

THE ROLES OF FISHING AND CLIMATE IN THE POPULATION DYNAMICS OF BOCACCIO ROCKFISH

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Abstract. Climate is an important force influencing the dynamics of populations and communities in many terrestrial, aquatic, and marine systems. The precipitous decline of stocks of bocaccio (*Sebastes paucispinis*) since the mid-1970s has been attributed to a combination of a shift in the climate regime in the eastern Pacific Ocean during the winter of 1976–1977 (leading to lower productivity) and overfishing. We used a bocaccio recruitment time series (1959–1997) and indices of climate and ocean condition (e.g., sea surface temperature, Northern Oscillation Index, El Niño–Southern Oscillation Index, and upwelling indices) to examine the relationship between bocaccio productivity (recruits per spawning output, R/S) and both interannual (e.g., ENSO) and interdecadal (regime shifts) scale variation in climate and ocean conditions.

We did not detect an effect of the 1976 climate regime shift on bocaccio productivity. Mean log R/S and the frequency of “good” recruitment years (log R/S > 1 SD above the long-term mean) were the same before and after the 1976 regime shift. Good recruitment years occurred about 13% of the time in both regimes. At an interannual time scale, cooler ocean temperatures during the period spanning egg production to the end of the larval stage correlated with higher log R/S both before and after the regime shift. Prior to the 1976 shift, high log R/S values were more likely when upwelling was low during the settlement period, but there was no relationship after the regime shift. A matrix population model suggested that in the absence of fishing a “good” recruitment year needs to occur 15% of the time to achieve a nonnegative population growth rate of ($\lambda \geq 1.0$), similar to the observed frequency of good recruitment events. Good recruitment years needed to occur >90% of the time under historic levels of fishing mortality to achieve a population growth rate ≥ 1.0 . Taken together, these results suggest that the 1976 regime shift did not contribute to the decline in bocaccio stocks through processes affecting recruitment, and that the degree to which populations of bocaccio can withstand fishing depends on the frequency of climatic conditions that promote strong recruitment.

Key words: bocaccio; El Niño–Southern Oscillation (ENSO); matrix model; Northern Oscillation Index (NOI); regime shift; sea surface temperatures (SST); *Sebastes paucispinis*; upwelling.

INTRODUCTION

Climate is a clear driving force underlying the dynamics of many populations and communities in a number of terrestrial, aquatic, and marine communities around the world. Interannual climate variability, such as El Niño events, and interdecadal variability associated with the Pacific Decadal Oscillation (PDO) or the North Atlantic Oscillation (NAO) generate substantial changes in precipitation and winds that are manifested as changes in primary production that propagate throughout ecosystems (Barber and Chavez 1983, Ottersen et al. 2001, Post and Forchhammer 2002, Strale 2002, Chavez et al. 2003). In terrestrial systems, for example, populations of arctic herbivores (Milner-Gulland and Mace 1998), large ungulates in Africa (Fritz and Duncan 1994), small mammals in Chile

(Lima et al. 2002), and kangaroos in Australia (Caughley et al. 1985) respond strongly to changes in vegetation associated with El Niño. North Atlantic Oscillation cycles synchronize Greenland populations of musk oxen and caribou that are separated by >1000 km of inland ice (Post and Forchhammer 2002). Similarly, changes in winds associated with El Niño and the PDO affect the upwelling of nutrients and productivity in marine systems, which ultimately affect the abundance of fish, seabirds, and mammals (Chavez et al. 2003, Gjerdum et al. 2003).

In populations of conservation concern that have been greatly reduced in size, it is critical to understand the role of climate in population dynamics. Conservation issues such as location and size of reserves, target population sizes, and allowable harvest rates will all be influenced by the extent to which populations respond to climate. If the distribution or dynamics of a species can be modeled as a function of climate, then resource managers will be better equipped to evaluate potential management alternatives. For example, in the

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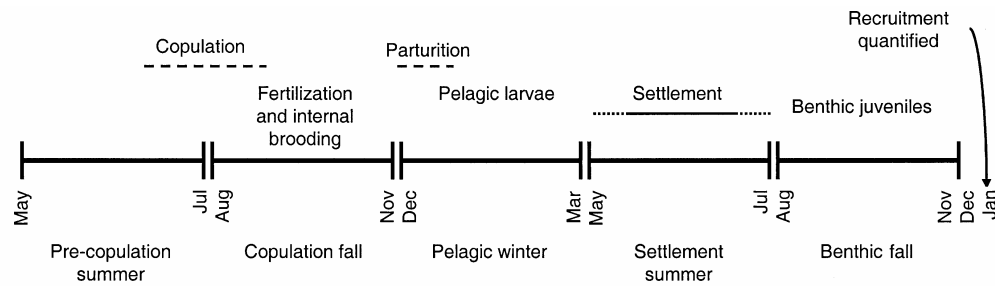


FIG. 1. Life history of bocaccio and terminology used. Bocaccio copulate in the late summer to early fall. Females brood larvae internally until parturition occurs in about December. Following a 3–5-month pelagic phase, larvae settle to shallow reefs and kelp. Recruitment is quantified on 1 January in the stock assessment model. Climate variables could affect recruits per spawning output (R/S) during several periods: the pre-copulation summer, copulation fall, pelagic winter, settlement summer, and benthic fall.

United States, the Magnuson-Stevens Fishery Conservation and Management Act requires that fishery management councils create and put into effect measures to rebuild over-harvested fish stocks. As a consequence, fisheries managers attempt to provide some harvest while allowing for recovery of the stock. However, if climate-induced downturns in productivity are not considered, harvest rates might be set too high resulting in further overfishing of stock (e.g., Manuta et al. 1997, Chavez et al. 2003).

Rockfishes (*Sebastes*) are an important part of recreational and commercial fisheries on the west coast of the United States. Recent stock assessments have indicated large declines for several species (PFMC 1999, 2002). In particular, bocaccio, *Sebastes paucispinis* (Ayers 1854), have declined 96% in the last 25 years (P. S. Levin, E. E. Holmes, and K. Piner, *unpublished manuscript*) and are now considered “critically endangered” by the International Union for Conservation of Nature and Natural Resources (IUCN). The demise of bocaccio coincided with a period of high fishing pressure, but it was also concurrent with a shift in the PDO that occurred during the winter of 1976–1977.

The PDO describes climate regimes that are similar to the El Niño–Southern Oscillation but are persistent over decadal scales (Manuta et al. 1997, Chavez et al. 2003). In the northeast Pacific Ocean from the 1950s to the mid-1970s, a cool regime persisted, characterized by a weak Aleutian low, strong California Current, cool sea surface temperatures (SST), shallow thermocline, and high productivity. A shift to a warm regime occurred during the winter of 1976–1977. This warmer regime was characterized by a stronger Aleutian low, weaker California Current, warmer SST, deeper thermocline, and lower productivity. A number of biological changes were associated with these regime shifts, from zooplankton (Brodeur and Ware 1992, Roemmich and McGowan 1995, Brodeur et al. 1996) to apex predators (Francis et al. 1998, Hare and Mantua 2000, Zhang et al. 2000, Sydeman et al. 2001), but the outcome of the regime shift varied among taxa. For example, anchovies were highly abundant under the cool

regime, but were replaced by sardines during the warmer regime (Chavez et al. 2003). The effects of regime shifts also vary geographically (Hare et al. 1999, Yasuda et al. 1999, Zhang et al. 2000, Hunt et al. 2002, Chavez et al. 2003, Levin 2003). Pacific salmon (*Oncorhynchus* spp.) from Alaska increased in abundance in response to the 1976 regime shift while populations from the Pacific Northwest declined (Hare et al. 1999).

While overfishing ostensibly caused the decline of bocaccio (Love et al. 1998, 2002), the role of climate in the population dynamics of bocaccio is poorly understood (MacCall 2002). Climate may influence how rapidly bocaccio stocks recover and how much harvest the species can sustain while recovering. In this paper we examine the effects of the climate regime shift that occurred during the winter of 1976–1977 and inter-annual climate variability on recruitment success of bocaccio. We determine whether the 1976 regime shift reduced bocaccio recruitment success and ask whether the relationship between recruitment success and ocean/climate conditions was the same under each regime.

METHODS

Study species

Bocaccio range from British Columbia to Baja California but are most common off the southern Californian coast. They are live bearers with copulation occurring in the fall followed by parturition in early winter (about December; Fig. 1). Pelagic larvae are abundant from December to April. Settlement occurs from February to August but is most intense from May to July (Love et al. 2002). Juveniles settle primarily to rocky areas covered by macroalgae or to eelgrass and sand. About two weeks after settlement, juveniles move to deeper waters (18–30 m) in some areas. Adults are most abundant at 50–250 m (Feder et al. 1974, Love et al. 2002). Because bocaccio are long lived, one would not expect spawner biomass to fluctuate in response to interannual climate variation (Warner and Chesson 1985, Love et al. 2002). Instead we focus on

recruitment of age-1 fishes and productivity or recruitment success defined as recruits per spawning output (R/S).

Biological patterns

We used time series data for bocaccio spawning biomass and recruitment (age-1 fishes) extracted from the STATc model 2003 stock assessment for bocaccio (MacCall 2003). The bocaccio assessment uses a stock synthesis length-based maximum likelihood model (Methot 1990). The model distributes the residual error among various types of data according to levels of variability and confidence (emphasis levels). In its simplest form, the model requires the following parameters: natural mortality, body mass for age class, age-specific availability to the fishery, abundance at age in the first year, recruitment, and fishing mortality in each year. In the fitting processes, each parameter can be given a different emphasis, which describes the contribution of that individual likelihood function to the overall likelihood of the model. The 2003 bocaccio model makes use of a number of data sources on fisheries catch, length, and abundance data. Catch data includes information from five fisheries segments using three gear groups, and northern and southern Californian recreational catches. Length information consists of data from the five fisheries segments and the National Marine Fisheries Service Triennial Surveys. Abundance data include trawl log book CPUEs (catch per unit of effort), recreational CPUEs, the Triennial Survey, and CalCOFI larval index of spawning output. Although three recruitment indices were developed, they were not used in the STATc model because of high imprecision. Recruitment was estimated with a Beverton-Holt stock-recruit relationship as the expected recruitment (A. MacCall, *personal communication*). However, there was no statistically detectable curvature to the stock-recruit relationship; the steepness parameter was estimated at 0.2 (a straight line). Also, the stock synthesis length-based maximum likelihood model used a low emphasis (0.1) for the stock-recruit relationship. Therefore, recruitment estimates tended to vary based on the age composition and survey abundance data (Methot 1990).

Our analyses divide each time series into two sections: before the 1976 regime shift (1959–1976) and after the regime shift (1977–1997). We refer to 1959–1976 as the “before” period and 1977–1997 as the “after” period. We made this division for two reasons. First, it allows us to consider the extent to which the dynamics within each climate regime differ. Secondly, because bocaccio stocks began declining around 1976, the role of ecological processes such as density dependence may have also changed. We begin the “before” period at 1959 because recruitment was held constant in the model prior to this point. We limit the “after” period to 1997 because another regime shift may have occurred at this point (Chavez et al. 2003),

although data are presented to 2003. Because estimates of recruitment are imprecise, we considered these data as indicators of magnitude (MacCall 2003). As such, we \log_{10} transformed all data on recruitment and R/S for the analyses.

We used regression analysis to examine relationships between recruitment, spawner output (measured in billions of eggs), and time. Recruits per spawning output (R/S) was quantified as the number of recruits per 10^9 eggs. Regression models were evaluated for autocorrelation using Durbin-Watson’s statistic, but significant autocorrelation was not detected.

Environmental variables

We looked at the association between a number of environmental variables and \log R/S. While absolute recruitment may be correlated with stock size, \log R/S is a measure of productivity and individual reproductive success that accounts for variation in spawning stock biomass. Recruits per spawning output can be reduced by density dependence at high population densities and by dispensation at low densities. However, we found no evidence of density dependence. Environmental variables included: the Northern Oscillation Index (Schwing et al. 2002), El Niño 3.4 Sea Surface Temperature Anomaly (*data available online*),² Sea Surface Temperature at 37° N, 122° W (Smith and Reynolds 2003), and the mean of upwelling indices for 36° N and 39° N (*data available online*).³ The Northern Oscillation and El Niño indices were chosen to represent basin-wide climate influences and changes. The sea surface temperature and upwelling indices are more specific to the Southern and Central California region, the target region of stock assessments (MacCall 2002). Upwelling may be important for production and larval survival, but it does not appear to affect larval condition (Rau et al. 2001). Upwelling and downwelling may be important for offshore and onshore transport of larvae (Larson et al. 1994, Bjorkstedt et al. 2002).

For each environmental variable, we calculated yearly averages in three seasons based on the life cycle of bocaccio (Fig. 1; Love et al. 2002). The seasons were: (1) fall (August–November), bocaccio have internal fertilization and copulate in late summer and early fall; (2) winter (December–March), parturition occurs in the winter followed by three to five months as pelagic larvae and juveniles; and (3) summer (May–July), juveniles settle in the late spring and early summer. Recruitment estimates (from the models) are for age-1 fishes quantified in the January following settlement. Therefore, climate variables could affect recruitment and R/S during several periods: the “pre-copulation summer,” “copulation fall,” “pelagic winter,” “settlement summer,” and “benthic fall.” To account for

² <http://ingrid.ldgo.columbia.edu/SOURCES/KAPLAN/Indices/>

³ <http://www.pfeg.noaa.gov/>

TABLE 1. Model information.

Age class (yr)	Name	Standard length (cm)	Mean no. eggs	Annual fishing mortality†	Annual survival†
Larval age 1	juvenile	NA	0	0	1.156×10^{-7} in “normal” years; 1.152×10^{-6} in “good” years
1–3	subadult	26.8	54 027	0.08	0.78
4–8	adult 1	49.8	387 727	0.18	0.68
9–15	adult 2	70.1	1 150 192	0.11	0.75
16–50	adult 3	82.8	1 952 731	0.10	0.76

† Mortality and survival are probabilities in the transition matrix (ranging from zero to 1.0).

the different times at which ocean conditions could affect bocaccio recruitment, we lagged each variable to match earlier stages giving us a total of 20 environmental variables (see Table 1 for variables included in the analysis).

We next ran these 20 environmental variables through a principal-components analysis (PCA). We chose this approach for several reasons. First, and most obviously, we needed to reduce the number of independent variables to a more manageable number. The PCA provided five uncorrelated principal components (PCs), which we used for further analyses. Second, because there were high levels of correlation among our environmental variables, we felt an approach such as stepwise multiple regression to be inappropriate. In preliminary analyses, we were able to produce a number of models with similar r^2 values but with different explanatory variables. The PCA approach combines correlated variables onto one new variable and does not require (or allow) the researcher to choose among correlated variables as to which one is specifically important. Therefore, this approach is more conservative in that it does not attempt to exclude correlated variables. Third, we chose to use the PCs from the analysis in an ANCOVA-type approach to examining the effect of both the regime shift and the environmental variables on recruitment of bocaccio. Principal components whose eigenvalues were >1.0 were retained. Finally, because there was only one response variable (log R/S), other multivariate approaches were not required.

We took two statistical approaches towards examining the relationship between bocaccio recruitment success (log R/S) and environmental variables (PCs). In the first approach, we used each principal component (PC) as a covariate in an analysis of covariance (ANCOVA) in which time period was the categorical factor. Separate models were run for each PC. For the second approach, we categorized years as having good recruitment success or not. We chose to do this for several reasons. First, bocaccio is a long-lived species in which episodic high recruitment success is probably a major factor driving population size (i.e., the storage effect; Warner and Hughes 1988). Second, recruitment estimates for both time series are imprecise and probably only represent magnitude. We defined a year with “good” recruitment success as one in which log R/S was more than one standard deviation (SD) above the

mean (for the log-transformed data) of the time series. We used a generalized linear model (GLM) with logit link and binary distribution to determine the relationship between environmental variables (represented by the PCs) and the probability of a year with good recruitment success. Principal components were included as continuous variables; “period” was a categorical variable. Separate models were run for each PC. Models were backfit by removing nonsignificant interaction terms. All statistical analyses were run using SAS 8.2 software (Littell et al. 1996, SAS Institute 1999).

The significance of climate in population dynamics

To illustrate the importance of climatic variation to bocaccio population dynamics, we developed a simple stage-based matrix model (Caswell 2001) for a hypothetical bocaccio population. To construct the population matrix, we first calculated survival of fish ≥ 1 year old by using estimates of the number of female bocaccio at ages 1 through 21 from 1960–2002 obtained from MacCall (2003). We then calculated the proportion of individuals in each year class in year t that were still alive in year $t + 1$. Survival in each class was considered to be the mean of ages that comprised that class (Table 1). Because our estimates of adult survival are derived from population counts, they include fishing mortality. We next estimated annual fishing mortality as the difference between natural survival (0.86; MacCall 2002) and our survival estimate (Table 1). We were thus able to examine population dynamics with and without fishing.

We estimated age-0 to age-1 survival as the product of a 90-d larval period and a 270-d demersal juvenile stage. An estimate of larval survival was not available for bocaccio. We used an instantaneous daily mortality for bocaccio larvae of 0.16, yielding a 90-d survival rate of 6×10^{-7} . This mortality rate is slightly higher than that reported for smaller preflexion shortbelly rockfish larvae ($Z = 0.11$; Ralston et al. 2003), and lower than the mean mortality rate for marine fish larvae ($Z = 0.24$; Houde 2002). No survival estimates are available for young-of-the-year bocaccio (270-d demersal stage). However, Adams and Howard (1996) estimated annual young-of-the-year survival of blue rockfish, *Sebastes mystinus*, as 0.19, and we used this value in our model. Our simple matrix model was density independent because we found no evidence sup-

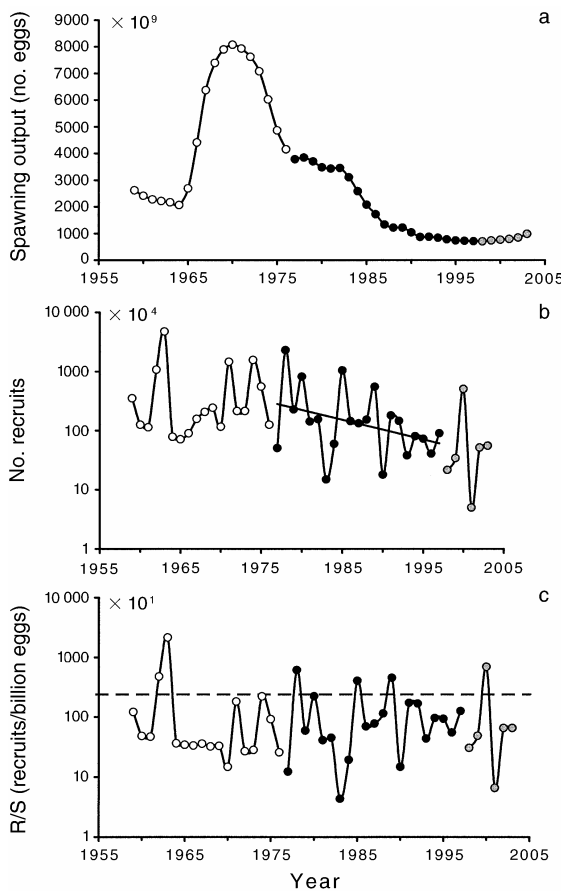


FIG. 2. (a) Spawning output of bocaccio off of southern California from 1951 to 2003, (b) abundance of bocaccio recruits from 1951 to 2003, and (c) trend in bocaccio R/S from 1951 to 2003. The dotted line in (c) indicates one standard deviation above the long-term mean and delineates "good" recruitment years. For statistical analyses, we begin the "before" period at 1959 because recruitment was held constant in the model prior to this point. We limit the "after" period to 1997 because a regime shift appears to have occurred at this point (Chavez et al. 2003), although data are presented to 2003. Open circles indicate data from prior to the 1976 shift. Black circles indicate data from after the 1976 regime shift. Gray circles are data for the period after 1997. Note the y-axis log scales in panels (b) and (c). Multiply the y-axis scale numbers by the factors shown above each panel for actual number of eggs and recruits.

porting a density-dependent model. This matrix produces a λ of 0.83, a value that matches the growth rate estimated from a time series of adult abundance (P. S. Levin, unpublished data).

To heuristically examine the importance of climate, we modeled the growth of a bocaccio population using two different population matrices as manifestations of "good" and "normal" states of the environment. Both models used identical young-of-the-year, subadult, and adult survivals as well as adult fertilities (Table 1). However, good years were characterized by larval sur-

vival that was one order of magnitude greater than normal years (Table 1). We chose one order of magnitude because it corresponded to the magnitude of good recruitment events (i.e., "good" log R/S) that we observed in the data. We then performed simulations in which one of the matrices was selected at random each year and multiplied by the most recent population vector. For these simulations, environmental conditions were assumed to be aperiodic and uncorrelated. We repeated these simulations using transition probabilities that included and excluded fishing mortality. In each case, we simulated 30 000 population growth increments and estimated the stochastic log growth rate by calculating the arithmetic mean of $\log[N(t+1)/N(t)]$ (Caswell 2001). We altered the frequency at which the two matrices were sampled and asked how frequently good years must occur in order to produce a population with a stochastic population growth rate of 1.0 (i.e., replacement) or greater.

RESULTS

Spawning output peaked in 1970 at 8.07×10^{12} eggs and then steadily declined to 9.84×10^{11} eggs in 2003 (Fig. 2a). Log recruitment was variable from 1959 to 1976, but there was no trend through time (Fig. 2b; $R^2 = 0.01$, $P = 0.72$). There was a marginally significant trend for a decline in log recruitment from 1977 to 1997 (Fig. 2b; $R^2 = 0.14$, $P = 0.09$). Log R/S varied annually, but did not decrease or increase over the course of the data series (Fig. 2c, $R^2 = 0.0009$, $P = 0.86$). Mean log R/S did not differ between periods (ANOVA, $F_{1,37} = 0.11$, $P = 0.75$) with a mean of 700 recruits per billion eggs (back-transformed mean and SE: upper SE bound = 2386; lower SE bound = 205). There was no evidence of density dependence across the 1959–1997 time series (Ricker recruitment curve, $R^2 = 0.07$, $P = 0.10$), or within either the before ($R^2 = 0.15$, $P = 0.11$) or after periods ($R^2 = 0.03$, $P = 0.40$).

Principal-component analysis and environmental variables

The principal-component analysis produced five principal components that explained 82% of the variance in the environmental variables, with PC1 and PC2 accounting for most of the variance (23% and 22%, respectively; Table 2). PC1 was primarily associated with upwelling during the copulation fall and temperature conditions during the pre-copulation summer, copulation fall, and pelagic winter. PC2 was associated with temperature conditions during the settlement and post-settlement periods. Upwelling conditions in general loaded on PC3, although upwelling during the pelagic winter loaded on PC4. The fifth principal component (PC5) was most strongly correlated with sea surface temperature during the pre-copulation summer.

TABLE 2. Component loadings (correlations between original variable and principal-component axis) from principal-components analysis on environmental variables.

Environmental variables	Principal component (percentage of variance explained)				
	PC1 (23)	PC2 (22)	PC3 (11)	PC4 (12)	PC5 (14)
El Niño copulation fall	0.923	0.045	-0.126	0.155	-0.163
El Niño pre-copulation summer	0.825	-0.041	-0.127	0.121	-0.384
El Niño pelagic winter	0.822	0.247	-0.15	0.301	-0.117
SST copulation fall	0.607	0.098	-0.042	0.003	-0.685
SST pelagic winter	0.561	0.245	0.059	0.415	-0.554
SST settlement period	0.264	0.561	0.006	0.57	-0.319
SST pre-copulation summer	0.206	0.108	0.039	0.048	-0.907
Upwelling benthic fall	0.117	-0.415	0.73	-0.015	-0.244
El Niño settlement period	0.048	0.896	-0.151	0.165	0.014
SST benthic fall	0.035	0.814	-0.085	0.373	-0.066
Upwelling pre-copulation summer	-0.017	0.119	0.716	0.168	0.542
NOI benthic fall	-0.069	-0.888	-0.085	0.15	0.005
Upwelling settlement period	-0.085	-0.165	0.699	-0.496	0.008
NOI settlement period	-0.111	-0.755	0.077	-0.214	0.124
Upwelling pelagic winter	-0.174	-0.071	0.067	-0.874	-0.074
El Niño benthic fall	-0.208	0.897	-0.088	-0.022	0.105
NOI pre-copulation summer	-0.469	0.137	0.067	-0.018	0.696
Upwelling copulation fall	-0.504	0.045	0.691	0.101	0.037
NOI pelagic winter	-0.543	-0.254	-0.135	-0.704	0.148
NOI copulation fall	-0.817	0.179	-0.097	-0.138	0.226

Notes: El Niño refers to the El Niño Southern Oscillation anomaly; SST is the sea surface temperature at 37° N, 122° W; NOI, Northern Oscillation Index. Upwelling is the mean of the upwelling indices calculated from wind stress for 36° and 39° N. All values are means for the time period, as defined in Fig. 1.

Recruitment success and oceanic conditions

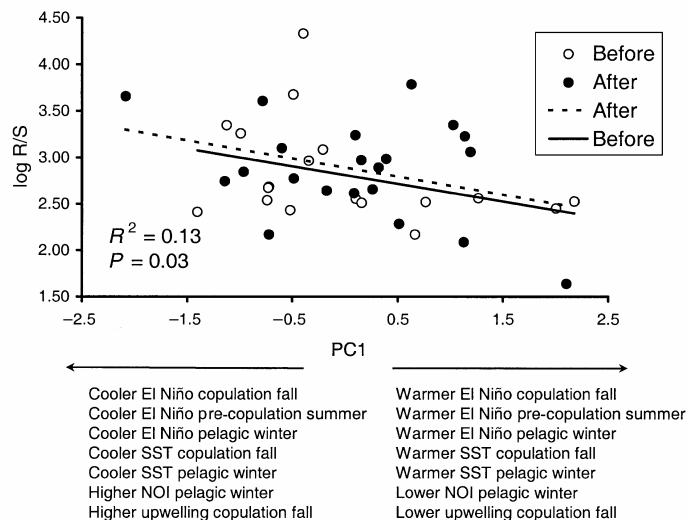
Log R/S was positively correlated with cooler ocean conditions during the pre-copulation summer, copulation fall, and pelagic winter, and higher upwelling during the copulation fall (Fig. 3; ANCOVA, PC1 as the covariate, $R^2 = 0.13$, $F_{1,38} = 5.22$, $P = 0.03$, slopes were homogeneous): there was no period effect (ANCOVA, $F_{1,38} = 0.24$, $P = 0.62$). The other PCs did not show correlations with log R/S ($P > 0.25$ for all).

In the second statistical approach, we modeled the probability of “good” log R/S in a given year. For PC1, the results were qualitatively similar results to the ANCOVA for PC1, although the relationship was

marginally significant (Fig. 4; GLM, $\chi^2 = 3.15$, $P = 0.07$). Additionally, the probability of good log R/S was related to the degree of upwelling in the pre-copulation fall, copulation fall, settlement summer, and benthic fall (PC3). However this relationship switched between periods (Fig. 5; GLM, period \times PC3 interaction, $\chi^2 = 4.60$, $P = 0.03$). Prior to 1977, good log R/S was more likely when upwelling was low. After 1977, good log R/S was more likely when upwelling was higher. The other PCs showed no correlation with the probability of high log R/S ($P > 0.12$).

We might have detected a statistical interaction because the relationship between high log R/S and PC3

FIG. 3. Results of ANOVA on the relationship between the bocaccio productivity (log R/S), regime (before/after the 1976 shift) and interannual climate variation, represented by the first principal component (PC1) as the covariate. Slopes were homogeneous, and there was no effect of regime ($P > 0.05$ for both). PC1 explained 13% of the variation in bocaccio productivity among years. Climate factors listed on the x-axis were those that loaded positively or negatively on PC1.



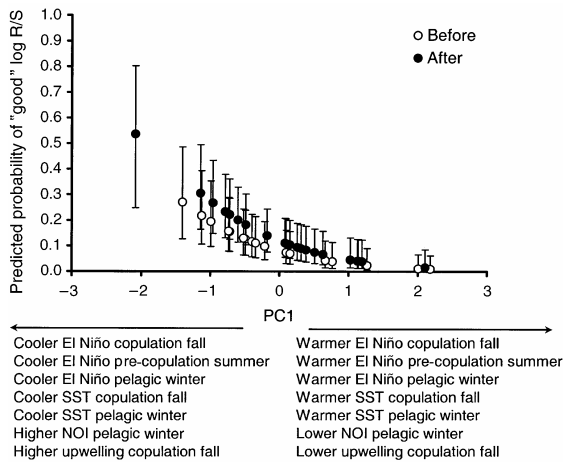


FIG. 4. Relationship between regime, interannual climate variation, and the probability of a “good” log R/S year. Note that the figure shows model predictions, not raw data, as the data are binary (0, 1). The model was run as a generalized linear model with logit link and binary distribution, in which regime (before/after the 1976 shift) was a categorical variable and the first principal component (PC1) was the covariate representing certain aspects of climate. There was a marginally significant relationship between PC1 and the probability of “good” log R/S ($P = 0.07$). The plot shows means ± 1 SE.

switched between periods, or because the relationship was significant in one period but not in the other. Therefore, we ran separate logistic regressions for each time period to test whether the relationship between high log R/S and upwelling was significant in both periods. During the cold regime (1959–1976), the probability of good log R/S increased when upwelling was lower ($\chi^2 = 6.39$, $P = 0.01$). During the warm regime (1977–1997), there was no relationship ($\chi^2 = 0.41$, $P = 0.52$).

The probability and importance of episodic recruitment events

An important question for managers is whether the probability of good recruitment events (where log R/S > 1 SD above the long-term mean) differs between the two climate regimes and how this affects the dynamics of the population. The probability of good log R/S did not differ between periods (GLM, binary distribution, logit link, $\chi^2 = 0.09$, $P = 0.77$) and was estimated as 0.13 (upper 95% CI bound = 0.19, lower 95% CI bound = 0.08). Nor was there a change in the probability of bad years (1 SD below the long-term mean, GLM, binary distribution, logit link, $\chi^2 = 1.70$, $P = 0.19$), or anomalous years (± 1 SD from the long-term mean, GLM, binary distribution, logit link, $\chi^2 = 1.45$, $P = 0.24$).

Our population models of bocaccio using stage-based matrices indicate that the frequency of high recruitment events is critical (Fig. 6). In the absence of fishing, our simulations suggest that years with log R/S values one order of magnitude greater than the long-

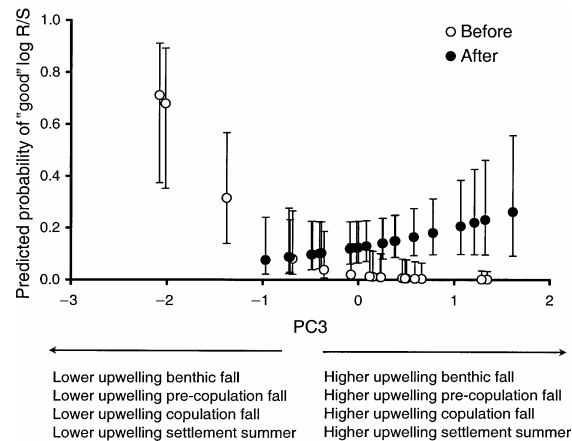


FIG. 5. Relationship between regime, interannual climate variation, and the probability of a “good” log R/S year. Note that the figure shows model predictions, not raw data, as the data are binary (0, 1). The model was run as a generalized linear model with logit link and binary distribution, in which regime (before/after the 1976 shift) was a categorical variable and the third principal component (PC3) was the covariate representing certain aspects of climate. There was a significant interaction between regime and PC3 ($P = 0.03$). The plot shows means ± 1 SE.

term mean must occur $\sim 15\%$ of the time in order to achieve a population growth rate equal to 1.0. We observed such recruitment events at a similar rate, $\sim 13\%$ of the time in our data. (Note that while slightly lower, the 95% CI for our estimate overlaps with the 15% value from the model output.) Thus, it appears that any change in the frequency of good recruitment episodes will have important consequences for bocaccio viability. Our model also suggests that historic levels of fishing were unsustainable given the frequency of “good” recruitment events (Fig. 6). When we included historic levels of fishing in the model, population growth was 0.86 when “good” recruitment events occurred 15% of the time. Even at the upper bound of the estimate for frequency of good recruitment events (0.19), population growth with fishing was < 1.0 . Indeed, in the

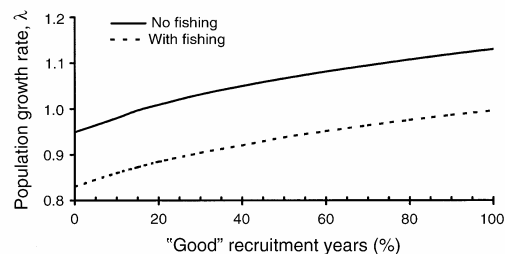


FIG. 6. Results of bocaccio population matrix models. Lambda (λ) is the dominant eigenvalue of the population matrix and indicates the population growth rate. Population size increases when $\lambda > 1.0$, decreases when $\lambda < 1.0$, and is stable at $\lambda = 1.0$.

presence of historical levels of fishing pressure, a population growth rate of ≥ 1.0 was achieved only when good recruitment events occurred $>90\%$ of the time.

DISCUSSION

The decline of the bocaccio stocks we explored here has been attributed to both poor climate conditions (i.e., the regime shift) and overfishing (Love et al. 1998, MacCall 2002). Understanding how bocaccio dynamics are influenced by climate clarifies both the historic role of fishing in the original stock decline as well as the appropriate strategy for rebuilding the now decimated population. For the bocaccio stock we explored here, climatic factors appear to have influenced the probability of episodic recruitment pulses and thus the ability of the stock to sustain exploitation. However, interpretation of the recruitment data for bocaccio is made difficult for two reasons. First, the mid-1970s saw both a dramatic increase in fishing activity and a climatic regime shift. As a consequence, disentangling how these two temporally confounded factors influenced patterns of bocaccio recruitment is problematical. Secondly, recruitment data for bocaccio are imprecise (MacCall 2002), and thus detailed descriptions of variability in the data are difficult. Despite these obstacles, our analyses provide insight into a number of issues influencing bocaccio stocks.

The role of regime shifts and climate variability in bocaccio recruitment

Our analyses suggest that the regime shift did not strongly contribute to the decline in bocaccio stocks through processes affecting recruitment. Previous workers have noted declines in the abundance of bocaccio larvae following the 1976 regime shift (Love et al. 1998, Moser et al. 2000), and such patterns appear to be at odds with our results. However, a decline in stock size as a result of fishing or any other cause would lower the absolute number of larvae in the absence of some compensatory mechanism. Consequently, it is not possible to separate effects of declining stock size and climate shifts on larval abundance. To circumvent this issue, we focused on log R/S as our metric because it is a quantity that accounts for variability in stock size (and, for bocaccio, log R/S seems statistically unaffected by population density). Using this measure, we found no change in the log R/S between time periods, and the probability of high log R/S was similar in both of the time periods we examined. These results suggest that the production and survival of fish from egg to recruitment (age-1) did not change with the regime shift. It then follows that the decline in bocaccio larvae following the 1976 regime shift was not the result of a change in per capita productivity, but rather the result of a factor (such as harvest) that resulted in a decline in bocaccio standing stock. Alternatively, reduced productivity following the regime shift may have affected juvenile and adult demographic rates, thereby yielding

a decline in population size that was independent of or compounded by fishing. Other species of rockfish have shown changes in fecundity (Ventresca et al. 1995) and growth during El Niño years (Lenarz et al. 1995).

While we did not observe a change in log R/S across the regime change, we did see an effect of interannual climate variability on bocaccio recruitment. In both the pre- and post-1976 time periods, log R/S was higher when waters were cooler during the copulation fall and pelagic winter and when upwelling was stronger during the copulation fall. Cooler waters and higher upwelling are generally associated with greater primary and secondary production (Chavez et al. 2003), and this enhanced production may influence the success of bocaccio recruitment at two points during their life. First, primary productivity prior to and during reproduction may affect female condition and drive parameters like egg size, egg quality, or the number of eggs produced by a female (Ventresca et al. 1995, Love et al. 2002). Additionally, because rockfishes are internal brooders, changes in productivity may also influence the number of viable larvae released by a female. These factors may interact to increase total larval production, survival, or both.

Climate may also affect recruitment by influencing food availability and thus growth and survival rates of larvae (Houde 1987, Suthers 1998). Weak upwelling results in low primary and secondary production and may result in poor recruitment because larvae are food limited (Ralston 1995). On the other hand, strong upwelling leads to higher turbulence, which impairs the ability of larvae to capture prey (Lasker 1981, Ainley et al. 1993), and again would yield poor recruitment despite high levels of productivity. Consequently, it is possible that intermediate levels of upwelling may lead to strong year classes by providing adequate food while also providing conditions in which larvae can successfully feed. However, there is little evidence to suggest that rockfish larvae in this region are food limited. For instance, Rau et al. (2001) were unable to find a correlation between upwelling and somatic condition of rockfish larvae. Similarly, Yoklavich and colleagues (1996) did not see evidence of starvation in rockfish larvae during the 1992–1993 El Niño. Ralston (1995) also noted no evidence that good larval growth resulted in improved survival of larval shortbelly rockfish, *Sebastes jordani*, to the juvenile stage. We did not detect this theoretical dome effect in our analyses, but our data set probably does not cover fine enough temporal and spatial scales to detect this type of effect. Despite the lack of support for the role of food availability in recruitment variability in rockfish, work in a number of systems strongly suggests that larval growth rates and the availability of food can significantly influence patterns of recruitment (Bailey et al. 1995, Bergenius et al. 2002, Comyns et al. 2003, Platt et al. 2003), and further investigation may yet uncover a similar effect in bocaccio.

Interestingly, the effect of climate on the success of bocaccio recruitment appears to have changed across regimes. During the cold (pre-1976) regime when upwelling was generally strong, we found that there was a higher probability of good recruitment when upwelling was weak. Conversely, during the warm (post-1976) regime when upwelling was generally weak and primary production low, we observed a higher probability of good recruitment when upwelling was strong. Why the role of upwelling changed between the regimes is a matter of conjecture. We hypothesize that this pattern results from tradeoffs between increased food availability and the increased likelihood of advection offshore associated with upwelling. Larval rockfishes are more abundant in or near upwelling fronts (Ainley et al. 1996, Wing et al. 1998, Bjorkstedt et al. 2002), and reduction of offshore transport associated with weak upwelling could increase recruitment. However, if weak upwelling results in low food availability, then favorable transport conditions may be irrelevant. On the other hand, during regimes of high productivity, food availability may be high enough to realize the benefits of short periods of low upwelling. Consequently, recruitment would increase during weak upwelling periods within cold regimes. During regimes when productivity is low, food availability may limit larval survival, and thus recruitment would increase during strong upwelling periods within warm regimes. Similar results have been seen in other species. Prior to the mid-1970s, survival of Oregon hatchery reared coho salmon (*Oncorhynchus kisutch*) was correlated with ocean upwelling (Nickelson 1986), but this relationship disappeared after the regime shift (Pearcy 1997, Botsford 2001).

Whatever the mechanism, our results show that variability in climate influences the probability of strong recruitment events. Because the dynamics of bocaccio populations appear to be driven by episodic recruitment, the frequency of climate conditions that favor strong recruitment is critical to bocaccio. Indeed, our stage-based matrix model of bocaccio indicated that, in the absence of fishing, pulses of recruitment that are one order of magnitude greater than the long-term mean must occur about 15% of the time in order to achieve population replacement. Interestingly, we observed recruitment pulses at nearly this same frequency, suggesting that over the long term, the intrinsic rate of increase of bocaccio populations is very low (Musick et al. 2000, MacCall and He 2002). Our model is meant to be conceptual rather than an application tool (Mangel et al. 2001), but it does raise important issues regarding the resiliency of bocaccio populations to fishing. When we included historic levels of fishing in our model, populations of bocaccio were not viable when strong recruitment pulses occurred 15% of the time. In fact, viable bocaccio populations were reached only when strong recruitment occurred nearly continually. While the demographic rates used to parameterize our model

are certainly only approximations of reality and likely vary geographically and temporally, this modeling exercise plainly illustrates that the degree to which populations of bocaccio can withstand fishing depends on the frequency of climatic conditions that promote strong recruitment. Historically, it appears possible that bocaccio populations could not sustain a viable fishery.

Paradoxically, in the absence of fishing, the matrix model concludes that bocaccio will have a population growth rate of $\lambda = 1.0$ under the frequency of good recruitment events observed in nature. Moreover, we did not detect a statistically significant level of density dependence in $\log R/S$. This would suggest that the population dynamics are governed by density-independent processes, a condition not conducive to persistence. There are a number of explanations for this result. As numerous authors have noted, density dependence need only occur at some place or time (Hanski et al. 1993, Murdoch 1994, Hixon and Carr 1997, Sale and Tolimieri 2000, Hixon et al. 2002); this time series may not have been the time. The combination of a productive regime during high population levels and low population (caused by fishing) during the low production regime may have prevented a density-dependent recruit-spawner relationship (Hallett et al. 2004). Alternatively, density dependence may have been present but not detectable statistically. For example, during the "before" period when populations were high, the Ricker recruitment curve had an $R^2 = 0.15$ and $P = 0.11$, which might be considered a trend indicative of weak density dependence. We did not include density dependence in the matrix model for simplicity and because we did not detect it statistically.

The future of bocaccio is uncertain. With a potential climate regime change in the late 1990s and strong recruitment of the 1999 and 2002 year classes, there is some optimism that improved ocean conditions associated with a cool regime will result in a timely recovery of bocaccio (MacCall and He 2002). However, our results suggest that a regime change per se may not be the issue, but rather how climate varies on a finer time scale. Several authors have suggested that looking for correlations between recruitment and environmental variables is misguided and often leads to spurious results, which break down over time (Myers 1998). However, our results do appear to have some predictive power. We examined from 1959 to 1997 and found that La Niña-like conditions prior to settlement should increase the probability of good recruitment; La Niña conditions prevailed in 1999 as did a strong year class. With the added complication of fishing pressure, the future of bocaccio is even more muddled. Nevertheless, we trust that approaches such as the one we employed here will aid resource managers as they attempt to manage harvest in the face of a dynamic environment.

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