

## Recruitment, Growth, and Survivorship of Black Abalone on Santa Cruz Island following Mass Mortality

Brian N. Tissot

Marine Science Department, University of Hawaii at Hilo,  
200 West Kawili Street, Hilo, Hawaii 96720-4091

*Abstract.* — Populations of black abalone experienced major declines in abundance throughout the California Channel Islands in the late 1980's. The focus of this research was to monitor the potential recovery of populations on Santa Cruz Island in 1990–1993 following mass mortality in 1987–1989. Abalone continued to decline in abundance between 1990–1993. These declines were associated with low survivorship and low relative weights, indicating that individuals were continuing to die from the withering syndrome (WS) which was associated with the principal mass mortality. Recruitment, and the movement of small abalone from their cryptic juvenile habitat unto open surge channels, was an important process maintaining adult abundance. However, major declines in the density of juvenile abalone occurred between 1991–1993. Small abalone (<70 mm in length) exhibited the greatest effects of WS and these effects decreased with increasing size. Temperature was indicated to be the single most important factor influencing population recovery. Oceanographic factors that result in elevated seawater temperatures, such as El Niño, will have a strong negative impact on the recovery of black abalone populations in southern California.

---

Prior to the mid-1980's populations of black abalone, *Haliotis cracheroidii*, occurred at extremely high densities ( $\approx 50\text{--}75\text{ m}^2$ ) throughout the California Channel Islands (Bergen 1971; Douros 1985, 1987). Shortly thereafter, populations on most of the islands began dramatic declines in abundance, often exceeding 90% (Davis et al. 1992; Haaker et al. 1992; Tissot 1988a). This precipitous decline, or mass mortality, occurred in conjunction with the "withering syndrome" (WS): abalone were shrunken in appearance, weakly attached to the substratum, and did not actively feed (Tissot 1991). At present the ultimate causes of the mortality are unclear, but possible factors include the effects of elevated temperatures, fluctuations in the abundance of drift algal foods, high abalone densities, and the spread of a pathogen (Culver and Richards 1992; Davis et al. 1992; Haaker et al. 1992; Lafferty and Kuris 1993; Steinbeck et al. 1992; Tissot 1991).

The focus of this research is to monitor changes, and potential recovery, of populations on Santa Cruz Island in 1990–1993 following major declines in 1987–1989 (Tissot 1991). I address the following questions:

- Did populations display any indication of recovery?
- Did WS continue to occur and did it influence survivorship?
- Was recruitment occurring and did it influence abundance?

I addressed these questions by monitoring the growth and survivorship of tagged abalone located along permanent transects established in 1987. Recruitment was monitored by surveying the abundance of juvenile black abalone, which primarily occur under rocks in boulder fields (Tissot 1988b).

### Materials and Methods

Study sites were located on the west end of Santa Cruz Island (34°00'N, 114°50'W), California. Intertidal transects were located in two general areas that differed in their exposure to ocean waves. The "wave-protected" site (hereafter referred to as "protected") was located 1 km SE of Forney Cove on the south side of the island. The "wave-exposed" site (hereafter referred to as "exposed") was located 0.2 km NE of Fraser Point on the north side of the island (see Tissot 1991).

In 1987, I established 3–4 permanent intertidal transects in surge channels at each study site. In 1990 I established 2 additional permanent transects in a boulder field at the protected site. Surge channel transects were 1 m wide and 5–15 m long; boulder field transects were 4 m wide and 25 m long. Transects were oriented perpendicular to the shore and extended from the mid- to the low-intertidal zones. I conducted surveys on a quarterly basis (winter, spring, summer, fall) between January 1987 and January 1990, and on an annual basis during the summer between 1990 and 1993.

I determined abalone abundance on each transect by counting the total number of individuals present. Density was calculated by dividing the total number of individuals by the total transect area after removing areas that were deemed uninhabitable by abalone. In 1990, I began measuring the shell length of all individuals on transects.

During surveys I tagged 5–75 haphazardly chosen abalone on, or adjacent to, each surge channel transect. Abalone were removed from the substratum using an abalone iron, their shells were cleaned with a wire brush, and they were tagged with an identifying number from a Dymo label maker applied to the shell with marine epoxy putty (Z-spar Splash Zone Compound). Damage to the foot resulting from handling was noted. Statistical comparisons between damaged and undamaged abalone revealed no significant differences in survivorship, rates of shell growth, weight gain, or net total movement (T-test, all  $P > 0.05$ ). For each individual I measured the length of the shell in the longest dimension with a caliper, and beginning in June 1988, the total wet abalone weight after the removal of shell growths, with a spring scale. Individuals that were abnormally underweight in appearance were noted.

Survivorship was measured by the recapture rate of tagged individuals. In order to make valid comparisons among survey intervals, which varied in duration, I calculated all recapture rates based on annual survivorship (e.g., summer 1987 to summer 1988).

I calculated shell growth as the change in length per unit time (mm/month). I derived an index of abalone "condition" using total abalone weight, hereafter referred to as "relative weight." Relative weight was calculated by measuring the percent deviation of abalone weight from a predicted weight, which was based on a logged length-weight regression calculated from field recaptured individuals

displaying both shell growth and increases in total weight between surveys in 1988–1990:

$$\text{Log}_e \text{predicted weight} = -9.36 + 3.15 \times \text{Log}_e \text{length}$$

( $r^2 = 0.97$ ,  $N = 87$ ,  $P < 0.01$ ). Relative weight was then calculated as a percent deviation from predicted weight:

$$\text{Relative weight} = \frac{\text{Weight} - \text{Predicted weight}}{\text{Weight}} \times 100$$

Although the calculation of a relative weight index using growing individuals as a standard was somewhat arbitrary, it served as a standard by which to make weight comparisons among years. Of the 49 individuals that were observed to be abnormally underweight during surveys, 88% ( $N = 43$ ) of their calculated relative weights were  $<0$  (the mean of “growing” individuals). Hence the method probably underrepresented the extent of withered abalone. Furthermore, since relative weights were based on total animal weight (shell + soft parts), the extent of shrunken soft parts was further underestimated. For example, based on measurements of 97 individuals from Santa Cruz Island the soft parts account for an average of 48.6% of the total weight (Tissot, unpublished data). Therefore, an abalone with a relative weight of  $-10\%$  actually had soft parts (foot + viscera) that were 20.6% below their predicted weight.

I obtained monthly surface seawater temperatures for the general area of Santa Cruz Island using satellite imagery data (NOAA 1987–1993). These temperatures were consistent ( $\pm 1.0^\circ\text{C}$ ) with values taken intertidally during surveys. Mean monthly temperatures were extracted for the years 1987–1993 and compared to average annual surface values derived for the Santa Cruz Island area for 1942–1969 from Robinson (1976). I calculated the annual temperature anomaly as the mean difference between actual monthly temperatures and average monthly temperatures from Robinson (1976).

### Results

Abalone density on surge channel transects exhibited a net decline throughout the 1987–1993 study period (Fig. 1A). Transects along the protected coast declined from a mean density of  $\approx 60/\text{m}^2$  in 1987 to less than  $1/\text{m}^2$  in 1993. Similarly, along exposed coasts, density declined from  $\approx 45/\text{m}^2$  to less than  $1/\text{m}^2$ . Rate of change in density was greatest between 1987–1988 surveys (Fig. 1B). There were small increases in abundance between surveys in 1989 in both study areas and between the 1990–1991 survey on the exposed coast, but further declines occurred between 1991–1993. The rate of decline of abalone density did not differ among transects (comparison among slopes:  $F = 0.67$ ;  $df = 7, 109$ ;  $P > 0.05$ ) indicating that declines were not related to initial abalone density.

Patterns of variation in abalone size differed among exposed and protected surge channel transects (Fig. 2). Individuals  $<80$  mm and  $>100$  mm decreased in abundance and eventually disappeared along exposed coast transects between 1990–1992. In contrast, the relative proportion of individuals  $<40$  mm increased and individuals  $>100$  mm decreased along protected coast transects during the same time period. There was a significant negative correlation between the mean

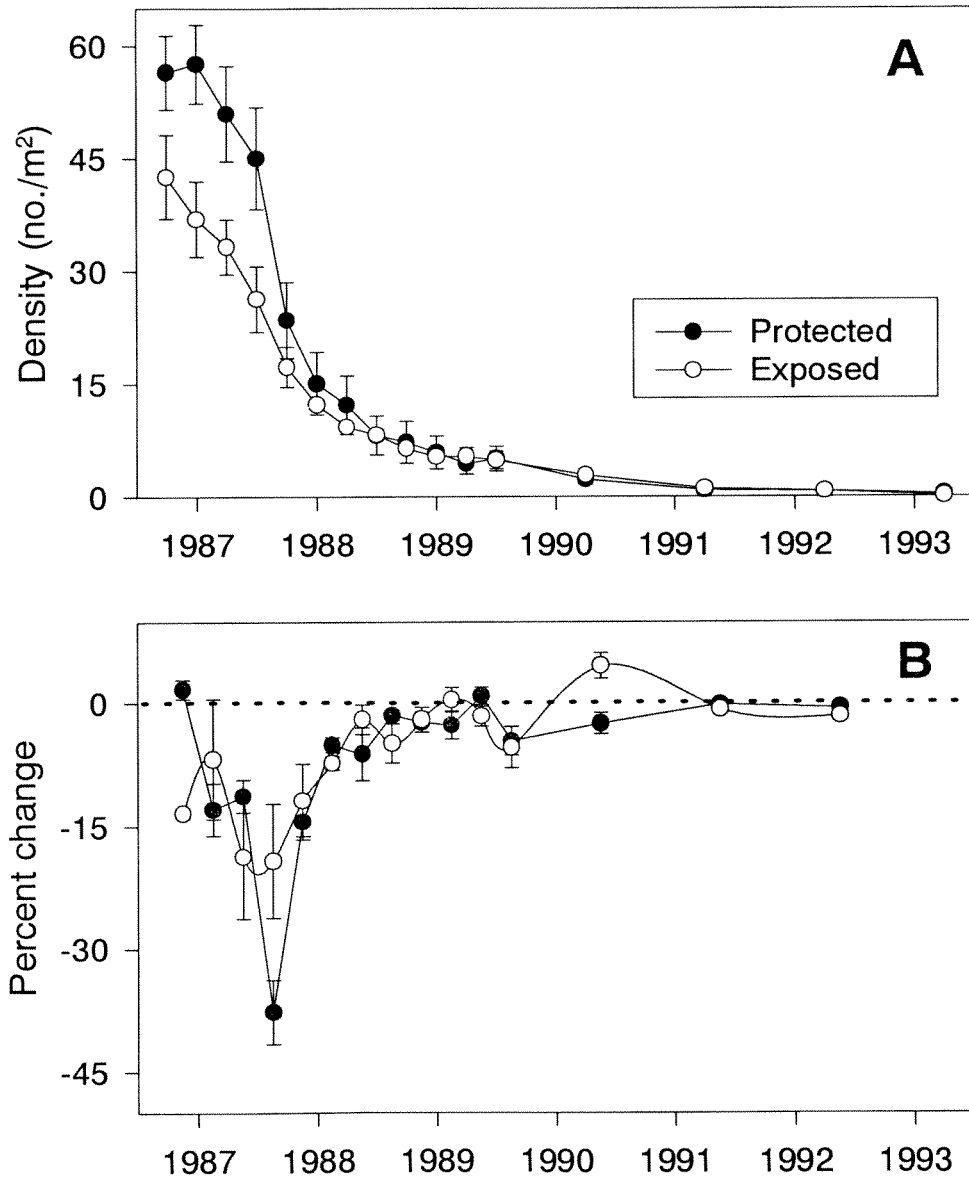


Fig. 1. Patterns of decline in abundance, 1987–1993. A. Mean density ( $\pm 1$  S.E.) on exposed vs. protected study areas. B. Percent change in mean density ( $\pm 1$  S.E.) relative to initial densities on exposed vs. protected study areas.

size of abalone on transects in 1990–1993 and their 1993 density ( $r = -0.62$ ,  $N = 8$ ,  $P < 0.05$ ), indicating that sites where abalone were relatively more abundant were composed primarily of small individuals.

Individuals on boulder field transects exhibited significant variation in size and density among years (Fig. 3). There were major declines in the density of all size classes between 1991 and 1992–1993. Total mean density varied from a high of  $1.4/\text{m}^2$  in 1991 to a low of  $0.51/\text{m}^2$  in 1993.

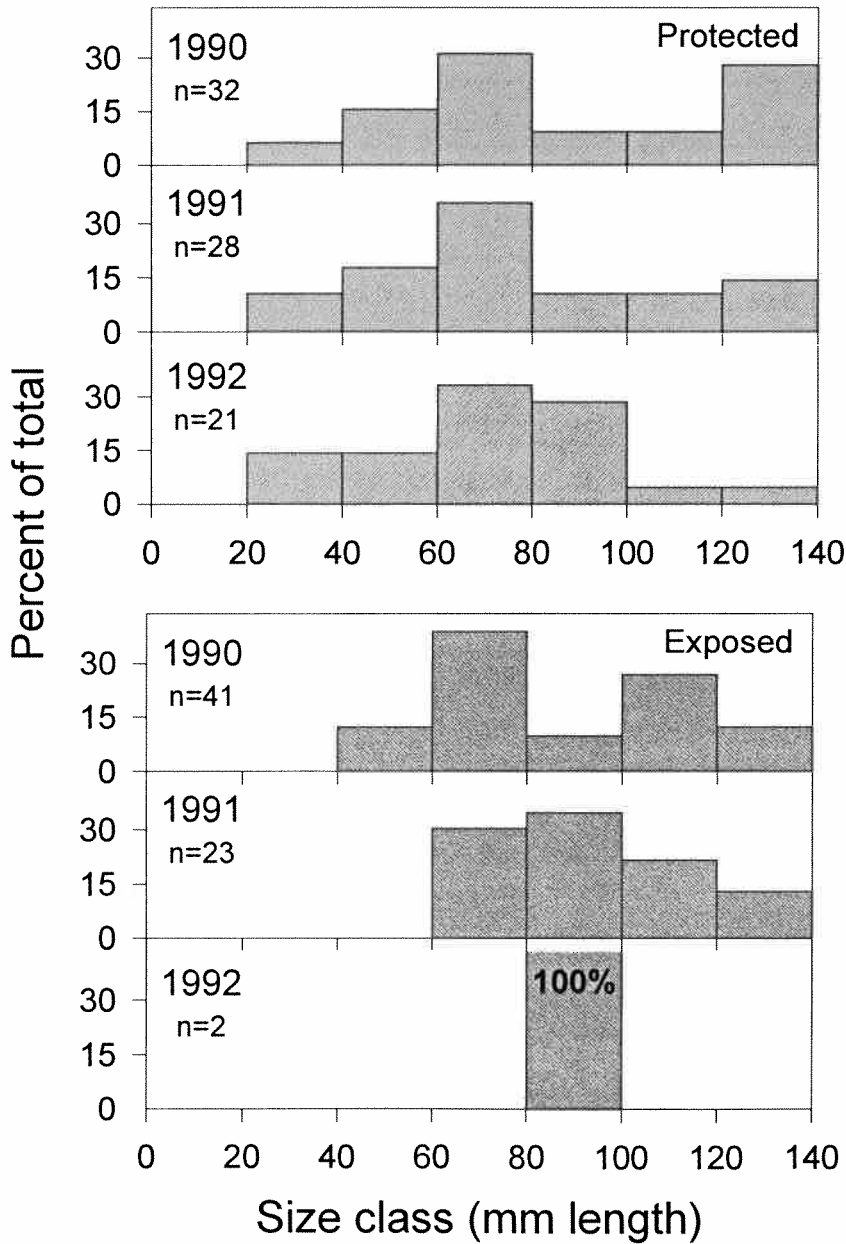


Fig. 2. Size frequency of abalone on surge channel transects in exposed and protected study areas (N = sample size).

Annual survivorship, as measured by the recapture rate of tagged abalone on surge channel transects, was significantly different among surveys (Kruskal-Wallis,  $H = 11.96$ ,  $N = 24$ ,  $df = 5$ ,  $P < 0.05$ ) (Fig. 4A). Recapture rates averaged 8% between summer surveys in 1987–1991 and 1992–1993, which were not significantly different from each other, and 31% between the 1991–1992 surveys (Tukey’s test,  $P < 0.01$ ).

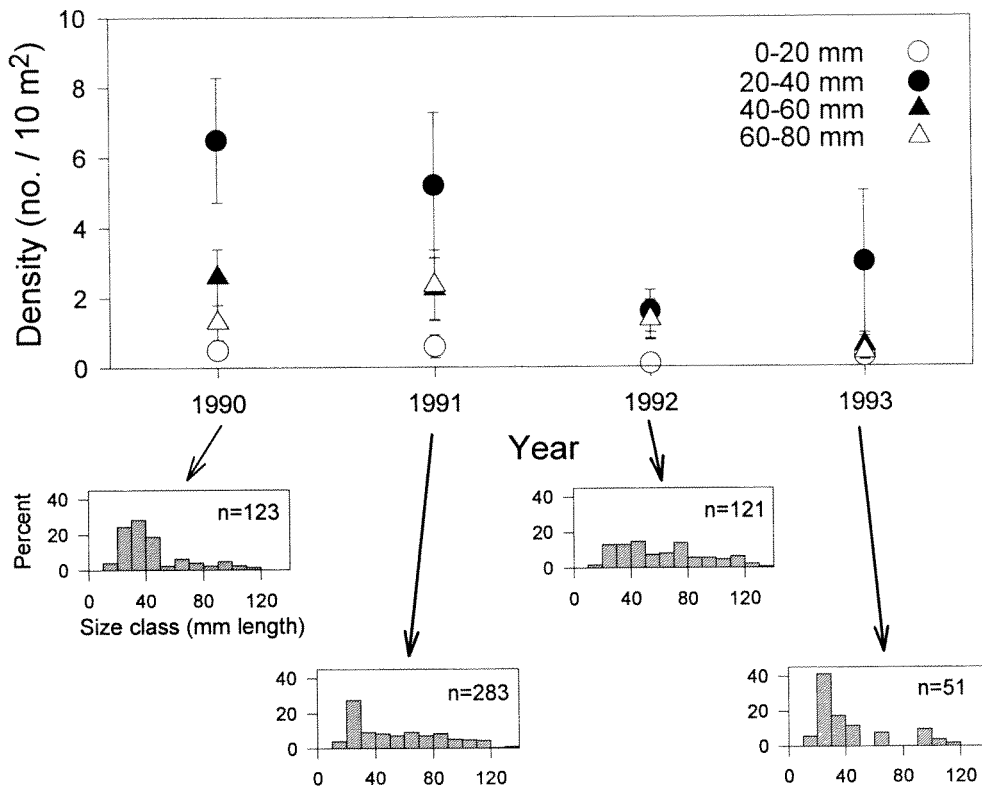


Fig. 3. Changes in mean density ( $\pm 1$  S.E.) of four size classes and size frequency of abalone on boulder fields ( $N$  = sample size).

The relative weight of individuals fluctuated during the study period (Fig. 4B). Mean weights were significantly different among years (Kruskal-Wallis,  $H = 39.5$ ,  $N = 405$ ,  $df = 5$ ,  $P < 0.01$ ): 1989 weights, which averaged 6.3% above predicted weight, were significantly different from all other years, which averaged 4.0% below predicted weight (Tukey's test,  $P < 0.01$ ). Mean relative weight of abalone  $\leq 70$  mm, which averaged 8.1% below predicted weight, was significantly different from abalone  $> 70$  mm, which averaged 1.5% below predicted weight (T-test,  $T = 2.93$ ,  $df = 192$ ,  $P < 0.01$ ).

Shell growth rates also exhibited high variability among years (Fig. 4C), however, there were no significant differences among years (Kruskal-Wallis,  $H = 4.71$ ,  $N = 59$ ,  $df = 4$ ,  $P > 0.05$ ).

Surface seawater temperatures were elevated above normal levels during all years of the study (Fig. 5). Average annual temperature anomalies were significantly different among years (Kruskal-Wallis,  $H = 24.5$ ,  $N = 84$ ,  $df = 6$ ,  $P < 0.01$ ) and varied from a mean of 1.2°C above average for 1987, 1988, 1990, 1992 and 1993, which were not significantly different from each other, to a mean of 0.41°C above average in 1989 and 1991 (Tukey's test, all  $P < 0.01$ ). Mean relative weights were significantly negatively correlated with mean winter temperature anomalies in 1987–1992 ( $r = -0.88$ ,  $N = 6$ ,  $P < 0.01$ ), but not with mean spring, summer, or fall temperature anomalies (all  $P > 0.05$ ).

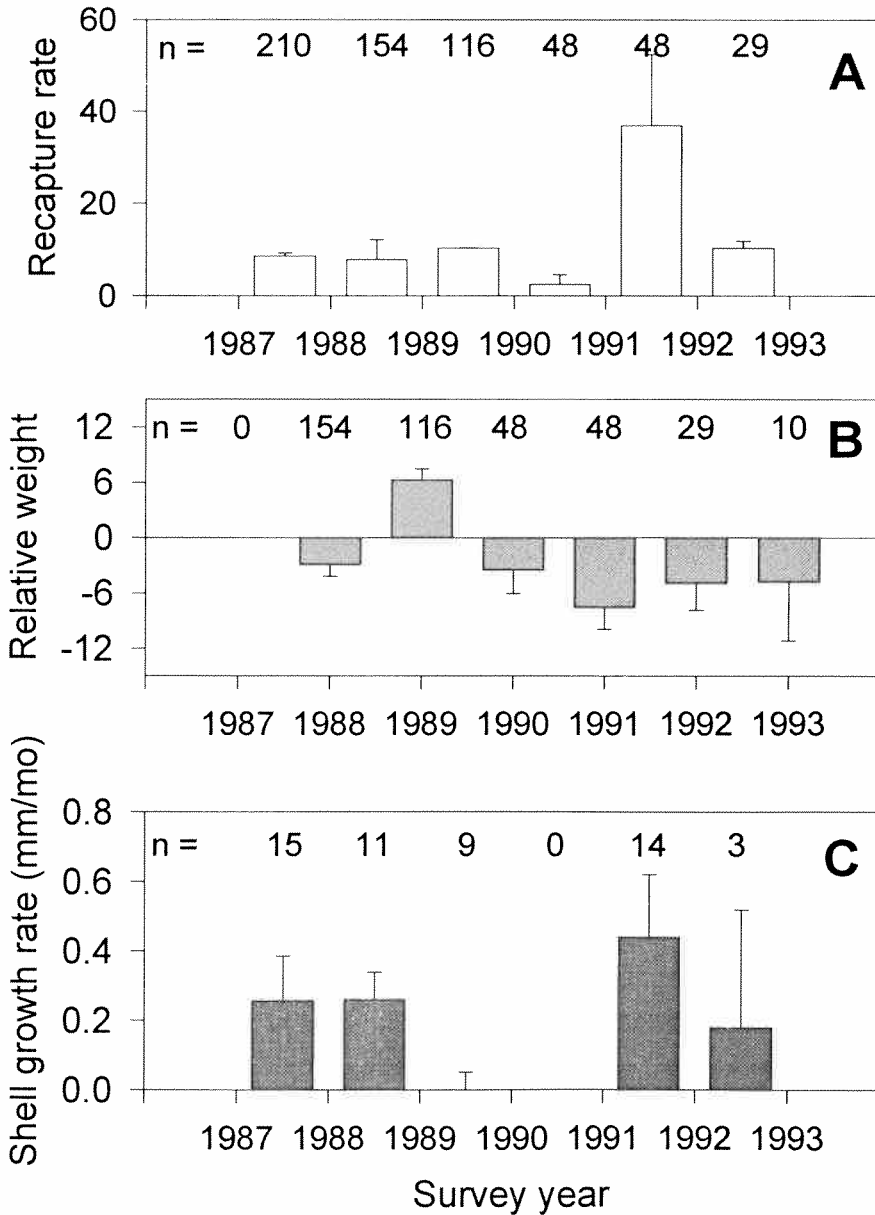


Fig. 4. Patterns of variation in growth and survivorship of tagged abalone (N = sample size). A. Mean recapture rate ( $\pm 1$  S.E.). B. Mean relative weight ( $\pm 1$  S.E.) (see text). C. Mean shell growth rates ( $\pm 1$  S.E.).

Discussion

Black abalone on Santa Cruz Island exhibited a net decline in abundance throughout the seven-year study period. Annual survivorship of tagged individuals, which averaged 8% in all years except 1991–1992, were low compared to other studies. Mean annual survivorship of ten species of abalone ranged from 0–92% but averaged 39% (Shepherd and Breen 1992). A better comparison can

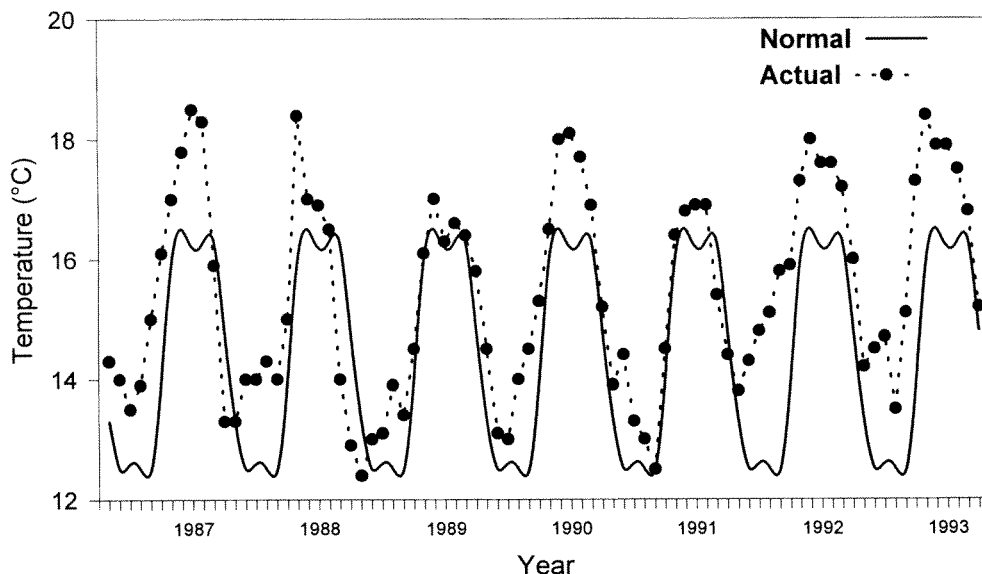


Fig. 5. Relationship between monthly seawater temperatures during the study period and average annual temperatures based on Robinson (1976).

be made using tagged black abalone on Año Nuevo Island in central California during 1987–1990 which did not exhibit WS, where annual survivorship averaged 33% (Tissot, unpublished data). In conjunction with low survivorship, relative abalone weights at Santa Cruz Island averaged 4.0% below predicted in all years except 1989. In contrast, using the same methodology to calculate relative weight at Año Nuevo Island, mean relative weights averaged 1.9% above predicted in 1988–1990. Thus population declines on Santa Cruz Island occurred in conjunction with low survivorship and low relative weights, indicating that elevated mortality rates continued to be associated with the withering syndrome. Important issues to be addressed are the effects of WS on the decline and recovery of the population and the role of ecological factors, such as seawater temperature, kelp abundance, and recruitment as they influence growth and survivorship.

The abundance of abalone on surge channel transects exhibited major declines between 1987 and 1993. Tissot (1991) has shown that these declines were primarily associated with mortality and not from handling injury, human disturbance, or emigration from study areas. Overall, the total decline between 1987 and 1993 has been 99.5%. In 1987 there were a total of 2630 abalone on all transects; 14 remained in 1993. Abundance has been reduced to zero on two of the eight transects, one each in exposed and protected study areas. If the current rate of decline continues, black abalone will be locally extinct on my study areas by 1997 ( $\pm 2$  years).

There was a strong relationship between the persistence of abalone on surge channel transects and their size composition. Study areas on the protected coast with the highest densities in 1993 exhibiting an influx of small abalone <40 mm into the study area. In contrast, lower density transects on the exposed coast were associated with an absence of small abalone. These observations indicate that recruitment, and the movement of small abalone from their cryptic juvenile

habitat into open surge channels, is an important process maintaining adult abundance. Similar observations have been made by Blecha et al. (1992) in central California. Boulder habitats suitable for small abalone are uncommon on the exposed coast of west Santa Cruz Island but are abundant on the protected coast. Therefore, a prediction from this study is: should abalone recovery occur in southern California, it will be higher in areas adjacent to intertidal boulder fields.

Newly recruiting and juvenile abalone in boulder fields exhibited high variation in abundance during 1990–1993. Declines in the density of all size classes occurred between 1991–1993 during abnormally warm temperatures associated with the 1992–1993 El Niño. There are at least two ways El Niño could have a negative effect on abalone recruitment and juvenile survivorship. First, ocean currents in southern California generally flow to the north during El Niño, transporting pelagic larvae from south to north (Cowen 1985). Because black abalone populations were decimated by mass mortality throughout southern California (Culver and Richards 1992), a northern flowing current might be sparsely laden with abalone larvae. In contrast, under normal oceanographic conditions, southern flowing currents would transport abalone larvae south from central California, where abalone are still abundant (Tissot 1991). A second mechanism is that elevated temperatures during El Niño enhance the effects of withering syndrome on juvenile abalone, resulting in elevated mortality.

Tissot (1991) demonstrated a strong relationship between the survivorship of tagged abalone and their relative weight, which thus served as a measure of the severity of WS. In this study relative weights of abalone were similar in 1990–1993 to those in 1988, when major mortality occurred. These observations demonstrate that WS has been present throughout the seven-year study period and associated with the continued high mortality. Perhaps more importantly, relative weight was strongly size dependent. Abalone <70 mm in length exhibited the greatest effects of WS and these effects decreased with increasing size. Thus, the continued presence of WS is having two major impacts on the populations: 1) low survivorship of adults; and 2) low survivorship of recruiting abalone which maintain adult populations.

Previous work by Steinbeck et al. (1992) and Tissot (1991) has shown temperature to have a strong effect on the incidence and severity of WS and resulting survivorship. Similar strong relationships between temperature, WS, and survivorship were evident in this study. Relative weights and survivorship were low during warm years in 1988, 1990, and 1992 but increased during oceanographically more normal years in 1989 and 1991. Moreover, low abalone weights were significantly correlated with elevated seawater temperatures during the winter season. Because black abalone store excess energy in the form of polysaccharides in the foot during the winter (Webber and Giese 1969), abalone mortality may be occurring due to a disruption of energy storage. Although the abundance of drift kelp, the principal food of black abalone, was unusually low during 1987–1988 during peak population declines (Tissot 1991), it did not appear to exhibit significant variation between 1989–1993, and thus was unlikely to be the continued cause of WS (Tissot, unpublished data). Therefore, temperature is the single most important factor influencing population recovery. Oceanographic factors that result in elevated seawater temperatures, such as El Niño, will have a strong negative impact on the recovery of black abalone populations.

### Acknowledgments

I thank Brandie Erbe, Jeremy Robinson, Eric Smith, John Steinbeck, and Susan Gaughan Tissot for assistance in the field. I would especially like to thank Eric Smith, who conducted the 1993 survey with Andy Barberena, Brandie Erbe, and Don Smith. I thank the US Navy and the Nature Conservancy for access to Santa Cruz Island and Lyndal Laughrin for invaluable logistic support. This work was partially supported by a grant from the University of Hawaii at Hilo.

### Literature Cited

- Bergen, M. 1971. Growth, feeding and movement in the black abalone, *Haliotis cracherodii* Leach 1817. Master's Thesis, University of California, Santa Barbara. 59 pp.
- Blecha, J. B., J. R. Steinbeck, and D. C. Somerville. 1992. Aspects of the biology of the black abalone (*Haliotis cracherodii*) near Diablo Canyon, central California. Chapter 18 in Proceedings of the First International Abalone Symposium: biology, fisheries, and culture. La Paz, Mexico. (S. Shepherd and M. Tegner, eds.), Blackwell Scientific Publications Ltd., Sydney.
- Cowen, R. K. 1985. Large scale patterns of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. *Journal of Marine Research*, 43:719-742.
- Culver, C. S., and J. B. Richards (editors). 1992. Black abalone mortality: establishing a research agenda. Summary of a Sea Grant workshop. Report No. T-CSGCP-024, California Sea Grant College, La Jolla, California. 32 pp.
- Davis, G. E., D. V. Richards, P. L. Haaker, and D. O. Parker. 1992. Abalone population declines and fishery management in southern California. Chapter 19 in Proceedings of the First International Abalone Symposium: biology, fisheries, and culture. La Paz, Mexico. (S. Shepherd and M. Tegner, eds.), Blackwell Scientific Publications Ltd., Sydney.
- Douros, W. J. 1985. Density, growth, reproduction, and recruitment in an intertidal abalone: effects of interspecific competition and prehistoric predation. Master's Thesis, University of California, Santa Barbara. 112 pp.
- . 1987. Stacking behavior of an intertidal abalone: an adaptive response or a consequence of space limitation? *Journal of Experimental Marine Biology and Ecology*, 108:1-14.
- Haaker, P. L., D. V. Richards, C. Friedman, G. E. Davis, D. O. Parker, and H. Tøgstad. 1992. Mass mortality and withering syndrome in black abalone, *Haliotis cracherodii*, in California. Chapter 17 in Proceedings of the First International Abalone Symposium: biology, fisheries, and culture. La Paz, Mexico. (S. Shepherd and M. Tegner, eds.), Blackwell Scientific Publications Ltd., Sydney.
- Lafferty, K. D., and A. M. Kuris. 1993. Mass mortality of abalone *Haliotis cracherodii* on the Channel Islands: tests of epidemiological hypotheses. *Marine Ecology Progress Series*, 96(3):239-248.
- National Oceanographic and Atmospheric Administration. 1987-1993. *Oceanographic Monthly Summary*. National Weather Service, Camp Springs, Maryland.
- Robinson, M. K. 1976. Atlas of North Pacific Ocean monthly mean temperatures and mean salinities of the surface layer. *NavOcean Reference Publication 2*.
- Shepherd, S. A., and P. A. Breen. 1992. Mortality in abalone: its estimation, variability and causes. Chapter 21 in Proceedings of the First International Abalone Symposium: biology, fisheries, and culture. La Paz, Mexico. (S. Shepherd and M. Tegner, eds.), Blackwell Scientific Publications Ltd., Sydney.
- Steinbeck, J. R., J. M. Groff, C. S. Friedman, T. McDowell, and R. P. Hedrick. 1992. Investigations into a mortality among populations of the California black abalone *Haliotis cracherodii*, on the central coast of California, USA. Chapter 16 in Proceedings of the First International Abalone Symposium: biology, fisheries, and culture. La Paz, Mexico. (S. Shepherd and M. Tegner, eds.), Blackwell Scientific Publications Ltd., Sydney.
- Tissot, B. N. 1988a. Mass mortality of black abalone in southern California. *American Zoologist*, 28:69A.
- . 1988b. Morphological variation along intertidal gradients in a population of black abalone *Haliotis cracherodii* Leach 1814. *Journal of Experimental Marine Biology and Ecology*, 117:71-90.

- . 1991. Geographic variation and mass mortality in the black abalone: the roles of development and ecology. Ph.D. Dissertation, Oregon State University, 271 pp.
- Webber, H. H., and A. C. Giese. 1969. Reproductive cycle and gametogenesis in the black abalone *Haliotis cracherodii* (Gastropoda: Prosobranchia). *Marine Biology*, 4:152–159.

Accepted for publication 26 December 1994.

4

4

4

4