0.000	0.634	0.236	0.000	0.018	
17	SD	0.56	0.00	0.303	0.000	0.269	0.500	0.232	0.000	0.000	0.213	0.000	0.419	0.359	0.000	0.073	
SCI	1970	MEAN	3.63	40.19	0.576	0.092	0.565	1.140	0.107	0.236	0.038	0.078	0.000	0.454	0.293	0.212	0.247
	16	SD	0.72	7.43	0.386	0.211	0.632	0.790	0.287	0.400	0.103	0.173	0.000	0.686	0.314	0.586	0.345

Table 7. Pearson product moment correlation coefficients (r) comparing early (8/04 and 8/05) and late (10/04 and 9/05) season sampling in each year, for bottom (*Btm*), mid-water (*MW*) and canopy (*Can*) transects. Mean $\log(x+1)$ transformed counts of all species observed in both sampling periods were used for correlation. A single asterisk indicates a significant correlation at the 0.05 level (*: $P < 0.05$). A double asterisk indicates the correlation is significant at the 0.01 level (**: $P < 0.01$).

Year	B.S. Rock (B)			Prisoner's to Pelican (PP)		
	<i>Btm</i>	<i>MW</i>	<i>Can</i>	<i>Btm</i>	<i>MW</i>	<i>Can</i>
2004	$r = 0.58^*$	$r = 0.87^{**}$	$r = 0.93^{**}$	$r = 0.92^{**}$	$r = 0.96^{**}$	$r = 0.95^{**}$
2005	$r = 0.88^{**}$	$r = 0.52^*$	$r = 0.98^{**}$	$r = 0.80^{**}$	$r = 0.82^{**}$	$r = 0.88^{**}$

Table 8. Species significantly correlated with kelp (*Macrocystis pyrifera*) abundance for bottom and canopy transects in each of three sampling periods. A single asterisk indicates the correlation is significant at the 0.05 level (*: $p < 0.05$). A double asterisk indicates the correlation is significant at the 0.01 level (**: $p < 0.01$). See Table 2 for species abbreviations.

	Bottom Transects			Canopy Transects		
	1970s N = 217	1996 N = 97	2000s N = 315	1970s N = 169	1996 N = 55	2000s N = 167
kbass	0.197**	0.291**	0.199**		0.384**	0.381**
sheep	0.235**		-0.168**			
bsmth	0.310**		-0.330**	0.358**		-0.368**
sen			-0.163**		0.522**	
gar		-0.260*	-0.229**			
half		-0.208*	-0.126*			
opal	0.170*			0.362**	0.300*	0.166*
bprch	0.146*		0.146*			0.179*
sprch						0.194*
pile						0.194*
rub	0.153*					
kprch			0.259**	0.257**		0.790**
krock		0.552**	0.452**			0.368**
blue			-0.214**	0.266**		
pgrn			-0.136*			

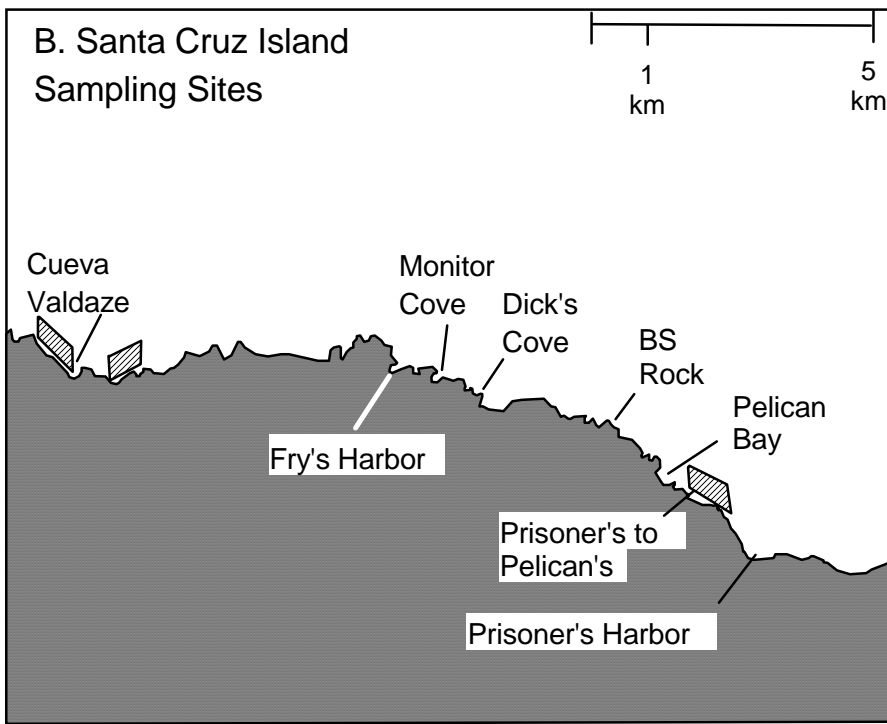
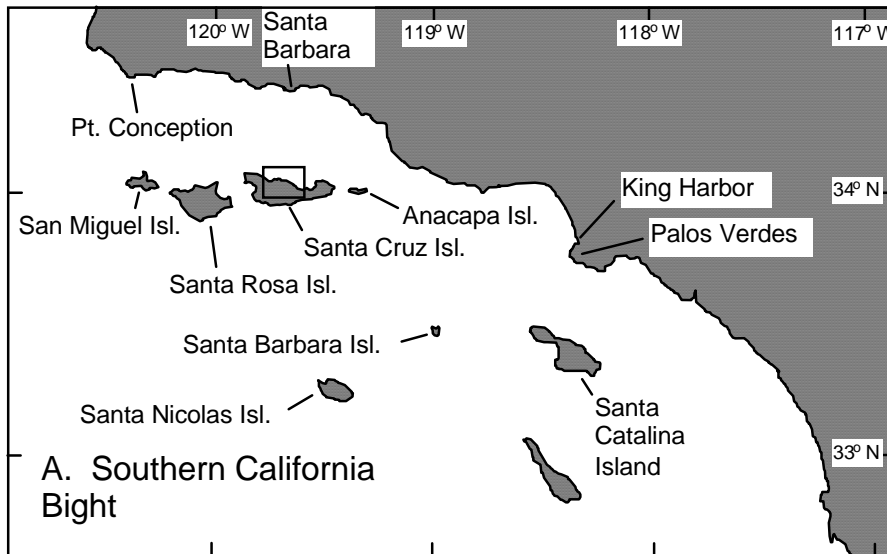


Figure 1. Locations of study sites. A. The southern California Bight. B. Study sites. Hatched areas show location of kelp forests.

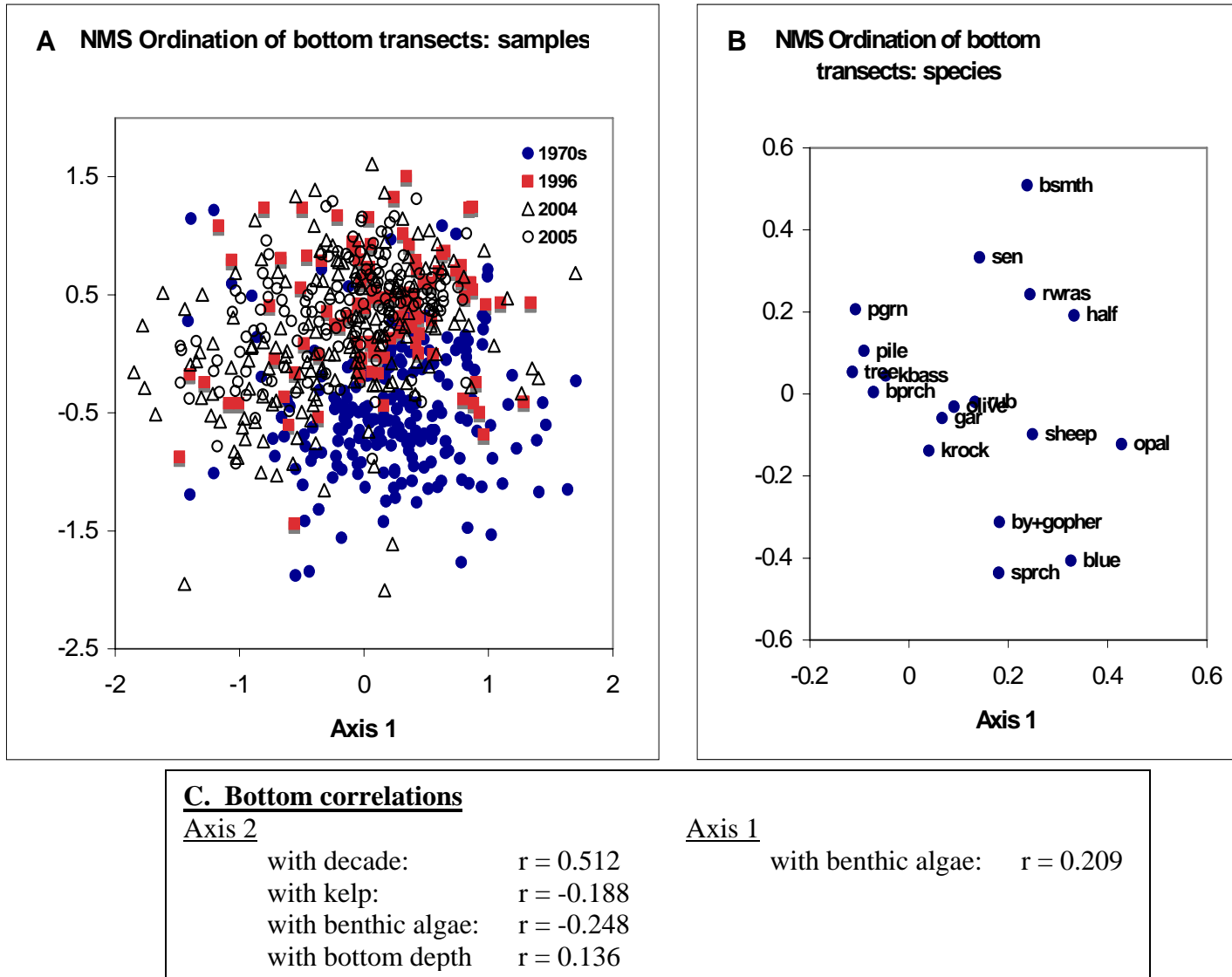


Figure 2. Nonmetric Multidimensional Scaling Ordination of bottom transects from sites on the north side of Santa Cruz Island, California. A. Ordination of transects from 1970s (solid blue circles), 1996 (red squares), 2004 (empty triangles) and 2005 (empty circles). B. Ordination of species. See Table 2 for species abbreviations. C. Correlations of scores on axes 1 and 2 with environmental variables.

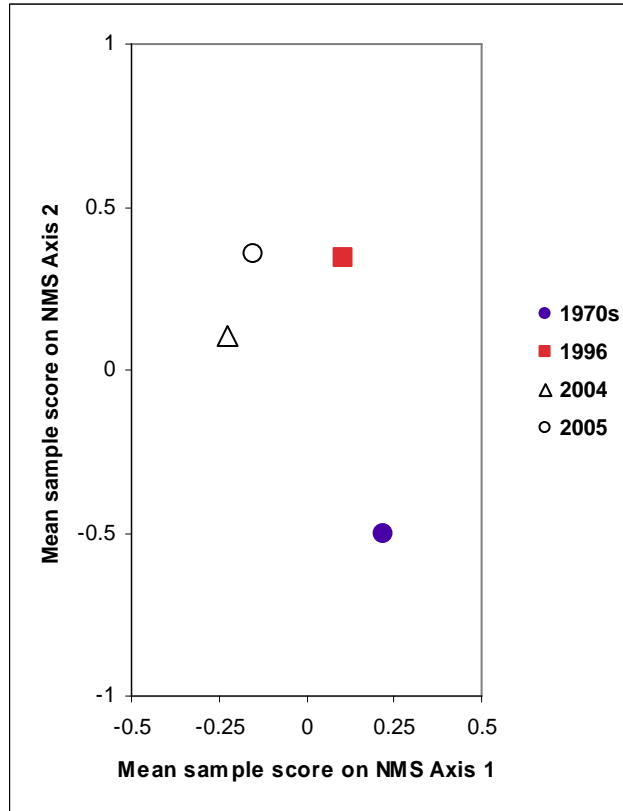


Figure 3. Centroids of bottom samples from 1970s, 1996, 2004 and 2005.

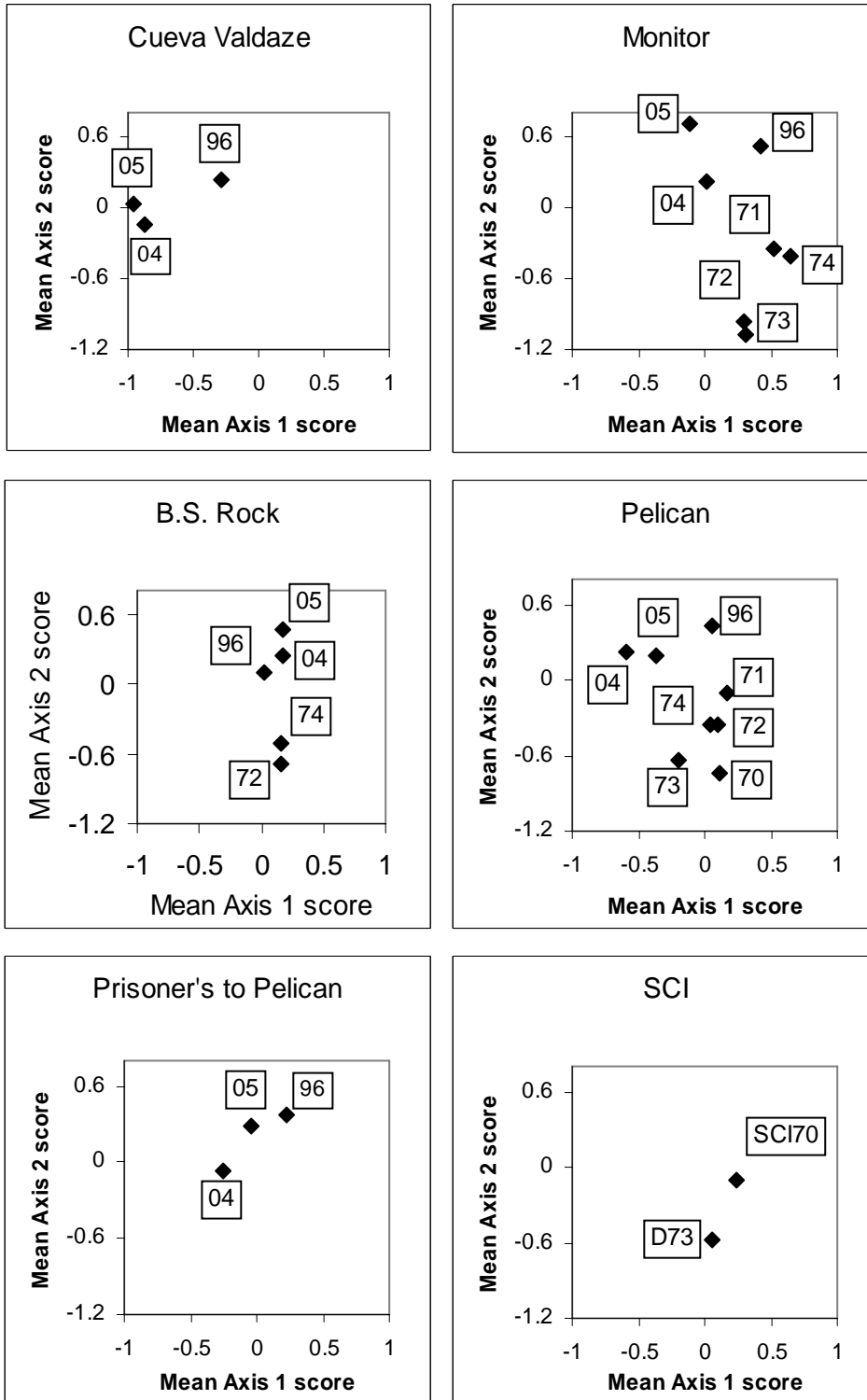


Figure 4. Centroids of yearly samples, by study site, for NMS ordination of bottom samples.

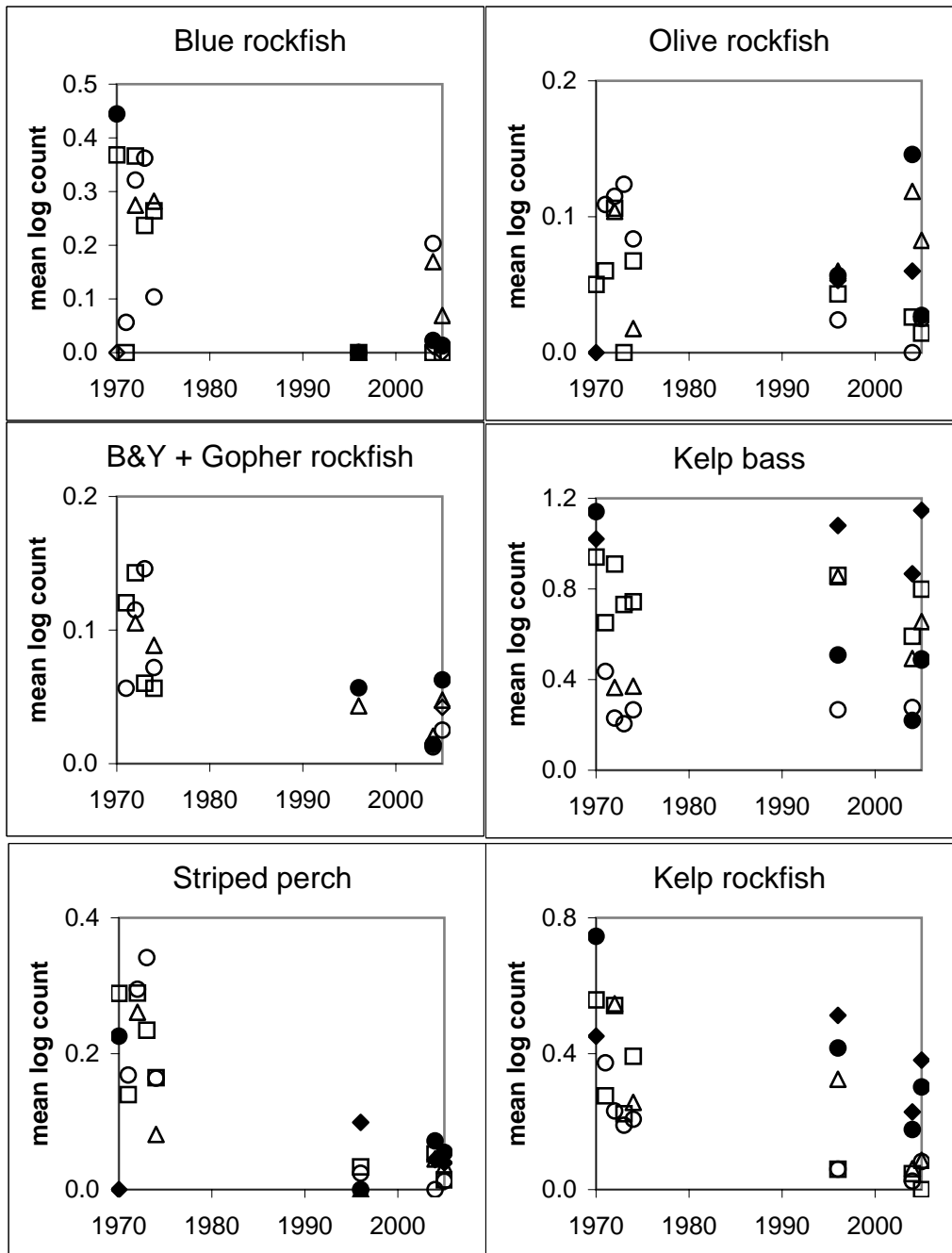


Figure 5a. Abundances of individual species in bottom samples

at the following sites:

◆ Prisoner's to Pelican
○ Monitor □ Pelican

● Cueva Valdaze
△ B.S. Rock

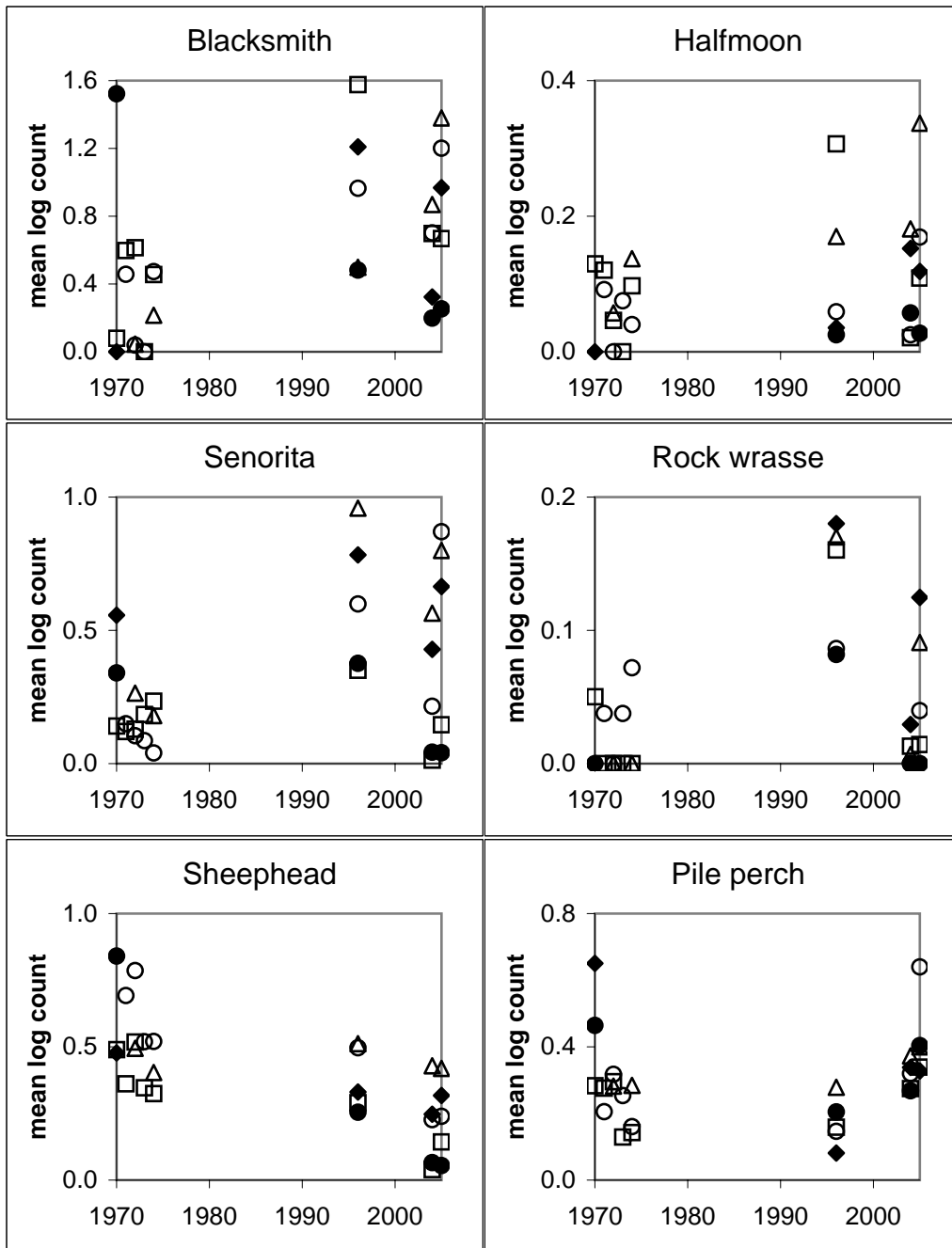


Figure 5b. Abundances of individual species in bottom samples

at the following sites:

◆ Prisoner's to Pelican
○ Monitor □ Pelican

● Cueva Valdaze
△ B.S. Rock

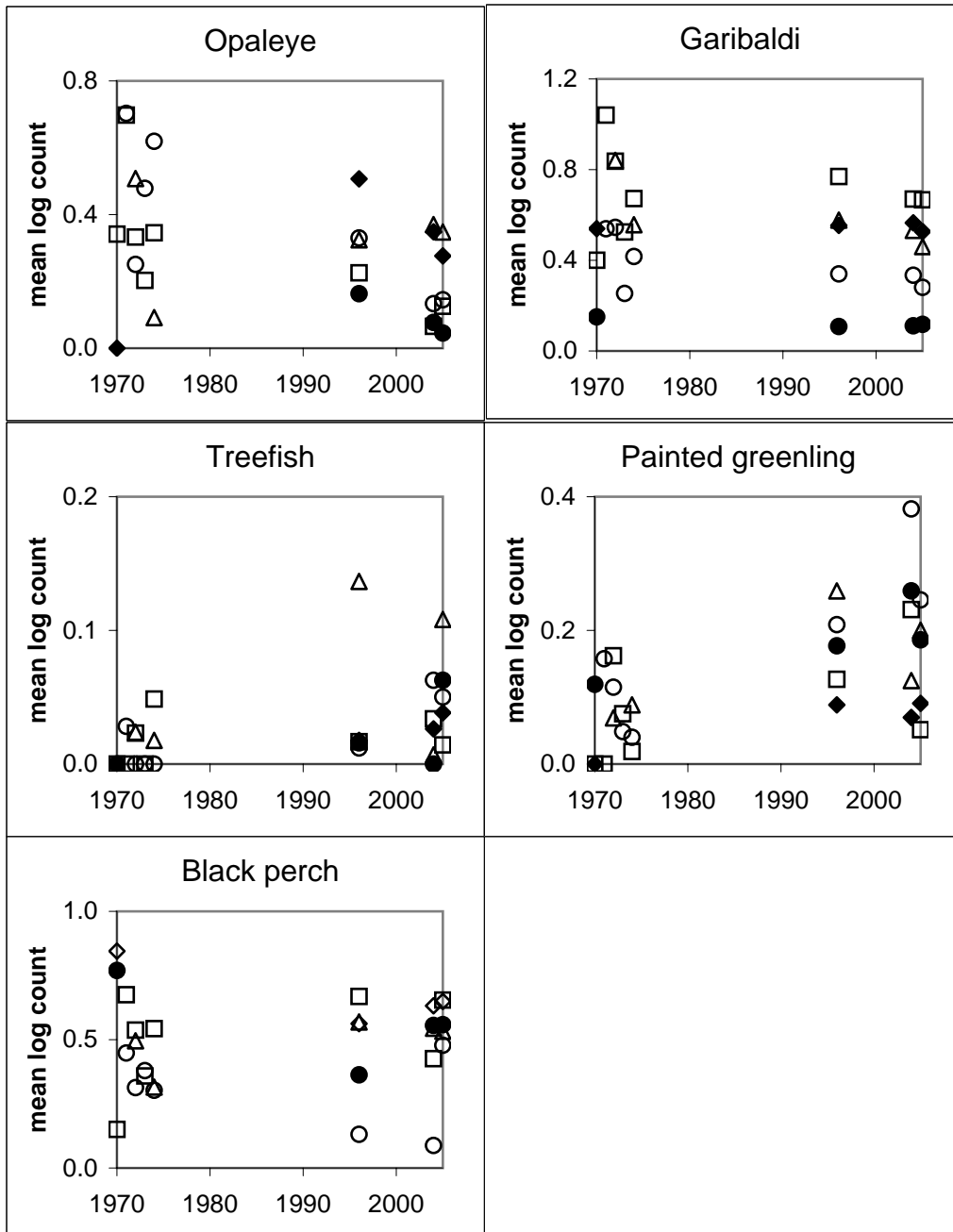


Figure 5c. Abundances of individual species in bottom samples

at the following sites:

◆ Prisoner's to Pelican
○ Monitor □ Pelican

● Cueva Valdaze
△ B.S. Rock

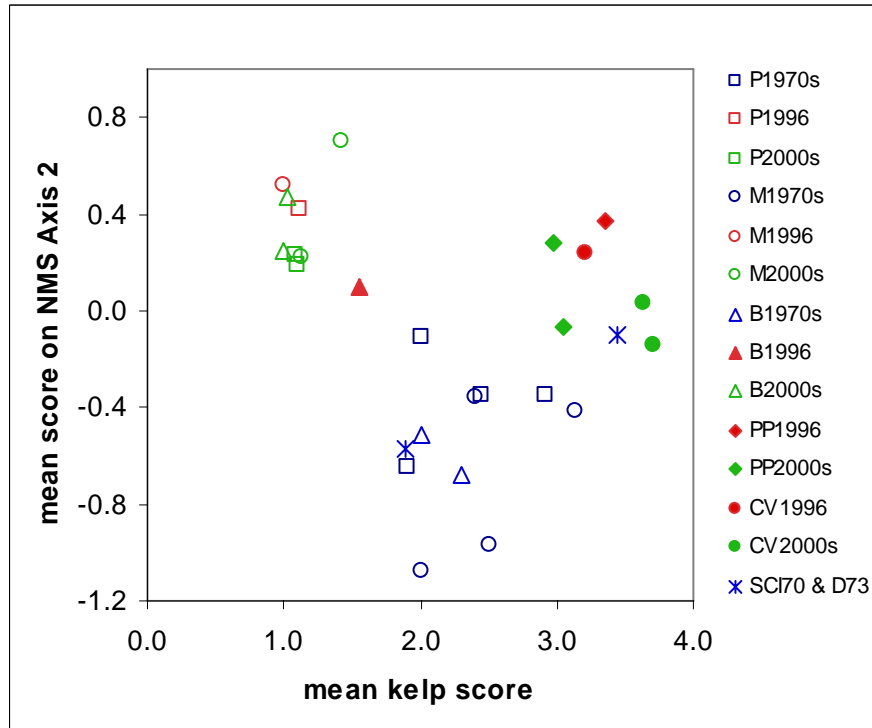


Figure 6. Means scores on NMS Axis 2 vs. mean kelp scores for sample sets of bottom transects.

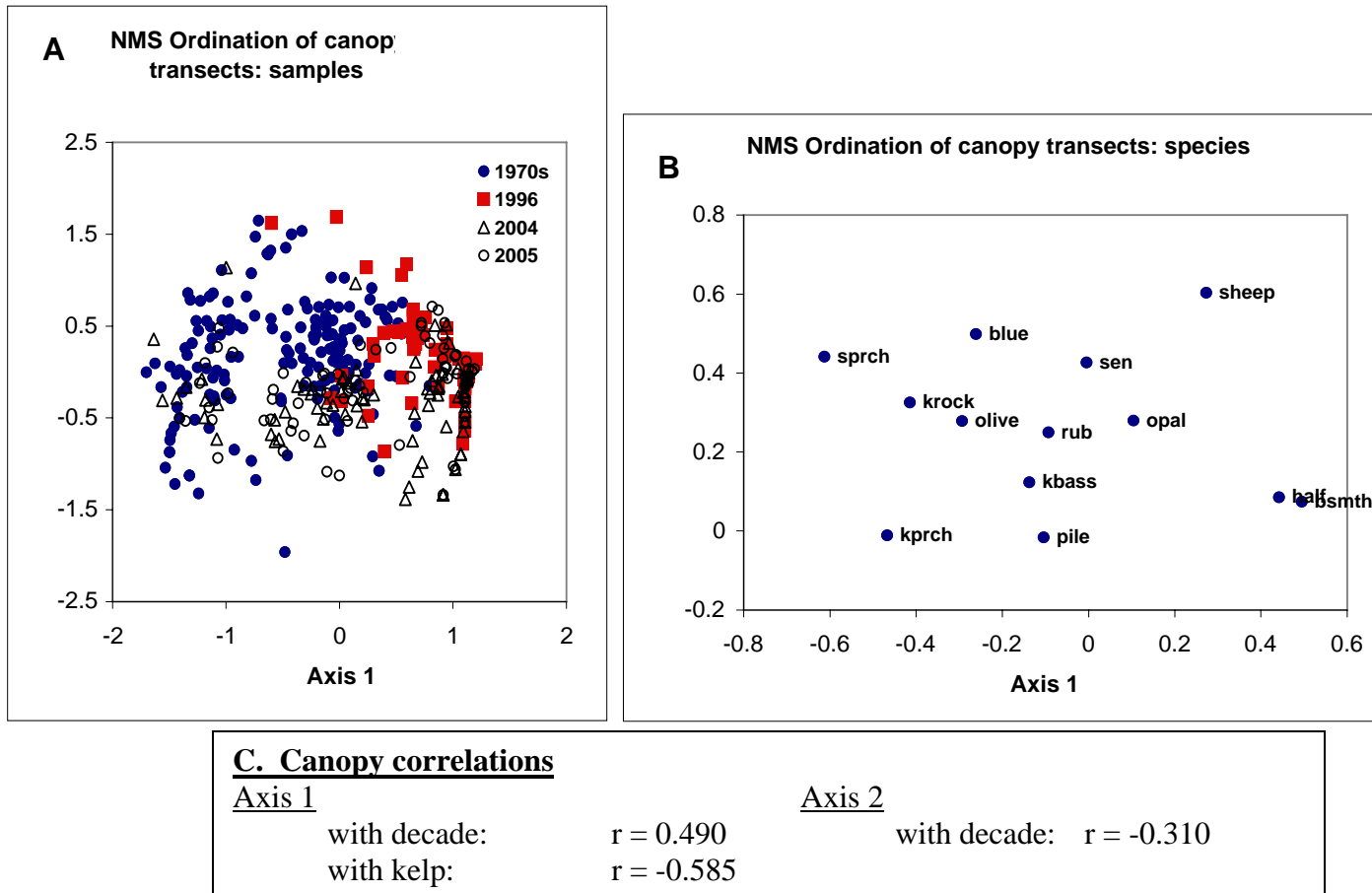


Figure 7. Nonmetric Multidimensional Scaling Ordination of canopy transects from sites on the north side of Santa Cruz Island, California. A. Ordination of transects from 1970s (solid blue circles), 1996 (red squares), 2004 (empty triangles) and 2005 (empty circles). B. Ordination of species. See Table 2 for species abbreviations. C. Correlations of scores on axes 1 and 2 with environmental variables.

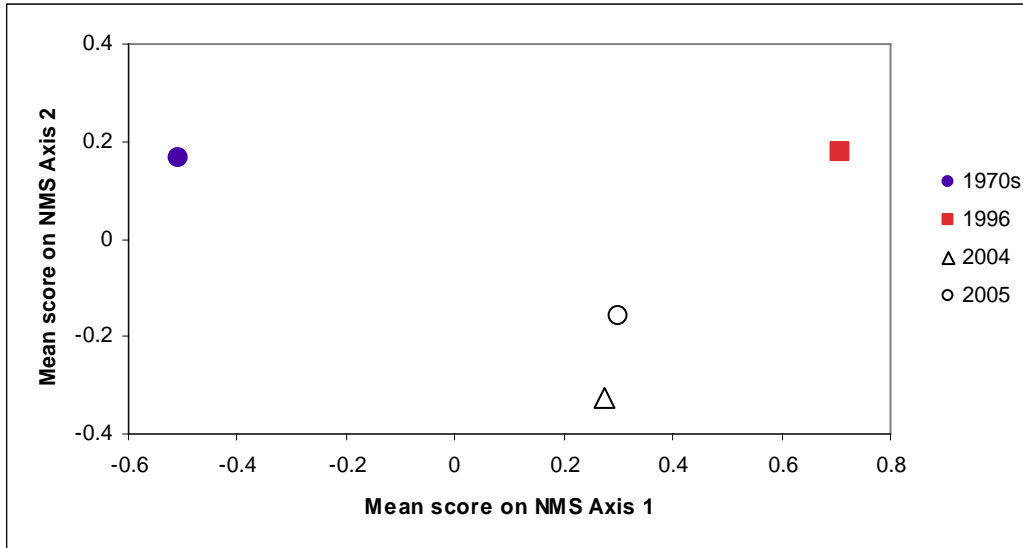


Figure 8. Centroids of canopy samples from 1970s, 1996, 2004 and 2005.

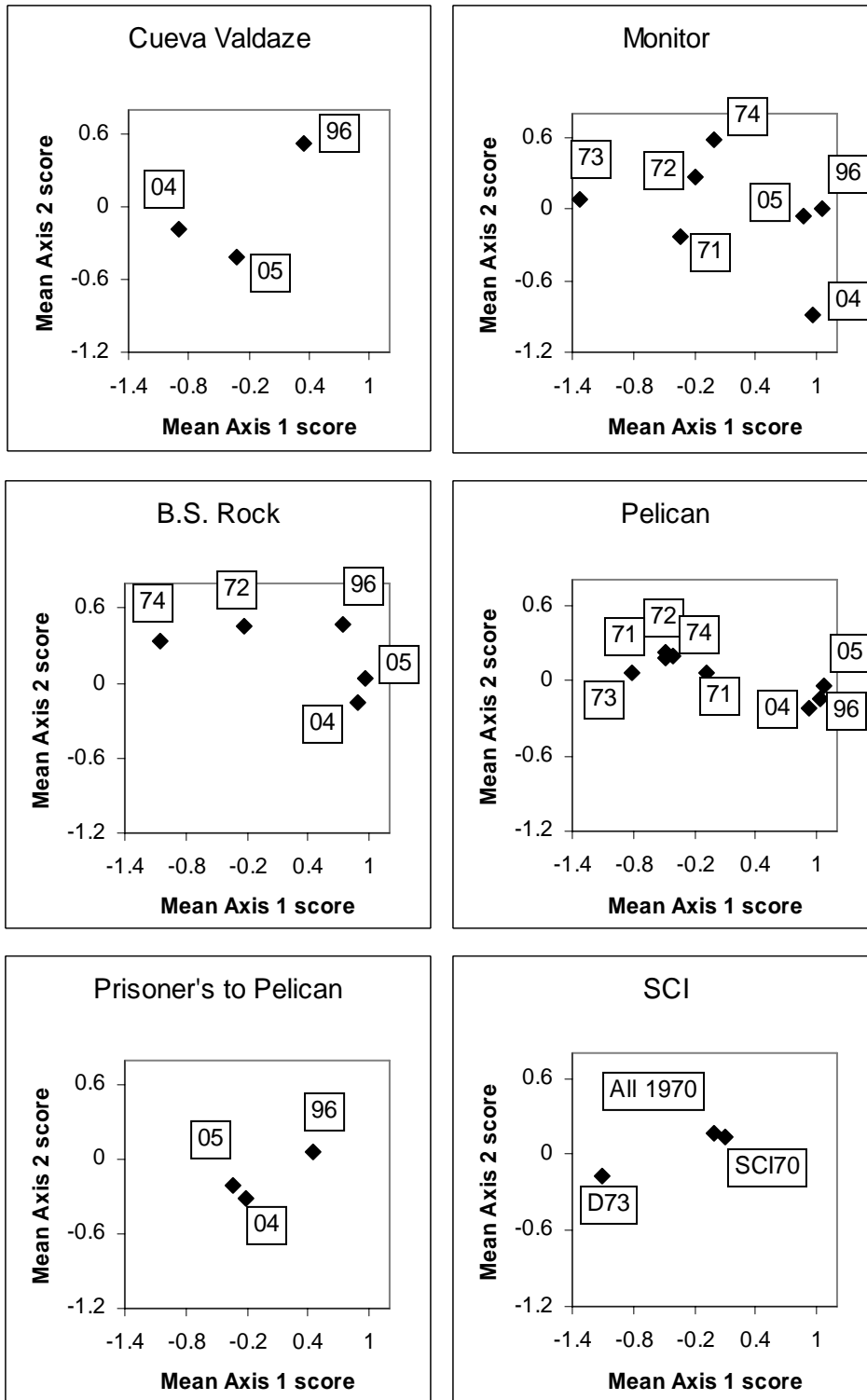


Figure 9. Centroids of yearly samples, by study site, for NMS ordination of canopy samples.

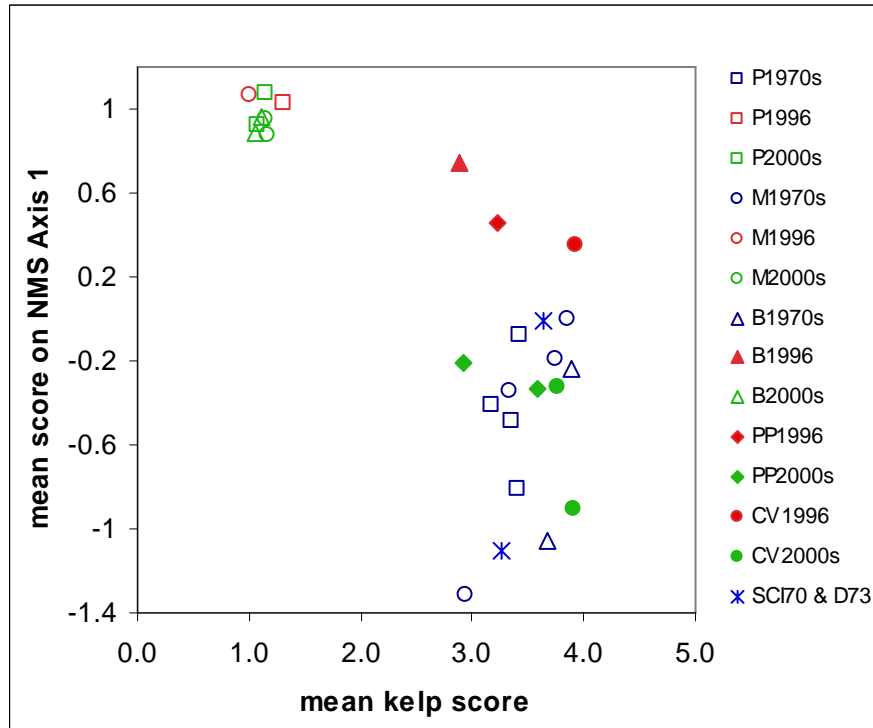


Figure 10. Means scores on NMS Axis 1 vs. mean kelp scores for sample sets of canopy transects.

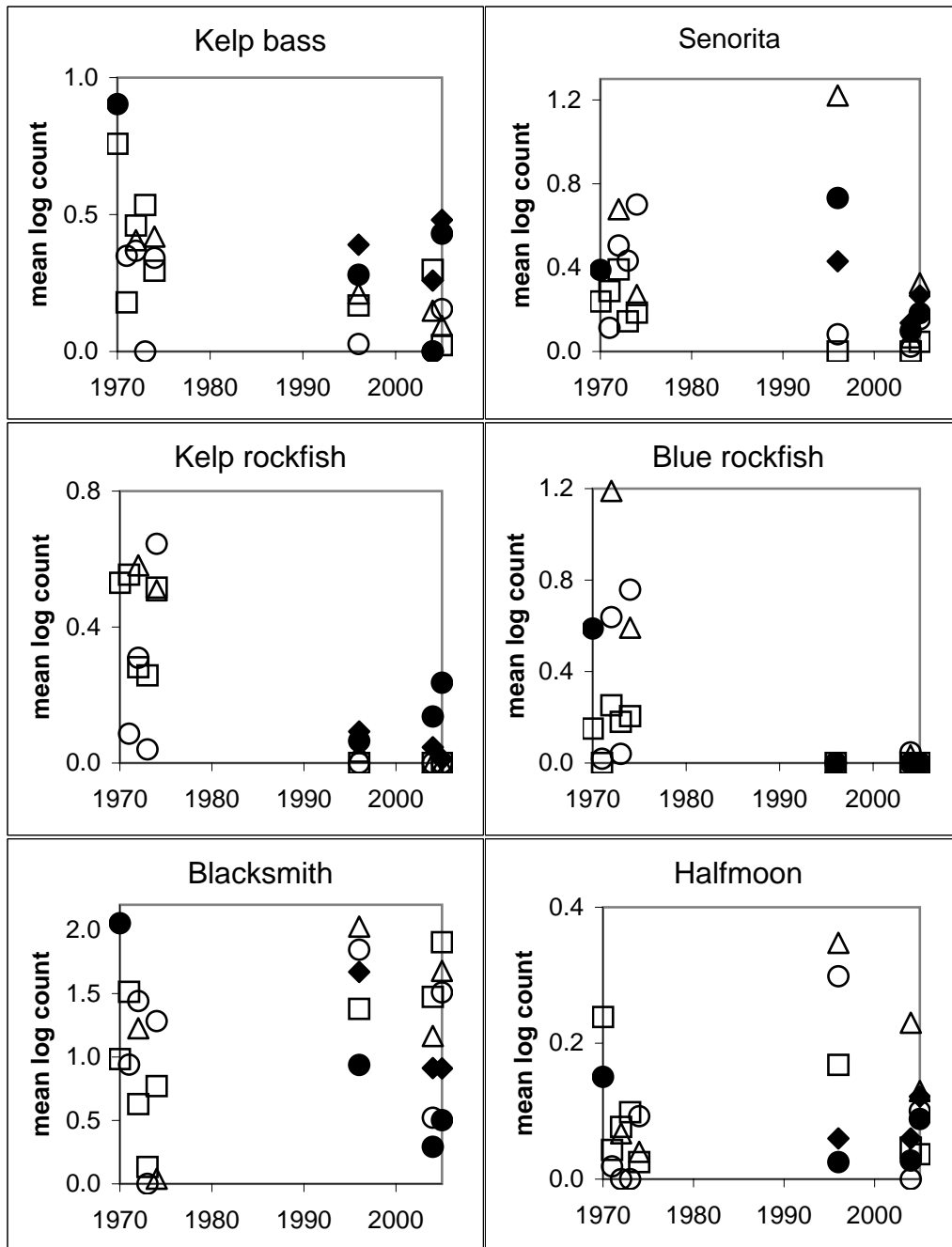


Figure 11a. Abundances of individual species in canopy samples

at the following sites:

◆ Prisoner's to Pelican

● Cueva Valdaze

○ Monitor □ Pelican

△ B.S. Rock

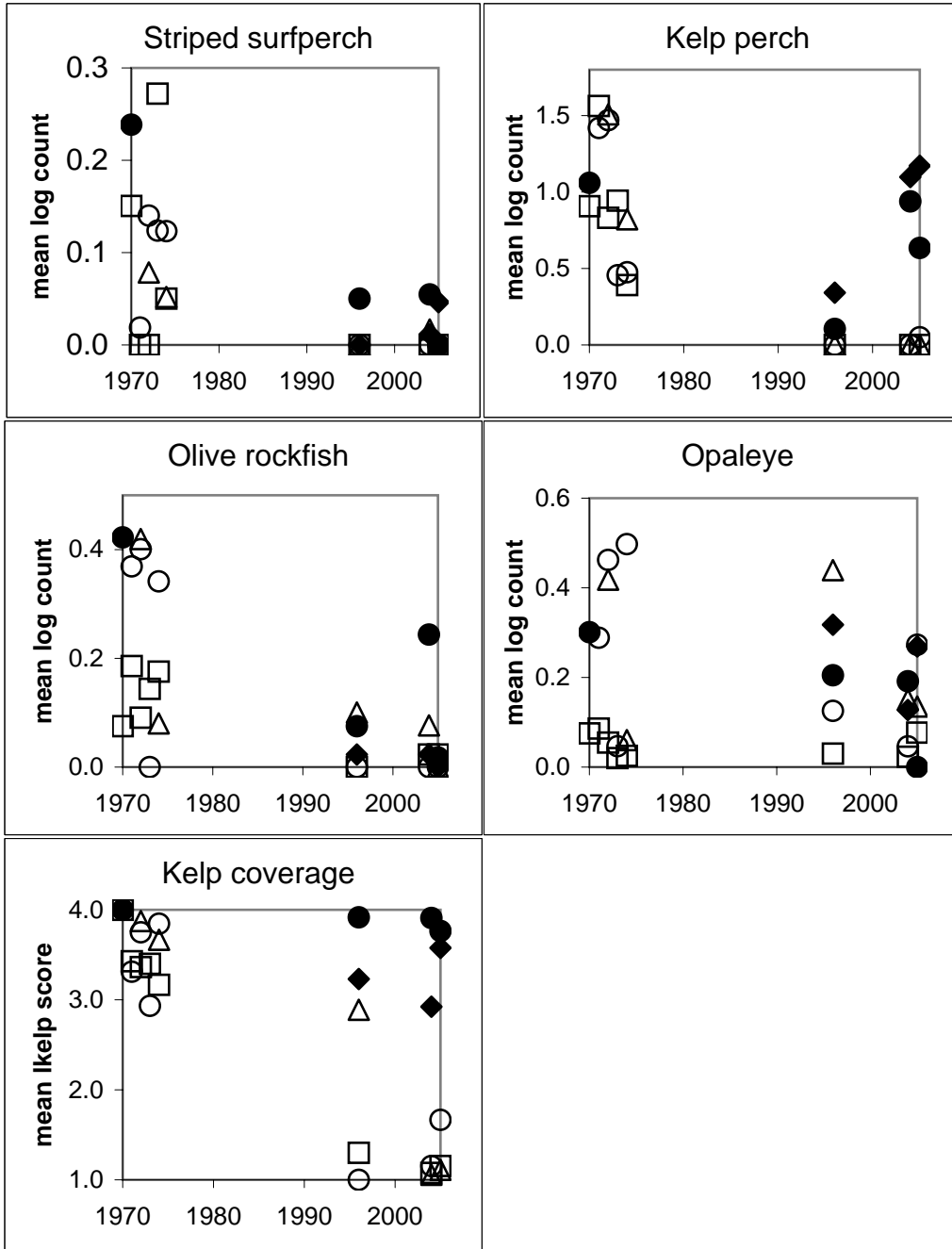


Figure 11b. Abundances of individual species in canopy samples

at the following sites:

◆ Prisoner's to Pelican
○ Monitor □ Pelican

● Cueva Valdaze
△ B.S. Rock