OCEAN WARMING EFFECTS ON GROWTH, REPRODUCTION, AND SURVIVORSHIP OF SOUTHERN CALIFORNIA ABALONE

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Abstract. Traditional fisheries management in southern California has failed, in part because it is based on an assumption of an unvarying environment and is focused on size limits rather than insuring the persistence of aggregations of large fecund individuals. The combined effect of low frequency climatic variability and anthropogenic perturbations can have dramatic consequences for abalone in southern California. Abalone species are tightly linked to kelp forest ecosystems that, besides furnishing habitat, also provide the main food source for abalone. In southern California, kelp canopies are very sensitive to oceanographic climate because the kelp depend upon high nutrients in the water column. Oceanic warming, in turn, results in decreased nutrients in the surface water, and this is correlated with marked reductions in giant kelp biomass.

Here we address the additive effects of ocean warming on two species of California abalone (the red abalone, *Haliotis rufescens*; and the green abalone, *H. fulgens*) by subjecting them to varied environmental conditions similar to cool, normal, and warm phases of the California current in the southern California Bight. Our experimental design simultaneously tested the synergistic effects of temperature and food quantity and quality on survivorship, growth, and reproduction. For red abalone, warm temperatures increased the onset of withering syndrome, a fatal abalone disease, and halted growth and reproduction. In contrast, green abalone survivorship, growth, and reproduction were relatively robust irrespective of temperature, while their growth and reproduction were most strongly influenced by food quantity. We found clear evidence suggesting that, combined with overfishing, California abalone populations are adversely affected by ecosystem responses to ocean warming: Cool-water red abalone suffer stronger consequences in warm water than do green abalone. Conservation, restoration, and recovery plans of remnant California abalone populations must consider these relationships when taking any action.

Key words: abalone; California current; climate change; global warming; Haliotis rufescens; Haliotis fulgens; *kelp;* Macrocystis pyrifera; *restoration.*

INTRODUCTION

Global warming, while often not dramatic in itself, may act additively and sometimes synergistically with other stresses, generating unfavorable consequences for a variety of marine species and ecosystems. Although biological responses to interdecadal shifts in climate have not been completely deciphered, it is now understood that variability in ocean climate plays a significant role in ecosystem dynamics (McGowan et al. 1998). Within the California current system, a lucrative abalone fishery of some 4000 annual metric tons once existed. In 1997, however, after almost three decades of dwindling landings, the fishery collapsed and was subsequently closed. One of the five abalone species once commercially harvested, the white abalone

(*Haliotis sorenseni*), is now listed as endangered under the Endangered Species Act (Federal Register 2001); others are severely depleted and will also need federal protection if restoration efforts are not successful (Karpov et al. 2000).

California abalone species are tightly linked to kelp forest ecosystems largely defined by giant kelp, *Macrocystis pyrifera*. While kelp forests furnish an important habitat for many species, their main importance to abalone is as a food source delivered via drifting fragments of kelp moved by currents or surge (Cox 1962). The health of giant kelp, in turn, is limited by nitrate availability dependent upon nutrient concentrations in the water column. Nutrient concentration in seawater is inversely correlated to temperature, hence nutrient-poor warm water is associated with reductions of nitrogen in kelp (Jackson 1977, Zimmerman and Kremer 1984), leaving consumer guilds less food of much lower quality during warm-water phases. The increased frequency and intensity of warm-water El
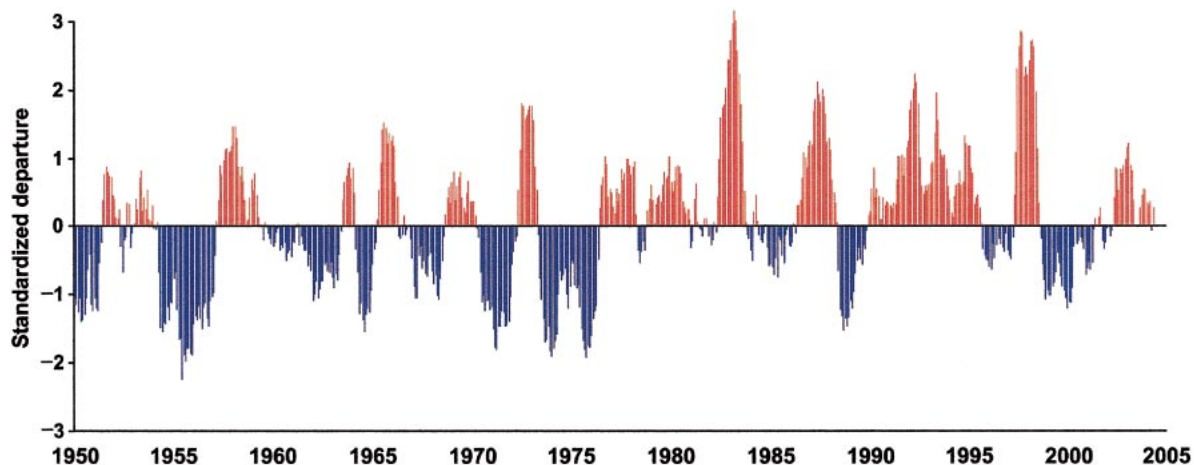
FIG. 1. Time series of a multivariate El Niño Southern Oscillation (ENSO) index that combines sea level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky over the tropical Pacific. Positive values are shown in red, and negative in blue; indices greater than 1 and less than −1 are considered strong El Niño and La Niña events, respectively. Monthly indices were acquired from the NOAA-CIRES Climate Diagnostic Center at the University of Colorado at Boulder (*available online:* ⟨http://www.cdc.noaa.gov⟩).

Niño Southern Oscillation (ENSO) phenomena (Fig. 1) since the 1976–1977 regime shift in the North Pacific is associated with a deepening of the thermocline and nutricline, causing warmer, nutrient-poor surface waters in the California current system. This trend has been correlated with surface water nutrient reductions associated with dramatic reductions in giant kelp densities. For example, coincident with the warming trends since 1957, the carrying capacity of giant kelp stipe density was reduced two-thirds in a southern California kelp forest (Tegner et al. 1996*b*). Finally, warm temperature has strong direct and indirect effects on abalone through its impact on withering syndrome, a fatal abalone disease (Friedman et al. 2000). Because the warming trends in sea surface temperature can facilitate disease outbreaks (Harvell et al. 1999), the effects of these atmospheric and oceanic warming trends need to be considered as part of any management and recovery efforts of southern California abalone stocks. Therefore, we hypothesize a link between the lack of recovery of California abalone species and the consequences of more frequent and intense warm-water ENSO events.

Here we evaluate the ecological impact of ocean warming on red and green abalone, *Haliotis rufescens* and *H. fulgens*. Of six depleted species present in the southern California region, these are the two species most likely to be restored. Therefore it is important to evaluate the probabilities of their success in the ensuing warming trend in the California current, by assessing the implications of predicted reductions in abundance and quality of kelp, as well as increased temperatures, on the growth, reproductive output, and survivorship of each species of abalone. Furthermore, we consider the impact of ocean warming on restoration and management plans in southern California. Historically, the red abalone, a species normally associated with cooler water, was the most important commercial abalone species in California, USA. In contrast, the most important commercial species in Baja California, Mexico, is the green abalone, a warm-water species.

METHODS

The experimental design for the sequential, yet otherwise identical, experiments with red and green abalone is shown in Fig. 2. Kelp forest habitat conditions under different ENSO regimes (La Niña, normal, and El Niño) were mimicked in the laboratory by altering three environmental factors: seawater temperature, food quantity (availability of kelp, *M. pyrifera*), and food quality (nitrogen content of kelp). Each experimental factor was stratified to three levels of treatment corresponding to previously recorded La Niña, normal, and El Niño conditions (Tegner and Dayton 1987, Seymour et al. 1989, Dayton et al. 1999). Daily mean values of the three temperatures for the duration of the experiments are shown in Fig. 3, with *H. rufescens* spanning 16 July 1999 to 27 June 2000, and *H. fulgens* spanning 19 March 2001 to 27 February 2002. Differences among temperatures were validated with a Friedman's two-way ANOVA ($P \ll 0.001$) with a posteriori tests indicating that all levels were different from one another. Variation of kelp nitrogen content was manipulated with the following protocol: (1) High quality kelp was collected from local kelp beds below the 15°C isotherm, and this kelp was then held in 12°C nutrient-enriched (KNO_3) seawater for three days prior to use. (2) Medium quality kelp was collected below the 15°C isotherm and held at 12°C for three days without nutrient enrichment. (3) Low quality kelp was collected from the surface canopy where the water is typically
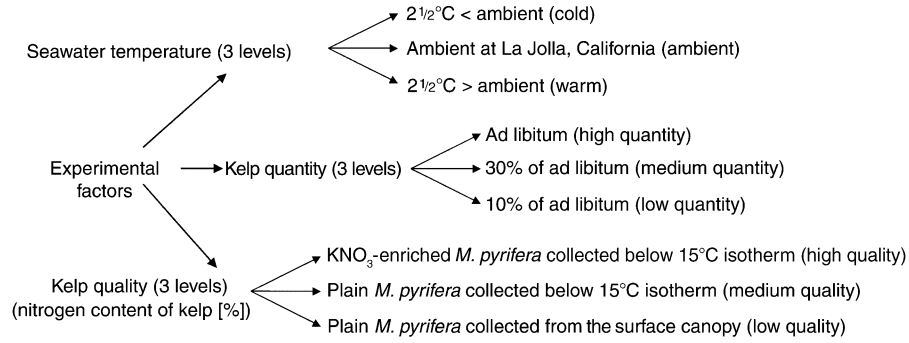
FIG. 2.   Flow chart of the experimental design showing the three experimental factors and the three corresponding levels of each factor. Experimental treatments were formed from all possible combinations of the three levels of each experimental factor, giving rise to 27 experimental treatments resembling kelp forest habitat conditions under different ENSO regimes (La Niña, normal, and El Niño). The kelp species is *Macrocystis pyrifera*.

warmer and lower in nitrates in comparison to water from below the thermocline.

Differences among nitrogen levels were tested by randomly sampling 13 sets of kelp quality levels over the period of the experiment, and determining the nitrogen content of each sample with a 2400 series CHN analyzer (Perkin-Elmer, Wellesley, Massachusetts, USA) using an acetanilide standard (71.09% C, 6.71% H, 10.36% N). Differences among kelp quality levels were validated with a Friedman's two-way ANOVA ($P \ll 0.001$), and a posteriori test indicated that all levels were different from one another.

Abalone were purchased from culture facilities in southern California, 600 red (90.00 $\pm$ 2.22 mm [means $\pm$ 1 SD]) and 600 green (95.58 $\pm$ 6.22 mm), all of which were tagged with coded stainless steel washers for identification. Both species were evaluated for withering syndrome by histological assessment of the withering syndrome aetiological agent, a Rickettsiales-like prokaryote (WS-RLP) found in the gastrointestinal epithelia (Friedman et al. 2000), by randomly testing 10

abalone from each species. Tissue sections from post-esophagus and digestive gland, the two tissues susceptible to WS-RLP infection (Friedman et al. 1997, Moore et al. 2000), were excised from each animal, placed in Invertebrate Davidson's solution (Shaw and Battle 1957) for 24 h and processed for routine paraffin histology. Deparaffinized 5-μm sections were stained with hematoxylin and eosin (Luna 1968) and viewed by light microscopy. In both species, tissue analysis confirmed light infections with the WS-RLP. In order to eliminate the WS-RLP in experimental animals, all abalone were injected with oxytetracycline according to the methods of Friedman et al. (2003). Abalone were given a series of nine intra-pedal muscle injections of 21 mg/kg live tissue weight of oxytetracycline (Liquamycin–LA 200, Pfizer, Groton, Connecticut, USA) using a sterile 1-mL syringe with 27 G, 1.12-cm (1/2-inch) needle (Friedman et al. 2003). Live tissue mass was estimated by sacrificing 15 animals from each species, taking into consideration that all size classes were included. For each animal, total mass minus shell mass
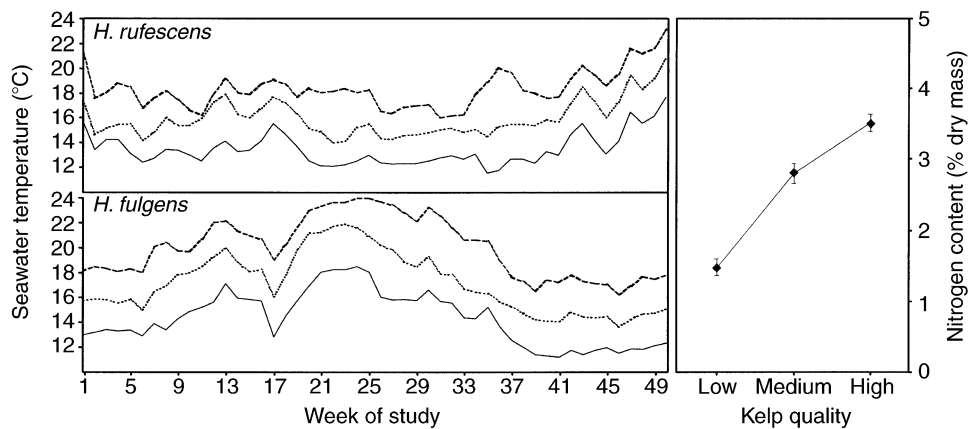

FIG. 3.   Temperature time series of daily mean values spanning the experimental period, and mean nitrogen content of kelp quality levels. Upper and lower plots correspond to red abalone, *Haliotis rufescens* (16 July 1999–27 June 2000), and green abalone, *H. fulgens* (19 March 2001–27 February 2002), respectively, and dashed, dotted, and solid lines correspond to warm, ambient, and cold seawater temperatures, respectively.

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TABLE 1. *F* values and probabilities from three-factor ANOVAs with equal replication, testing the effects of varying temperature, food quantity, and food quality on abalone growth, reproductive output, disease, and mortality.

| | | Growth | | | | | | Reproduction (GBI) | | |
| | | Length | | | Mass | | | | | |
Source of variation	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Haliotis rufescens										
Temperature	2	0.05	181.87	0.00	1.80	276.15	0.00	0.22	3.87	0.03
Quantity	2	0.08	272.42	0.00	1.40	215.86	0.00	1.86	32.51	0.00
Quality	2	0.02	79.22	0.00	0.51	79.08	0.00	0.50	8.74	0.00
Temperature : Quantity	4	0.00	4.16	0.01	0.02	3.71	0.01	0.05	0.90	0.47
Temperature : Quality	4	0.00	4.76	0.00	0.03	5.30	0.00	0.03	0.55	0.70
Quantity : Quality	4	0.00	10.22	0.00	0.06	9.55	0.00	0.29	5.14	0.00
Temperature : Quantity : Quality	8	0.00	0.34	0.94	0.01	1.06	0.41	0.03	0.59	0.78
Residuals	54	0.00			0.01			0.06		
H. fulgens										
Temperature	2	0.00	11.34	0.00	0.01	2.41	0.10	0.84	8.05	0.00
Quantity	2	0.12	690.91	0.00	1.57	474.76	0.00	7.32	70.11	0.00
Quality	2	0.02	133.68	0.00	0.29	88.96	0.00	0.36	3.45	0.04
Temperature : Quantity	4	0.00	9.10	0.00	0.05	14.36	0.00	0.52	4.99	0.00
Temperature : Quality	4	0.00	1.46	0.23	0.00	0.85	0.50	0.13	1.24	0.30
Quantity : Quality	4	0.00	22.46	0.00	0.03	10.10	0.00	0.05	0.47	0.76
Temperature : Quantity : Quality	8	0.00	0.82	0.59	0.00	1.08	0.39	0.08	0.78	0.62
Residuals	54	0.00			0.00			0.10		

Notes: Growth was evaluated through standardized changes in animal mass and shell length [(initial − final value)/initial value]. Reproductive output was evaluated from gonad bulk indices (GBI). Disease was evaluated by the burden of withering syndrome, Rickettsiales-like prokaryote (WS-RLP) and scores of morphological changes associated with withering syndrome (digestive gland atrophy [DGA] and foot muscle degeneration [FM-DG]), and accumulated mortalities. All variables were derived from cell means since that was the experimental unit and not individual abalone (see *Methods* for details). A posteriori tests were run on those treatments with significant effects (see Appendix).

was calculated, and the mean percentage of tissue mass for red and green abalone was 67.47% and 64.70% of total mass, respectively. Oxytetracycline injections were given every other day over a 5-day period, followed by 16 days of recovery. This protocol was repeated three times for a total of nine doses over seven weeks. Injection sites were rotated around the foot muscle to minimize local tissue damage. After termination of antibiotic treatment, abalone were allowed one month to stabilize prior to initiation of the experiment. An insufficient number of animals were available to retest the presence of WS-RLP. Since each abalone received an equal antibiotic treatment, they were considered to have the same baseline of no infection or very low infection (Friedman et al. 2003). Subsequent reinfection was anticipated because southern California is within the endemic range of the WS-RLP, and local facilities have WS-RLP infected abalone (J. D. Moore and C. S. Friedman, *personal observation*).

Randomly selected abalone were placed in rigid 1.3-cm plastic mesh floating cages subdivided into nine cells. Cages were placed in tanks receiving flowing seawater at one of the three temperature levels (Fig. 1). Each cell per cage corresponded to one of the nine combinations of food availability and quality and was assigned randomly. Seven abalone were placed in each cell, and the entire design was replicated three times. All abalone were periodically measured (every 6–8 weeks) for changes in shell length, total mass, and gonad maturation throughout the length of the experi-

ment. After termination of both abalone experiments, three abalone per cell were selected at random and sacrificed for assessment of gonad bulk index, WS-RLP infection intensity, and morphological changes associated with withering syndrome. Volumetric gonad bulk indices were derived from measurements of cross sections of the gonadal appendage and were calculated as described by Tutschulte and Connell (1981). Tissue sections for histological analyses included postesophagus, digestive gland, and foot muscle tissues. Microscopic evaluations of WS-RLP infection intensity and withering syndrome associated morphological changes were conducted blindly in order to prevent bias during assessment. WS-RLP burdens were quantified in post-esophagus and digestive gland tissue using the scale of Friedman et al. (1997) based on the average number of bacterial inclusions per 200× magnification field of view: (0) absent, (1) 1–10, (2) 11–100, or (3) >100. Morphological changes associated with withering syndrome were assessed visually using integral scales from 0 to 3, where for both evaluations, 0 represented a normal healthy appearance. Changes in the architectural morphology of the digestive gland were characterized by the percentage of the gland occupied by connective tissue vs. functional glandular tissue as follows: (1) 5–10%, (2) 11–25%, and (3) >25%. Foot muscle degeneration scores of 1, 2, and 3 denotes muscle fibers comprising 76–90%, 51–75%, and <50% of the foot muscle, respectively. Since the two experiments were not run simultaneously, the abundance of

TABLE 1. Extended.

	Disease and morbidity											
WS-RLP			DGA			FM-Deg			Mortality		
MS	F	P	MS	F	P	MS	F	P	MS	F	P
4.74	19.64	0.00	2.64	25.32	0.00	1.80	9.48	0.00	0.38	41.11	0.00
0.34	1.40	0.25	1.78	17.07	0.00	2.08	10.90	0.00	0.04	3.97	0.02
0.07	0.28	0.76	0.40	3.84	0.03	0.98	5.13	0.01	0.00	0.08	0.92
0.19	0.79	0.54	0.32	3.05	0.02	0.15	0.81	0.53	0.03	3.49	0.01
0.10	0.41	0.80	0.15	1.43	0.24	0.05	0.25	0.91	0.00	0.20	0.94
0.31	1.29	0.28	0.02	0.23	0.92	0.24	1.24	0.30	0.00	0.16	0.96
0.35	1.45	0.20	0.12	1.14	0.35	0.08	0.43	0.90	0.00	0.34	0.94
0.24			0.10			0.19			0.01		
0.02	0.86	0.43	0.00	1.00	0.37	0.08	1.19	0.31	0.00	2.00	0.15
0.00	0.21	0.81	0.00	1.00	0.37	0.05	0.81	0.45	0.00	0.50	0.61
0.02	0.86	0.43	0.00	1.00	0.37	0.26	3.94	0.03	0.00	0.50	0.61
0.02	1.07	0.38	0.00	1.00	0.42	0.03	0.50	0.74	0.00	0.50	0.74
0.03	1.71	0.16	0.00	1.00	0.42	0.07	1.09	0.37	0.00	0.50	0.74
0.02	1.07	0.38	0.00	1.00	0.42	0.04	0.63	0.65	0.00	1.25	0.30
0.01	0.64	0.74	0.00	1.00	0.45	0.05	0.69	0.70	0.00	1.25	0.29
0.02			0.00			0.07			0.00		

the withering syndrome bacterium in the water source could have differed between experiments; however, histological analyses concluded WS-RLP presence and infection in both species, so presumably both experiments were similarly exposed.

The effects of varying temperature, food quantity and quality on abalone growth, reproductive output, disease and mortality were tested using three-factor ANOVAs with equal replication ($\alpha = 0.05$). The percentage of change in growth was evaluated through standardized changes in animal mass and shell length using the following equation:

$$\left(\frac{\text{initial} - \text{final value}}{\text{initial value}}\right) \times 100.$$

Reproductive output was evaluated from gonad bulk indices. Disease and morbidity were evaluated from scores of WS-RLP burden and withering syndrome associated morphological changes (digestive gland condition and foot muscle degeneration) and accumulated mortalities. All of these variables were derived from cell means, which were considered the experimental unit rather than individual abalone. Tukey a posteriori tests were run on those treatments with significant effects. In addition to traditional ANOVA tests, a multivariate analysis combining all variables was also applied to the data. The similarities of standardized means, corresponding to the 27 temperature–kelp quantity–kelp quality factor level combinations, were assessed with dendrograms and two-dimensional multidimensional scaling based on Euclidean distances.

RESULTS

Growth

All three experimental treatments (water temperature, food quantity, and food quality) had strong effects on abalone growth, both individually and synergistically. At the individual-factor level, red and green abalone growth responded significantly to all experimental factors, with the exception of green abalone, where temperature showed no significant effect (Table 1). With the exception of the two-way interaction between temperature and food quality with the green abalone, all two-way interactions were also significant. Although growth of both species reacted strongly to environmental stimuli, seawater temperature seemed to have a much stronger influence on red abalone. Simple linear regressions based on least squares were fit to interpret growth rates of the nine combinations of temperature and food quantity; these are shown in a matrix format in Fig. 4. The decrease in the slopes of the growth rates in red abalone with increasing water temperature was more dramatic than observed for green abalone, even when food quantity remained constant. An overall trend of decreasing slopes was observed for both species when exposed to warm temperatures and low food quantity. Fig. 5 shows the sensitivity of mass gain in both species to temperature and food conditions: Red abalone have a clear adverse response to warmer temperatures, while green abalone show no effect at all. Warm temperature halted red abalone growth, and was associated with significant mass loss when combined with poor food conditions. Conversely, colder seawater promoted red abalone growth even with limited food availability (Figs. 4 and 5). Green abalone, on the other hand, grew robustly at all temperatures with warmer temperatures stimulating growth when combined with good food conditions. Growth of both species decreased in response to reduced food availability and quality, with food availability being more important than quality; this may be deduced from Fig. 4 in the quality and quantity interaction plots.
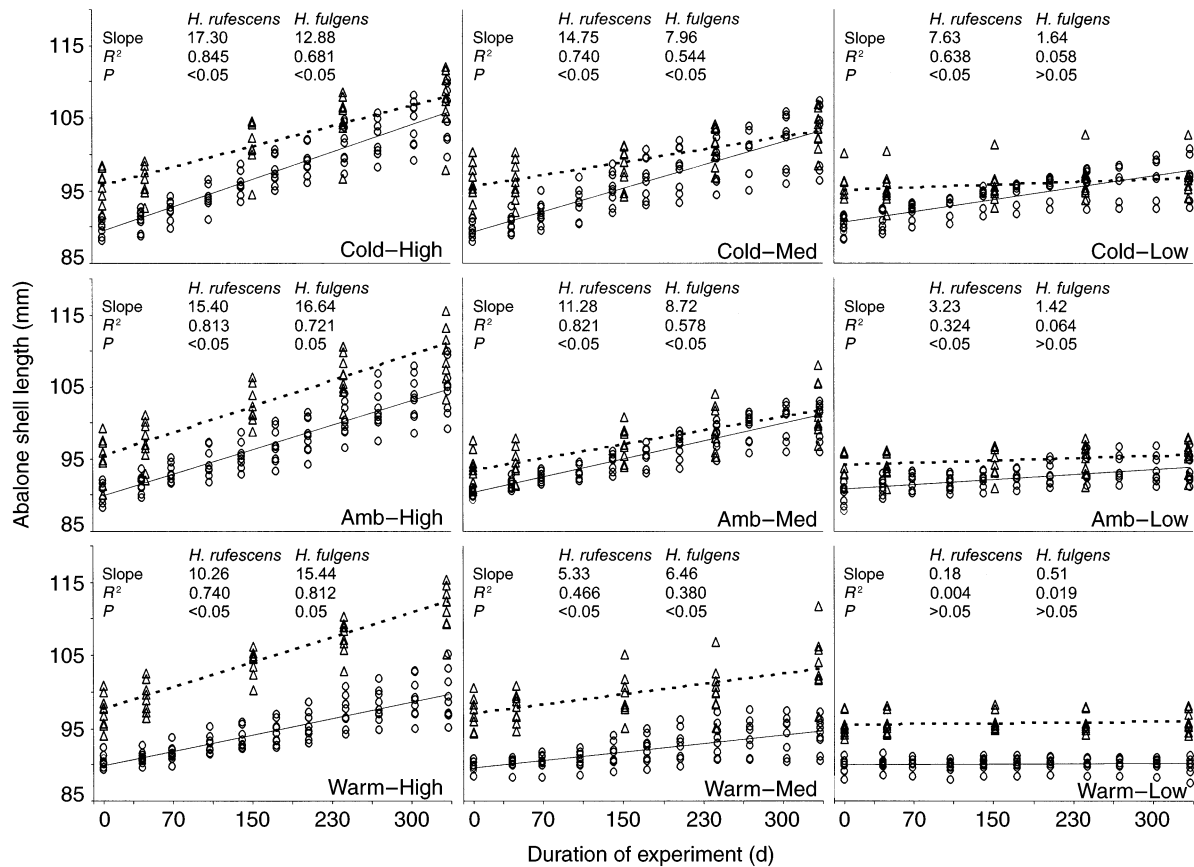
FIG. 4. Mean durations of temperature–food quantity treatment combinations for red abalone (circles) and green abalone (triangles) with superimposed least-square fits of shell length to time. The nine possible temperature–food quantity combinations (bottom right of each plot) are shown in a matrix format with slopes, R^2, and regression probabilities in the top left of each plot.

Reproduction

Reproductive output decreased in response to poor food conditions; however, green abalone were able to maintain their reproductive potential throughout all experimental treatments. Overall, red abalone were less reproductive than green abalone, with their gonad development being more responsive to changes in temperature and food conditions. When combined with optimum food conditions, varying temperature triggered opposing reproductive responses; red abalone became more gravid with colder temperatures, while green abalone became more gravid with warmer temperatures (Fig. 6).

Disease and morbidity

Differences in environmental conditions resulted in distinct consequences of disease outcomes for each species (Fig. 7). Microscopic examination of green abalone tissues revealed very low WS-RLP bacterial burdens, as well as associated digestive tract and foot muscle morphological changes. With the exception of the significant effect food quality had on foot muscle degeneration ($P = 0.025$), all green abalone disease and morbidity variables showed nonsignificant responses to treatments and interactions thereof. In contrast, pathogenic effects were much more conspicuous in red abalone, which demonstrated higher sensitivity to environmental variability and warmer temperature induced proliferation of WS-RLP, resulting in morphological changes with increased mortality from the disease (Fig. 7).

Multivariate analyses

Cluster and multidimensional scaling analyses combining growth (percentage of change in length and mass), reproduction (gonad bulk index), and disease (WS-RLP burden, digestive gland atrophy, foot muscle degeneration, and accumulated mortality) variables revealed clear grouping of treatments resembling similar environmental regimes (Fig. 8). Each species of abalone, however, showed particular patterns in the way treatment combination clusters were segregated. Treatment combinations among red abalone formed three tight clusters resembling environmental regimes expressed during normal, warm ENSO (El Niño), and cold ENSO (La Niña) conditions (with the unrealistic
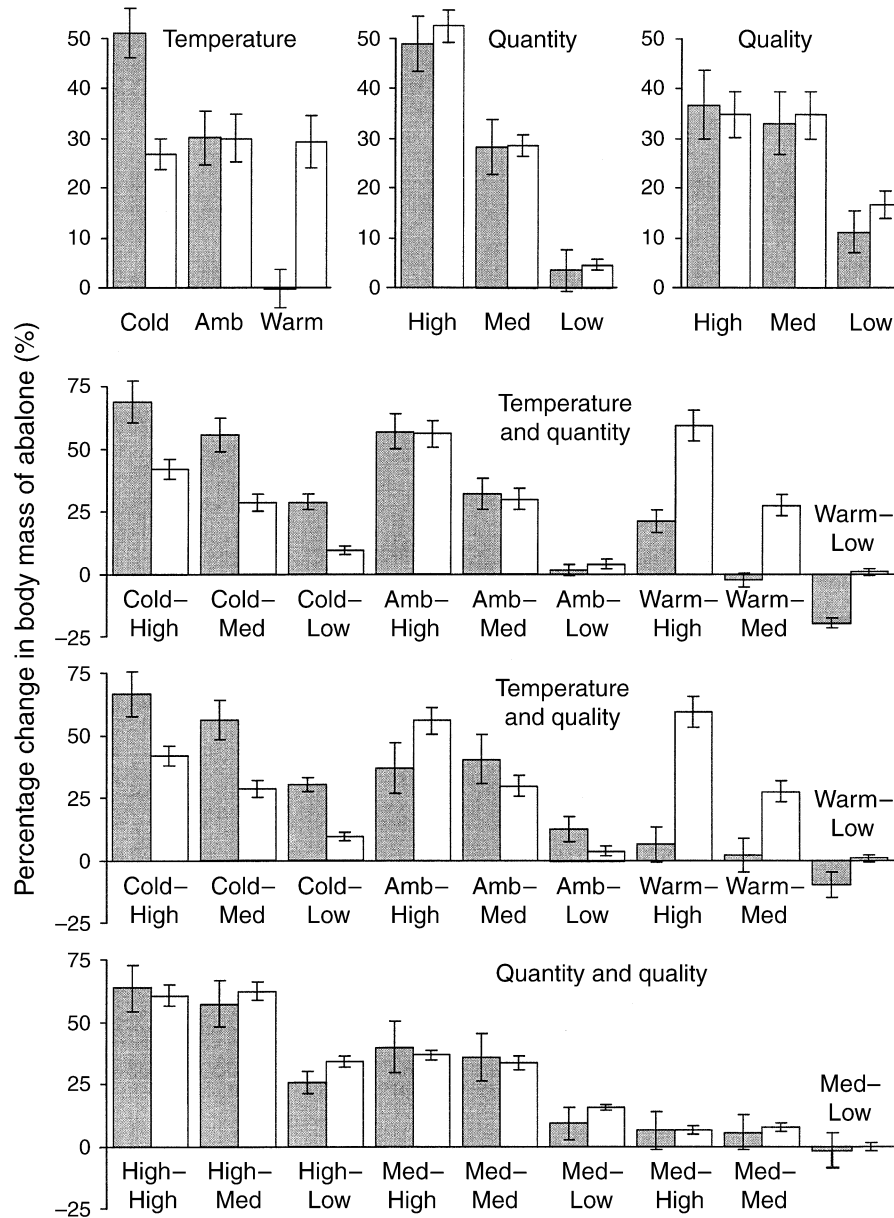
Fig. 5. Mean (±1 SE) percentage change in body mass of abalone in response to the three experimental factors and their three two-way interactions. Gray and white bars correspond to *Haliotis rufescens* and *H. fulgens*, respectively.

warm water and good food conditions falling in the cluster corresponding to La Niña). In marked contrast, treatment combinations among green abalone showed clustering impartial to environmental conditions, forming one large group with all but one of the treatments and a second cluster with one treatment that resembled warm ENSO conditions.

DISCUSSION

Ramifications of ecological impacts of global warming have yet to be incorporated into fisheries management and restoration. In hopes of stimulating successful restoration and management, we review the relevance

of the implications of these findings and integrate them with relevant literature, as well as discuss the most serious management shortcomings.

As in our study, abalone growth in the wild is strongly influenced by environmental variability (e.g., changes in sea surface temperature and consequences thereof). A six-year tagging study (1978–1984) approximating von Bertalanffy growth parameters (asymptotic length, L_∞, and Brody coefficient, K) for red abalone at Santa Rosa Island, reported significantly less growth during a warm-water phase (1982–1983) when $K = 0.12$, while in previous years, K values had averaged 0.26 (Haaker et al. 1998). A compilation of similar
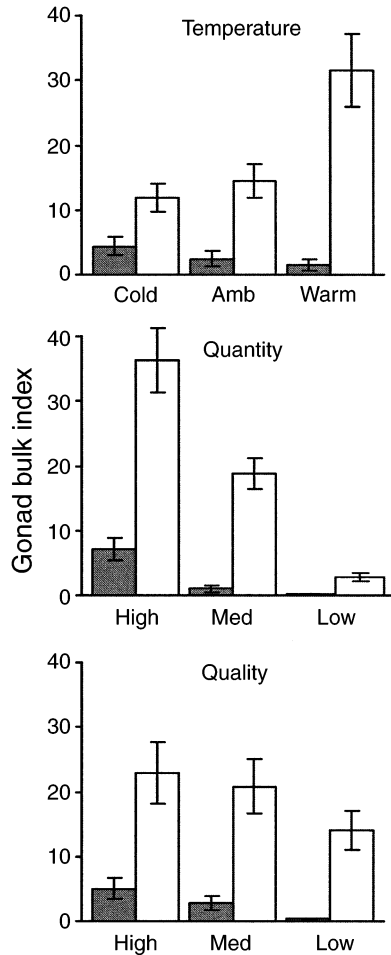
FIG. 6.   Mean (±1 SE) gonad bulk indices for the three experimental factors. Gray and white bars correspond to *H. rufescens* and *H. fulgens*, respectively.

studies done on green abalone demonstrated higher growth rates at the southern end of their geographical range, where sea surface temperatures are greater (K = 0.10 at 33° N, K = 0.34 at 27° N, K = 0.88 at 26° N; Tutschulte and Connell 1988, Shepherd et al. 1991, 1998, Guzman del Próo 1992). Although several factors may vary with latitude, these studies and our results imply that green abalone are able to tolerate higher frequency temperature fluctuations. An example of the high sensitivity of red abalone to temperature is nicely shown within the California Bight by Tegner et al. (2001) in the Channel Islands, where a longitudinal temperature gradient was correlated to a decrease in abalone landings.

Reproductive potential of the two species exhibits similar trends, both in our study and in the wild. Red abalone in the much cooler northern California waters do not show a seasonal reproductive cycle and consequently are gravid year-round; southern California red abalone are also reproductive year-round, but show an increase in gonad size during winter months when

temperatures drop (Boolootian et al. 1962, Giorgi and DeMartini 1977). Green abalone, on the other hand, are reported to have a marked seasonality with summer reproduction, when temperatures rise (Tutschulte and Connell 1981).

Disease also appears to be temperature dependent with species-specific differences. Moore et al. (2000) concluded that, in red abalone, warm water enhances the severity of the pathogenic effects of the withering syndrome aetiological agent. Our results also show that expression of withering syndrome in red abalone is much reduced in colder water; thus, cooler water may serve as a thermal refuge in which there is a reduced ability of the WS-RLP to proliferate. Furthermore, we found a strong difference in susceptibility between red and green abalone, with red abalone much more susceptible to withering syndrome than green abalone. Because red abalone are more vulnerable to warm-water stress, they will be adversely affected by even slightly increased temperatures in the California current. Another California abalone species, the black abalone (*H. cracherodii*), is nearly absent from southern California due to withering syndrome (Haaker et al. 1992, Altstatt et al. 1996). However, this species is still present in cooler central and northern California waters, despite the presence of the withering syndrome bacterium. Hence, temperature appears to influence withering syndrome in several species.

Active recovery/restoration

What implications do these results have for management, restoration, and recovery efforts for southern California abalone stocks? Traditionally, management of California abalone was based on the assumption of a constant marine environment, failing to integrate the fluctuating oceanographic climate with adequate reproductive natural history. These shortcomings represent a consistent pitfall in fisheries management. This is especially true for abalone, long-lived species needing 7 to 10 years to enter the fishery (Tegner 1989). Any recovery efforts must incorporate oceanic and atmospheric warming trends. Our understanding of both ENSO phenomena and the 1976–1977 regime shift of the North Pacific is sufficient enough that we can anticipate that ocean warming will be associated with a shoaling of the source of upwelled waters and consequent warmer nutrient-poor surface water in the California current system (McGowan et al. 2003).

Considering that abalone densities are orders of magnitude below the Allee threshold (Allee 1931), active restoration efforts consisting of: (1) continued enforcement of fishery closures and protected areas to allow natural population recovery; (2) broodstock transplants or aggregations to create circumstances for adequate fertilization success and larval supply; (3) outplanting of hatchery-reared larvae, juveniles, or adults, will be needed. One southern California enhancement effort, where 4456 adult, sexually mature green abalone were
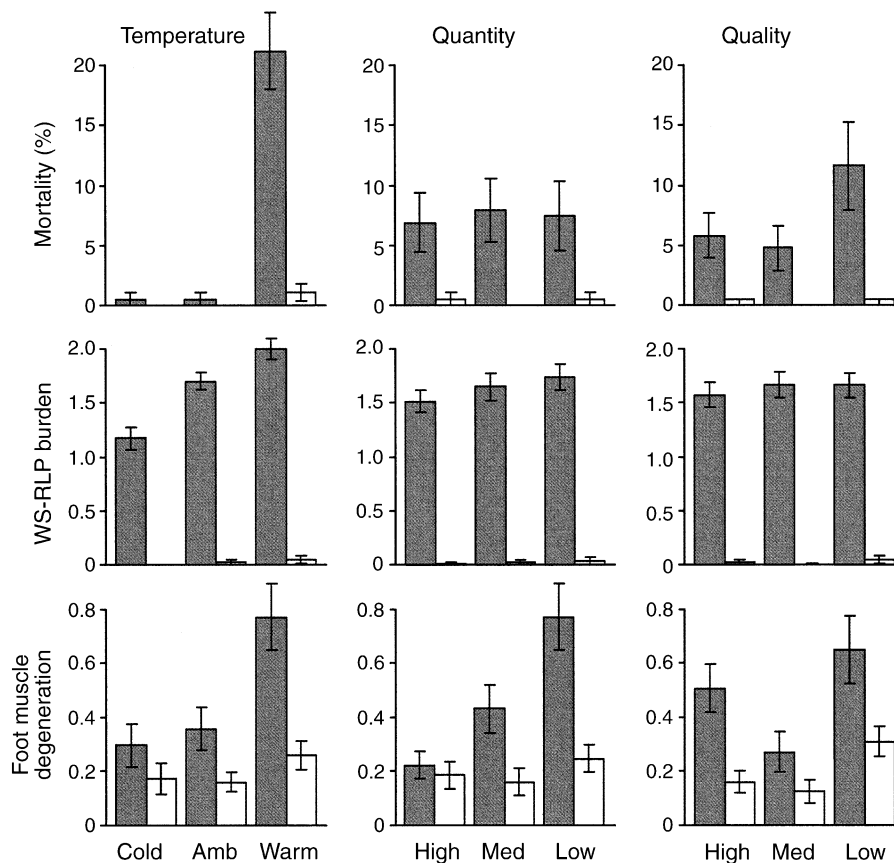
FIG. 7. Means (± 1 SE) of accumulated mortality, withering syndrome Rickettsiales-like prokaryote (WS-RLP) burdens, and foot muscle degeneration for the three experimental factors (see Methods for descriptions of WS-RLP burden and foot muscle degeneration). Gray and white bars correspond to *H. rufescens* and *H. fulgens*, respectively.

transplanted to Palos Verdes was successful, with a recruitment pulse observed in the region three years after the transplants (Tegner 1992). Unfortunately, the entire broodstock was poached, thereby terminating the experiment. However, the fact that there was a marked recruitment shadow demonstrates the utility of such outplanting techniques and supports the hypothesis that larval supply is a key issue. Nevertheless, high mortalities have been repeatedly observed in both seeded and native juvenile abalone, indicating that larval supply is not the only pressure limiting abalone populations (Tegner and Butler 1985). The limited recapture of seeded abalone observed to date suggests that strategies for abalone enhancement need further evaluation, including balancing the net gains of outplanting efforts by significantly increasing the number and size of outplanted animals since larger individuals have higher survivorship. Thus, more and larger individuals will contribute larvae into the system sooner. Aggressively enforced protected areas will be essential to recover patches of self-maintaining abalone populations and enhance populations. Thus, continued fisheries closures and enforcement, in conjunction with various outplanting efforts, may be successful but abalone abundances

are not likely to change rapidly. Our study suggests that future restoration efforts in southern California are more likely to succeed with green abalone than red abalone, given the changing temperature regime and the presence of withering syndrome in this region (Friedman et al. 1997, Harvell et al. 1999)

The Allee effect and recruitment overfishing

Five of the seven California abalone species once supported a lucrative commercial fishery of some 4000 metric tons annually. A decreasing trend in the landings began after 1969, and continued until the eventual collapse and closure of the fishery in 1997, when a moratorium was imposed on all abalone fishing south of San Francisco, California. The genesis of this decline has been a major focus of research (Tegner 1989, Davis et al. 1992, Karpov et al. 2000). Fisheries independent egg-per-recruit analyses (Tegner 1989) failed to consider fertilization success. Another shortcoming of such size specific analyses is that the biological rates are uncertain, and our results suggest that mortality, growth, and reproductive rates are functions of ocean temperature regimes. Thus, catch restrictions based only on size ignore many important variables, espe-
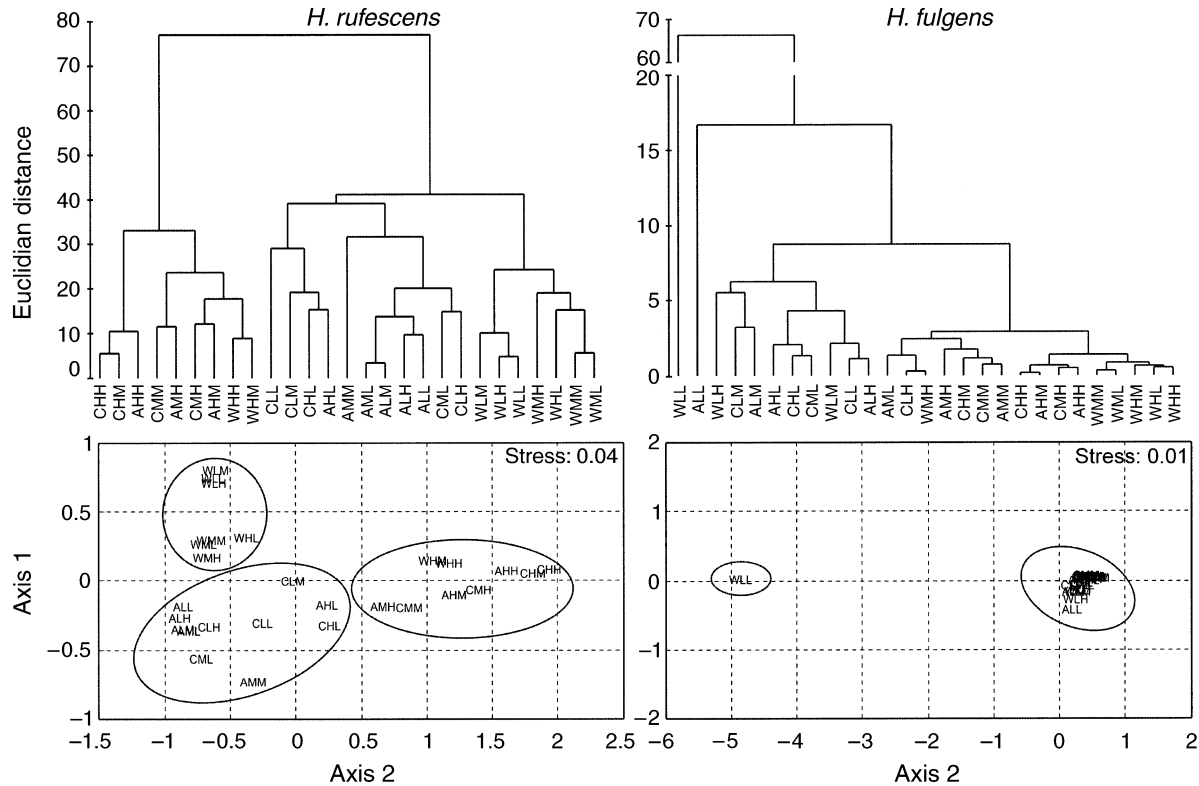
Fig. 8. Dendrograms and multidimensional scaling plots based on Euclidean distances between standardized means of all experimental treatment combinations. In the top two plots, *x*-axis labels correspond to factor-level combinations in the order of temperature, then food quantity, and then food quality. The two lower plots show results from two-dimensional multidimensional scaling analysis with overimposed clusters based on separations from the dendrograms. Abbreviations are: C, cold; A, ambient; W, warm; H, high; M, medium; and L, low.

cially the importance of population densities and aggregations to ensure gamete fertilization and adequate larval production, as well as inaccurate assumptions of constant growth, reproduction, fertilization success and survival in varying ocean climates. This is not a new concern; nearly a century ago, Edwards (1913) warned of the "threatened extermination of the abalone," stating that removing large individuals of legal size does not secure reproduction of the most prolific breeders. And the consequences of reducing the density of broadcast spawners below a threshold that ensures gamete fertilization was also understood at that time (Lillie 1915), and reiterated by Stokesbury and Himmelman (1993), and Claereboudt (1999). This is especially true for abalone, in which fertilization is usually not successful when mating individuals are farther than one to two meters apart (Tegner et al. 1996*a*, Babcock and Keesing 1999). Obviously, recruitment overfishing, where the main source of larval supply is removed by fishing pressure, has been taking place for over a century, and it is not surprising that these fishing pressures have caught up with the California abalone. With the exception of northern California red abalone, densities of surviving abalone in southern California are so low that almost all surviving individuals are so far apart

that their gametes are not ensured successful fertilization (Karpov et al. 2000). At this point, their populations are orders of magnitude less than would be necessary to reverse this trend. Thus, restoration and recovery efforts must insure that aggregations of abalone are protected, and since reproductive output is exponentially associated with age and size, we need to protect many such aggregations.

Localized extinctions and range reductions

Long-term warming trends in recent years are coincident with an increase in low frequency climatic variability of the California current system (McGowan et al. 1998). Not until recently have the ecological consequences and extinction risks of climate shifts become apparent (Walther et al. 2002, Thomas et al. 2004). For example, interdecadal to decadal shifts in biomass and organism abundance within the California current have been observed (Barry et al. 1995, Roemmich and McGowan 1995, Veit et al. 1996). Other north Pacific eastern boundary ecosystems have also been affected (Anderson and Piat 1999, Hare and Mantua 2000, Miller and Niklas 2000). Tucked away within the California bight, southern California coasts have less northern cold-water influx from the California current than cen-

tral California; therefore, kelp forests in this region depend upon localized upwelling. The deepening of the thermocline with the subsequent deepening of the source of cool nutrient-rich waters in southern California will have strong negative effects on the kelp; this in turn will affect dependent herbivores. The green abalone's robust thermal tolerance and ability to maintain growth and reproduction so long as food is not limiting will be advantageous in southern California, where this abalone species inhabits a larger suite of habitats having wider varieties of food sources in the subtidal and intertidal regions. During warm ENSO events, thermal stress will hinder red abalone growth and reproduction, and result in a much higher mortality of red relative to green abalone. Red abalone, therefore, will suffer greater ecological consequences if a warming trend in the California current persists. If warmer seawater continues moving north, southern California may no longer be a suitable red abalone habitat. This conclusion closely parallels the prediction of the Hobday and Tegner (2002) modeling study. Additionally, the expansion of sea otters (*Enhydra lutris*) south of Point Conception into the California Bight (Vowel 2000), will further complicate red abalone recovery in the region.

Conclusions

Temperature fluctuations associated with current warming trends have both direct and indirect effects on abalone and the potential for meaningful restoration and management. The implications of a deepening thermocline (the source of cool, nutrient-rich waters), with the attendant stress on kelp reduces the quantity and quality of available food; this has significant consequences for the two species of abalone we studied. Future restoration efforts of all California abalone species (including the white abalone, *H. sorenseni*) should take current warming trends into consideration. The implications of global warming on the recovery of depleted resources are of profound importance to conservation and management. While we focused on two localized species in southern California, our conclusions may be applicable to other depleted species whose conservation and management hinges on oceanographic climate. It is evident that overfishing was the main force driving the demise of California abalone stocks. However, it is also evident that a warming trend in the California current acted in concert with overfishing to amplify the effects of recruitment overfishing, disease, and low densities, and thus limiting the ability of abalone populations to recover.

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APPENDIX

Results of Tukey a posteriori tests for variables showing significance with the ANOVA test are available in ESA's Electronic Data Archive: *Ecological Archives* A015-013-A1.