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Title: Geographic Variation and Mass Mortality in the Black Abalone: the Roles of Development and Ecology

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Studies of geographic variation are central to understanding ecological and evolutionary processes. Geographic variation in the shell of the black abalone (*Haliotis cracherodii*), a marine intertidal gastropod, involves both clinal and local variation along the eastern Pacific coast in the number and size of tremata (=respiratory pores) on the shell. The goals of my studies were to determine the ecological causes of this morphological variation and to evaluate the contribution of developmental processes to morphological patterns. My field studies included 22 surveys conducted over three years (1987-1990), during which I monitored 2715 tagged abalone, at two study sites in California: Año Nuevo Island and Santa Cruz Island.

I depicted the ontogeny of trema number and size using multivariate ontogenetic trajectories: a path describing trema development relative to changes in allometric size. Because variation in the slope of ontogenetic trajectories was associated with latitudinal variation in the habitat of intertidal abalone, I proposed that dissociation between size and trema development by heterochrony was responsible for geographic variation.

Spatial and temporal variation in the abundance of drift algal foods had strong effects on the intertidal distribution and feeding preferences of abalone, which are largely sedentary. The availability of drift algae was primarily controlled by the abundance of local algal stocks and the extent of water movement.

On Santa Cruz Island, marked fluctuations in the abundance of drift algal foods occurring during the 1986-87 El Niño resulted in mass mortality of abalone in 1986-88. Survivorship during mass mortality had strong interactions with abalone shore-level size gradients and seasonal movement patterns, and was an important factor influencing geographic variation in population structure.

Variation in trema number along geographic and wave-exposure gradients was an allometric consequence of variation in shell growth rate, which in turn, was largely controlled by the abundance of drift algal foods. In contrast, shore-level gradients in trema number resulted from a combination of growth-induced allometry, differential survivorship, and complex movement patterns. Trema size varied with the extent of water movement as a response to variation in respiratory efficiency. Overall, morphological patterns resulted from environmentally-induced phenotypic plasticity and not heterochrony.

Geographic Variation and Mass Mortality in the Black Abalone: the Roles of Development and Ecology

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DEDICATION

To my great aunt,

Gabrielle Tissot Mulvane,

who opened my eyes to nature

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CHAPTER 4

Geographic Variation and Mass Mortality in the Black Abalone: the Roles of Development and Ecology

INTRODUCTION

Geographic variation in organismal biology has long intriqued both ecologists and evolutionary biologists. Among ecologists, geographic variation in physical and biological processes has provided insight into factors influencing population dynamics (e.g., Connell, 1961). Similarily, among evolutionary biologists, studies of geographic variation have advanced our understanding of evolutionary processes, such as adaptation (e.g., Mayr, 1941). However, a major challenge in evolutionary ecology, and the goal of this dissertation, is to examine components of geographic variation that incorporate both these ecological and evolutionary perspectives.

Ontogenetic development, and associated changes in organismal size and shape, is important in both ecological and evolutionary processes. On ecological scales, ontogenetic variation is associated with large changes in the effects of biological and physical processes on individual fitness. As a result, variation in body size alone explains 75% of the variation in organismal physiology, reproduction, and behavior (Calder, 1984). On evolutionary scales, ontogeny represents both a constraint on the development of form (Maynard-Smith et al. 1985) and a source of new morphological combinations (Gould, 1977). Thus, ontogeny is a biological process that is important on both ecological and evolutionary time scales.

This dissertation is focused on geographic variation in the shell morphology of the black abalone, *Haliotis cracherodii*, a marine, intertidal gastropod. My primary aim is to elucidate *ecological* factors which have an

important influence on the *development* of morphological features. In chapter 1, I define a statistical method of measuring ontogentic variation using multivariate techniques. These methods are used to examine the *pattern* of geographic variation in the shell morphology of the black abalone and develop hypotheses concerning the causes of these patterns.

In the next two chapters, 2 and 3, I investigate ecological factors which have a *causal* effect on abalone growth, distribution, and abundance. Because black abalone are sedentary herbivores and feed in drifting marine algae, in chapter 2 I examine the role of a major component of abalone growth: the availability of drift algal food. This study serves to elucidate the influence of spatial and temporal variation in food supply on abalone abundance, distribution, and feeding preferences. During the course of my studies I inadvertently documented a large decline in abalone abundance, or mass mortality, at my study site on Santa Cruz Island. Because mass mortality represents a strong selective agent with important evolutionary consequences (Kinne, 1980), in chapter 3 I examine the effects of this event on population dynamics. The chapter investigates patterns of abalone abundance, growth, distribution, and survivorship in relation to the effects of abnormal oceanographic conditions, or El Niño events, on the kelp-forest community which supplies drift algal foods.

In Chapter 4, I examine patterns of abalone morphology with respect to allometric growth and potential causal factors. I evaluate four hypotheses on the effects of natural selection and differential growth on morphology due to spatial variation in desiccation and water movement. This chapter serves to integrate the results of the previous chapters by examining morphological *patterns* in relation to developmental *mechanisms* as influenced by ecological *causes*.

Chapter 1

MULTIVARIATE ANALYSIS

Abstract

Heterochrony, or changes in the timing of developmental events during ontogeny, is an important evolutionary mechanism that invokes multiple changes in organismal morphology. In this chapter I described the rationale behind multivariate methods applied to studies of ontogenetic and geographic variation. These methods are applied to patterns of geographic variation in the black abalone, *Haliotis cracherodii*.

My primary goal was to quantify a character's ontogenetic trajectory, a path depicting the development of a character within a space defined by age, size, and shape. Principal components analysis, or PCA, represents a transformation and rotation of original variable axes to new variable axes, or components, which almost invariably describe variation in organismal size and shape. Component scores derived from PCA serve as metrics of size and shape in the calculation of ontogenetic trajectories.

Developmental variation in the black abalone involves increases in the number of respiratory pores, or tremata, on the shell with increasing size. Moreover, morphological variation among populations of the black abalone involves tremata number and size, *a priori* evidence that heterochrony is the mechanism underlying geographic variation.

Analysis of covariance of multivariate ontogenetic trajectories indicated significant divergence among populations in the slopes of trajectories. Ontogeny among individuals from lower latitudes resulted in more small, closely-spaced tremata when compared to the ontogeny of individuals at higher latitudes. Based on

these observations I proposed that heterochronic processes are dissociating trema development from shell growth rates in response to geographic variation in intertidal habitat.

Introduction

This chapter focuses on the multivariate analysis of morphological variation resulting from heterochrony, or changes in the timing of developmental events during ontogeny (de Beer, 1958). My goals are three-fold: 1) outline the steps in a multivariate analysis, 2) illustrate the methodology with data on a recent marine gastropod, the black abalone *Haliotis cracherodii*, and, 3) discuss conceptual difficulties associated with the application of multivariate techniques to problems involving heterochrony.

Heterochrony invokes multiple changes in organismal morphology. Most traits change ontogenetically and are functionally, developmentally, or genetically correlated with other traits (Falconer, 1981; Atchley, 1984; Maynard Smith et al., 1985). Thus, heterochronic change is multivariate and the measurement and simultaneous description of these changes require a multivariate approach. Bivariate techniques are an additional tool for examining heterochrony; they are useful for dissecting out changes in individual characters and describing dissociations among traits (McKinney, 1988a).

Historical Perspective

A history of the ideas leading to our current understanding of heterochronic processes was reviewed by Gould (1977). My goal here is to review the development of quantitative multivariate descriptions of ontogeny and their application to problems involving heterochrony.

Descriptions of ontogenetic change began with Thompson (1917) and Huxley (1932) -- see McKinney (1988a). Examination of covariation among characters did not occur until the advent of computers in the late 1950's. Early multivariate studies examined polymorphism (Blackith, 1957), growth (Rao, 1958), geographic variation (Jolicoeur, 1959), sexual dimorphism (Jolicoeur and Mosimann, 1960), and

interspecific variation (Blackith, 1960) using discriminate analysis and principal component analysis [reviews by Cock (1966) and Gould (1966)]. Links between bivariate and multivariate allometry were provided by Jolicoeur (1963a,b) -- see Shea (1985) for examples.

Gould's (1969) factor analysis of paedomorphosis in Bermudian land snails was perhaps the first explict application of multivariate techniques to problems of heterochrony. His *Ontogeny and Phylogeny* (1977) laid the foundations for a synthesis of the fields of heterochrony and the quantitative allometric approach. The clock model of heterochronic change, although qualitative, was the basis for the semi-quantitative model of Alberch et al. (1979) and most current studies of heterochrony are extensions and elaborations of their model (bivariate: Alberch and Alberch, 1981; Shea, 1983; McKinney, 1984, 1988a; multivariate: Shea, 1985; Schweitzer et al., 1986; Tissot, 1988).

Metrics of Heterochrony

Alberch et al. (1979) proposed a model of heterochrony involving size, shape, and age as independent variables. Relying on the quantification of a character's *ontogenetic trajectory*, a path depicting the development of a character, the model is intended to distinquish between different forms of heterochrony. Within a space defined by age, size, and shape, different trajectories describe variation in three parameters: a, the size (or age) of onset of growth of a character; b, the size (or age) of termination (offset) of growth of a character; and k, the rate of change of shape relative to size (or age). A major problem with the use of their model is a general lack of data on age. As heterochrony, by definition, describes shifts in developmental timing, examination of size and shape describes *allometric heterochrony* rather than pure heterochrony (see McKinney, 1988a).

In order to measure quantitative heterochronic changes analytical methods must supply the following: 1) multivariate metrics of size and shape; 2) calculation

of ontogenetic trajectories; 3) discrimination among ancestor-descendent trajectories with respect to slopes, intercepts, and developmental events; and, 4) a technique to incorporate age into the morphological framework. Below I describe methods that fulfill objectives 1-3; objective 4 will be treated in the discussion.

Multivariate Methodology

In this section I outline the steps in the multivariate analysis of ontogenetic variation. Problems associated with samples, standardizing data, and choosing an appropriate dispersion matrix for analysis are discussed. I describe the use of principal component analysis (PCA) for deriving multivariate measures of size and shape and their formulation into ontogenetic trajectories.

Samples

The goal is to sample individuals from a population or species from which information relating to ontogenetic variation can be obtained. Typical samples in morphometric studies constitute mixed cross-sections of populations: a series of individuals of varying sizes (Cock, 1966). As the age of individuals is unknown, size and shape are usually confounded with age due to temporal variation in growth. A longitudinal sample, data on the growth of individuals throughout their ontogeny, is required to measure the influence of age on size and shape (Cock, 1966). Longitudinal samples, however, are difficult or impossible (in the case of most fossils) to obtain. Mixed cross-sectional samples are frequently used in morphometric studies, and represent average growth patterns within populations (Cock, 1966). Based on information presented by Dudzinski et al. (1975), a minimum sample size for PCA is 30 to 40 individuals.

Data

Data are grouped by their functional level of representation, that of the operational taxonomic unit (OTU), which is the lowest ranking taxa employed in a study (Sneath and Sokal, 1973). OTU's may represent individuals, populations, or species and are grouped by general factors such as age, sex, population, or species.

Before analysis by PCA, raw data are frequently transformed to alternate scales of measurement in order to equalize variances, remove scaling effects, and

promote linearity (Sokal and Rohlf, 1981). Raw data are rarely used in PCA due to scale effects. As PCA describes patterns of covariation among variables based on their magnitude, the raw variances of variables directly determine the resulting components (Pimentel, 1979). Log data may circumvent this problem as logarithmic transformation promote independence of the variance and the mean (Sokal and Rohlf, 1981; Bryant, 1986).

Many data sets constitute a mixed array of quantitative and qualitative date types of different units (e.g., millimeters, degrees, counts, character state codes) (Sneath and Sokal, 1973). As with raw data, log-transformed mixed-mode data introduce scale effects that influence subsequent principal components. Separate analysis of continuous and discontinuous variables can circumvent this problem (Humphries et al., 1981). If the number of traits is small, however, this approach may be unfeasible. Moreover, separate analyses of different types of data expands rather than simplifies our descriptions of ontogeny. Transformation of the data to z-scores eliminates problems of mixed mode variables. Variances are standardized by dividing data values by standard deviations (Sokal and Rohlf, 1981). PCA of standardized data results in a more even weighing of variables and has proven useful in taxonomic studies (Thorpe, 1980; Pimentel, 1981).

PCA examines patterns of variation among measures of dispersion of a sample. Two general types of dispersion matrices are defined, based on whether OTU's or OTU traits provide the variation (Pimentel, 1981). In R-mode analyses, the dispersion matrix describes variation among OTU traits. In Q-mode analyses, the dispersion matrix measures variation among OTU's. Both modes are commonplace in morphometric studies and may produce similar results; R-mode techniques are more common in the literature (see Thorpe, 1980; Pimentel, 1981) and will be the focus of my analysis.

In R-mode PCA, the dispersion matrix is based on variances and covariances, or on correlations, among traits. When variables are linear distance measures the covariance matrix is preferred as it is supported by a large amount of statistical theory (Anderson, 1963; Dillon and Goldstein, 1984) and by links between bivariate and multivariate allometry (Jolicoeur, 1963a). The correlation matrix is used when variables are mixed-mode, as correlations are independent of scale. When data are standardized the covariance matrix is equivalent to the correlation matrix (Pimentel, 1981).

Analytical Methods: *Size and Shape*

Our goal is to obtain metrics of size and shape that we can combine into ontogenetic trajectories. Factor analysis, or PCA in the case where factors are orthogonal, is a multivariate technique that is concerned with the identification of structure within a set of observed variables (Dillon and Goldstein, 1984). In data sets with OTU's that vary in size, PCA almost invariably produces components that describe variation in size and shape.

PCA represents a transformation and rotation of original variable axes to new variable axes, or components, that describe successively smaller partitions of the variation in the dispersion matrix, subject to the constraint that axes are orthogonal or uncorrelated. The amount of variation described by each axis is measured by the component's length, or eigenvalue. Eigenvector coefficients, or directional cosines, are the cosines of angles between components and original variable axes. Eigenvector loadings are equivalent to the allometric loading of variables on components. Component scores represent values for each OTU based on relationships to component eigenvectors; scores are derived from a linear combination of the raw data and component loadings. Component correlations (often called variable loadings) represent product-moment correlations between principal component scores and the original data. Additional PCA metrics that aid

in interpretation of components are the amount of variation attributed to each trait or OTU on each component (Pimentel, 1979).

Although PCA has been a common approach in morphometric studies (Jolicoeur, 1959, 1963b; Jolicoeur and Mosimann, 1960; Gould, 1969; Tissot, 1984; Shea, 1985), it has three problems. First is the observation that the first principal component (PC1) does not always measure pure (or isometric) size. Because traits have different allometric loadings with general size, variation in shape is inextricably associated with changes in size (see Discussion). Much of the confusion associated with the use of PC1 as a metric of size is semantic: PC1 derived from ontogenetic data does not simply describe variation in size, but in addition, variation in shape related to allometric growth (Shea, 1985). PC1 should therefore be labeled a size-allometry axis (hereafter referred to as "*allometric size*"). Second, the mathmatical constraint of orthogonality between components removes shape variation contained in PC1 from subsequent components, which are thus not measures of pure (or allometric) shape. Components subsequent to PC1 describe variation in shape that is mathmatically independent of allometric growth. These shape axes describe differences in growth attributable to changes in the slope and intercepts of ontogenetic trajectories (Shea, 1985; Tissot, 1988). A third problem pertains to the extrapolation of PCA, originally intended for single group analysis, to the multigroup case. Differences in size among groups can confound size and shape variation among principal components, in addition to their functional and mathmatical mingling above.

The shear-PCA was proposed by Humphries et al. (1981) as a solution to the intergroup size problem. Shear-PCA measures the confounding of intergroup size and shape on PC1 by comparing unmodified principal components to those based on group-free dispersion: a pooled within-group dispersion matrix in which intergroup size differences have been eliminated by mean-centering data within

group. Using PC1 from the group-free dispersion matrix (the within-group size-allometry axis), residual shape variation in the original PC1 is measured and placed (or sheared) into subsequent components (Humphries et al., 1981). This procedure amounts to calculating a vector orthogonal to the group-free PC1 but within the plane of the original components. The shearing method ignores divergence among groups in PC1, a limitation that should be explored by separate PCA's of each group (see Discussion). When compared to PCA from unmodified multigroup data, shear-PCA shows enhanced group discrimination (Humphries et al., 1981; Bookstein et al., 1985) and clear separation of allometric size and size-independent shape.

Computer algorithms for PCA are listed by Blackith and Reyment (1971), Cooley and Lohnes (1971), Mather (1976), and Bookstein et al. (1985). Several statistical packages offer conventional PCA: BIOSTAT (Pimentel, R. A. and J. D. Smith, 1985, Sigma Soft, Placentia, CA), BMDP (Dixon and Brown, 1979), SAS (SAS Institute, Cary, NC), SPSS (SPSS Inc., Chicago, IL), and SYSTAT (SYSTAT Inc., Evanston, ILL). A SAS procedure for performing a shear-PCA is listed by Bookstein et al. (1985). Programs that perform both conventional and shear-PCA are available from the author for use on IBM personal computers.

After a PCA or shear-PCA run, one is faced with the problem of determining which components to examine and the biological interpretation of axes. Eigenvalues, eigenvectors, component correlations, component scores, and percent variation due to variables and OTU's are helpful interpretative aids. Of course, the ultimate basis for interpretation of components is whether they make biological sense (Oxnard, 1978; Pimentel, 1979).

Eigenvalues are measures of the amount of variability described by each component and aid in determining which components describe significant amounts of variation. Several techniques are available: 1) examining axes until 90% of the total variation is described, 2) examining axes with eigenvalues that are larger than

average, 3) scree tests in which eigenvalues are plotted against axis number and visually or statistically examined for breaks in their pattern of decline, and 4) comparisons between real and random eigenvalues (Anderson, 1963; Horn, 1965; Cattell, 1966; Dillon and Goldstein, 1984). In most cases the 90% rule combined with biological interpretation is sufficient for separation of real from trivial components.

Of greater difficulty is the objective interpretation of components. In general, significant component correlations indicate which eigenvector loadings to interpret, while the percent variation attributed to each variable explains the amount of variation being described on a variable-by-variable basis. Isometry tests which compare eigenvectors with a theoretical component having equal loadings are useful for detecting isometric size components (Jolicoeur, 1963a, 1984). Since increases in general size almost invariably involve allometric change among variables, deviation from isometry is expected (Gould, 1966; Sprent, 1972). Multivariate methods that force the first principal axis to isometry create relationships among character that are not likely to exist (Somers, 1986). The correlation between eigenvector loadings and allometric loadings of variables on a measure of body size, such as length, mass, or volume is a way of examining PCA size in relation to bivariate allometric size (Tissot, 1988). Significant correlation between eigenvector and allometric loadings will identify the size-allometry axis, which is invariably the first component in ontogenetic samples.

Component scores are useful in several ways: they aid in the interpretation of components via group ordination, and serve as measures of multivariate variation in the calculation of ontogenetic trajectories. Examination of group ordinations based on component scores is helpful towards identifying outliers and detecting nonlinearity in the data (Pimentel, 1979).

Analytical Methods: *Multivariate Ontogenetic Trajectories*

After interpretation of components as contrasts of allometric size and statistically independent measures of shape, component scores serve as metrics of size and shape in the calculation of ontogenetic trajectories. By using component scores as linear combinations of the original variables, PCA reduces a multivariate system to a series of bivariate relationships. Linear regression is used to measure relationships between allometric size and shape. The resulting linear equation predicts shape on the basis of size and serves as a depiction of the average path of ontogeny of OTU's within groups in the size-shape space defined by component axes.

As neither size nor shape can be considered a dependent variable the appropriate method of analysis is model II regression. As principal component scores are in the same units (those of the combined variables), the slope of the major (or principal) axis for each group is the best estimate of the interrelationships between size and shape (Sokal and Rohlf, 1981). The problem with using model II regression is that methods for discriminating among group slopes and intercepts (analysis of covariance) are based on model I regression in which one variable is considered dependent on the other. Thus, in order to discriminate among group trajectories, model I techniques, such as least-squares regression must be used.

In reference to the allometric outcomes of the Alberch et al. (1979) model, the slope of the regression is an estimate of shape change relative to size (k), while the intercept serves to delineate onset or offset signals (a and b). Intercepts on ontogenetic trajectories represent average shape scores at size scores of zero. In order to make intercepts biologically meaningful, PCA scores need to be centered based on consistant criteria (e.g., the size score at which length is zero). Developmental events are incorporated into ontogenetic trajectories by calculating the intercept of their regression on size components (i.e., predicting the size at which the event occurs) (see Tissot, 1988).

Ontogenetic trajectories are examined for complex allometry by comparing F-ratios of regressions using higher order size and shape terms (McKinney, 1984). Once trajectories are linear, discrimination among groups can be accomplished by analysis of covariance which tests for differences among slopes and intercepts of regressions (Sokal and Rohlf, 1981).

An Example: Intraspecific Divergence and Allometric Heterochrony in the Black Abalone, *Haliotis cracherodii*

To illustrate the multivariate measurement of heterochronic change I present an analysis of ontogenetic variation in a recent marine gastropod. The data analyzed are typical of most morphometric studies: simple, mixed-mode traits describing, in this case, shell morphology.

Introduction

The black abalone, *Haliotis cracherodii*, is a common gastropod of the intertidal and subtidal zones of the eastern Pacific coast from San Francisco to southern Baja California (Cox, 1962). Developmental variation in the black abalone involves increases in the number of respiratory pores, or tremata, on the shell with increasing size (Figure 1.1). Associated with increasing trema number are changes in trema diameter and spacing (Figure 1.1). In addition, black abalone ontogeny is marked by a well-defined developmental event: the attainment of a muscle scar on the shell. Development of the muscle scar coincides with a slowing or cessation in shell growth.

Intraspecific divergence among populations of the black abalone involves ontogenetic processes. Individuals from populations at lower latitudes possess more numerous tremata at a given size than individuals from populations at higher latitudes. As the number of tremata varies with ontogeny, geographic variation in size-trema relationships is *a priori* evidence that heterochrony is promoting intraspecific divergence.

Materials

Samples of black abalone were obtained by haphazardly collecting ontogenetic series of animals from several localities. Samples were obtained from four geographically separate populations: Año Nuevo Island, San Mateo County, CA (n=54; 37° 6' N, 122° 20' W); Valley Anchorage, Santa Cruz Island, CA (n=47;

34° N, 119° 40' W); Natividad Island, Baja California (n=41; 27° 40 N, 115° 20 W); and Guadalupe Island, Baja California (n=64; 29° N, 118° 15 W). As the age of specimens was unknown, collections represented mixed, cross-sectional samples of populations.

Seven traits were measured on the shell of each individual (Figure 1.2). Length, width, trema length, and height describe the overall size of the shell; trema number, size, and spacing describe developmental variation in shell shape (Figure 1.1). The muscle scar was recorded as the proportion of the muscle attachment area covered by scar nacre.

Multivariate Analysis

As the data were of mixed-mode (millimeters and counts) the raw data were transformed to z-scores prior to analysis. The pooled correlation matrix of variables was analyzed using both PCA and shear-PCA (R-mode analyses). As the results of both techniques were similar I will present the shear-PCA and indicate differences between analyses where they occurred.

Two components from the shear-PCA described greater than 90% of the total variation among variables and had eigenvalues close to or greater than average eigenvalues ($\bar{l} = 1$ for correlation matrix analyses) (Table 1.1). Based on component correlations and the percent variation due to each trait, the first two components described most of the variation among variables and were significantly correlated with the original data (Table 1.1).

The first principal component described 78% of the total variation in the correlation matrix. Eigenvector loadings for PC1 deviated significantly from isometry ($p < 0.001$) and were significantly correlated with the allometric loadings of each variable on shell length ($r = 0.94$, $p < 0.05$). I thus interpreted the first component as the size-allometry axis: variation in shape attributable to allometric growth.

Multigroup PCA revealed small but significant divergence among samples in the size-allometry axis. The angles between PC1 from pooled shear-PCA and PC1's based on single group analyses were: 2.6° (Año Nuevo Island), 7.3° (Santa Cruz Island), 9.3° (Natividad Island), and 5.7° (Guadalupe Island) (all angles $p < 0.01$ from zero). Although group divergence in size-allometry was statistically significant, the magnitude of these differences was small and not likely to confound the use of PC1 as a measure of size. Group differences in allometric size resulted from statistical interactions among the allometry of traits within samples (Table 1.2).

Component two described 13% of the total variation (Table 1.1). Eigenvector loadings and component correlations indicated that this axis contrasts variation among individuals in the number, diameter, and spacing of tremata. Variable loadings indicated that as tremata increase in number, relative trema diameter and spacing decreases. These traits covaried in a manner consistent with the initial observations on the ontogeny of black abalone and were interpreted as describing ontogenetic variation among individuals.

Multigroup PCA revealed significant group divergence in the second principal component (PC2) (all $p < 0.01$). The angles between PC2 derived from pooled and single group analyses were: 16.7° (Año Nuevo Island), 22.6° (Santa Cruz Island), 19.4° (Natividad Island), and 18.4° (Guadalupe Island) (all angles $p < 0.01$ from zero). This pattern illustrates two points: 1) the pooled analysis describes variation due principally to the extreme samples (high latitude Año Nuevo Island and low latitude Guadalupe Island), and 2) PC2 is not simply a measure of size-independent shape but also describes variation *among* samples. As the shear-PCA removes intergroup size differences, PC2 describes divergence in shape that is independent of allometric growth.

The shear-PCA produced greater group discrimination than conventional PCA. Based on analysis of variance of second axis principal component scores,

shear-PCA produced larger F-ratios based on size-independent shape ($F = 222.0$, $p < 0.01$) than conventional PCA ($F = 219.5$, $p < 0.01$). In essense the shear-PCA removed intergroup differences in shape on the first axis ($F = 10.7$, $p < 0.01$ on PC1; $F = 0.0$, $p = 1.0$ on shear PC1) and placed this residual variation into the second axis, thus enhancing group discrimination.

Multivariate ontogenetic trajectories were calculated using model I linear regression analysis on first and second axis component scores as measures of allometric size and shape, respectively (Figure 1.3). Shape was assumed to be dependent on size. Within groups, trajectories described the average path of trema ontogeny with increasing allometric size. As individuals were derived from mixed cross-sectional samples, trajectories contrasted variation in shape resulting from variation in allometric growth and age.

The allometric size at the onset of muscle scar development was estimated by a series of second-order curvilinear regressions of PC1 scores on the proportion of scar nacre in the muscle attachment area (all $R^2 > 40\%$). Using the regression equations I estimated the size at which the proportion of scar cover was equal to 0.5 in each sample (Figure 1.4).

Analysis of covariance of ontogenetic trajectories indicated significant divergence among trajectory slopes. All slopes were significantly different from one another (all $p < 0.001$) and varied inversely with latitude. Ontogeny among individuals from lower latitudes (e.g., Guadalupe Island) resulted in more small, closely-spaced tremata when compared to the ontogeny of individuals at higher latitudes (e.g., Año Nuevo Island), which possessed fewer, larger, more distantly spaced tremata at comparable allometric sizes (Figure 1.3). This dissociation of allometric size and shape covaried with a shift in the maximum size of individuals, shells were larger at higher latitudes, and the size (and possibly age) at which muscle scar development begins. The muscle scar develops at smaller sizes in low

latitude populations when compared to high latitude populations (Figures 1.3 and 1.4).

Biological Interpretation

Latitudinal dissociation of size and tremata development is associated with a latitudinal habitat shift: individuals in northern populations occur in the mid- and low-intertidal zones while individuals in southern populations are found in the low intertidal and shallow subtidal zones (chapter 4). Based on these observations I propose that heterochronic processes are dissociating trema development from shell growth rates in response to geographic variation in intertidal habitat.

Discussion

The analytical methods presented were successful with respect to their initial goals: the multivariate description of ontogeny and heterochronic change. Using a combination of PCA and linear regression, I obtained metrics of allometric size and developmental shape and described their relationship by calculating ontogenetic trajectories. The methods measured the onset of a developmental event relative to size, and discriminated among group trajectories. Below I discuss the interpretation of PCA size and shape and its usefulness in ontogenetic studies. I conclude by examining future prospects of multivariate techniques as they apply to the measurement of heterochrony.

Size and Shape

A conceptual difficulty associated with the use of PCA towards the elucidation of ontogenetic processes is the biological interpretation of PCA size and shape. The question is: to what extent is our biological understanding of organismal size and shape consistent with their PCA metrics?

Body size is not a single character, such as length, mass, or volume; size is an unmeasured latent trait. Our goal is to obtain an estimate of size by calculating a general size factor. As organisms increase in size the absolute magnitude of most morphological traits increase. General size, therefore, is defined as a linear combination of variables that most parsimoniously accounts for observed covariances or correlations among traits of organisms of varying sizes (Bookstein et al., 1985). R-mode PCA extracts linear contrasts of variables that account for the largest proportion of variation among trait dispersion. Thus, with respect to general size, PCA is consistent with the biological definition of the term.

Most of the controversy associated with the use of PCA size as a measure of general size is based on an ignorance of allometry. Few organisms exhibit traits that

increase isometrically with size (Sprent, 1972; Schmidt-Nielsen, 1984). As a result, variation in size is inextricably associated with changes in shape (Gould, 1966). Therefore, a measure of general size *by definition* contains variation in shape. Relabeling of PC1 as the size-allometry axis emphasizes this notion (Shea, 1985). In taxonomic studies the inseparability of size and allometric growth on PC1 is regarded as a disadvantage, as evidenced by the multitude of techniques designed to remove size (e.g., Lemen, 1983). From an allometric perspective, however, the merging of size and allometric shape on PC1 is the *goal* of the analysis (Shea, 1985).

Another source of confusion regarding PCA relates to the multigroup problem: intergroup differences in size introduce intergroup variation in shape into the size-allometry axis. When intergroup size differences are significant, results of shear-PCA are distinct from those of conventional PCA and group discrimination is significantly enhanced (Humphries et al., 1981; Bookstein et al., 1985). To the extent that patterns of group size-allometries are similar, shear-PCA is an effective technique for removing these intergroup differences. However, the reliance of shear-PCA on similar intergroup size variation is a major problem of the method. When groups diverge significantly in their pattern of size allometry, shear-PCA would calculate non-sensible components. Further, the level of PC1 divergence at which problems would occur is unknown. In my intraspecific example, PCA and shear-PCA produced similar results, largely due to small differences in allometric size among samples and little divergence on the size-allometry axis. Analysis of interspecific divergence is likely to involve more significant differences in size and patterns of within-group size. For these reasons shear-PCA should always be examined in relationship to single group PCA's.

A more difficult question is to what extent PCA axes beyond the first measure biological attributes of shape. As with size, shape is an unmeasured latent trait: the orientation of a vector in an attribute space after the removal of scale

(Mosimann, 1970). Studies of ontogeny require a metric of development, a measure of trait change through time. Because the goal is to separate the timing of trait development from allometric growth (Gould 1977: 235-238), metrics of size and shape that are biologically uncorrelated are needed. The question is: are there aspects of development uncoupled from allometric growth?

The concept of dissociation of developmental events (Gould, 1977) and onset-offset signals (Alberch et al., 1979) emphasizes that some aspects of development are uncoupled from allometric growth. Moreover, several studies illustrate biological independence of growth and development of traits (Atchley, 1984; Atchley and Rutledge, 1980; Atchley et al., 1981) and heritability of PCA size and shape (Atchley, 1983). The problem with the use of PCA to obtain a metric of shape is due to the required orthogonality of PCA axes: shape variation is extracted independent of allometric growth *regardless* of whether such a relationship exists. That is, if there is little structure in the data beyond that of size-allometry, components subsequent to PC1 will describe trivial variation that is not related to biological processes. The only solution to this dilemma is a thorough understanding of the system under investigation and a biological interpretation of axes on a case-by-case basis.

Future Prospects

Our methods are far from complete with respect to measuring the full gamut of heterochronic relationships. One obvious omission is the incorporation of developmental time into our size-shape relationships. Implicit in the concept of heterochrony is the notion of time. The terms hypermorphosis, progenesis and displacement *by definition* describe shifts in timing. If we ignore time we ignore the growth rate of morphological characters, which is another mechanism whereby heterochrony operates (e.g., Shea, 1983). Unless we label our definitions with

morphological terms (e.g., allometric neoteny; see McKinney, 1988a), we need to incorporate age into our multivariate analyses.

I have presented a technique that incorporates developmental events potentially resulting from timing into a morphological framework, i.e., the location of events on ontogenetic trajectories. On the average, body size is a predictor of 75% of the variation in an organisms morphology, life history, and behavior (Calder, 1984; Peters, 1984). Therefore, in many cases, size *per se* is perhaps of more interest than age, and my approach may be sufficient. Several other approaches are: 1) plotting age against size-allometry and shape axes; 2) combining age, size, and shape into a three dimensional plot (Alberch et al., 1979); or, 3) using age as a variable in a factor-analytic approach in which axes are rotated to describe common associations among traits. In order to assess the importance of timing in heterochrony, empirical studies that describe relationships between developmental time and multivariate form are needed.

Finally, it cannot be overstated that any interpretation of morphological divergence resulting from heterochrony must be viewed in a phylogenetic context. Ancestor-descendent relationships are implict in the terminology of heterochronic outcomes (Fink, 1982, 1988). To determine the direction of evolutionary change, the spatial relationships of ontogenetic trajectories need to be supplemented by a phylogenetic analysis of character states (e.g., Wiley, 1981). This procedure amounts to integrating a cladogram with PCA. Bookstein et al (1985: 206-211) present an example of this approach.

In conclusion, I would like to emphasize that a multivariate analysis of form is only a first step in the biological investigation of heterochrony. If heterochrony is limited to morphological terms, then it serves only as a mechanistic redescription of evolutionary change. The ultimate significance of heterochrony must lie in its relation to selective factors promoting dissociations of developmental events and

their relationships to ecological processes (Gould, 1977; Fischer, 1985; McKinney, 1986, 1988b).

Table 1.1. Results of shear-PCA on 206 individual black abalone from four localities. Component correlations significantly different from zero are indicated in boldface ($p < 0.05$). Measured variables are diagrammed in Figure 1.2.

	Eigenvectors			Component Correlations			Percent Variation		
Variable	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Length	0.42	0.09	-0.05	**0.99**	-0.08	-0.03	97.3	0.2	0.1
Width	0.42	0.04	-0.08	**0.99**	-0.04	-0.05	97.2	0.0	0.2
Height	0.41	0.20	-0.10	**0.96**	**-0.19**	-0.06	92.2	0.5	0.4
Trema Number	0.23	0.74	0.16	**0.54**	**-0.69**	0.09	28.9	67.3	0.9
Trema Length	0.42	0.14	-0.13	**0.98**	-0.13	-0.07	96.0	0.5	0.5
Trema Spacing	0.36	-0.31	-0.48	**0.85**	**0.29**	**-0.28**	72.7	9.6	7.9
Trema Diameter	0.34	-0.52	0.84	**0.80**	**0.49**	**0.49**	64.6	10.2	24.2
Eigenvalues	5.49	0.88	0.34						
Percent Variation	78.4	12.6	4.9						

Table 1.2. Allometric loadings of variables on shell length for four samples of black abalone. Divergence in allometric size among groups is due to interactions among allometric relationships of traits within samples. All loadings are significantly different from zero at $p < 0.01$.

	Sample Location				
Variable	Año Nuevo Island	Santa Cruz Island	Natividad Island	Guadalupe Island	All Data Pooled
Width	1.11	1.07	1.01	1.07	1.08
Height	1.25	1.21	1.35	1.38	1.24
Trema Number	0.17	0.18	0.26	0.40	0.26
Trema Length	1.08	1.10	0.99	1.12	1.11
Trema Spacing	0.94	0.83	0.71	0.67	0.67
Trema Diameter	0.59	0.75	0.52	0.45	0.61
Sample size	54	47	41	64	206

Figure 1.1. Allometry in black abalone from Santa Cruz Island, California. The relationship between variation in shell length and six morphological variables is presented. See Figure 1.2 for a diagram of variables. Table 1.2 lists the allometric loadings of each variable on shell length

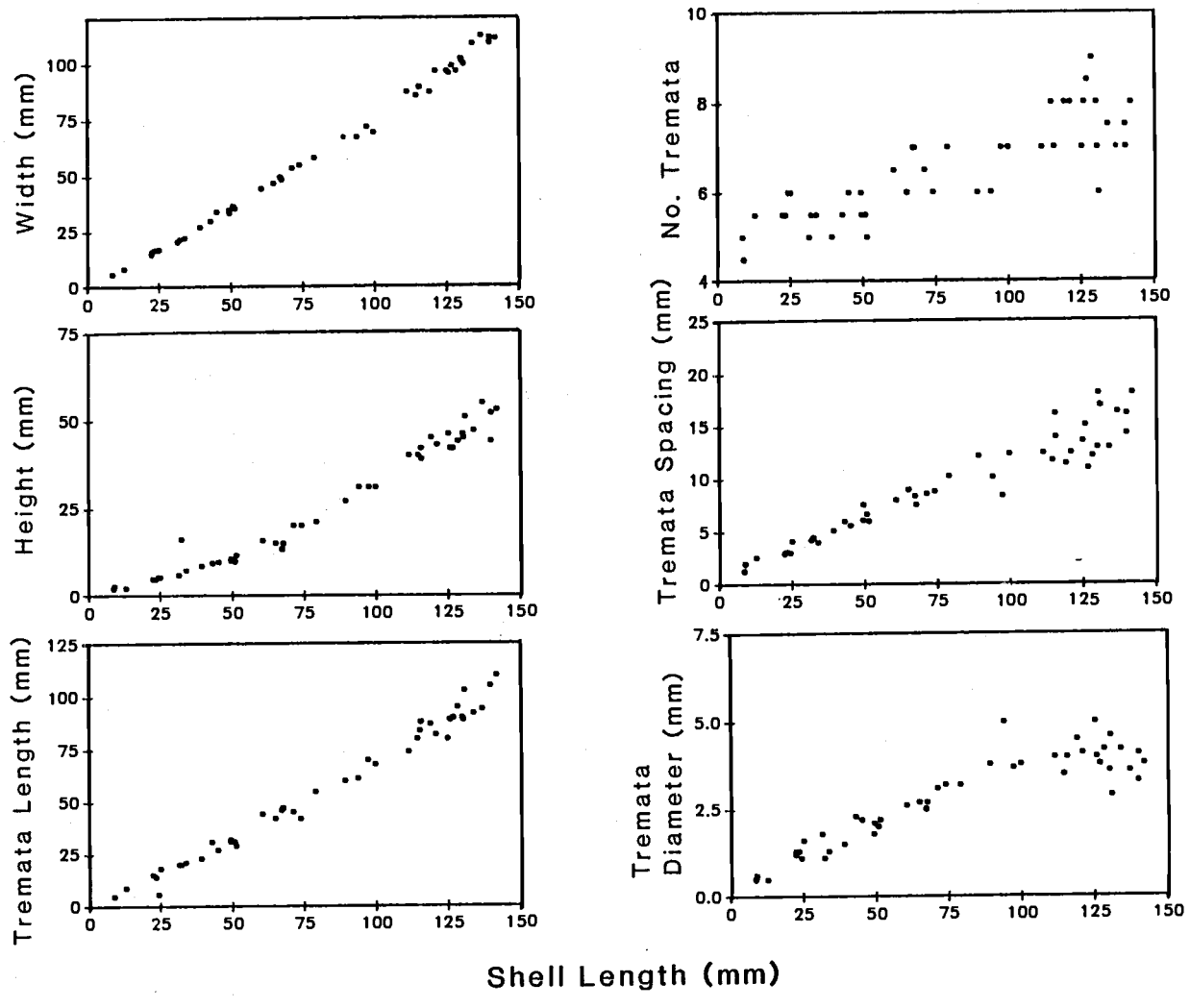

Width (mm)
Height (mm)
Tremata Length (mm)
No. Tremata
Tremata Spacing (mm)
Tremata Diameter (mm)
Shell Length (mm)

Figure 1.1

Figure 1.2. Morphometric variables used to describe the size and shape of black abalone shells.

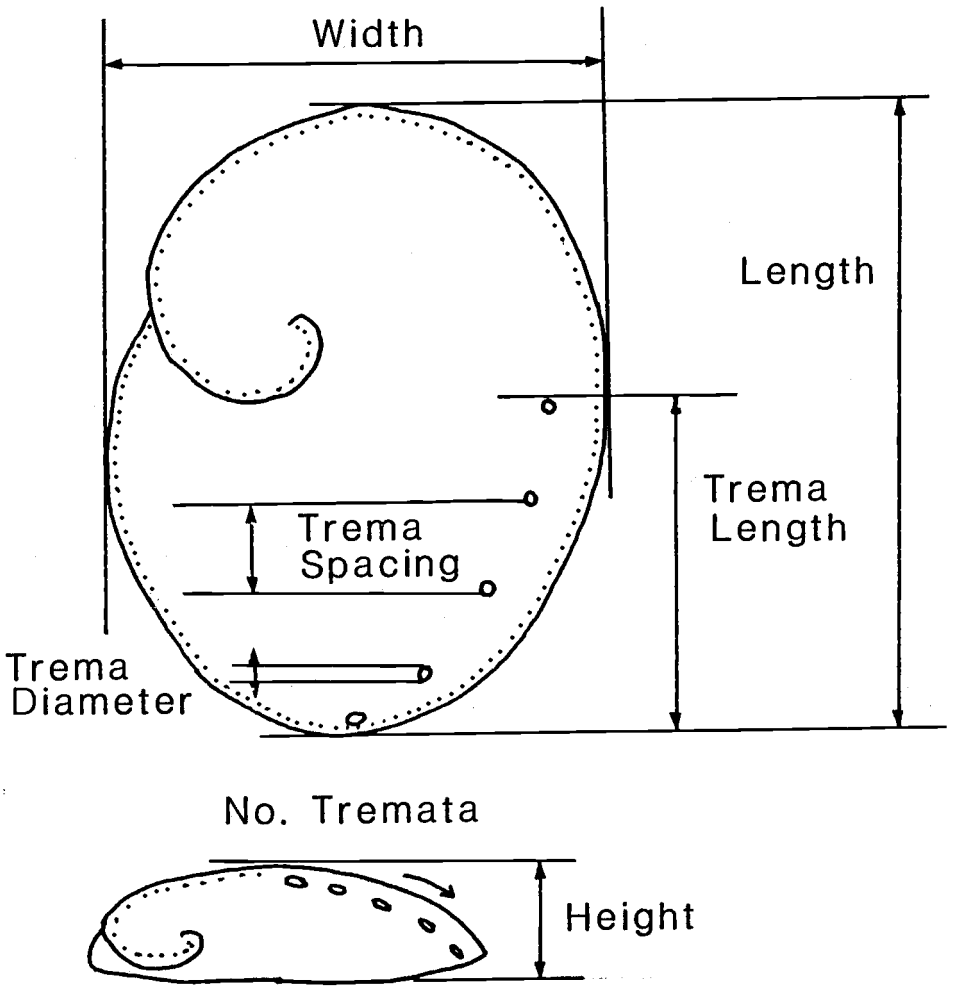

Width
Length
Trema
Length
Trema
Spacing
Trema
Diameter
No. Tremata
Height

Figure 1.2

Figure 1.3. Geographic variation and heterochrony in the black abalone. Ontogenetic trajectories for four populations based on first (PC1) and second axis (PC2) principal component scores are presented in relation to the size at the onset of muscle scar development (see text), which is denoted by arrowheads on the length of trajectories. Population samples are denoted by symbols: Guadalupe Is. (open circles), Natividad Is. (closed circles), Santa Cruz Island (open triangles), and Año Nuevo Island (closed trinagles). Analysis of covariance revealed significant divergence among populations in trajectory slopes: the rate of change of tremata development relative to general size. Low latitude populations (e.g., Guadalupe Island) display accelerated morphological development relative to high latitude populations (e.g., Año Nuevo Island). Dissociation of allometric size and tremata shape covaries with maximum size and a shift in the size at which muscle scar development begins.

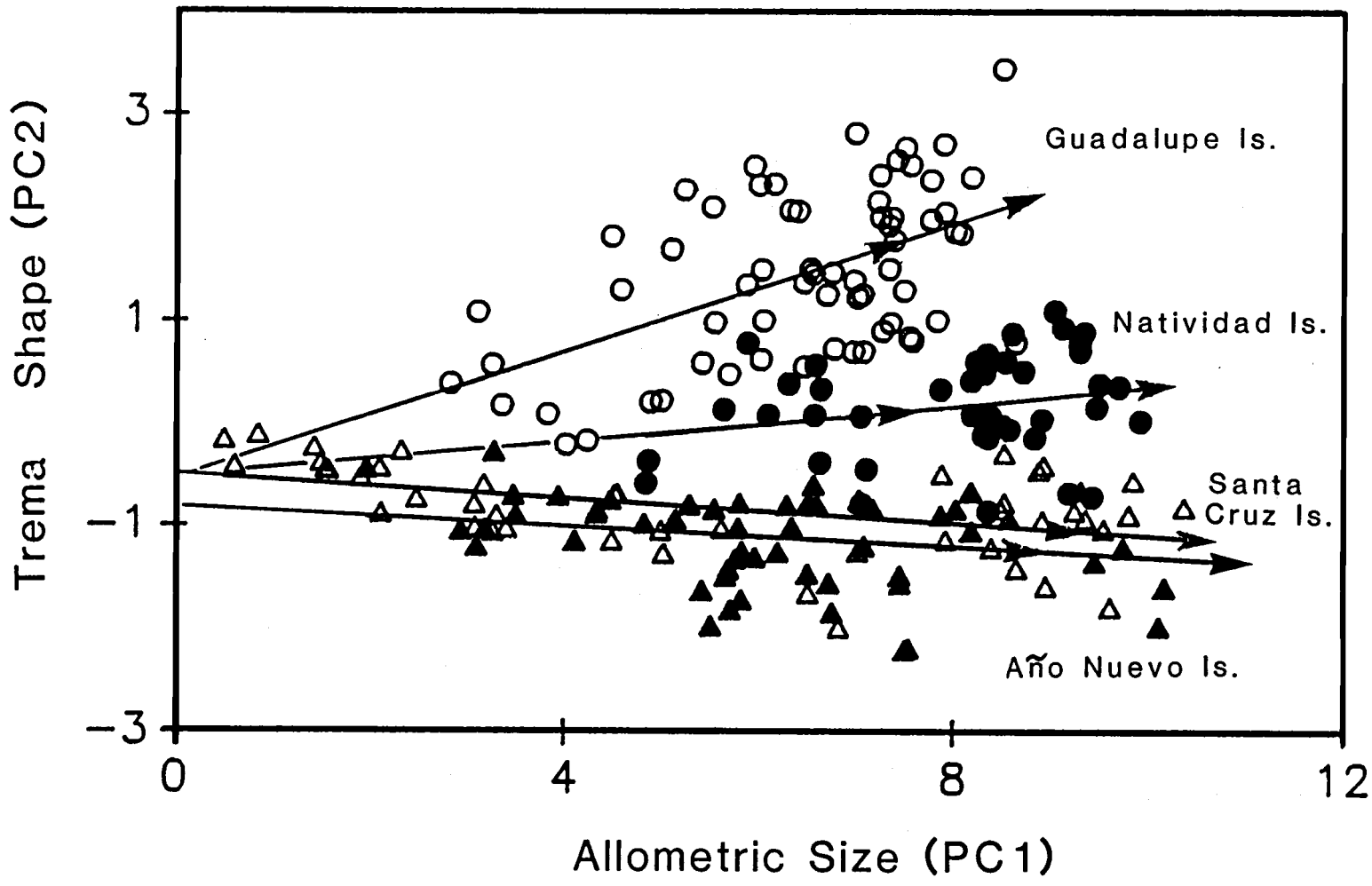

Trema Shape (PC2)
3
1
−1
−3
0
4
8
12
Allometric Size (PC1)
Guadalupe Is.
Natividad Is.
Santa Cruz Is.
Año Nuevo Is.

Figure 1.3

Figure 1.4. Relationships between allometric size and muscle scar development in four populations of black abalone. The size at the onset of scar development was estimated by second-order curvilinear regression analysis of scar cover on first axis principal components scores (PC1), which are shown for each sample.

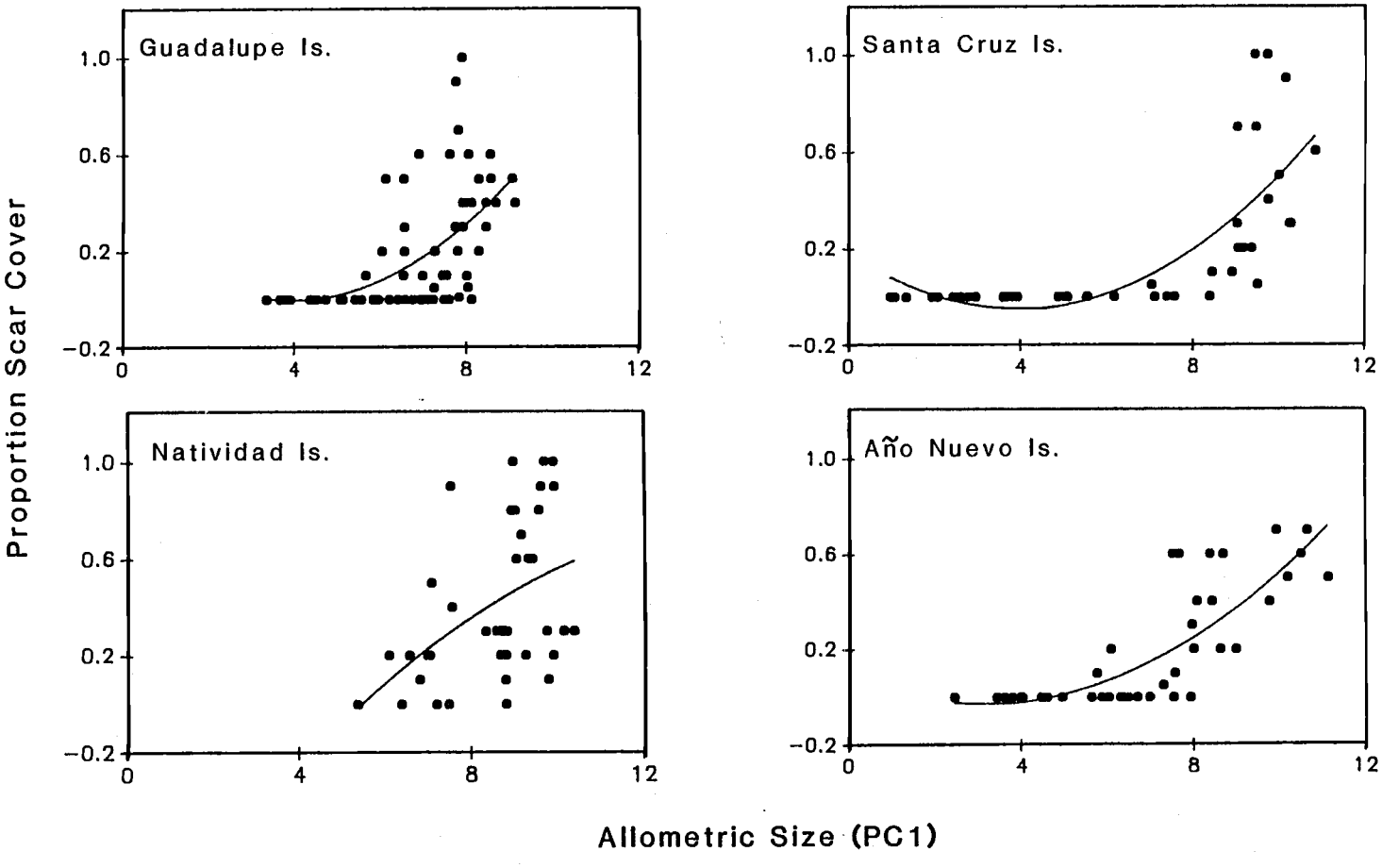

Guadalupe Is.
Santa Cruz Is.
Natividad Is.
Año Nuevo Is.
Proportion Scar Cover
Allometric Size (PC1)
1.0
0.6
0.2
-0.2
0
4
8
12

Figure 1.4

Chapter 2

GEOGRAPHIC VARIATION IN THE AVAILABILITY OF DRIFT MACROALGAL FOOD TO BLACK ABALONE: CAUSES AND CONSEQUENCES

Abstract

Drifting macroalgae is an important food resource for a wide variety of marine organisms. Despite its importance, very little is known about factors which influence the availability of drift algae to individual herbivores. In this chapter I focused on geographic variation in the availability of drift macroalgae to a rocky intertidal herbivore: the black abalone, *Haliotis cracherodii*. Black abalone are highly dependent on drift algae as a food source and spatial and temporal variation in drift algae is likely to have a strong influence on abalone distribution and abundance. Accordingly, in this study I examined the abundance of drift algae along three spatial gradients: 1) shore-level, 2) wave exposure, and 3) latitudinal.

Along shore-level gradients within study sites on Santa Cruz Island and Año Nuevo Island abalone abundance was significantly correlated with the availability of drift algae. In contrast, among sites along wave-exposure gradients, abalone abundance was not associated with drift algal availability. Black abalone feeding preference among taxa of drift algae differed between study sites. As a result, the diet of abalone varied latitudinally in conjunction with geographic variation in the species richness of drift algae.

The composition and abundance of drift algae exhibited marked spatial and temporal variation in availability to intertidal black abalone. The abundance of drift algae was largely controlled by the standing crop of local

algal stands, the extent of water movement, and the topography of the intertidal habitat.

Introduction

Kelp forests are a dominant feature of rocky temperate shores and constitute one of the world's most productive ecosystems. As in terrestrial forests, most kelp-derived productivity is transported out of the system in the form of drifting plants or detached pieces of algae (Gerard, 1976). The amount of drift algae produced in kelp forests can be tremendous, often exceeding 10 kg/m^2 (Foster and Schiel, 1985), and is an important food resource for a wide variety of organisms (e.g., bacteria: Koop and Griffiths, 1982; crustaceans: Gore et al., 1981; echinoderms and polychaetes: Bedford and Moore, 1984; fish: Kulczycki et al., 1981). Despite its importance, very little is known about factors which influence the availability of drift algae to individual herbivores. This paper focuses on geographic variation in the availability of drift macroalgae to a rocky intertidal herbivore: the black abalone, *Haliotis cracherodii* Leach 1814.

The black abalone is a common intertidal inhabitant of the eastern Pacific coast. Abalone are sedentary and feed almost exclusively on drift algae, which are captured by extending the anterior portion of the foot into the water column (Cox, 1962; Shepherd, 1973). Because black abalone seldom actively search for food and often occur in dense aggregations, they are highly dependent on drift algae as a food source (Wright, 1971; Douros, 1987). As a result, spatial and temporal variation in drift algae is likely to have a strong influence on the distribution and abundance of black abalone.

Numerous factors are known to influence the abundance of drift algae in a particular area. Of primary importance is the biomass of live plants: drift algae exhibit strong seasonal variation which parallels the standing crop of local algal stands (ZoBell, 1971; Gerard, 1976; Ebeling et al., 1985; Harrold

and Reed, 1985; Virstein and Carbonara, 1985). However, the actual transport of drift algae is caused by water movement, which thus modifies its local availability (Schwenke, 1971; Norton and Mathieson, 1983). Additional factors, which may affect the abundance of drift algae on a local scale, include the topography of the depositional area (ZoBell, 1971), the density of live plant material (Virstein and Carbonara, 1985), and interactions between drift supply and the direction of local currents (Schwenke, 1971).

Previous studies have focused exclusively on weight per unit area as a measure of drift algal abundance (e.g., ZoBell, 1971; Ebeling et al., 1985; Harrold and Reed, 1985). However, algal weight may not be an adequate measure of the *availability* of drift algae to herbivores. For example, a weight metric would rank equally the frequent supply of small pieces of algae and the infrequent deposition of huge algal rafts, although these two conditions may have different levels of importance to a sedentary herbivore. In particular, the *density* (number of food items per unit area) of drift in a particular area could have a strong influence on the spatial distribution of herbivores. Moreover, the *frequency* (number of food items per unit time) of drift deposition could have strong effects on the growth and reproduction of herbivores.

This paper represents a portion of a larger study focused on ecological factors influencing geographic variation in the morphology, growth, distribution, and survivorship of the black abalone. In order to relate causal factors to geographic patterns it is necessary to examine their covariation along several spatial scales (see Schiel and Foster, 1986). Accordingly, this study examines the abundance of drift algae along three spatial gradients: 1) shore-level, 2) wave exposure, and 3) latitudinal. My primary goal was to identify physical and biological factors which influence the weight, density,

and frequency of drift algal deposition in the rocky intertidal zone. I assessed the influence of variation in drift algae on black abalone by examining relationships between algal abundance and abalone feeding preferences and distributional patterns. The relationships of these parameters to abalone growth will be examined elsewhere (Tissot, in preparation).

Materials and Methods

Field Methods

The two study areas were located on the west end of Santa Cruz Island (34° 00' N, 114° 50' W), 25 km east of Santa Barbara, and on Año Nuevo Island (37° 6' N, 122° 20' W), 65 km south of San Francisco (Figure 2.1). I located two permanent intertidal transects in two general sites at each study area that differed in their exposure to ocean waves. On Santa Cruz Island (hereafter "SCI") the "protected" site was located 1 km SE of Fourney Cove on the south side of the Island; the "exposed" site was located 0.2 km NE of Fraser Point on the north side of the Island (Figure 2.1). The exposed site was open to the prevailing N-NW ocean swell and wind while the protected site was largely sheltered from N-NW swells but received S-SW swells during the summer and early fall. On Año Nuevo Island (hereafter "ANI") the "exposed" site was located on the SE corner of the island while the "protected" site was located on the NW side. Although the prevailing ocean swells were from the N-NW and more directly approached the protected site, the transects occurred on eastern facing slopes and were sheltered behind several large rock outcrops. In contrast, the exposed side of the island was directly open to S and SW swells, which occurred in the summer and fall, and N-NW swells wrapping around the southern extent of the island (Figure 2.1).

Within each study site at each island I established two intertidal transects in areas inhabited by black abalone. The one-meter wide transects extended from the high (2.0 m above MLLW) to the low-intertidal (-0.5 m below MLLW) at varying slope and were between five and 25 m in length. On SCI, transects were located in surge channels bounded by vertical walls of irregular shape and covered a total area of 36 m^2. Transects on ANI covered

74 m^2 and occurred on flat, layered mudstone with a 20 degree E-SE slope (see Weber, 1981). I monitored transects on a quarterly basis (winter, spring, summer, fall) at SCI and three times a year (winter, spring, fall) at ANI for periods of 5-14 d. The study period spanned two years: spring 1988 to winter 1990.

I measured black abalone abundance along intertidal transects by counting the total number of abalone visible in one m transect intervals (i.e., one square meter) during each survey.

I measured water movement daily during surveys using dynamometers similar to those described by Palumbi (1984). Along each transect 3-6 dynamometers were systematically positioned at several tidal elevations and sampled during low tides. Dynamometers measure maximal wave forces. I assumed that all forces were due to drag, and converted them to maximal water velocity using formulae described in Vogel (1981).

I measured the amount of drift algae accumulated in each transect area during a 24 hr period at low tide. Pieces of algal debris were located along permanently affixed transects using both horizontal and vertical coordinates, identified to species, and weighted to the nearest gram using a Pesola spring scale. The weight of large algal rafts (> 1 kg) was estimated by taking 3-4 measurements on subsamples and extrapolating. Individual drift items were counted as distinct if they occurred greater than 10 cm from adjacent pieces or if they were of different taxa. *Phyllospadix*, which was not eaten by black abalone, and algae weighing less than one gram were not measured. I also noted pieces of algae held by abalone.

I estimated the abundance of drift algae with three metrics: 1) *weight* was calculated by summing the total weight of drift algae accumulated along a transect divided by the area of the transect (g/m^2); 2) *density* was

calculated by counting the number of pieces of drift items along a transect relative to the total transect area (no./m^2); and 3) *frequency* was calculated by counting the number of times drift algae was present along the transect relative to the total time surveyed. To quantify intertidal patterns of drift deposition, frequency was measured by counting the number of days drift was present at 0.25 m vertical intervals relative to the total number of days sampled. Among-survey patterns of drift frequency were calculated by counting the number of times drift was present at each one meter transect interval per day relative to the total number of interval-days possible.

I measured the standing crop of giant kelp (*Macrocystis*) on SCI by measuring the area of kelp surface canopies using aerial infrared photographs taken during the summer months of 1987-1989. These photographs, obtained from Ecoscan (Freedom, CA), primarily recorded the offshore canopy of *Macrocystis pyrifera* and inshore canopies of *Egregia menzesii*. I traced kelp canopies from projected slides using a 1:10,000 scale and digitized them using an IBM personal computer.

In order to estimate the source of drift algal material I initiated two kelp tagging experiments on SCI in July 1989. In both experiments pieces of *Macrocystis*, 0.3 m in length, including several blades and pneumatocysts, were freshly cut from live kelp plants and tagged by tying a marked piece of brightly colored plastic flagging to the middle of the stipe. In the first experiment, samples of 100 tagged blades were released by boat at six locations around the protected coast study site. Four samples were released at the outer edge of *Macrocystis* beds (100 m offshore): two were located near the study site, but 300 m apart, one was 0.5 km east of the study site, and another was 0.5 km west (Figure 2.1). The two final samples were released at the inner edge of the *Macrocystis* beds (50 m offshore), directly inshore from

the outer kelp-bed locations (Figure 2.1). The second experiment involved an additional 250 blades, 125 of which were released at the outer edge of the *Macrocystis* forest near the study site, and 125 were released at the inner edge, directly inshore. For five days following their release I intensively searched the study site for tagged kelp at low tides with two additional observers (total beach distance 0.50 km).

I examined the feeding preference of black abalone by calculating algal availability relative to observations of feeding abalone. Food availability was estimated using the total number of drift items for each species. Selection by abalone was estimated by summing the number of feeding observations for each drift species relative to the total number of all feeding observations. I calculated preference using the method described in Johnson (1980) which uses the difference between ranked food items as a measure of resource selection. The ranking procedure is superior to other methods of examining resource preference (e.g., electivity indices) because the results are independent of the number of food items included in the analysis (Johnson, 1980).

Data Analysis

I examine the statistical significance of differences along exposure gradients and among surveys in water movement and algal abundance using a nested two-way analysis of variance (ANOVA). This procedure tested for seasonal and interannual variation between protected and exposed sites at each island. Individual transects served as nested replicates for each study area. Because tests of significance of nested ANOVAs are inexact when sample sizes are unequal (Sokal and Rohlf, 1981), ANOVAs were conducted on the mean values of variables. Prior to ANOVA, samples were examined using Bartlett's test for homogeneity of variances. In the few cases where

variances were unequal a transformation was chosen that minimized differences among sample variances. Significant main effects were further examined using a Student-Newman-Keuls multiple range test (Sokal and Rohlf, 1981). Differences between SCI and ANI were analyzed using a Mann-Whitney two-sample rank test.

Relationships between the abundance of abalone and drift algal were examined using parametric correlation analysis. For each transect the proportion of the total number of abalone occurring in each one meter interval was compared to corresponding average values of algal abundance.

Results

During the course of eight surveys on Santa Cruz Island (SCI), 729 pieces of drift algae were examined in relation to 688 dynamometer readings on 52 observation days. On Año Nuevo Island (ANI), 743 pieces of drift algae and 229 dynamometer readings were recorded during six surveys on 27 observation days.

Abalone abundance

At both study sites the intertidal distribution of feeding abalone was significantly correlated with the intertidal abundance of drift algae by weight (SCI: $r = 0.972$, $p < 0.01$; ANI: $r = 0.707$, $p < 0.05$). Within transects there were significant correlations between the abundance of abalone and drift algae at both sites (Table 2.1a). On SCI, abalone abundance was significantly correlated with both the weight and number of drift items but not their frequency. On ANI, the abundance of abalone was significantly correlated with the weight of drift algae along transects but not their number or frequency. Among transects there were no significant correlations between abalone density and drift algal abundance at both study sites (Table 2.1b).

Drift Macroalgae: *composition*

The composition of drift algae varied among study sites and along exposure gradients within sites (Tables 2.2 and 2.3). At SCI, drift algae was composed of 11 taxa. However, 90% of the drift, both by number of occurrences and by weight, was composed of two taxa, *Macrocystis pyrifera* and *Egregia menzesii* (Table 2.2). In contrast, on ANI, drift algae was comprised of 22 taxa, with 10 taxa comprising 90% of the drift (Table 2.2). In general there was moderate correspondence between measures of drift algal weight, density, and frequency at both study sites (multiple $r^2 = 0.28$, $p <$

0.01). Exceptions to this trend included *Botryoglossum*, which occurred frequently in numerous small pieces, and *Nereocystis luetkeana* which occurred infrequently in large rafts (> 5 kg). At both islands the number of taxa of drift algae varied along exposure gradients: species richness was 36% and 18% higher at SCI and ANI, respectively, on exposed relative to protected transects (Tables 2.2 and 2.3).

The weight of individual pieces of drift algae varied over four orders of magnitude (Figure 2.2). At both sites pieces of drift ranged from one gram in weight (the smallest size measured) to 10+ kg rafts of *Macrocystis* (SCI) and *Nereocystis* (ANI). The average size of drift algae was significantly larger at ANI (259 grams) than SCI (133 grams) (Mann-Whitney, $p < 0.01$).

For several morphologically complex species, the drift was composed of different components of the plant. For example, on SCI drift *Macrocystis* was composed primarily of blades and stipes (74.6% by weight), and secondarily by blades only (10.3%), stipes (7.7%), and holdfasts (7.4%). Similarly, on ANI, drift *Laminaria setchellii* was composed of blades (46.5% by weight), whole plants (32.1%), and stipes (21.4%).

Spatial Variation: *shore-level gradients*

Along shore-level gradients there were marked spatial variation in maximal water velocities and the deposition of drift algal material. Dynamometers indicated that water velocities varied irregularly along intertidal transects in exposed and protected sites at each island (Figure 2.3). Along exposed transects at SCI water velocities were greater at high relative to low intertidal positions. In contrast, along protected transects at SCI, and all transects at ANI, water velocities varied irregularly with intertidal position.

In a similar manner the distribution of drift algae displayed irregular distributions along exposure gradients at both sites (Figure 2.4). At protected sites at SCI drift algae was more abundant by weight and density in the low- and mid-intertidal regions. However, based on the frequency of deposition, drift occurred more evenly. In contrast, on exposed transects at SCI, infrequent deposition of large *Macrocystis* rafts in the high intertidal resulted in high abundance of drift algae by weight in both the mid- and high-intertidal. However, drift algae occurred more frequently and at higher density in the low- and mid-intertidal regions.

The intertidal distribution of drift algae on ANI was distinct from patterns on SCI (Figure 2.4). In protected areas, drift algae was more abundant by weight in the mid-intertidal, due to the occasional deposition of large *Nereocystis* rafts, but occurred at higher densities and more frequently in the upper mid-intertidal. In contrast, along exposed transects, drift algae were more abundant by weight and number in the mid-intertidal but occurred frequently across both mid- and high-intertidal regions.

Overall, drift algae on SCI occurred significantly lower on the shore (0.43 m above MLLW) than on ANI (0.88 m above MLLW) (Mann-Whitney, $p < 0.01$). There were no significant correlations between the intertidal distribution of drift algae and maximal water velocities at either site (SCI: $r = -0.46$, $n = 11$, $p > 0.05$; ANI: $r = 0.01$, $n = 16$, $p > 0.05$).

Spatial Variation: *wave exposure gradients*

Overall, average maximum water velocities were higher in exposed areas at both islands relative to protected sites (Figures 2.3 and 2.5). Two-way ANOVA indicated that water velocities on SCI were significantly higher on exposed relative to protected transects (Tables 2.3 and 2.4). Although exposed areas on ANI had higher average velocities than protected areas, a

significant interaction between study area and survey indicated that exposure gradients varied seasonally on ANI (see Temporal Variation below).

In general, the abundance of drift algae on all measures was greater in exposed relative to protected areas at both islands. On SCI, drift algae occurred in significantly greater numbers in exposed relative to protected areas (Tables 2.3 and 2.4). Although drift algae were higher by weight and frequency on exposed relative to protected transects (Table 2.3), a significant interaction between study area and survey indicated seasonal variation in these measures of drift abundance along exposure gradients (Table 2.4; see Temporal Variation below).

On ANI, two-way ANOVA indicated that drift algae occurred in greater numbers and frequency on exposed relative to protected areas (Tables 2.3 and 2.4). However, due to the occasional deposition of large *Nereocystis* rafts on protected transects, there were no significant differences in the abundance of drift algae by weight along exposure gradients (Table 2.4).

On SCI, there were significant correlations between average maximal daily water velocities and average drift density ($r = 0.32$, $p < 0.01$) and frequency ($r = 0.35$, $p < 0.01$): drift algal abundance increased with increasing water velocities (Figure 2.6). Similarly, on ANI there was a significant correlation between drift frequency and water velocity ($r = 0.30$, $p < 0.05$) but not with drift weight or density (both $p > 0.05$).

Spatial Variation: *latitudinal gradients*

Drift algae occurred at significantly greater frequencies on SCI (0.30) relative to ANI (0.20) (Mann-Whitney, $p < 0.05$). However, there were no significant differences between islands in the weight or density of drift algae (Mann-Whitney, both $p > 0.05$), although SCI had both greater mean

weights and number of drift plants (21.0 g/m^2/d and 0.43 pieces/m^2/d) than ANI (14.3 g/m^2/d and 0.33 pieces/m^2/d).

Temporal Variation: *short-term patterns*

The deposition of drift algae in the intertidal zone displayed marked daily variation. On SCI, where these patterns were most pronounced, algae accumulated in irregular pulses in which the weight of drift fluctuated 3-5 fold over the course of several days. During the summer and fall of 1988, and in spring 1989, algal pulses generally followed increases in water motion interrupted by a one to three day calm period (Figure 2.7). During summer 1989, a pulse occurred at peak water motion following a four day increase in wave height. In contrast, on ANI there were no relationships between drift algal pulses and changes in water motion (Figure 2.7).

Temporal Variation: *long-term patterns*

Islands differed dramatically with respect to the extent of seasonal and interannual variation in the amount of drift algae (Figure 2.8). On SCI, two-way ANOVA indicated significant seasonal variation in the frequency, number, and weight of drift algae (Table 2.4). Based on drift density, multiple range tests separated survey means into three homogeneous subsets: spring and summer 1988 and spring 1989 surveys, which had low drift density; fall 1988 and winter 1990 surveys, which had intermediate drift densities; and winter, summer, fall 1989 surveys, which had high drift densities (Figure 2.8). In contrast, on both a weight and frequency basis there was a significant interaction between study area and survey, which resulted from two different seasonal patterns in drift algal availability: 1) abundance increased from a minimum in the spring to a maximum in the winter; and 2) abundance increased from a minimum in the spring to a maximum in the fall decreasing in the winter. Overall, a winter peak in drift abundance was observed more

during 1988-89 while the fall peak predominated in 1989-90 (Figure 2.8). Drift algae was significantly more abundant in 1989 relative to 1988 by weight (30.4 vs 13.8 g/m^2/d, respectively), density (0.59 vs 0.31 pieces/m^2/d), and frequency (0.37 vs 0.23) (Mann-Whitney, all $p < 0.01$).

Drift algae on ANI displayed similar but less pronounced seasonal variation in abundance that usually peaked in the fall (Figure 2.8). Although there were no significant differences among surveys in drift algal abundance by weight (Table 2.4), both algal frequency and density displayed significant seasonal variation. Multiple range tests separated survey means into two homogeneous subsets: the fall 1988 and 1989 surveys, which had a numerous, frequent pieces of drift, and all other surveys, in which abundance was significantly reduced (Figure 2.8). Drift algae on ANI was significantly more abundant by weight in 1989 relative to 1988 (25.3 vs 7.4 g/m^2/d, respectively: Mann-Whitney, $p < 0.05$) but not by density or frequency (Mann-Whitney, all $p > 0.05$).

Algal Abundance: *giant kelp canopy*

There was marked interannual variation in the summer canopy of *Macrocystis* at SCI (Figure 2.9). Between 1988 and 1989 the *Macrocystis* canopy decreased slightly at the exposed study site but increased dramatically at the protected site. Changes in giant kelp canopy were paralleled by proportional fluctuations in the weight of drift algae deposited along transects at both sites.

Kelp Transport: *tagging experiment*

Recovery of tagged kelp fronds on SCI indicated that some intertidal drift algae was derived from local kelp beds (Figure 2.10). In the first experiment, five of the 600 tagged kelp fronds were recovered within the next five days, a recapture rate of 0.83%. No tagged kelp was recovered from the

two release sites 0.5 km distant of the study area. All of the recovered fronds were from adjacent kelp beds: two were released on the outer edge of the bed and three from the inner edge. The average minimum distance travelled by tagged kelp was 286 m (range 60-450 m) (Figure 2.10a).

Results of the second experiment indicated that more drift algae was derived from the outer edge of the kelp bed relative to the inner edge (Figure 2.10b). Of the 250 fronds released, 10 were recovered on the shore, a recapture rate of 4%. Nine of these were from the outer edge of the kelp bed and one was from the inner edge. Three tagged fronds were located by boat entrained on the surface canopy of a kelp bed, 200 m west of their release sites (Figure 2.10b). One additional tagged frond released from the inshore edge was recovered on the beach three months after the tagging experiment. The average minimum distance travelled was 331 m (range 90-420 m).

Abalone food preference

Abalone on SCI were observed feeding on three of the 11 (27%) possible food items: *Macrocystis*, *Egregia*, and *Cystoseira* (Table 2.5). In contrast, abalone on ANI had a broader diet consisting of 11 of 22 (50%) possible drift taxa. At SCI there were no significant differences among the utilization of the three drift foods (Table 2.5). In contrast, at ANI abalone exhibited a significant preference for some drift items relative to others. In general, rare food items such as *Postelsia, Macrocystis, Alaria, Cystoseira, Nereocystis, Gigartina spp,* and *Egregia* were preferred over abundant food items such as *Laminaria, Dictyoneurum, Botryglossum and Pterygophora.*

Discussion

The composition and abundance of drift algae at sites in central and southern California exhibited marked spatial and temporal variation in availability to intertidal black abalone. On Santa Cruz Island (SCI), the drift was dominated by a single species, *Macrocystis pyrifera*, which originated from large offshore surface canopies. In contrast, drift algae on Año Nuevo Island (ANI), was dominated by numerous benthic species, such as *Laminaria setchellii*, *Botryoglossum farlowianum*, and *Pterygophora californica*. Despite major differences in species composition, seasonal patterns of drift algal abundance were remarkably similar at both sites. In contrast, the distribution of drift algae differed between sites along intertidal gradients. Below I review the roles of standing crop, water movement, and intertidal topography as factors influencing drift availability and their effects on abalone feeding preference and intertidal distribution.

Causal Factors: *algal abundance*

The most pronounced pattern of variability in drift algal abundance resulted from seasonal variation in local algal stocks. On SCI, there was a direct relationship between the areal extent of offshore kelp canopies and the abundance of drift algae (principally *Macrocystis*) on intertidal transects. Moreover, recovery of tagged kelp fronds indicated that at least some drift kelp was derived locally, and deposited in the intertidal zone within days of detachment from live plants directly offshore. Overall, drift algal abundance was minimal in the spring and maximal in the fall and winter. Similar patterns of abundance have been described for algal communities in southern California (ZoBell, 1971; Harrold and Reed, 1985; Tegner and Dayton, 1987), central California (Gerard, 1976), Scotland (Bedford and

Moore, 1984), and south Australia (Shepherd, 1973). In California, seasonal variation in drift availability is largely due to flux in *Macrocystis* abundance which peaks in mid- to late-summer and deteriorates in the fall and winter when growth declines and storms destroy the canopy (North, 1971; Gerard, 1976; Dayton, 1985; Foster and Schiel, 1985).

Laminaria, which was a dominant component of the drift at ANI, exhibits seasonal patterns in growth and abundance similar to *Macrocystis* (Kitching, 1937; Kain, 1979). However, on ANI seasonal variation in drift abundance was less pronounced than at SCI. There are two likely reasons for this difference: 1) *Laminaria* is more resistant to environmental disturbance than *Macrocystis* and experiences smaller fluctuations in abundance (Foster and Schiel, 1985); and 2) algal biomass on ANI is influenced by nutrients derived from locally abundant pinnipeds. The Año Nuevo area supports large populations of California sea lions (*Zalophus californianus*), northern elephant seals (*Mirounga angustirostris*), Steller sea lions (*Eumetopias jubata*), and harbor seals (*Phoca vitulina*) (Le Bouef, 1981). Hansen (1971, 1972) found strong correlations between pinniped abundance and ammonium-nitrogen concentrations, which peaked in the summer, and the standing crop of *Iridaea cordata* at Año Nuevo. Moreover, several species of algae are known to utilize ammonium-nitrogen in the presence of other nitrogenous compounds (Hansen, 1980). Thus, algal stocks on ANI, and in turn the abundance of drift algae, may vary in response to two factors -- season and pinniped abundance -- which covary and result in similar seasonal patterns to those measured at SCI, but with less amplitude.

Causal Factors: *water movement*

Although algal abundance had a strong effect on drift algae availability, the actual transport of drift to intertidal abalone was largely controlled by water movement. In this study interaction between drift abundance and water movement was manifested on several different scales. On a daily scale, fluctuations in water movement often resulted in fluctuations in the weight of intertidal drift algae on SCI. These pulses could result from elevated rates of plant destruction by grazers, such as sea urchins and crustaceans (Dayton, 1985), during calm periods. Subsequent increases in water movement would transport this accumulated drift from the kelp forest to intertidal regions.

Along intertidal transects, drift algal deposition was not correlated with the distribution of maximal water velocities. On this scale, intertidal topography appears to be more important than water movement (see below). However, there were pronounced differences in both the abundance and composition of drift algae between areas that varied in exposure to waves and currents. Both study sites designated as "exposed" had higher average maximal water velocities than sites designated as "protected", although on ANI there was seasonal variation in wave exposure. One common consequence of increased water movement was an increase in species richness, abundance, and intertidal distribution of drift algae in exposed relative to protected areas. At both islands, drift algae occurred at higher densities and was more frequent in exposed relative to protected areas. Moreover, by weight, drift algae occurred across a broader range of the intertidal on exposed relative to protected transects. These patterns indicate that water movement is an important factor influencing the deposition of drift algae and, in turn, supplying food to intertidal abalone.

Causal Factors: *intertidal topography*

The shape and location of the deposition area was an additional factor which influenced the intertidal availability of drift algae. On a small scale, intertidal cracks and boulders served to enhance the entrapment of drift material as well as providing refuge for abalone (personal observations). On ANI, the gently sloping sedimentary rock acted as a reservoir which appeared to promote the transport of drift to abalone in cracks. As noted by ZoBell (1971), gently sloping areas promote greater deposition of drift algae than steeply sloping shores.

The direction and magnitude of local currents also had profound effects on the local accumulation of drift algae. The frequent recovery of tagged kelp fronds in adjacent intertidal areas emphasized the clumped nature of drift algal accumulation. The distribution of intertidal black abalone, which are generally restricted to surge channels and the sides of boulders, may largely be controlled by factors which cause clumping of drift algae.

Effects on Abalone Feeding Preference

Black abalone preference for drift algae varied geographically in conjunction with differences in the species richness of food items. At SCI there were no observed preferences among food items. In contrast, on ANI abalone exhibited a preference for rare drift items (e.g., *Postelsia* and *Macrocystis*) relative to abundant food items (*Laminaria* and *Pterygophora*). Both Poore (1972) and Shepherd (1973) found similar geographic variation in diet among abalone in New Zealand and south Australia, respectively. In this regard it would be interesting to examine the nutritional quality of algae around Año Nuevo in order to assess the effects of pinniped abundance on

herbivore nutrition. The high diversity of invertebrates in the Año Nuevo area indicates a strong positive effect of nutrient enrichment (Pearse, 1981).

Effects on Abalone Abundance

Relationships between food availability and abalone abundance serve as a measure of the influence of spatial and temporal variability in drift algae on abalone distribution. This study examined three measures of drift algal abundance: the weight, density, and frequency of deposition. Overall, abundance by weight was the best correlate of abalone distribution. One explanation for this result stems from patterns of drift deposition: large amounts of algae are commonly trapped in cracks and around boulders where black abalone are abundant. Thus, weight may be a strong correlate due to its association with suitable abalone habitat.

The density of drift was also significantly correlated with abalone abundance in several instances. High drift densities, in addition to their high correlation with drift weight, could enhance the availability of algae to individual abalone. In contrast, the frequency of drift deposition was the poorest overall correlate of abalone abundance. Because black abalone are resistant to starvation and can survive 10-12 months without food (Bergen, 1971; Chapter 3), the frequency of food availability may not be as important as sporadically abundant food near suitable habitat.

Along shore-level gradients, abalone abundance was significantly associated with the availability of drift algae. A major feature of geographic variation in the black abalone is an intertidal shift in distribution with latitude: abalone on ANI occur higher on the shore than SCI (Tissot, 1988b; Chapter 4). Interestingly, these patterns are consistent with differences in the intertidal distribution of drift algae, which also occurred higher on the shore at ANI relative to SCI. These results support the hypothesis that the

intertidal distribution of drift algae is a major factor determining the intertidal distribution of black abalone.

In contrast, along wave-exposure gradients, abalone abundance was not associated with drift algal availability. Abalone in exposed areas occurred at lower (SCI) or similar densities (ANI) than those at protected sites despite more abundant drift along exposed transects. Although higher water velocities promote higher drift algal abundance, they can also have negative effects on feeding rates of abalone. As demonstrated by Shepherd (1973), the proportion of successful drift feeding abalone was greatest during times of intermediate water movement. During calm periods, or period when the water was too rough, drift was not available to abalone (Shepherd, 1973). Additional factors, such as recruitment, suitable habitat, or wave forces could also have strong effects on microgeographic distribution. However, the abundance of abalone predators is generally greater at protected relative to exposed areas at both sites (Tissot, unpublished data).

Geographic variation in abalone density, at least in recent times, is associated with latitudinal variation in the abundance of drift algae. On SCI, where drift algae was more abundant overall, black abalone occur at higher densities (125 - 25/m^2) relative to ANI (8-12/m^2) at least until a mass mortality in 1986-88 (Chapter 3). Although there is a strong component of human exploitation in this trend (SCI is less exploited than ANI) these patterns have persisted for at least several decades (Cox, 1962; Buzz Owen, personal communication). Although latitudinal variation in abalone density is undoubtedly a response to numerous factors, especially recruitment, drift algae abundance is likely to play an important role.

One factor that may have a profound effect on abalone population dynamics is latitudinal variation in the temporal variability of drift algae. At

ANI in central California, *Macrocystis* was uncommon and drift algae was dominated by benthic species, such as *Laminaria*, *Botryoglossum*, and *Pterygophora*, which are generally not as productive as giant kelp but less susceptible to environmental stress (Foster and Schiel, 1985). In contrast, at SCI in southern California, drift algae was dominated by *Macrocystis* which occurred in extensive offshore canopies that provided large amounts of material to the intertidal zone. However, giant kelp displayed pronounced seasonal and interannual variation in abundance. *Macrocystis* is very vulnerable to environmental disturbances, such as El Niño-induced storms and low nutrient, high temperature conditions, which results in considerable interannual variability (Dayton and Tegner, 1984; Ebeling et al., 1985; Tegner and Dayton, 1987). Increases in giant kelp on SCI between 1987-89 represented recovery from the 1986-87 El Niño (Chapter 3), which has been implicated as one cause of the 1986-88 starvation-induced mass mortality of black abalone throughout southern California (Tissot, 1988c; Davis et al., in press; Chapter 3).

In summary, although there was considerable spatial and temporal variation in the composition and abundance of drift algae along the California coast, drift abundance were largely controlled by several related factors: algal standing crop, water movement, topography, and local currents. Variability in these factors, and their subsequent effects on the abundance of intertidal drift algae, had marked effects on the diet and intertidal distribution of black abalone. What remains to be ascertained is the importance of drift algae to abalone abundance relative to additional ecological factors such as recruitment, habitat, and predation.

Table 2.1. Pearson correlations between abalone abundance and three measures of drift algal abundance: weight/m^2, number /m^2, and the frequency of occurrence (see Methods). **A.** Within transects at each island. **B.** Among transects at each island.

A. WITHIN TRANSECTS

	TRANSECT				
	Protected		*Exposed*		
Location	1	2	1	2	Overall
Santa Cruz Island (n = 5-15)					
Weight	0.06	0.99**	-0.30	0.96**	0.37*
Number	-0.18	0.90**	0.37	-0.09	0.38*
Frequency	-0.11	0.89**	-0.10	-0.06	0.27
Año Nuevo Island (n = 7-25)					
Weight	0.69*	0.29	0.05	0.57**	0.43**
Number	0.51	0.54*	-0.25	0.65**	0.04
Frequency	0.78**	0.46	-0.43*	0.50*	-0.05

B. AMONG TRANSECTS (n = 4)

	LOCATION	
	Santa Cruz Island	*Año Nuevo Island*
Weight	0.40	0.40
Number	-0.40	0.80
Frequency	0.18	0.60

Significance Levels: * - $p < 0.05$, ** - $p < 0.01$

Table 2.2. Macroalgal species collected as drift along intertidal transects at Año Nuevo and Santa Cruz Island. All species were found along exposed study sites at both islands. Species also found at protected sites are indicated by an *.

Año Nuevo Island			*Santa Cruz Island*		
Species	Percent Number	Total Weight	Species	Percent Number	Total Weight
**Laminaria setchellii*	35.2	21.4	**Macrocystis pyrifera*	76.2	80.9
**Botryoglossum farlowianum*	22.8	8.2	**Egregia menzesii*	12.8	16.2
**Pterygophora californica*	11.7	18.7	**Gigartina* spp.	2.3	0.3
**Dictyoneurum californica*	5.6	2.1	**Cystoseira osmundacea*	1.8	1.6
**Egregia menzesii*	4.7	6.7	**Iridaea* spp.	0.6	<0.1
**Iridaea* spp.	3.2	0.7	*Unidentified red algae	0.6	0.1
Coralline algae	2.4	0.6	**Laminaria setchellii*	0.4	<0.1
*Unidentified red algae	2.3	0.7	*Porphyra* sp.	0.4	0.1
**Gigartina* spp.	1.8	0.4	*Gelidium* sp.	0.1	<0.1
**Nereocystis luetkeana*	1.7	35.5	*Pterocladia* sp.	0.1	<0.1
**Cystoseira osmundacea*	1.2	0.6	*Prionitis* sp.	0.1	<0.1
**Ulva* spp.	1.1	0.1			
**Macrocystis integrifolia*	0.8	2.4			
**Alaria marginata*	0.7	0.7			
*Unidentified brown algae	0.7	<0.1			
**Neoptilota densa*	0.7	0.2			
**Prionitis* sp.	0.5	0.1			
**Gymnogongrus* sp.	0.3	<0.1			
**Postelsia palmaeformis*	0.3	0.8			
Eisenia arboretum	0.1	<0.1			
Laminaria sinclarii	0.1	<0.1			
Microcladia coulteri	0.1	0.1			

Table 2.3. Differences between study areas and between wave-exposure gradients in measures of drift algal composition and abundance and maximum water velocity.

	STUDY SITE			
	Exposed		*Protected*	
Study Area	Mean	SE	Mean	SE
Santa Cruz Island				
Species richness (# taxa)	11	--	7	--
Drift weight (g)	38.8	5.85	85.1	18.2
Algal Weight (g/m^2)	21.7	4.37	20.5	6.18
Algal Density ($no./m^2$)	0.63	0.08	0.25	0.03
Algal Frequency ($freq/m^2$)	0.34	0.03	0.24	0.02
Water Velocity (m/s)	2.27	0.03	2.05	0.02
Año Nuevo Island				
Species richness (# taxa)	22	--	18	--
Drift weight (g)	20.1	2.17	123.7	72.6
Algal Weight (g/m2)	3.3	1.45	8.7	11.4
Algal Density (no./m2)	0.42	0.04	0.23	0.04
Algal Frequency (freq/m2)	0.26	0.03	0.11	0.02
Water Velocity (m/s)	2.40	0.05	2.04	0.04

Table 2.4. Results of nested two-way analysis of variance testing the effects of sites (wave-exposure gradients) and surveys (season) on drift algal weight, number, and frequency, and maximum water velocities.

		F-VALUES		
Variable	df	Site	Survey	Site * Survey
Santa Cruz Island				
Water Movement	16	4.65*	4.34**	0.35
Algal Weight	16	0.02	8.69**	4.91**
Algal Density	16	10.08**	5.39**	1.98
Algal Frequency	16	9.67**	12.55**	3.03*
Año Nuevo Island				
Water Movement	12	0.07	9.01**	3.51*
Algal Weight	12	0.13	2.09	1.27
Algal Density	12	9.93**	7.37**	2.66
Algal Frequency	12	20.10**	4.65*	1.64

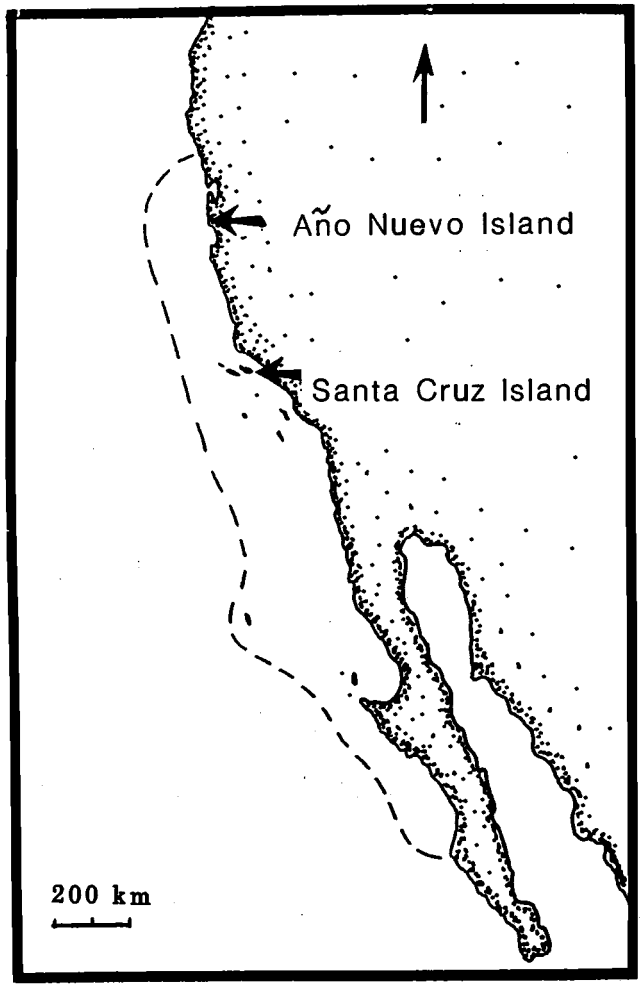
Significance Levels: * - $p < 0.05$, ** - $p < 0.01$

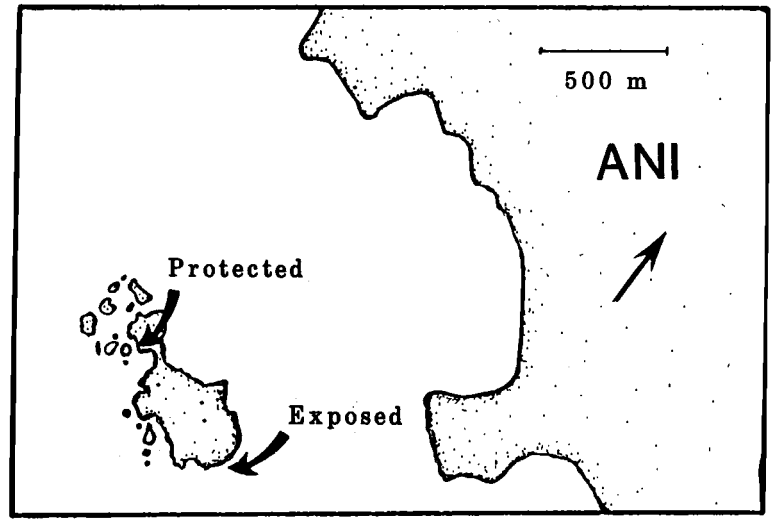
Table 2.5. Feeding preferences of intertidal black abalone on drift macroalgae at Santa Cruz and Año Nuevo Islands. The F-value testing for significance differences among food items is presented relative to the rank order of food items (lowest = most preferred) and significant ranges based on methods presented in Johnson (1980).

Location/Species	Number of Observations: Drift	Number of Observations: Feeding	Rank Order	Significant Ranges
Santa Cruz Island: $F_{2,3} = 0.115$				
Cystoseira osmundacea	14	3	1	|
Macrocystis pyrifera	592	37	2	|
Egregia menzesii	93	7	3	|
Año Nuevo Island: $F_{10,10} = 4.129$*				
Postelsia palmaeformis	2	1	1	|
Macrocystis integrifolia	7	3	2	|
Alaria marginata	5	2	3	|
Cystoseira osmundacea	9	1	4	|
Nereocystis luetkeana	7	1	5	|
Gigartina spp.	16	2	6	| |
Egregia menzesii	35	16	7	| |
Laminaria setchellii	264	59	8	| |
Dictyoneurum californica	42	7	9	| |
Botryoglossum farlowianum	171	14	10	| |
Pterygophora californica	88	12	11	| |

Significance Levels: * - $p < 0.05$

Figure 2.1. Map of study areas in relation to the geographic range of the black abalone. **A.** Exposed and protected study sites at Año Nuevo Island (ANI). **B.** Exposed and protected study sites at Santa Cruz Island (SCI). Kelp tagging sites are indicated by stars (see text).


Año Nuevo Island
Santa Cruz Island
200 km


500 m
ANI
Protected
Exposed

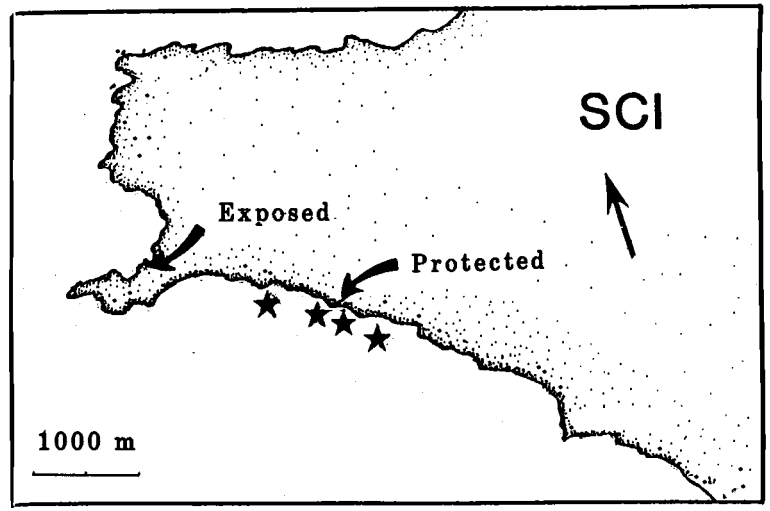

SCI
Exposed
Protected
1000 m

Figure 2.1

Figure 2.2. Size distribution of drift algal pieces.

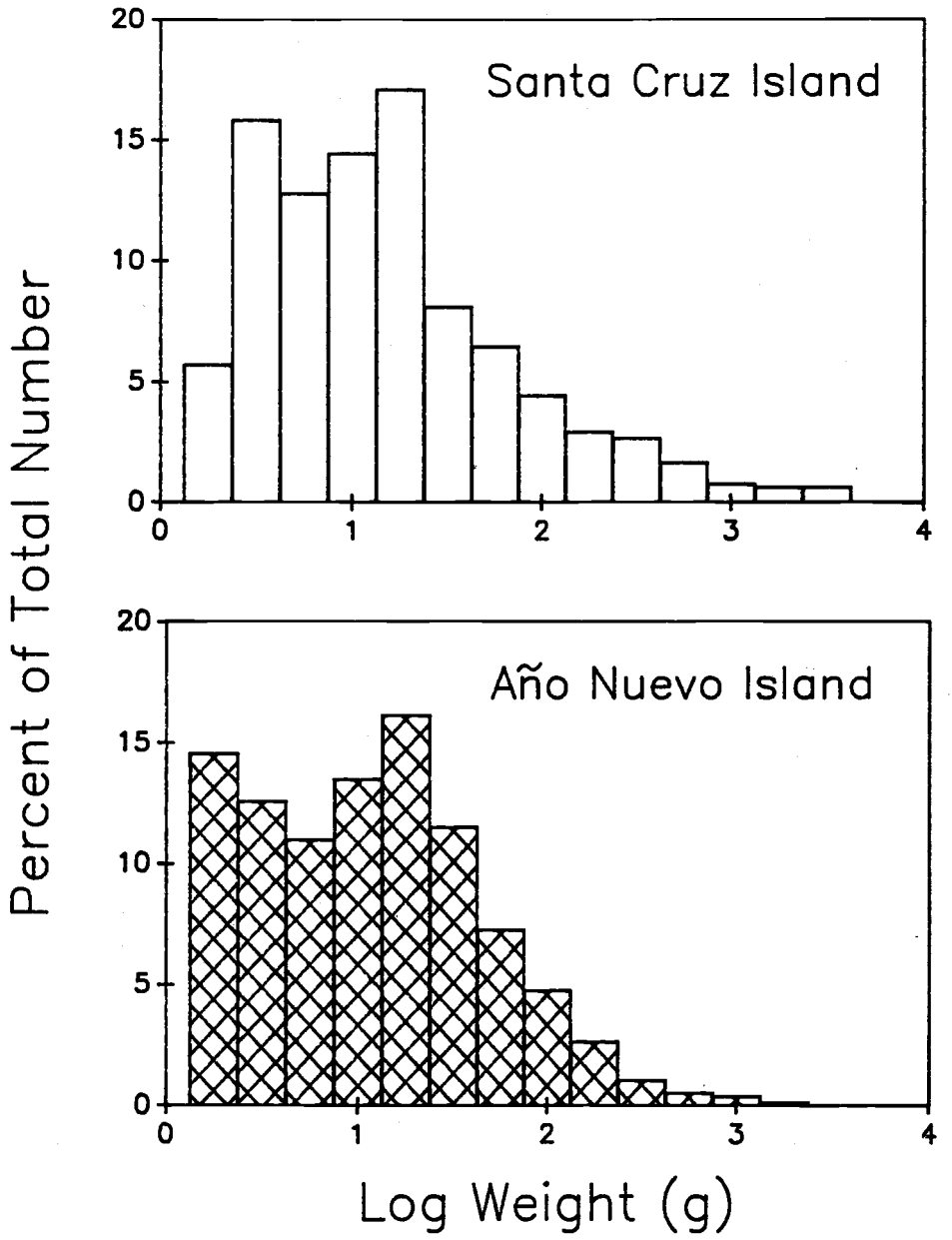

Santa Cruz Island
Año Nuevo Island
Percent of Total Number
Log Weight (g)
0
5
10
15
20
0
1
2
3
4

Figure 2.2

Figure 2.3. The intertidal distribution of average maximal water velocities (± 1 SE) along exposure gradients at two study sites. Water velocities were measured using dynamometers. ND = no data available.

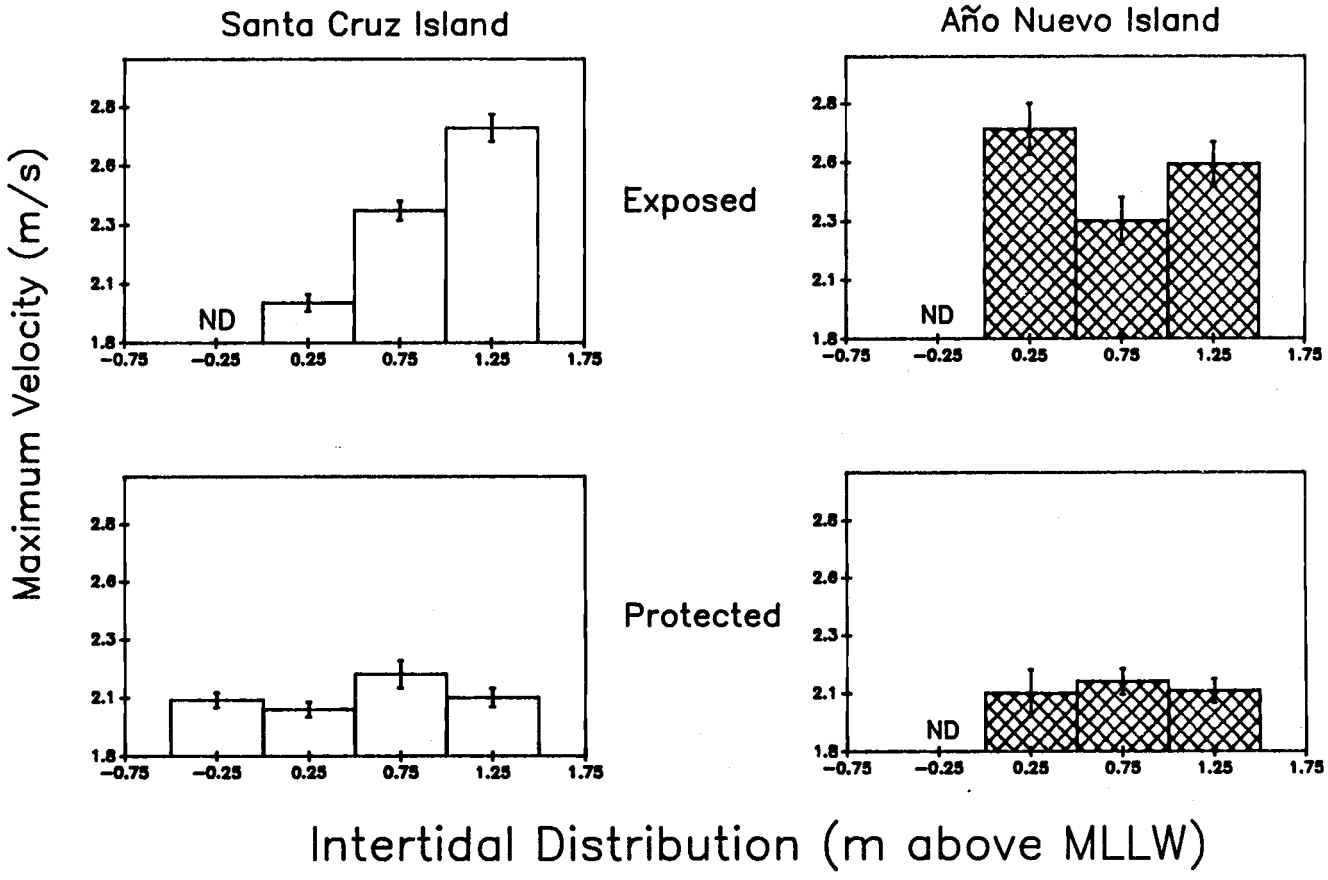

Santa Cruz Island
Año Nuevo Island
Exposed
Protected
Maximum Velocity (m/s)
Intertidal Distribution (m above MLLW)
ND
ND
ND
2.8
2.6
2.3
2.1
1.8
−0.75
−0.25
0.25
0.75
1.25
1.75

Figure 2.3

Figure 2.4. The intertidal distribution of three measures of drift algal abundance along exposure gradients at the two study islands. The range of intertidal heights corresponds to the intertidal areas occupied by transects in each study area.

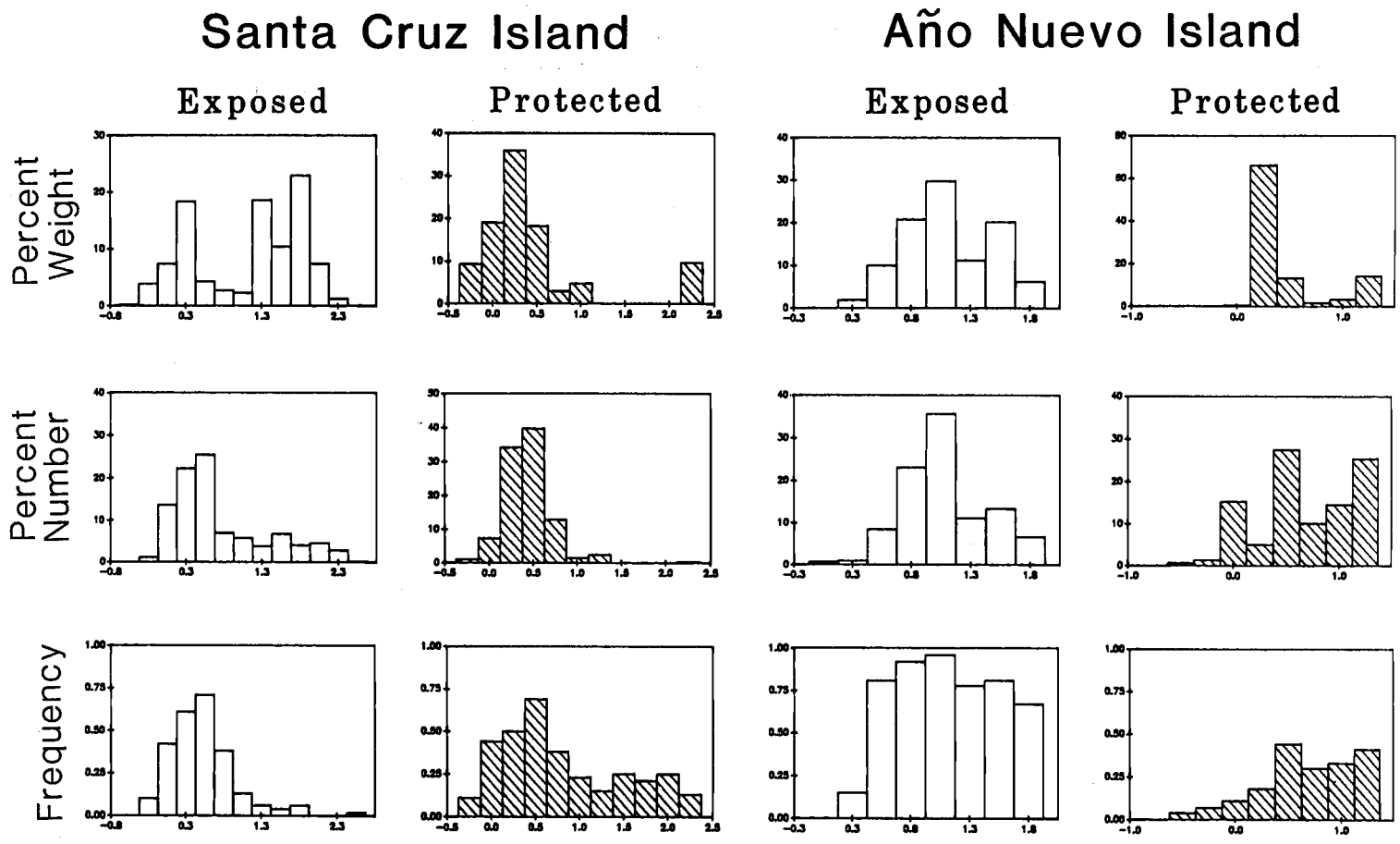

Santa Cruz Island
Año Nuevo Island
Exposed
Protected
Exposed
Protected
Percent Weight
Percent Number
Frequency
Intertidal Distribution (m above MLLW)

Figure 2.4

Figure 2.5. Temporal variation in average maximal water velocities ($\pm$ 1 SE) along exposure gradients at the two study islands. Water velocities were measured using dynamometers.

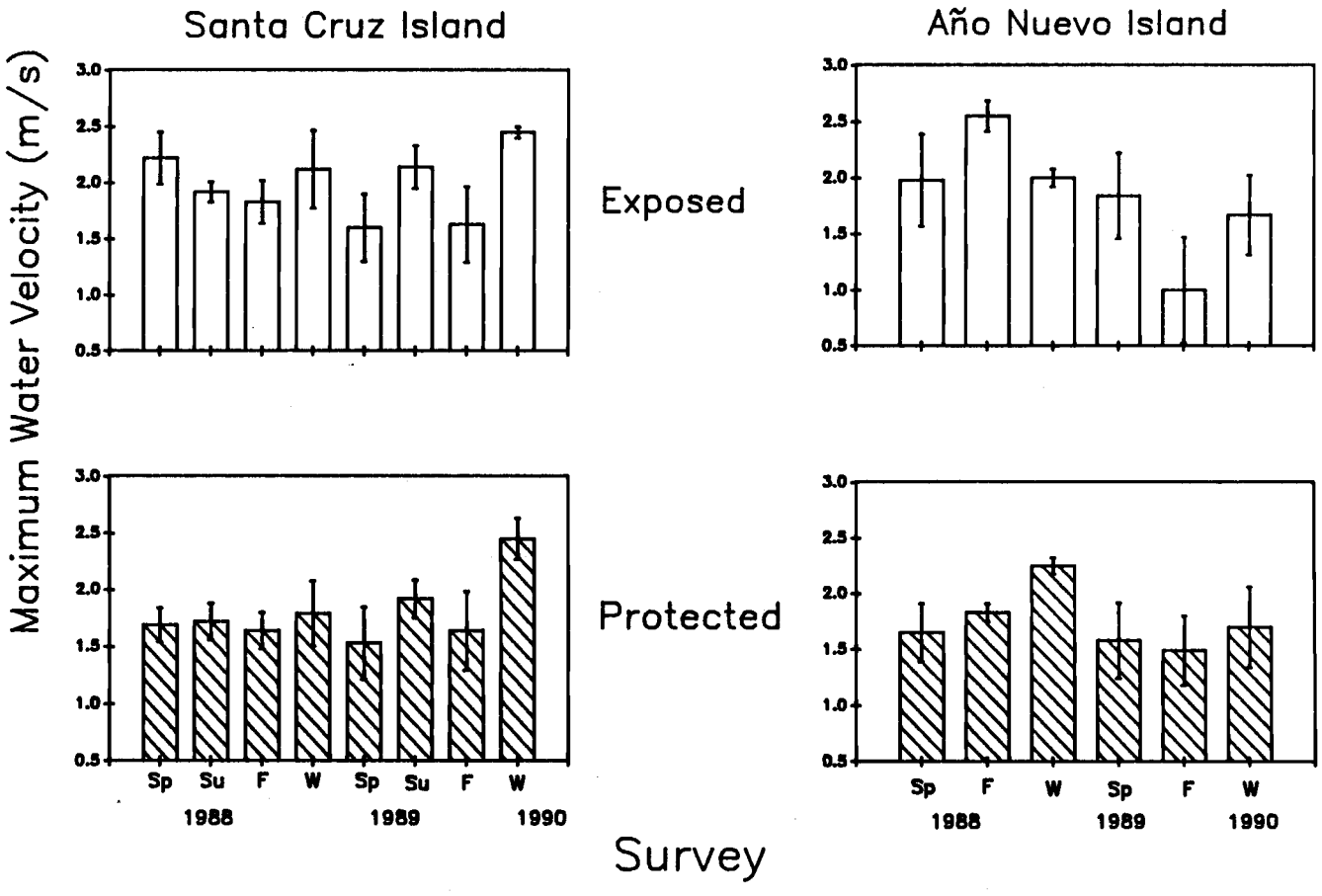

Santa Cruz Island
Año Nuevo Island
Maximum Water Velocity (m/s)
3.0
2.5
2.0
1.5
1.0
0.5
Exposed
Protected
Sp Su F W Sp Su F W
1988 1989 1990
Sp F W Sp F W
1988 1989 1990
Survey

Figure 2.5

Figure 2.6. The frequency of drift algal deposition along transects in relation to daily average maximal water velocities measured using dynamometers.

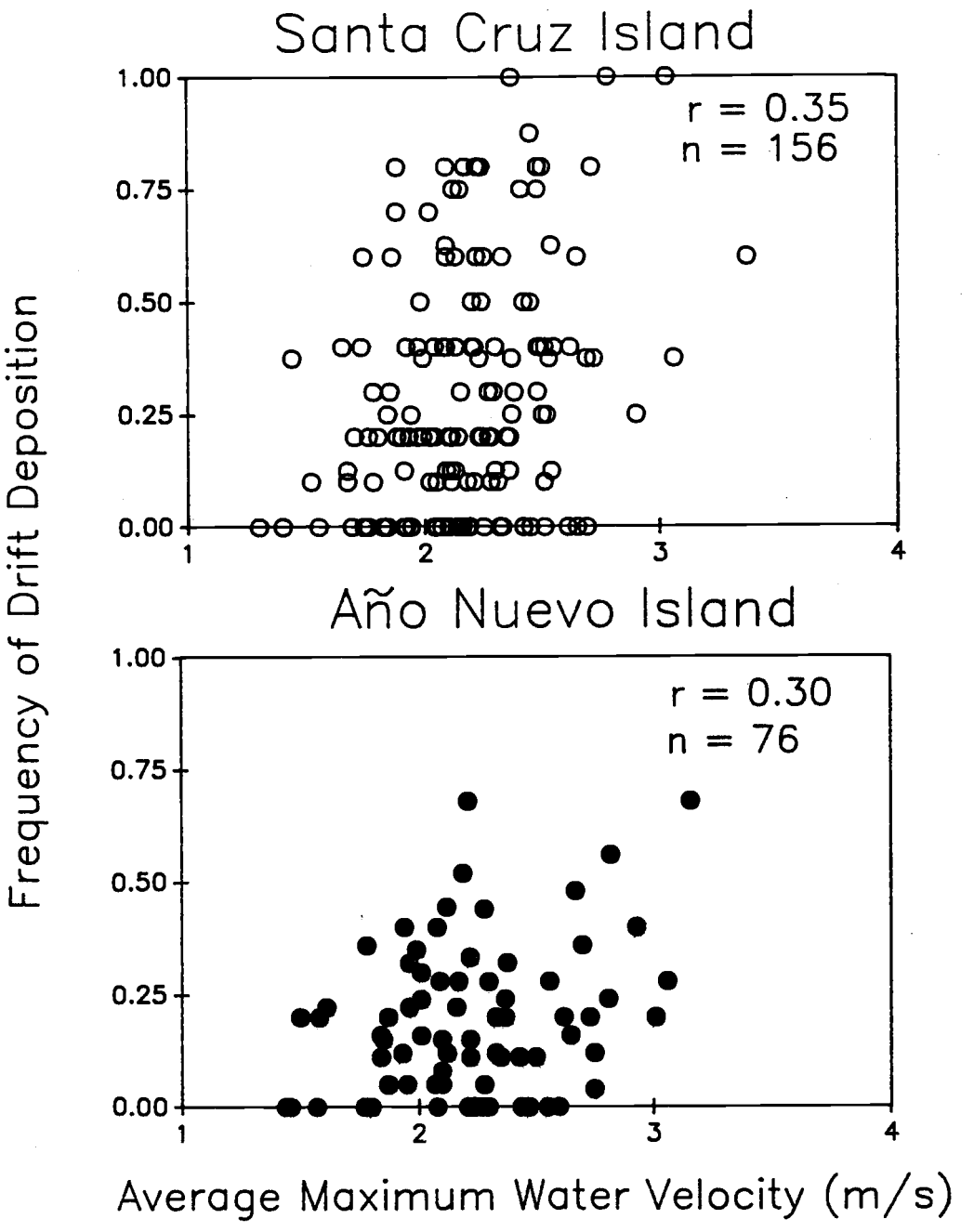

Santa Cruz Island
r = 0.35
n = 156
Año Nuevo Island
r = 0.30
n = 76
Frequency of Drift Deposition
Average Maximum Water Velocity (m/s)
1.00
0.75
0.50
0.25
0.00
1
2
3
4

Figure 2.6

Figure 2.7. Daily variation in drift algal weight in relation to average maximum water velocities at two study sites for surveys that exceeded four days in length.

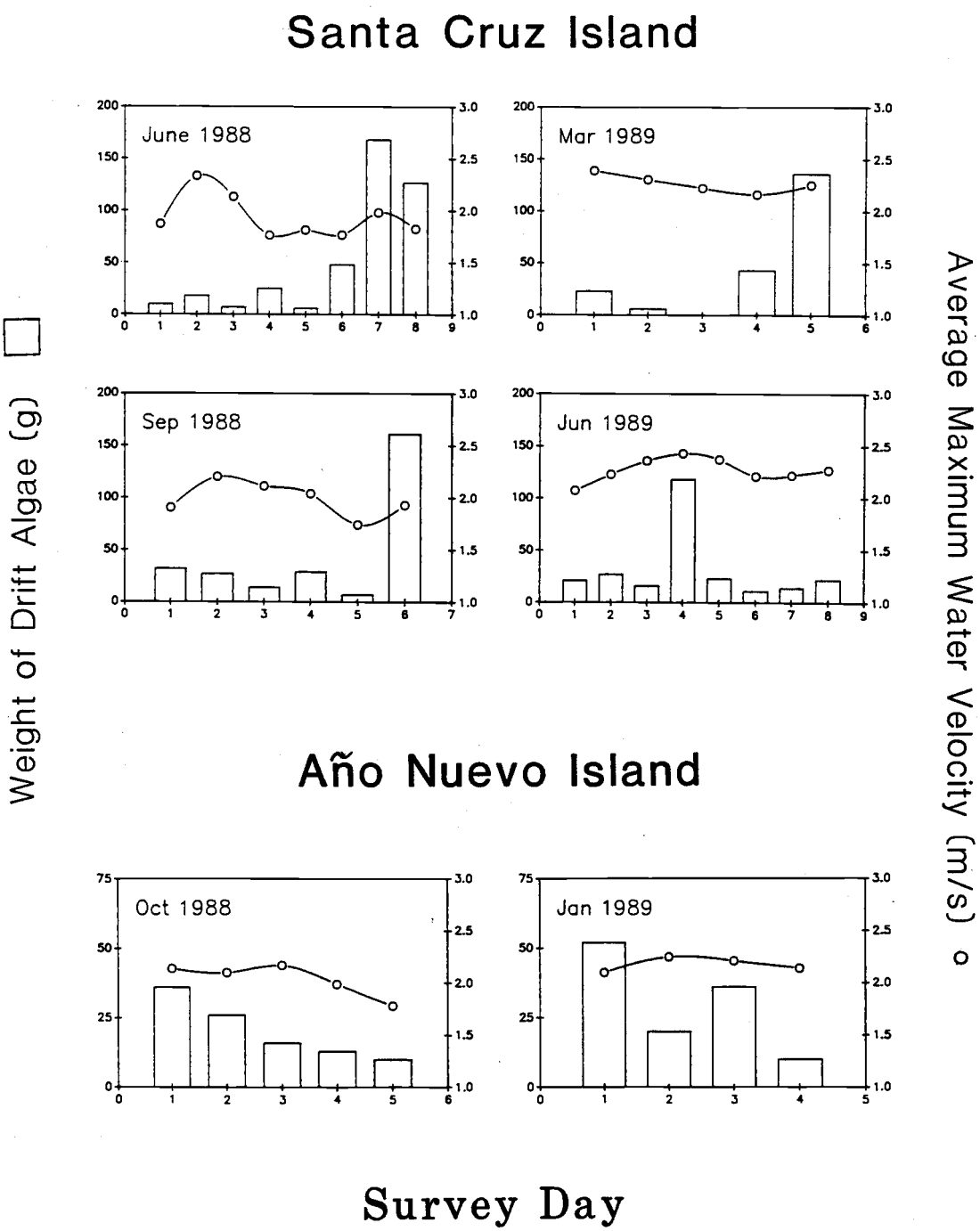

Santa Cruz Island
June 1988
Mar 1989
Sep 1988
Jun 1989
Año Nuevo Island
Oct 1988
Jan 1989
Weight of Drift Algae (g)
Average Maximum Water Velocity (m/s)
Survey Day

Figure 2.7

Figure 2.8. Temporal variation in three measures of drift algal abundance (± 1 SE) along exposure gradients at two study sites.

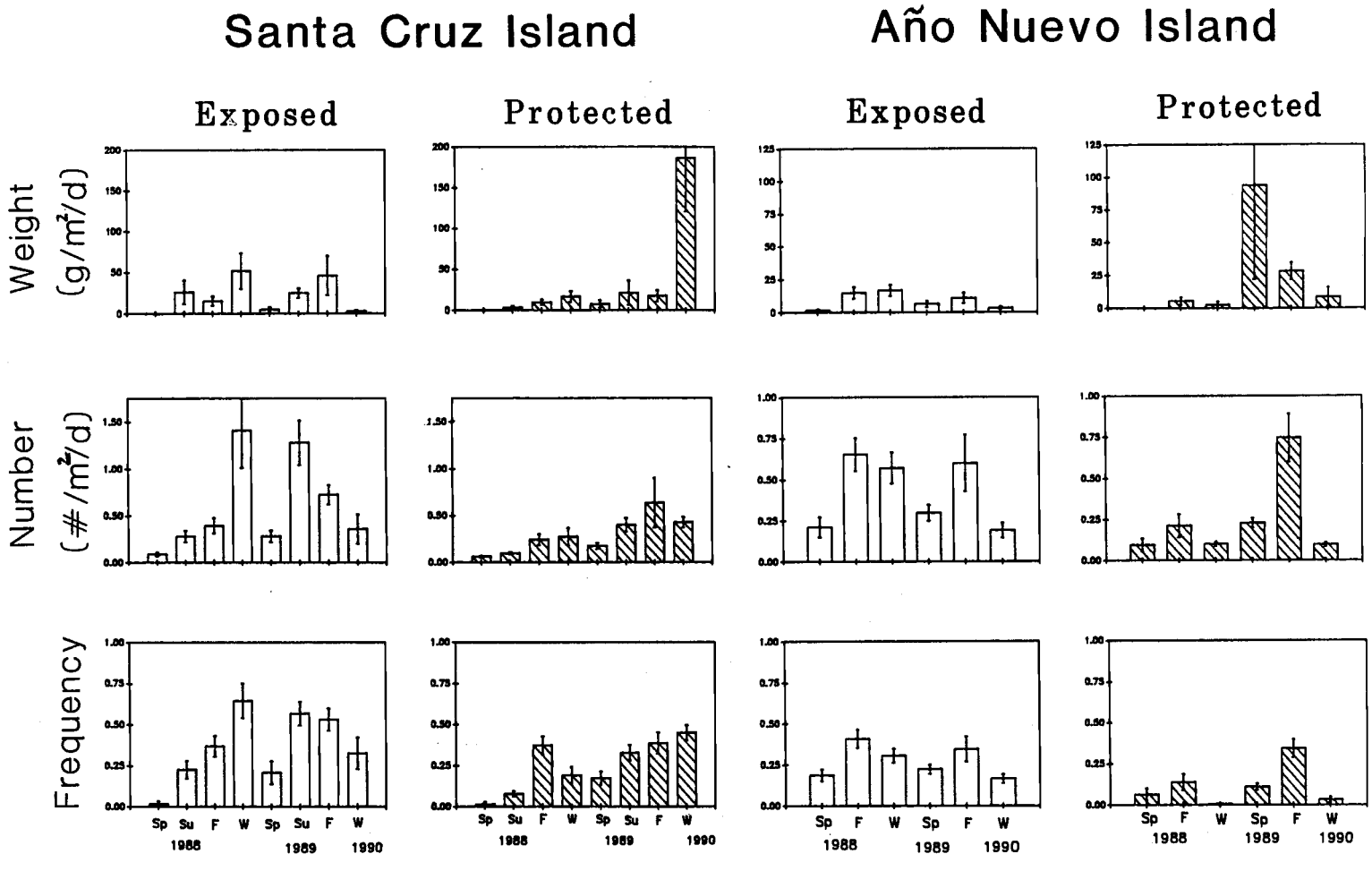

Santa Cruz Island
Año Nuevo Island
Exposed
Protected
Exposed
Protected
Weight (g/m²/d)
Number (#/m²/d)
Frequency
Sp Su F W Sp Su F W
1988
1989
1990
Survey

Figure 2.8

Figure 2.9. The abundance of drift algae by weight in g/m2 (histograms) in relation to the area of *Macrocystis* canopy in m^2 (dots) at two study areas on SCI in 1988 and 1989.

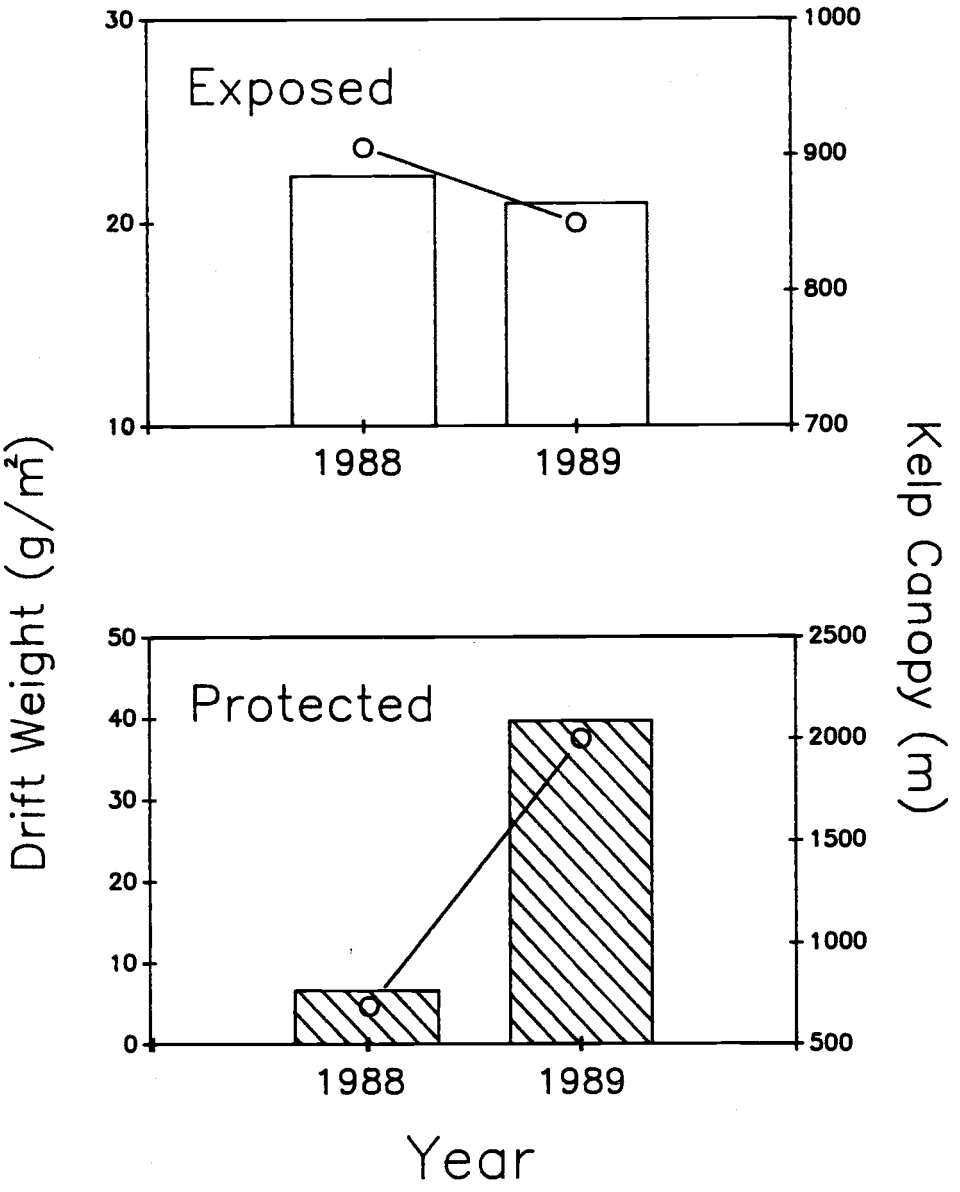

Exposed
Protected
30
20
10
50
40
30
20
10
0
1000
900
800
700
2500
2000
1500
1000
500
1988
1989
1988
1989
Drift Weight (g/m²)
Kelp Canopy (m)
Year

Figure 2.9

Figure 2.10. Minimum paths of recaptured tagged *Macrocystis pyrifera* fronds in relation to kelp beds and intertidal abalone transects (A, B, E, F) on the protected study area of Santa Cruz Island. Each arrow represents the net movement of one tagged frond. **A.** Experiment #1, in which 100 pieces of tagged kelp were released at six sites. Four of these sites are indicated by stars. Two sites not shown were located 0.5 km east and west of the protected study site (see Figure 1). **B.** Experiment #2, in which 125 pieces of tagged kelp were released at two sites, indicated by stars.

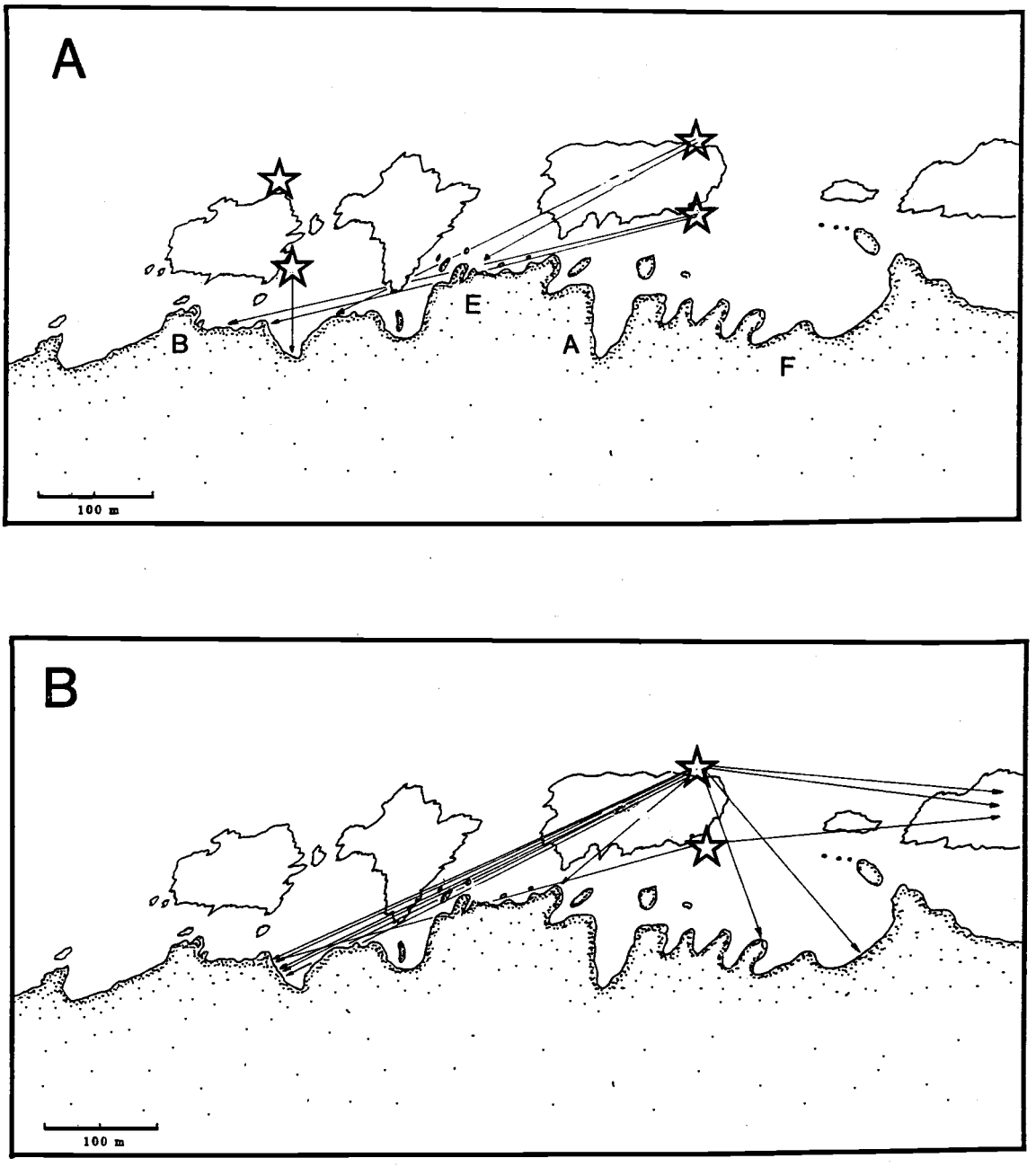


Figure 2.10

Chapter 3

POPULATION DYNAMICS OF BLACK ABALONE DURING MASS MORTALITY IN SOUTHERN CALIFORNIA

Abstract

Mass mortality represents a strong selective agent that has the potential of eliminating entire species. Between 1986 and 1988, black abalone (*Haliotis cracherodii*) populations experienced 40-100% declines in abundance throughout southern California. I documented this decline on Santa Cruz Island, California, and proposed hypotheses concerning the cause(s) of the mortality.

I examined 1000 tagged abalone quarterly over the course of three years (1987-1990), both during and after the mass mortality. Measurements of tagged abalone indicated that growth, reproduction, and behavior were significantly different from "normal" both during and after the mass mortality. Density-dependent declines in abundance, associated with high rates of movement, low body weights, depressed shell growth, and irregular gonad development, indicated that a disease was present during the mass mortality.

Because the population decline occurred during a period of low drift algal abundance, associated with fluctuations in the extent of offshore kelp forests, I propose that mortality primarily occurred in response to starvation. Although black abalone appear to be adapted to long periods of starvation, individuals on Santa Cruz Island experienced low food abundance for at least a year in 1987-88. Fluctuations in the abundance of giant kelp (*Macrocystis*), their principal food, occurred in response to the 1983-84 and 1986-87 El Niños and high densities of purple sea urchins, *Strongylocentrotus purpuratus*, which may exploitatively compete with abalone for drift macroalgae.

A strong decrease in the thermal tolerance of black abalone between 1982 and 1987 indicated a reduction in the ability of individuals to endure physiological stress. However, because the thermal tolerance of black abalone is high, it is unlikely that elevated seawater temperatures during El Niño were a cause of the disease, although they may have contributed to its onset.

Although high abalone densities in the northern Channel Islands are clearly abnormal, these densities have persisted for at least 30 years. One hypothesis is that high density populations in the northern Channel Islands have been experiencing chronic starvation stress in response to high seasonal and interannual variation in kelp abundance. Another hypothesis is that this chronic stress decreased the resistence of abalone to infection by pathogens, which, in turn, may have caused the mass mortality. Although persistant mortality and depressed rates of shell growth among abalone 18 months after food became abundant supports this hypothesis, there is currently little evidence in support of a pathogen as the primary cause of the mass mortality.

Introduction

Mass mortality, a major decline in abundance, represents a selective agent that has the potential of eliminating entire species. In the early 1800s, cases of mass mortality were used to confirm Cuvier's theory of catastrophes (Brongersma-Sanders, 1957), and sudden extinction events are a dominant feature of the fossil record (Boucot, 1981). The causes of such extinctions can be inferred by examining mass mortality in recent populations, and represents a challenging subject that is not well understood (e.g., Lessios, 1988).

In the marine environment mass mortality has been attributed to plankton blooms, disease, storms, earthquakes, vulcanism, and changes in currents, sea level, salinity, and temperature (see Brongersma-Sanders, 1957 and Sindermann, 1970 for reviews). Disease represents the least understood of these causes and is virtually unstudied as an ecological factor in community ecology (Kinne, 1980; Anderson, 1982). Undoubtedly, disease can play a major role in the regulation of animal populations (May, 1983) and biotic pathogens have been implicated in several recent cases of mass mortality in the marine environment. Interactions between pathogens and abnormally warm water has been attributed to the disappearance of the seastars *Heliaster* and *Pisaster* along the eastern Pacific coast (Dungan et al., 1982), the wasting disease of the eelgrass *Zostera* in the Atlantic (Rasmussen, 1977), and die-offs of the sea urchin *Strongylocentrotus droebachiensis* in Nova Scotia (Scheibling and Stephanson, 1984). Similarly, mass mortality of the Caribbean sea urchin *Diadema antillarum* has been attributed to the introduction of an exotic pathogen (Lessios et al., 1984). One of the major challenges in understanding these events is distinguishing secondary

infections from the primary causal agent(s). In the majority of cases a specific cause of the mortality is never conclusively identified (Sindermann, 1970).

Mass mortality is virtually unstudied as an ecological phenomenon due to its apparent rarity and rapid sweep through populations. Because observations have been limited to changes in density and/or geographic distribution, little is known about the ecological interactions which may influence survivorship during mass mortality. The recent well-documented die-off of *Diadema* serves as a striking example: a wave of mortalities swept the entire Caribbean within nine months; individual populations declined 94-100% within 7-45 days after contact by the mortality front, which may have been a current-borne bacterium (Lessios, 1988). Given the rapidity and severity of these kinds of events, obtaining ecological information beyond measures of abundance is often more fortuitous than insightful. However, because the survivors of these catastrophes play a major role in the restructuring of populations after mortality, the influence of ecological factors during mortality events can have profound effects on the population dynamics of recovering species.

Mass Mortality of the Black Abalone

The black abalone, *Haliotis cracherodii* Leach 1814, is a common intertidal gastropod that occurs from Point Arena, California, to southern Baja California along the eastern Pacific coast. Abalone are herbivorous and feed by capturing pieces of drifting algae, largely kelps, carried by the current (Cox, 1962; Shepherd, 1973). Historically, the black abalone has been the basis of an intense aboriginal fishery extending over 5000 years (Muratto, 1984) and subjected to predation by the California sea otter, *Enhydra lutris*, over at least the last 500,000 years (Kenyon, 1975). However, by 1900 both of these sources of mortality were eliminated in California and commercial

harvesting of littoral abalone was prohibited until 1969. Although a strong recreational fishery for black abalone occurred along the populous mainland coasts, on offshore islands, such as the California Channel Islands (Figure 3.1), black abalone stocks were largely unharvested and became extremely dense (Cox, 1962). In 1984, intertidal densities greater than $75/m^2$ were not uncommon throughout the northern Channel Islands (Douros, 1987). Between 1986 and 1988, however, black abalone populations throughout southern California sharply declined (Davis, 1988; Tissot, 1988c) (Figure 3.2). In contrast, populations north of Point Conception have shown few noticeable declines (Tissot, 1988c).

This paper describes the population dynamics of black abalone during mass mortality on Santa Cruz Island, California between 1987 and 1990. The goals of this investigation were two-fold: 1) to describe population dynamics during mass mortality; and 2) to generate hypotheses concerning cause(s) of the population decline. Because disease represents a common cause of mass mortality (Sindermann, 1970) my studies were focused on measuring symptoms of disease processes: negative deviations from "normal" survival, growth, and reproduction (Kinne, 1980). Moreover, due to the occurrence of the mortality episode during an environmental perturbation, the 1986-87 El Niño, particular attention was given to several specific hypotheses.

El Niño is an unusually warm current that periodically occurs off the coasts of Ecuador and Peru which can have strong effects on southern Californian oceanographic processes and nearshore communities (Glynn, 1988). The 1982-84 El Niño, which preceeded the mass mortality, was the largest event in recorded history (Tegner and Dayton, 1987) and devasted kelp forest communities throughout southern California (Dayton and Tegner, 1984). Because black abalone are sedentary and strongly dependent

on algal productivity (Leighton and Boolootian, 1963), sharp fluctuations in kelp forest standing crop could have had strong effects on the dense populations of abalone in the northern Channel Islands. Accordingly, this study examined survivorship during mass mortality in relation to the abundance of drift algal foods and kelp forest standing crop. Moreover, because other herbivores, such as the sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus*, are known to have a strong influence on both drift algal supply (Harrold and Reed, 1985) and kelp standing crop (Lawerence, 1975), the structure of the kelp forest community was also examined.

Materials and Methods

A. Study Sites and Transects

The study sites were located on the west end of Santa Cruz Island (34° 00' N, 114° 50' W), California, 25 km south of Santa Barbara, CA (Figure 3.3). Intertidal and subtidal transects were located in two general areas that differed in their exposure to ocean waves (see Chapter 2). The "protected" site was located 1 km SE of Fourney Cove on the south side of Santa Cruz Island. The "exposed" site was located 0.2 km NE of Fraser Point in a large cove on the north side of the island (Figure 3.3). The exposed site was open to the prevailing N-NW ocean swell and wind. The protected site was largely sheltered from N-NW swells but received S-SW swells during the summer and early fall.

At both sites the substrate consisted of irregular breccias and basalts largely bare of fleshy macroalgae and dominated by abalone, barnacles, mussels, limpets, and erect and crustose coralline algae. At the protected site, black abalone occupied open substrates along the vertical and horizontal walls of surge channels, under large boulders, and in shallow crevices. In contrast, abalone only occupied crevices at the exposed site. In January and March of 1987 I established seven permanent transects at each study site. Transects were located at the base and sides of surge channels, were 1 m wide and 5-15 m long, and extended from the high to the low intertidal throughout the range of abalone distribution.

I conducted a total of twelve surveys on a quarterly basis (January, March, June, September) between January 1987 and January 1990. One survey (January 1988) was missed due to bad weather. 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.

B. Abalone Tagging and Survivorship

During each survey I tagged 5-75 abalone on each transect. I located individual abalone by systematically sampling the entire length of the transect, haphazardly choosing individuals within any one transect area. Abalone were removed from the substrate, their shell was 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). For each individual I measured the following traits: 1) *Shell Length*: length of the longest dimension; 2) *Shell Width*: width of the shell perpendicular to length; 3) *Shell Height*: maximum height of the shell; 4) *Number of Tremata* (= respiratory pores): number of open holes on the shell; 5) *Trema Length*: the distance tremata traverse on the shell; 6) *Trema Spacing*: distance between the two anterior-most tremata; 7) *Trema Diameter*: maximum diameter of the anterior-most trema; 8) *Total weight* (after June 1988): total weight of abalone after the removal of shell growths, measured using a Pesola spring scale; 9) *Degree of Sculpture*: a ranked index: 1 = no shell sculpture, 2 = faint sculpture, 3 = well defined sculpture, and, 4 = strong sculpture; 10) *Shell Growths*: proportion of the total shell surface initially covered by shell growths; and 11) *Shell Erosion*: proportion of the total shell surface eroded down to the nacreous layer (see Tissot 1988b; Chapter 4).

Abalone location was marked along each transect using three coordinates -- X (downshore), Y (vertical), and Z (alongshore) -- which were calibrated relative to mean lower low water (MLLW = 0.0 m) using a transit. Repeated measurements indicated that locations were accurate to within $\pm$

0.1 m. I measured overall net movement of abalone by the minimum distance between tagging locations on sequential surveys. I measured net vertical movement by calculating the change in position relative to MLLW between sequential surveys.

During each survey I intensively searched an area 10-30 m around each transect for tagged abalone and dead tagged shells. As no tagged abalone were found further than 20 m from their initial position this method was deemed sufficient. At the protected site, I also searched the subtidal area adjacent to each transect using SCUBA. Survivorship of tagged abalone was measured using the Jolly-Seber method as described in Krebs (1988). I estimated relationships between measures of morphology, growth and behavior, and survivorship by calculating the product-moment correlation between variables and the number of recaptures of individual abalone, a method recommended by Endler (1986).

C. Gonad Indices

I monitored the reproductive condition of abalone by collecting 10 individuals from the protected study site during each survey beginning in June 1988. Abalone were frozen and transported to the lab, where the following traits were measured: 1) total weight (shell + soft parts); 2) foot weight; 3) gonad length from apex to tip; 4) gonad width at mid-length; 5) gonad height at mid-length; 6) hepatic gland width at mid-length; and 6) hepatic gland height at mid-length. I estimated total gonad volume using the method described in Tutschulte and Connell (1981). I derived a gonad index by:

$$Gonad\ Index = Gonad\ Volume / Foot\ Weight \quad (1)$$

which measured the size of the gonad relative to the foot.

D. Algal Abundance

Beginning in March 1988 I examined drift algal availability by measuring the weight of drift algal material accumulated along two transects at each study site during 24 hr periods at low tide. Pieces of algal debris were located along transects using both horizontal and vertical coordinates, identified to species, and weighted to the nearest gram using a Pesola spring scale. Individual drift items were counted as distinct if they occurred greater than 10 cm from adjacent pieces or if they were of different taxa. *Phyllospadix*, which was not eaten by black abalone, and algae weighing less than one gram were not measured. I noted pieces of algae held by abalone and sea urchins.

I estimated the areal cover of kelp on the west end of Santa Cruz Island using aerial infrared photographs for the years 1984-1985 and 1987-1988 taken during the summer months. These photographs primarily recorded the offshore canopy of *Macrocystis pyrifera*. Aerial photographs were obtained from Ecoscan (Freedom, CA) and Kelco Co. (San Diego, CA). I traced kelp canopies from projected slides using a 1:10,000 scale and digitized them by computer.

E. Kelp Forest Community Structure

I established subtidal transects to estimate the densities of sea urchins (*Strongylocentrotus purpuratus* and *S. fransiscanus*), seastars (*Pycnopodia helianthoides*, *Pisaster giganteus*, and *Patiria miniata*), and macroalgal cover. Transects were sampled in three general areas: at the protected study site, at Black Point, and at south Fraser Point (Figure 3.3). Subtidal transects were 5-15 m in length and sampled using 0.25 m^2 quadrats at one meter intervals.

At the protected site, five 15 m transects were established and surveyed in September 1988 and June 1989; three transects were located in the shallow 2-6 m zone, 25 m offshore of abalone transects; two additional transects were located in *Macrocystis* beds 100 m offshore at 6-9 m depths. At Black Point, five quadrats were randomly sampled in June 1989 at each of 10, 8 and 4 m depths. At south Fraser Point, I sampled five quadrats in June and September 1989 at each of 10 and 12 m depths. At the exposed study site, north Fraser Point, I made qualitative observations in nearshore *Macrocystis* beds at 5-15 m depths in March 1989.

F. Sea Water Temperatures

I obtained monthly surface seawater temperatures for the general area of Santa Cruz Island using satellite imagery data (NOAA, 1982-1989). These temperatures were consistent ($\pm$ 1.0 C) with values taken intertidally during surveys. Mean monthly temperatures were extracted for the years 1982-1989 and compared to average annual surface values derived for the Santa Cruz Island area for 1942-1969 from Robinson (1976).

G. Laboratory studies

I conducted a series of laboratory studies to test specific predictions derived from the disease and starvation hypotheses. Abalone for these studies were collected from three localities in 1987: at the protected site on Santa Cruz Island, on Año Nuevo Island in central California, and at Punta San Quintin, Baja California (Figure 3.1). All abalone were transported in aerated ice chests to the Hatfield Marine Science Center, Newport, OR, and held in a partially recirculating seawater system. Mortality during transportation was generally less than 1%. Ambient seawater temperatures in the lab varied between 10-16 C and the salinity varied between 29-34 ppt.

In order to examine feeding rates of individual abalone in relation to growth, I made observations on individuals collected from Santa Cruz Island in September 1988. Abalone were individually fed to excess on a weighed portion of *Alaria marginata* and/or *Laminaria dentigera*. At weekly intervals abalone were weighed, and the amount of algae consumed was calculated relative to uneaten controls.

I examined the effects of starvation on weight loss by holding 30 abalone collected from Año Nuevo Island in April 1989 without food in a 100 gallon holding tank. The tank was supplied with fresh, aerated, filtered seawater and maintained in darkness to prevent algal growths. Individuals were weighed on a monthly basis. When mortality reached 50%, the remained abalone were feed to excess on a diet of *Alaria marginata*.

I examined the effects of temperature stress on abalone growth and survival using individuals from each of three populations (Año Nuevo Island, Santa Cruz Island, and San Quintin) cultured together in each of three seawater temperatures (12, 15, and 18 C). Individuals were fed *ad libitum* on a diet of *Alaria marginata*, *Laminaria* spp., *Iridaea cordata* and/or *Hedophyllum setchelli*. The 12C treatment was maintained by a Tecumseh refrigeration unit which held the temperature at 12.5C (SD = 0.5). The 15C and 18C treatments were maintained by submerged electrical heaters which held temperatures at 15.4C (SD = 0.9) and 19.2C (SD = 0.9) during the experiment, which was conducted between Aug 1987 and Aug 1988.

H. Data Analysis

I calculated shell growth rates by measuring the maximum increment of new shell material between surveys. Growth increments were transformed to represent changes in shell length (dL) using the relationship:

$$dL = 0.36 * \textit{growth increment} \qquad (2)$$

which I derived using field measured growth increments in relation to changes in shell length. Shell growth rates (mm/month) were calculated by:

$$Shell\ Growth\ Rate = dL / dt \quad (3)$$

where *dt* was the elapsed time between recaptures in months.

I transformed all measures of growth to scales independent of size (as measured by shell length) in order to allow comparisons among tagged abalone that varied in size among transects and surveys. Relative shell growth rates were calculated by using the deviations of shell growth from a linear regression predicted growth from shell length using all recaptured abalone:

$$Predicted\ Shell\ Growth = 0.534 - (0.004 * Length) \quad (4)$$

($r^2 = 0.07$, $n = 660$, $p < 0.01$). Residuals from predicted shell growth examined growth rates independently of shell size. I standardized relative shell growth values to z-scores (mean = 0, standard deviation = 1) in order to present growth in units of sample standard deviations (see Sokal and Rohlf, 1981).

For comparative purposes, I also calculated relative shell growth rates from the studies of Wright (1975) and Douros (1985) which were conducted at the west end of Santa Cruz Island. Data were converted to similar units (mm/month) and pooled with the data from this study. Relative shell growth rates were calculated as deviations from predicted growth using the equation:

$$Predicted\ Shell\ Growth = 1.51 - (0.012 * Length) \quad (5)$$

($r^2 = 0.18$, $n = 865$, $p < 0.01$) and were similarly transformed to z-scores. I examined statistical differences among studies using analysis of covariance of shell growth rate with shell length serving as a covariate.

I converted changes in total abalone weight between surveys to relative changes in weight using deviations from the regression:

$$\textit{Relative Weight Change} = 4.92 - (0.066 * \textit{Length}) \quad (6)$$

($r^2 = 0.53$, $n = 287$, $p < 0.01$). Relative weight change values were transformed to z-scores and represented deviations from average values in standard deviation units.

I derived an index of abalone "condition" using total abalone weight. Relative total weight was calculated using deviations of weights from a log-linear regression predicting "normal" abalone weight from shell length. Field recaptured individuals displaying both shell growth and increases in weight between surveys were used to derive the equation:

$$\textit{Log Predicted Weight} = 9.74 + (3.24 * \textit{Log Length}) \quad (7)$$

using base e logs ($r^2 = 0.97$, $n = 65$, $p < 0.01$). Deviations from this equation measured total abalone weight relative to "normal" abalone and were transformed to z-scores.

I examined the statistical significance of differences between wave-protected and wave-exposed study sites using a one-way analysis of variance (ANOVA). Because measures of abalone growth and behavior were derived from repeated recaptures of tagged individuals between surveys, I used a repeated-measure design, which controlled for the covariance between non-independent measures (Winer, 1971). Individual transects served as replicates for each site. Prior to ANOVA, samples were examined using Bartlett's test for homogeneity of variances. In the cases where variances were unequal, I chose a transformation that minimized differences among sample variances. Significant ANOVA's were not analyzed with *a posterori* tests because means from repeated measure analyses are not statisticallly independent (Day and Quinn, 1989). Instead, I plotted the mean values of variables ($\pm$ 1 standard error) across surveys and study sites.

I examined multivariate relationships among measured variables using canonical correlation analysis (CCA), which maximizes correlations among two sets of variables relative to minimizing correlations within sets (Pimentel, 1979). In this study I used CCA to quantify associations between measures of abalone growth, behavior and mortality, and potential causal factors. An important interpretative aid in CCA is the redundancy coefficient: a measure of the variation in one variable set predicted by variation in the other variable set. When canonical correlations are significant, a high redundancy coefficient implies a strong overall association among variable sets. In contrast, a low redundancy coefficient results when only several variables are highly correlated (Pimentel, 1979). Data for analysis were derived using mean values of variables. In the first analysis, which included data from all surveys, I examined shell growth rates, movement, and changes in abalone density for interactions with abalone density, mean quarterly ambient seawater temperatures, and the mean quarterly deviations of ambient seawater temperatures from long-term temperature averages. In the second analysis, which included data collected from June 1988 to June 1989, I examined associations between shell growth rates, changes in weight, total movement, survivorship, and changes in abalone density, and their interaction with abalone density, drift algal weight (g/m^2), drift algal density ($\#/m^2$), ambient seawater temperatures, and the deviations of ambient seawater temperatures from long-term averages.

Results

I tagged a total of 1000 abalone over the course of 12 surveys. Repeated recaptures (2-6) of tagged abalone resulted in 1805 measurements. The overall recapture rate was 45%.

Abundance

All transects displayed striking declines in abalone density between 1987 and 1990 (Figures 3.4 and 3.5). Densities of abalone in early 1987 averaged 58.4/m^2 on the protected transects (range 76-40/m^2) and 38.4/m^2 at the exposed site (range 47-30/m^2). Overall declines in density were greatest at the protected site, where the average density in January 1989 was 5.6/m^2, an overall decline of 90%. On exposed transects the average density in January 1989 was 8.2/m^2, an overall decline of 79%. Throughout 1987 and early 1988, large accumulations of empty shells were observed on the beach and many of these shells contained the remains of dead abalone.

The rate of decline was significantly lower on exposed relative to protected transects (Table 3.1). In protected areas, abalone densities declined from the first survey in January 1987 to maximum declines between September 1987 and March 1988 of 7% per month (Figure 3.6). The majority of mortality occurred during this 6-month period. Between March and June 1988 declines leveled off, and several transects increased in density between March and June 1989. Overall, however, abalone density at the protected site continued to decline throughout the study period.

At the exposed site, declines in density followed a similar pattern but were lower in intensity and more variable among transects (Figure 3.6). Declines in early 1987 were greater on the exposed relative to the protected coast, but peak mortality, which averaged 3.3% per month, occurred over a

larger time interval from June 1987 to March 1988. Several transects displayed density increases in September 1988 and March and June of 1989. However, average abalone density on the exposed site declined throughout the study period.

Intersurvey changes in density were significantly related to initial densities ($r = -0.47$, $n = 43$, $p < 0.01$), indicating that declines were density-dependent. As a result, abalone density after mass mortality was not significantly related to initial densities ($r = -0.18$, $n = 7$, $p > 0.05$). Black abalone were 62% more dense on the protected relative to the exposed site in 1987 but 46% less dense after mass mortality.

Distribution

Coincident with mass mortality were shifts in the intertidal distribution of abalone (Figure 3.7). Changes were most pronounced on the protected site where individuals which once covered most open space occupied cracks and crevices (Figure 3.4). Throughout the study period there were shore-level size gradients: a significant negative correlation between shell length and vertical distribution indicated that smaller individuals occurred higher on the shore than larger individuals ($r = -0.25$, $n = 662$, $p < 0.01$).

Survivorship

Estimates of survivorship were based on the assumption that tagged abalone not recovered were dead. This assumption could be partially examined in abalone because dead tagged shells are unequivocal evidence of death. Recovery rates of dead tagged shells were 9.8% on the protected coast and 5.6% on the exposed coast and all dead shells were recovered within 100 m of the transect in which they were originally tagged. No recovered shells showed evidence of mortality due to predation. Analysis of variance revealed

that the shell lengths of recaptured, missing (i.e., assumed dead), and dead tagged shells were significantly different (Figure 3.8). A Student-Newman-Keuls mutiple range test indicated that dead tagged shells were significantly larger than recaptured or missing abalone, which were not significantly different. The frequency of recovered dead shells at intervals along intertidal transects was not significantly different from the frequency of missing tagged individuals (Chi-Square, $n = 6$, $p > 0.05$).

Jolly-Seber survivorship of tagged abalone varied between exposed and protected sites (Figure 3.9). Overall, tagged abalone along exposed transects experienced significantly higher survivorship (0.69) relative to abalone at the protected site (0.54) (Table 3.1). At both sites the probability of survivorship between surveys followed a similar annual pattern in 1987-88: survivorship was high during the summer and low during the fall and winter. Low survivorship between September 1987 and March 1988 was partially due to the missed survey of January 1988 and hence a longer time interval (6 vs. 3 months) between surveys. Variability in survivorship was inversely proportional to its magnitude: low survivorship was uniformly low but high survivorship was variable.

Survivorship, as measured by recapture rate, also varied among size classes of abalone. However, this pattern differed among sites and years (Table 3.2). At the exposed site there was a decrease in the overall recapture rate of abalone as size increased: large abalone (length > 100 mm) had 9% lower survivorship than small abalone (30-70 mm). In contrast, at the protected site recapture rates were roughly equal among size classes (Table 3.2).

Rate of recapture also varied along intertidal gradients. At both sites the recapture rate of tagged abalone was reduced in the low- relative to the mid-intertidal zone (Figure 3.10).

Several traits were associated with greater survivorship during the study period, as measured by their correlation with the number of recaptures of individual abalone (Table 3.3). There were no significant correlations between the number of recaptures and shell length, shell erosion, shell cover, and relative weight. However, low shell growth rates, and low changes in relative weight were associated with high survivorship. There was a significant correlation between the number of recaptures and the shell sculpture index, indicating that more heavily sculptured abalone had higher survivorship than smooth abalone. Significant positive correlation between the number of recaptures and vertical movement indicated that survivorship was higher in individuals that moved upward into the intertidal relative to those that moved downward. Moreover, a significant correlation between recapture rate and net total movement at the protected site indicated that survivorship was higher in individuals that moved greater distances.

Movement

The magnitude and direction of net total abalone movement displayed strong spatial and temporal variation (Figure 3.11). Mean distances travelled between surveys was significantly higher on protected transects (2.14 m/survey) relative to exposed transects (0.92 m/survey) (Table 3.1) and displayed strong seasonal variation. Although patterns of movement were irregular, overall, abalone moved greater distances in the winter and spring relative to the summer and fall (Figure 3.12).

There was also pronounced variation among study sites in the net vertical movement of individuals (Table 3.1). At the exposed site, vertical

movement followed an annual pattern: individuals moved up in the intertidal in the summer, and down in the intertidal in the spring and fall (Figure 3.13). In contrast, vertical movement patterns were different at the protected site: individuals moved upshore during the summer and fall of 1987, downshore throughout 1988, and upshore in the spring and summer of 1989 (Figure 3.13). Overall, the direction of vertical movement was significantly different among sites: individuals at the protected site displayed a net downshore movement relative to individuals at the exposed site (Table 3.1).

Growth

Shell growth rates, as measured by standardized relative growth values, varied dramatically during mass mortality (Figure 3.14). Due to the high variability of shell growth, there were no significant differences among study sites (Table 3.1). However, shell growth displayed seasonal variation: growth rates, and the proportion of growing abalone, were higher in the spring and summer relative to the fall and winter (Figure 3.12). Overall, mean relative growth rates did not vary along intertidal gradients ($r = -0.05$, $n = 662$, $p > 0.05$). The highest mean growth rate occurred during the summer of 1988 and the lowest during the fall and winter of 1987-88.

Shell growth rates were depressed in 1987-1989 relative to growth rates measured in earlier studies of black abalone on Santa Cruz Island (Table 3.4). Both Wright's 1969-71 study at north Christi Beach (4 km east of the protected site; see Figure 3.3) and Douros' 1984 study (at the protected site) measured significantly higher growth rates than reported here for 1987-1989 (Figure 3.15). Analysis of covariance indicated that relationships between shell growth rate and shell length were significantly different among studies ($F = 127.3$, $n = 865$, $p < 0.01$). In the previous studies, 63-89% of the abalone exhibited shell growth. During 1987-89, the percent of abalone

exhibited growth declined from 52% to 43% to 30%, respectively, between years (Table 3.4).

Due to high variability, rates of relative weight gain were not significantly different among sites (Table 3.1) although mean rates of weight gain were higher at the exposed site (39% increase by weight/month) relative to the protected site (18%/month) (Figure 3.16). In general, abalone gained weight in the spring and lost weight during the summer, fall, and winter. Relative weight changes were significantly correlated with shell growth rates ($r = 0.42$, $n = 76$, $p < 0.01$) which were also highest in the spring and summer (Figure 3.12). Overall, large abalone exhibited greater weight losses relative to small abalone (Figure 3.17a).

There were no significant differences between sites in abalone condition, as measured by total abalone weight relative to "normal" abalone (Table 3.1). I defined "normal" as the relative weight of abalone both gaining weight and growing shell between surveys (see Methods). However, the seasonal pattern of relative weight varied between sites (Figure 3.18). At the protected site, abalone were severely underweight in June 1988 and gradually increased throughout 1988-89, reaching a peak in June 1989 after weight gains during the spring (Figure 3.16). In contrast, the mean relative weight of abalone on the exposed site was above normal in June 1988, declined in the winter of 1988 and spring of 1989, and increased in the spring of 1989. However, in contrast to weight gains, relative weight did not vary with shell length (Figure 3.17b).

A strong negative relationship between recapture rate and relative body weight indicated that underweight abalone at both sites were less likely to be recaptured than normal, heavier abalone (Figure 3.10). Recapture rates varied between 100% for abalone 2-3 standard deviations above normal

weight to 20% for abalone 1-3 standard deviations below normal weight. These results indicated that abalone greater than one standard deviation below normal weight (about 50% below predicted weight) were less likely to survive the three months to the next survey period. These severely underweight abalone occurred in all size classes (Figure 3.17). However, relative abalone weight did not vary along intertidal gradients: at both sites the proportion of abalone above healthy weight were approximately equal at all intertidal intervals (Figure 3.19).

Gonad Condition

There was strong interannual variation in reproductive condition between 1988 and 1989. In 1988, the gonad index declined in both sexes from peak values in the summer to low values in the fall and winter (Figure 3.20). In contrast, in 1989 the gonad index for both sexes increased from low values in the spring to peak values in the fall, declining into the winter.

Gonad volume was significantly more variable in June of both 1988 and 1989 relative to June 1984 data collected by Douros (1985) (Figure 3.21). Analysis of covariance revealed significant differences among the y-intercepts of the gonad volume-body weight regression for the three years: abalone had more gonad relative to their body weights in 1988 relative to 1984 or 1989, which were not significantly different ($F = 3.63$, $df = 56$, $p < 0.05$). Moreover, as indicated by the r-squared values for the regressions, reproductive output was more variable in 1988 ($r^2 = 0.22$) and 1989 ($r^2 = 0.08$) relative to 1984 ($r^2 = 0.50$).

There was a significant correlation between the gonad index and relative abalone weight ($r = 0.52$, $n = 27$, $p < 0.01$), indicating that underweight abalone produced less gonad than abalone of normal weight. The gonad index was also significantly correlated with vertical distribution:

high intertidal abalone had large gonad indices relative to low intertidal abalone ($r = 0.53$, $n = 16$, $p < 0.05$).

Drift Macroalgae

Drift algae displayed marked spatial and temporal variation in abundance along intertidal transects. A two-way ANOVA indicated a significant interaction between sites and surveys in the abundance of drift algae measured by weight (interaction $F = 4.91$, $df = 16$, $p < 0.01$). Although drift algae was generally more abundant at the exposed (33.8 g/m^2) relative to the protected site (21.9 g/m^2), this pattern was reversed in January 1990 (Figure 3.22).

At both sites drift algal was rare along transects in March 1988: a time of major declines in abalone abundance, low survivorship, and low growth rates (Figures 3.5, 3.9, 3.14). However, in the spring of 1988 I observed strong recruitment of both *Macrocystis* and *Egregia* on the west end of Santa Cruz Island: numerous tiny laminarian sporophytes occurred along intertidal transects as high as +0.5 m MLLW and at subtidal depths to 10 m. As a result, drift algae increased significantly between March and June 1988, especially at the exposed site (Figure 3.22). The abundance and frequency of drift algae continued to increase into 1989. During March 1989, drift algae was 64-fold more abundant than the previous spring.

Although drift algae was more abundant in the low relative to the high intertidal (Figure 3.19), there were no significant correlations between the abundance of drift algae and relative shell growth rates or rates of weight gain along intertidal transects (all $p > 0.05$). Moreover, there were no significant correlations between relative shell growth rates or rates of weight gain and the abundance of drift algae among surveys (all $p > 0.05$). Along intertidal transects, 14% of all measured drift algae was captured by purple

sea urchins (*Strongylocentrotus purpuratus*), while 7% was held by black abalone.

Kelp Canopy

There was marked interannual variation in the summer canopy of *Macrocystis* along the west end of Santa Cruz Island both prior to and during mass mortality (Figure 3.23). In 1984, kelp beds were 52% of their area in 1985. In contrast, during the population decline in 1987, surface canopies were reduced to 64% of their 1985 area. Following the spring 1988 recruitment episode, however, kelp beds recovered significantly at the exposed site, but continued to decline at the protected site.

Seawater Temperatures

Seawater temperatures for 1982-1989 derived from satellite imagery indicated abnormally warm surface water around Santa Cruz Island both prior to and during the mass mortality (Figure 3.24). The normal seasonal pattern is for a minimum of 12C during upwelling in late winter and early spring, and a maximum of 16C between September and December (Robinson, 1976).

Between the eight year period 1982-1989 only two years, 1985 and 1989, had seawater temperatures similar to temperatures derived from the 1942-1969 averages reported by Robinson (1976). During 1983-84 there were several large temperature anomalies: summer seawater temperatures in 1983 and 1984 averaged 19C, 3C above average summer temperatures. In 1986-87 there were several additional abnormally warm periods: seawater temperatures were 1-2 C above average during mass mortality in the spring and summer of 1987 (Figure 3.24). There was a significant correlation between the temperature anomaly (i.e., average quarterly deviations of seawater temperatures from the 1942-69 means) and inter-survey density

declines on the exposed site ($r = -0.76$, $n = 11$, $p < 0.01$). Among transects on the protected coast, however, this correlation was not significant ($r = -0.46$, $n = 11$, $p > 0.05$).

Subtidal Communities

Subtidal transects along the shallow protected coast were dominated by high densities of purple sea urchins, which often exceeded $80/m^2$ (Table 3.5). Between Black Point and Fourney Cove (the protected site), purple sea urchins formed a largely continuous "carpet" at 3-6 m depths. In these areas, fleshy algae (especially *Macrocystis*) was rare to non-existent. Below 8 m, however, sea urchins decreased and kelp became more abundant. At the more exposed south Fraser Point, purple sea urchins occurred at reduced densities in cracks and under boulders (Table 3.5). I failed to observe any sea urchins at 5-15 m depths at north Fraser Point (the exposed site). In contrast to the protected site, the exposed site was dominated by dense stands of *Macrocystis* and *Egregia*.

All species of seastars (*Pisaster giganteus*, *Pycnopodia helianthoidies*, and *Patiria miniata*) were rare in the shallow subtidal at 2-7 m depths. In kelp beds below 8-10 m, however, these species were more abundant (Table 3.5). Along intertidal abalone transects only one *Pisaster ochraceus* was observed over the course of 3 years.

Feeding observations

In the laboratory underweight abalone collected in the field were weak and consumed considerably less macroalgae (*Alaria* and *Laminaria*) than heavier abalone (Figure 3.25). Although food was supplied *ad libitum*, three of the six abalone died during the 10-week observation period. Death resulted after sharp declines in body weight, which commonly spanned 10-14

days, and occurred at 1.2 - 5 standard deviations below average normal weight.

Starvation Experiment

Abalone collected from Año Nuevo Island began dying from starvation 300 days after collection; 50% mortality occurred after 460 days. The time course of mortality was size-biased: there was a significant positive correlation between shell length and the number of days required for death by starvation ($r = 0.66$, $n = 16$, $p < 0.01$), indicating that large individuals survived for longer periods of time without food than small individuals (Figure 3.26). Death occurred at an average relative weight of 4.2 standard deviations (95% confidence interval = $\pm$ 0.56) below normal weight, based on individuals from Año Nuevo Island (unpublished data).

Abalone continued to die from starvation after food was supplied on day 460. In the six week period following the resumption of feeding, an additional 5 individuals died (17%). I observed that underweight abalone were weak and many did not feed although they were placed directly on algal blades. Moreover, of the remaining 12 individuals, 9 (75%) continued to lose weight in the presence of food.

Temperature Experiment

Survivorship of abalone in the laboratory showed a strong interaction with temperature when food was provided *ad libitum* (Figure 3.27). The results of growth experiments during two time periods, August to December 1987 and December 1987, to August 1988, produced similar results: between 15-18C, abalone showed reduced tolerance to elevated temperatures. In the earlier time period, there were differences among populations in the effects of temperature: abalone from the southernmost population (San Quintin) had higher survivorship at 18C than abalone from the northernmost

population (Año Nuevo Island), with the intermediate latitude population (Santa Cruz Island) having intermediate survivorship.

Underweight abalone were present in all temperature treatments (Figure 3.28) but mortality was significant only at 18C. Abalone died at 1-3 standard deviations below normal weight (30-90% underweight) and attempts to revive emaciated abalone at lower temperatures were unsuccessful.

The thermal tolerance of black abalone in these studies in 1987 was reduced compared to studies conducted at the Diablo Canyon Power Plant in 1979-82 (Hines et al., 1980; Pacific Gas & Electric, 1982, 1983) (Table 3.6). In these previous studies the black abalone displayed a consistent LT_{50} (i.e.. the temperature at which 50% mortality occurred) of 26.1-31.5C during a variety of exposures to elevated temperatures (Table 3.6). In contrast, in this study, abalone from three populations experienced greater than 50% mortality at 18C.

Multivariate Analysis

Canonical correlation analysis revealed significant associations between measures of abalone growth, movement, and mortality, and potential causal factors (Table 3.7; Figure 3.29). The first analysis, which spanned the entire 1987-89 study period, primarily documented interactions occurring during the population decline of 1987-88. Chi-Square tests indicated that only the first canonical axis represented a significant association among variables sets (Table 3.7). The first canonical axis associated large, negative changes in density among transects with high density sites and a high temperature anomaly. Although close to 50% of the variance among sets was explained by this axis, the redundancy of each set (i.e., the proportion of variation in one set predicted by the other) was low,

indicating that there was little overall association among data sets. The significant canonical correlation resulted from a strong correlation between density declines and the temperature anomaly. Canonical variate scores, which measured the contribution of sites and surveys to this pattern, contrasted temperature-dependent mortality among years in decreasing order of intensity: 1987 > 1988 > 1989 (Figure 3.29a).

The second analysis examined associations among additional measures of abalone dynamics (body weight changes and Jolly-Seber survivorship) and additional potential causal factors (drift algae weight and density). Due to the incomplete measurement of these variables, the analysis was limited to the period between June 1988 and June 1989 and thus measured interactions occurring among survivors of the 1987-1988 population decline. Chi-square tests indicated that the first canonical correlation was significant (Table 3.7). However, because sample sizes were small (n = 25) and the canonical correlation was high (0.80) I also examined the second canonical axis.

The first canonical axis contrasted high rates of movement and low shell growth occurring at low density sites during low temperature periods (Table 3.7). However, low redundancy coefficients indicated that overall associations between variable sets were low. A plot of canonical variate scores for this axis contrasted winter and spring surveys, where movement was high and shell growth was low, with summer and fall surveys, where movement was low and shell growth was high (Figure 3.29b).

The second canonical axis described an association among variable sets uncorrelated with the first: declines in density occurred at high density sites where drift algae by weight was abundant (i.e., the exposed transects) (Table 3.7). Again, however, low redundancy coefficients indicated a low

overall association among variable sets. These results indicated that density-dependent declines occurred in 1988-89 despite abundant food resources. Plots of canonical variate scores contrasted differences in the rate of decline between sites: in 1988-89 the higher density exposed site experienced greater mortality than the lower density protected site (Figure 3.29c).

Discussion

Black abalone on Santa Cruz Island experienced striking declines in abundance between 1987 and 1990. Densities decreased over 90% from an average of $50/m^2$ in 1987 to $6/m^2$ in 1990. The population decline was associated with high rates of movement, low body weights, depressed shell growth, and irregular gonad development. These results indicate that a disease, a negative deviation from normal conditions (Kinne, 1980), was present during the mass mortality. The major question to be addressed is: what caused the disease?

Unfortunately, the causes of disease are exceedingly difficult to document because they occur in response to a wide variety of interacting factors (Kinne, 1980). Several potential factors relevant to this study include food shortages, abnormal crowding, environmental perturbations, physiological disorders, and invasion by pathogens (Sindermann, 1970; Kinne, 1980). Accordingly, the following discussion is divided into four sections which evaluate hypotheses on the causes of mass mortality: 1) the geographic distribution of the mortality; 2) relationships of causal factors to survivorship; 3) the interaction of mass mortality with population dynamics; and 4) similarities between the abalone decline and other mass mortalities.

Geographic Distribution of Mass Mortality

The geographic distribution of abalone mortality indicates that rates of mortality were temperature- and density-dependent. The earliest signs of black abalone decline, although limited, occurred in the warmest regions of the Southern California Bight. In Laguna Beach, a population of sub-adult black abalone declined between 1983 and 1985 (Tissot, 1988d), went locally extinct in early 1986, and has not recovered as of January 1990 (unpublished

data). A sharp decline in black abalone abundance was also observed along the Palos Verdes peninsula during 1983-86 (Alan Miller, personal communication). Satellite imagery indicates that these areas experienced 2-4C higher surface temperatures than the northern Channel Islands, including Santa Cruz Island (NOAA, 1982-1984). In 1985, when the National Park Service and the California Department of Fish and Game began studies on the black abalone in the northern Channel Islands, these populations were just beginning to decline (see Figure 3.2): population declines began at Anacapa in early 1986 and at Santa Rosa Island in late 1986 (Davis et al., in press). However, the commercial catch of black abalone, largely from the northern Channel Islands, had been declining since 1983 (Haaker et al., in press). In contrast, populations of black abalone in colder areas of the Southern California Bight, such as San Miguel, San Nicholas, and northern Santa Rosa Island, experienced either moderate declines (San Miguel and northern Santa Rosa) or no mortality (San Nicholas), despite similar high densities of black abalone (Davis et al., in press) (Figure 3.2). At Año Nuevo Island in central California, no mortality was observed between 1987 and 1990 (unpublished data; Chapter 4). In Baja California, where seawater temperatures are generally higher than southern California (NOAA, 1982-1984), only a few instances of mortality have been reported (personal communications). However, because black abalone are harvested both commercially and recreationally throughout Baja California, they rarely occur at densities above $5/m^2$ (personal observations). In July 1986, I observed no symptoms of the disease in black, green, or pink abalone on Natividad Island off Baja California. Between December 1987 and July 1988, however, I noticed declines in black abalone abundance at Punta San Quintin.

There is some evidence to suggest that mortality spread to low-density sites in 1988-89 after mass mortality at high density sites in 1986-88. Black abalone in the thermal discharge at the Diablo Cove Nuclear Power Plant, the northernmost record of mortality, did not display symptoms of the disease until mid-1988, although the plant had been operating since 1985 (Steinbeck et al., in press; Blecha et al., in press). Temperatures in the Diablo Cove thermal discharge averaged 16-23 C (2-7 C above ambient temperatures). Moreover, some low density (5-10/m^2) populations, such as Santa Barbara Island, did not experience mortality until 1989 (Davis et al., in press).

Overall, these patterns of decline indicate that mass mortality was density-dependent and was higher in warm-water, relative to cold-water populations. Mortality was probably greatest in the northern California Channel Islands because they had a combination of both unusually warm water and high abalone densities. These patterns, combined with observations on Santa Cruz Island during the mass mortality, indicate that population declines occurred in reponse to *four* interacting factors: 1) low abundance of drift algae, which in turn was associated with, 2) high sea urchin densities, 3) elevated seawater temperatures, and 4) high abalone densities. Below I discuss each of these factors, and the potential role of biotic pathogens, in relation to survivorship during mass mortality.

The Role of Starvation

Mass mortality occurred during a period of low drift algal abundance associated with marked fluctuations in the extent of offshore kelp forests. This observation alone strongly suggests the hypothesis that mortality occurred in response to starvation. Additional evidence was provided by the starvation experiment: starved abalone were weak and underweight, similar

symptoms to those observed in the field. Moreover, the starvation experiment demonstrated that mortality and weight loss continued to occur after food became abundant. Similarly, mortality and weight loss in the field continued to occur for 18 months after an increase in food abundance.

Because drift macroalgae was more abundant on wave-exposed relative to protected transects, higher survivorship and higher rates of weight gain in abalone at the exposed relative to the protected site was also consistent with the starvation hypothesis. However, these results are inconclusive because additional factors unique to the exposed site may also have been important: 1) cooler seawater temperatures (personal observation); 2) higher water motion; and 3) lower densities of black abalone.

Drift algae typically displays strong spatial and temporal variation in availability (Gerard, 1976; Chapter 2). Black abalone are particularly dependent on drift algae because they often occur at high densities and rarely actively search for food (Bergen, 1971; Douros, 1985; Blecha et al., in press). However, like most organisms that feed on drift algae, they also appear to be adapted to long periods of starvation (Tegner and Levin, 1982). Previous experiments indicated that black abalone could survive 60 (Leighton and Boolootian, 1962) to 261 days (Bergen, 1971) without food. In this study abalone from Año Nuevo Island in central California survived over 460 days without food. Interestingly, Leighton's study occurred during the 1957-59 El Niño, when abalone mortality was also attributed to starvation (see below).

During the mass mortality offshore kelp canopies were sparse compared to previous years and drift macroalgae was rare in the intertidal. I estimate that drift algae was about 50% less abundant in June 1987

compared to June 1988. In March 1988, when I began measuring drift algal abundance, drift algae was very scarse. Thus, abalone on Santa Cruz Island experienced low food abundance, in conjunction with elevated sewater temperatures, for at least a year in 1987-88 and perhaps longer if drift algae was scarce during 1986.

Measurements of offshore kelp canopies derived from aerial infrared photographs indicated large declines in the abundance of giant kelp (*Macrocystis pyrifera*) between 1985 and 1987 when mass mortality began. Giant kelp is the major source of drift algae for black abalone in southern California (Leighton and Boolootian, 1962; Douros, 1985, 1987). At Santa Cruz Island, giant kelp comprised 81% by weight of all measured drift algae in 1988-90, and 79% of all abalone feeding observations (see Chapter 2). Fluctuations in giant kelp abundance at Santa Cruz Island occurred during two El Niño events: periods characterized by unusually warm seawater temperatures, low nutrient conditions, and larger than average storm events (Glynn, 1988). However, on Santa Cruz Island, declines in giant kelp abundance during the minor 1986-87 El Niño were of a greater magnitude than the devastating 1983-84 El Niño, an event which had strong effects on kelp forests throughout southern California (Dayton and Tegner 1984; Tegner and Dayton, 1987). The paradoxical stronger effect of the lesser 1986-87 El Niño may have been due to the interaction of additional factors unique to the northern California Channel Islands: 1) a severe winter storm which occurred in January 1988 (Seymour et al., 1989); 2) the location of these islands in a temperature-transition zone; and 3) the establishment of extensive sea urchin barrens after 1983.

Storms have a major effect on kelp forest communities, especially giant kelp, which is notably sensitive to strong wave-action (Dayton and

Tegner, 1984; Dayton, 1985; Ebeling et al., 1985). The storm in January 1988 was the most intense disturbance to hit the Santa Barbara area in 25 years, including major storms during the 1983-84 El Niño (Seymour et al., 1989). In addition to further lowering the abundance of giant kelp, the strong waves associated with the storm would have had devastating effects on abalone weaken by previous starvation. Thus, the storm may be the proximal cause of peak abalone mortality between the September 1987 and March 1988 surveys.

The negative effects of warm water and low nutrient conditions on *Macrocystis* are well known (Jackson 1977; North and Zimmerman, 1984). Kelp forests in the northern Channel Islands, particularly Santa Cruz and Santa Rosa, are notably vulnerable to nutrient fluctuations because this area lies in a transition zone between the cold, nutrient-rich California current and the influence of the warm, nutrient-poor Davidson counter-current (Murray et al., 1980; Seapy and Littler, 1980). During El Niño events, these islands experience fluctuations around the critical temperature of 16C: a temperature which coincides with a critical level of nitrate availability in giant kelp (Jackson, 1977, 1983). Thus, the kelp forest communities in the northern Channel Island may be particularly sensitive to El Niño events.

The Role of Sea Urchins

Differences in the recovery of kelp beds on Santa Cruz Island after kelp recruitment in 1988 were associated with variation in the extent of sea urchin barrens. At the protected site, Black Point to Fourney Cove, giant kelp beds were rare in shallow (2-7 m), rocky areas where sea urchin barrens, primarily *Strongylocentrotus purpuratus*, predominated (Table 3.5). At this site, as in other nearby sites (Ebeling et al., 1985), kelp beds were confined to the narrow, deeper portions of the shore where urchins were not abundant.

In contrast, at the exposed site near Fraser Point, giant kelp beds occurred at a range of depths from 5 to 25 m. Possibly due to high water motion, purple urchins were not abundant at shallow depths and were restricted to cracks and holes on the reef.

There were major increases in the density of sea urchins between 1984-1986 in response to strong recruitment during the 1983-84 El Niño (Davis et al., in press; M. Tegner, personal communication). On Santa Cruz Island, the combined density of urchins (*S. purpuratus* and *Lytechinus anamensus*) increased from 4.8 to 40.8/m^2 between 1984 and 1986 (Davis et al., in press). At the west end of Santa Cruz Island, densities of purple sea urchins averaged 91/m^2 in shallow water and 32/m^2 in kelp forests in 1988 and 1989 (Table 3.5).

Sea urchins are known to have strong effects on both the distribution of kelp plants and the abundance of drift algae (reviewed by Lawerence 1975). At the protected site on Santa Cruz Island, sea urchin barrens eliminated live kelp plants from nearshore areas, which serve as a source of drift algae (see Chapter 2). In addition to removing live plants, subtidal sea urchins consumed a significant portion of intertidal drift algae. Along intertidal transects, where purple sea urchins averaged 5/m^2 in the low intertidal, they captured twice as much drift algae as that held by abalone. Thus, sea urchins may exploitatively compete with abalone for drift macroalgae, both by their removal of live plants and by their consumption of drift algae. Tegner and Levin (1982) provided experimental evidence of competition for drift algae between red abalone, *Haliotis rufescens*, and red sea urchins, *Strongylocentrotus franciscanus*.

Ironically, these sea urchin barrens, which I propose contributed to the mass mortality by reducing the availability of drift algae, were partially

due to a previous mass mortality: that of the seastars *Patiria miniata*, *Pisaster giganteus*, *P. ochraceus*, and *Pycnopodia helianthoides*. Two outbreaks of a disease in 1978 and 1981 caused extensive mortality of these seastars in shallow water areas throughout the Southern California Bight (Dungan et al., 1982; Davis, 1985; Tegner and Dayton, 1987). On Santa Cruz Island, seastars were rare on subtidal transects between 1982 and 1989 (Davis et al., in press). At the west end of Santa Cruz Island, seastars were only abundant below 10m depths (Table 3.5); they have yet to recolonize shallow water urchin barrens. Although the extent to which seastars control purple sea urchins populations is not known, the decline of *Pycnopodia* -- a voracious predator on purple urchins (Mauzey et al., 1968) -- is considered to have had the strongest effect. I have observed *Pycnopodia* eating purple sea urchins on Santa Cruz Island. Additional causes of sea urchin barrens which also may have been important include: 1) reductions in the abundance of other urchin predators such as the California sea otter, *Enhydra lutris* (Kenyon, 1975); the spiny lobster, *Panulirus interruptus* (Tegner and Levin, 1983); and the California Sheephead, *Semicossyphus pulcher* (Cowen, 1983); and, 2) reductions in the abundance of purple urchin competitors, such as the red sea urchin, *S. franciscanus* (Schroeter, 1978), which has been severely reduced on Santa Cruz Island by commercial fishing (personal observation).

The Role of Temperature

Declines in abundance were significantly correlated with elevated seawater temperatures in 1987-88 associated with El Niño. Furthermore, survivorship of tagged abalone was reduced during high seasonal temperatures in the fall of 1988 and 1989 despite peak abundances of drift algae. In the laboratory, mortality was also higher at 18C relative to 16C and 12C, although food was supplied *ad libitum*. These studies demonstrate that

temperature had an adverse effect on survivorship independently of food abundance. Furthermore, comparison of these results with earlier studies of thermal tolerance indicate that black abalone had significantly reduced tolerance to thermal stress during mass mortality.

In 1987 abalone from three populations experienced greater than 50% mortality at 18C in this study, and 38% mortality at 18C in a similar experiment conducted at Diablo Canyon in 1988-89 (Steinbeck et al., in press). These values indicate a 6-8C reduction in thermal tolerance between 1982 and 1987 and suggest a reduction in the ability of abalone to endure physiological stress. However, considering that black abalone displayed tolerance to high temperatures prior to 1982, it is unlikely that seawater temperatures during the 1983-84 and 1986-87 El Niños, which reached maximum values of 20C, were a cause of the disease. It is likely, however, that this thermal stress, in conjunction with a food shortage, may have contributed to the onset of the disease.

The Role of Abalone Density

Population declines throughout the Southern California Bight indicated that mortality was density dependent. On Santa Cruz Island, mortality was density dependent and varied along a wave-exposure gradient: mortality was higher at the protected site, where densities were 34% higher prior to mass mortality, than the wave-exposed site (Figure 3.5). Further evidence in support of density-dependent mortality is provided by reciprocal transplantation of abalone between wave-exposed sites on Santa Cruz Island in 1987 (Chapter 4). Survivorship among transplanted individuals was inversely proportional to changes in density: abalone moved to higher density sites diplayed decreased survivorship relative to abalone moved to lower density sites. Moreover, shell growth rates were higher among individuals

from the exposed site, both transplants and controls, relative to abalone derived from the protected site. These results indicate that density, in addition to having a strong effect on survivorship, may have influenced the intensity of the disease.

Abnormal crowding is a common cause of disease because high densities can induce a wide variety of stresses (Kinne, 1980; Long, 1973). Although high abalone densities in the northern Channel Islands are clearly abnormal, due to removal of their main predators, these densities have persisted for at least 30 years (Cox, 1962; B. Owen, personal communication). Thus, it is paradoxical that high densities would have a negative effect after years of apparent stability. One explanation is that abalone populations in the northern Channel Islands have been experiencing chronic starvation stress in response to high seasonal and interannual variation in kelp abundance. Because drift algal abundance is not correlated with abalone density among transects (Chapter 2), high density sites would be subjected to greater starvation stress than low density sites. Another hypothesis is that thermal stress during the 1983-84 and 1986-87 El Niños, in combination with reduced food abundance, produced sufficient stress to induce an abalone disease.

The Role of Pathogens

Although biotic pathogens are a common cause of mass mortality in marine organisms (Sindermann, 1970) there is no available evidence supporting a pathogen as the primary cause of the abalone mortality in southern California. Moreover, because changes in environmental conditions often disrupt host-parasite relationships (Kinne, 1980), biotic infections are commonly associated with population declines although they are not the proximal cause of the decline (e.g., Rasmussen, 1977). Therefore, one

hypothesis is that high abalone density, in conjuction with a food shortage and high temperatures, decreased the resistence of abalone to infection by pathogens, which may have secondarily caused the mass mortality. Continued mortality and depressed rates of shell growth among abalone 18 months after kelp recruitment in Spring 1988 is consistent with this hypothesis. Additional evidence was provided by lack of correlation between survivorship and drift algal abundance along intertidal transects and the geographic spread of mass mortality in 1988-89.

One potential pathogen is the coccidial protozoan discussed in Steinbeck et al. (in press). Coccidia infect the kidneys of red, pink, and black abalone and may cause considerable tissue damage and inflammation (Steinbeck et al., in press). A similar coccidial infection has been described in the littleneck clam (Morado et al., 1984). However, there is little evidence supporting coccidia as the cause of abalone mortality. Infections by coccidia occur throughout the range of the black abalone and are not related to population declines (C. Friedman, personal communication). Moreover, in the temperature experiment reported by Steinbeck et al. (in press), the extent of coccidiosis was inversely proportional to temperature: infections occurred in 25% of the surviving individuals at 18C but 100% of individuals at ambient temperatures (10-15C). Thus, there is currently no evidence to support coccidia as a cause of the mass mortality in abalone.

Effects on Population Dynamics

There were several aspects of abalone growth, distribution, and behavior that interacted with survivorship during mass mortality. Inverse relationships between the extent of abalone movement and drift algal abundance indicated that movement represented foraging during periods of low food availability. Similar relationships between movement and food

availability have been described for sea urchins (Harrold and Reed, 1985). Moreover, high rates of movement was related to higher survivorship during mass mortality, suggesting that increased foraging for food may have reduced the effects of the disease. However, an alternate hypothesis is that survivorship was not higher in individuals with high rates of movement *per se*, but higher among individuals that migrated upward in the intertidal, a behavior also correlated with higher survivorship during the mass mortality. Black abalone exhibit seasonal variation in movement and usually move into the low intertidal in the fall when spawning occurs (Tissot, 1988d). Although drift algae was more abundant in the low-intertidal, abalone survivorship was reduced in the low- relative to the mid-intertidal. However, these patterns are paradoxical in that growth in generally limited by the availability of drift macroalgae (Leighton and Boolootian, 1962).

One potential cause of intertidal variation in survivorship is a decrease in metabolic rate in conjunction with aerial exposure. Under conditions of stress or low food availability reductions in metabolic rate can have profound effects on survival (Bayne and Newell, 1983). Black abalone exhibit a temperature-dependent reduction in metabolic rate upon exposure to air: respiration is 68% less at 12C and 38% less at 16C in black abalone exposed to air relative to submerged individuals (Tissot, unpublished data). Due to greater periods of time out of water, mid-intertidal abalone would have considerably reduced metabolic rates relative to low-intertidal abalone. Thus, survivorship may have been greater in the mid-intertidal because aerially-exposed abalone are more metabolically efficient than submerged abalone.

Body size was another important trait that appeared to interact with survivorship during the mass mortality. Although the the recapture rate of

small abalone was 10% greater than large abalone at the wave-exposed site, body size was not correlated with survivorship at the protected site. However, the larger size of dead tagged shells relative to missing tagged shells indicated that small tagged abalone were more likely to be missed during surveys. Recovered dead shells are an accurate estimate of the mean size of mortalities but they underestimate the variance due to frequency-independent transportation and breakage of shells (Tissot, unpublished data). Thus, in contrast to the reduced survivorship of small relative to large abalone in the starvation experiment, there is some evidence that small abalone had higher survivorship than large abalone during the mass mortality.

There are several reasons why small abalone could have had higher survivorship during the population decline. First, shore-level size gradients indicated that small abalone occurred higher on the shore than large abalone, where survivorship was greater (see Chapter 4). Second, although not documented in this study, small abalone generally move greater distances than large abalone (Bergen, 1971; Blecha et al., in press), and may be more efficient foragers. Third, smaller abalone, being younger, may be more resistant to infection by diseases (Anderson and Crombie, 1985). Thus, there are several reasons, two of which are unique to black abalone, that may have promoted higher survivorship among small individuals during mass mortality.

Abalone with strong shell sculpture were also favored during mass mortality although this factor was not correlated with any previously described gradient in survivorship (i.e., wave-exposure or intertidal position). However, sculpture was weaky correlated with two factors associated with higher survivorship: 1) small body size; and 2) high shell growth rates. Thus, higher survivorship of this trait during the mass mortality may be due to its

correlation with characteristics that were favored during the population decline.

Relationships to other Mass Mortalities

Previous episodes of mortality in abalone share several similarities with this study. Previous reports of underweight black abalone in southern California were reported by Young (1964) and Leighton and Boolootian (1963) from 1956-1959 at White Point on the Palos Verdes peninsula. These authors attributed this condition to starvation resulting from the negative effects of sewage on algal abundance. MacGinitie and MacGinitie (1966) reported a similar incidence of sewage-induced starvation in pink abalone, *H. corrugata*, in Laguna Beach in 1959. To test this hypothesis, Young (1964) conducted a reciprocal transplantation of black abalone between Palos Verdes, where algae was scarse, and Santa Catalina Island, where algae was abundant. Weight gain among transplants at Catalina and mortality among transplants at Palos Verdes was consistent with the starvation hypothesis (Young, 1964). During the strong 1957-59 El Niño, Cox (1962) reported several incidences of starvation in red and pink abalone throughout central and southern California. Mortality, reduced shell growth, and shrunken soft parts were attributed to declines in the abundance of *Macrocystis* and *Nereocystis* (Cox, 1962), which was strongly influenced by the 1957-59 El Niño (Radovich, 1961). When these kelps increased in abundance in 1960-61, large increments of thin, new shell material were added in red and pink abalone within several months (Cox, 1962). A similar growth surge was measured during this study at the exposed site in the summer of 1988 and in several pink abalone collected on Santa Cruz Island in 1988 (Tissot, unpublished data). Similar reports of underweight abalone have been described in Japan, where mortality was attributed to declines in the availability of kelp (Tanaka

et al., 1986). These previous episodes of abalone mortality differ in one important respect from the 1986-88 decline in southern California: abalone recovered after the restoration of abundant food. In contrast, abalone on Santa Cruz Island continued to decline, lose weight, and display depressed shell growth rates 18 months after increases in food abundance in mid-1988. Mass mortality in southern California can thus be attributed to a combination of temporal fluctuations in food abundance, which are not uncommon among abalone populations, and the effects of a chronic disease.

Mass mortality of the black abalone also shares several similarities with die-offs in other marine organisms. As in the case of the sea urchin *Strongylocentrotus* in Nova Scotia (Scheibling and Stephenson, 1984), the seastar *Heliaster* in the Gulf of California (Dungan et al., 1982), and the eelgrass *Zostera* in the Atlantic (Rasmussen, 1977), black abalone declined during periods of abnormally warm water. In all of these cases, thermal stress appeared to play a major role in increasing the susceptibility of the host to infection by pathogens, although in most cases a specific pathogen was never identified.

An additional similarity between the abalone mortality and other cases of mass mortality is their occurance in abundant species. In addition to the black abalone, *Zostera* in the Atlantic, *Heliaster* in the Gulf of California, *Strongylocentrotus* in Nova Scotia and Santa Cruz, and *Diadema* in the Caribbean, were exceptionally abundant prior to mass mortality (Pearse et al., 1977; Rasmussen, 1977; Dungan et al., 1982; Miller and Colodey, 1983; Scheibling and Stephenson, 1984; Lessios, 1988). Although the causes of these mortalities are largely unknown, high density is indicated to have a strong effect on rates of abalone mortality in the northern Channel Islands.

Alternatively, we may only be detecting mass mortality in abundant species because their declines are more obvious.

Unique to the black abalone die-off were several features not previously described. Of greatest importance was the rate of mortality: in contrast to the rapid course of most die-offs (e.g., 7-45 d in *Diadema*) the slow two-year decline among black abalone allowed measurement of several ecological factors that appeared to interact with survivorship during mass mortality. The most striking patterns involved variation in movement and survivorship along intertidal and wave-exposure gradients. These spatial patterns are important because they determined the demographics of the population after mass mortality. The genetic structure of the post-mortality population could be quite different from that prior to mass mortality if there is genetic variation along these ecological gradients.

Perhaps of greatest interest in this study was the number of factors that interacted during the course of the population decline. Spatial and temporal variation in growth, distribution, behavior, wave exposure, seawater temperature, abalone density, and algal, sea urchin and seastar abundance all appeared to play roles in the abalone mortality. This study thus serves as an example of the multivariate nature of shallow-water marine communities and the complexity that can underlie a mass mortality. It is hoped that by documenting this population decline we will be in a better position to understand, and perhaps prevent, future mass mortalities.

Table 3.1. Results of repeated-measure one-way analyses of variance testing for differences among exposed and protected study sites for variables measured on black abalone at Santa Cruz Island.

Variable	Mean Values *Exposed*	*Protected*	F-Value
Change in Density	-7.550	-9.955	7.09**
Survivorship	0.687	0.545	6.58**
Total Movement	0.920	2.143	3.13*
Vertical Movement	-0.051	-0.058	2.76*
Relative Shell Growth	-0.181	-0.093	1.30
Relative Weight Change	0.108	-0.016	1.43
Relative Total Weight	0.172	0.159	1.83

Significance Levels: * - $p < 0.05$, ** - $p < 0.01$

Table 3.2. Percent recaptures of tagged black abalone among three size classes from 1987-1989 at two sites on Santa Cruz Island.

	Shell Length (mm)					
	Exposed Site			*Protected Site*		
Year	30-70	70-100	> 100	30-70	70-100	> 100
1987	34.8	48.8	31.6	41.8	41.5	43.0
1988	68.0	50.0	45.8	33.3	37.5	33.7
1989	58.6	40.0	51.0	30.0	41.2	47.8
Mean	51.8	45.3	40.7	37.9	40.6	40.7

Table 3.3. Correlations between the number of recaptures of abalone and variables describing abalone biology at wave-exposed and wave-protected study sites.

Variable	*Exposed* N	r	*Protected* N	r
Length	451	-0.001	581	0.033
Shell Erosion	245	-0.082	318	0.011
Shell Cover	245	0.032	318	0.094
Sculpture	245	0.158**	318	0.168**
Shell Growth Rate	202	-0.140*	234	-0.200**
Relative Total Weight	243	-0.054	189	0.011
Relative Weight Change	112	-0.211**	69	0.022
Total Movement	202	0.054	234	0.119*
Vertical Movement	202	0.183**	234	0.135*

Significance Levels: * - $p < 0.05$, ** - $p < 0.01$

Table 3.4. Comparison of relative shell growth rates and the percent of growing black abalone at Santa Cruz Island measured by Wright (1975), Douros (1985), and this study for 1987-1989. See text for a description of relative shell growth.

Study	N	Study Dates	Raw Shell Growth Rate (mm/mo)	Relative Shell Growth Rate	Percent Growing
Wright	73	1969-71	0.548	0.354	63.0
Douros	129	1984	1.218	1.164	89.3
Present	300	1987	0.206	0.048	51.7
	193	1988	0.196	0.042	43.0
	172	1989	0.172	-0.131	29.6

Table 3.5. Subtidal community structure at western Santa Cruz Island. Densities (no/m^2) of purple (*Strongylocentrotus purpuratus*) and red (*S. franciscanus*) sea urchins, and seastars are reported relative to the percent cover of erect and crustose coralline algae, fleshy macroalgae, and giant kelp, *Macrocystis pyrifera*. For each sample, N = the number of 0.25 m^2 quadrats sampled. For localities see Figure 3.3.

Year/Site	N	Sea Urchins		Seastars			Coralline		Fleshy Algae	
		Purple	Red	*Patiria*	*Pisaster*	*Pycnopodia*	Crust	Erect	Other	Kelp[1]
1988: Urchin Barrens, 2-6 m										
Protected	30	72.6	2.4	0	0	0	48.1	7.5	7.0	0
Protected	30	87.9	1.2	0	0	0	4.8	18.6	10.6	0
Protected	30	102.8	2.2	0	0	0	48.1	5.9	2.0	0
1989: Urchin Barrens, 2-6 m										
Protected	15	89.9	4.8	0.8	0.3	0	56.0	1.3	3.3	1.3
Protected	15	112.8	0.8	0	0	0	12.0	2.0	3.5	0
Protected	15	83.5	0.3	0	0	0	20.0	2.0	3.1	0
Black Pt.	5	62.4	9.6	0	0	0	0	0	0	0
1989: *Macrocystis Pyrifera* forest, 3-15 m										
Protected	12	69.1	1.9	0	0.5	0	3.3	1.7	3.3	1.7
Protected	10	17.6	10.4	0	0	0.4	>1.0	22.0	6.0	4.0
Black Pt.	5	21.6	1.6	0	0.8	0	0	0	12.0	2.0
Black Pt.	5	8.0	1.6	0	2.4	0	0	0	6.0	14.0
S. Fraser+	5	52.0	0.8	0	1.6	0	26.0	14.0	0	10.0
S. Fraser	5	12.8	2.4	0	1.6	0	0	6.0	8.0	8.0
N. Fraser[2]	0	-	-	+	+	-	+	+	++	++

1 - Kelp = *Macrocystis pyrifera* and *Egregia menzesii*
2 - Qualitative Observations only: ++ = abundant; + - Present; - Absent

Table 3.6. Summary of thermal tolerance studies conducted on black abalone. Reported are LT_{50}s, the temperature at 50% sample mortality. Abalone were acclimated at ambient (12-15C) temperatures (Previous studies: Hines et al., 1980; Pacific Gas and Electric, 1982, 1983; and Steinbeck et al. in press).

Study Period	Year of Study	LT_{50}(C)
Previous Studies: Diablo Canyon, CA		
96 hr	1979	26.1
90 d	1979	> 24.0
1 hr	1982	31.5
180 d	1988	19.0
Present Study: Newport, OR		
90 d	1987	18.0
180 d	1988	17.0

Table 3.7. Canonical correlation analysis: measures of association between abalone growth, behavior, and decline, and potential causal factors during surveys in 1987-1989. Chi-square values test the significance of canonical correlation coefficients. Significant canonical loadings are indicated in bold type.

	Canonical Loadings		
	Analysis #1	Analysis #2	
Variable	First Axis	First Axis	Second Axis
Canonical Correlation	0.564	0.893	0.801
Chi-Square	18.23	41.03	19.50
DF	9	25	16
Probability	0.04	0.03	0.20
Potential Effects:			
Density Change	**-0.929**	0.340	**-0.868**
Total Movement	0.297	**0.778**	0.066
Shell Growth	0.187	**-0.626**	0.166
Survivorship	---	-0.092	0.193
Weight Change	---	0.211	0.288
Variance Explained:	0.329	0.233	0.186
Redundancy:	0.104	0.186	0.118
Potential Causes:			
Temp. Anomaly	**0.987**	**-0.430**	0.071
Density	**0.867**	**-0.534**	**0.630**
Temperature	0.255	**-0.786**	-0.318
Algal Weight	---	-0.225	**0.592**
Algal Frequency	---	-0.149	-0.086
Variance Explained:	0.597	0.232	0.172
Redundancy:	0.190	0.185	0.113

Figure 3.1. Study sites in Alta and Baja California in relation to the geographic range of the black abalone (dashed line)

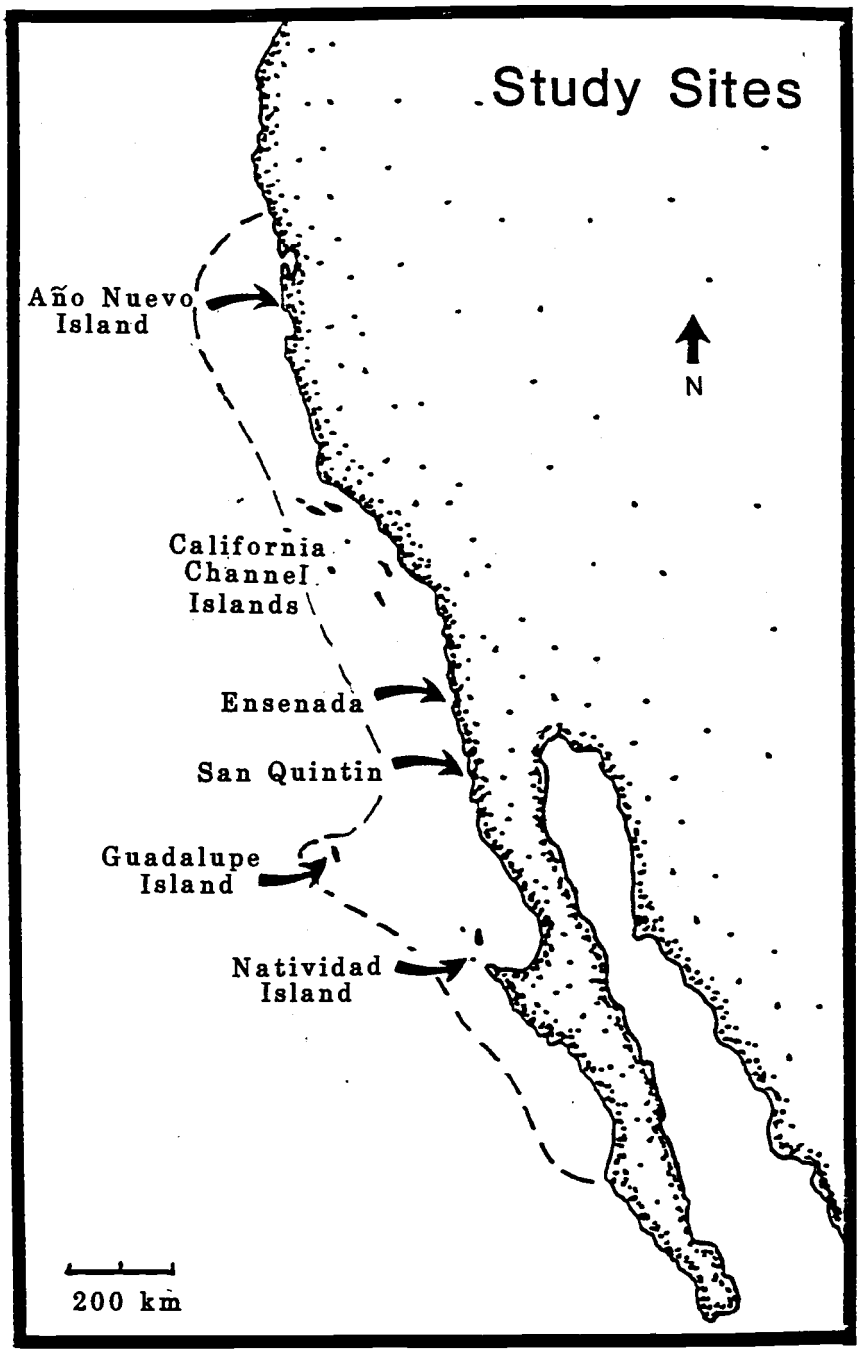

Study Sites
Año Nuevo Island
N
California Channel Islands
Ensenada
San Quintin
Guadalupe Island
Natividad Island
200 km

Figure 3.1

Figure 3.2. Principal sites of mass mortality in southern California and the percent declines in abundance. Mortality figures for sites are derived from Davis et al. (in press), Haaker et al. (in press), Steinbeck et al. (in press), this study, and personal communications.

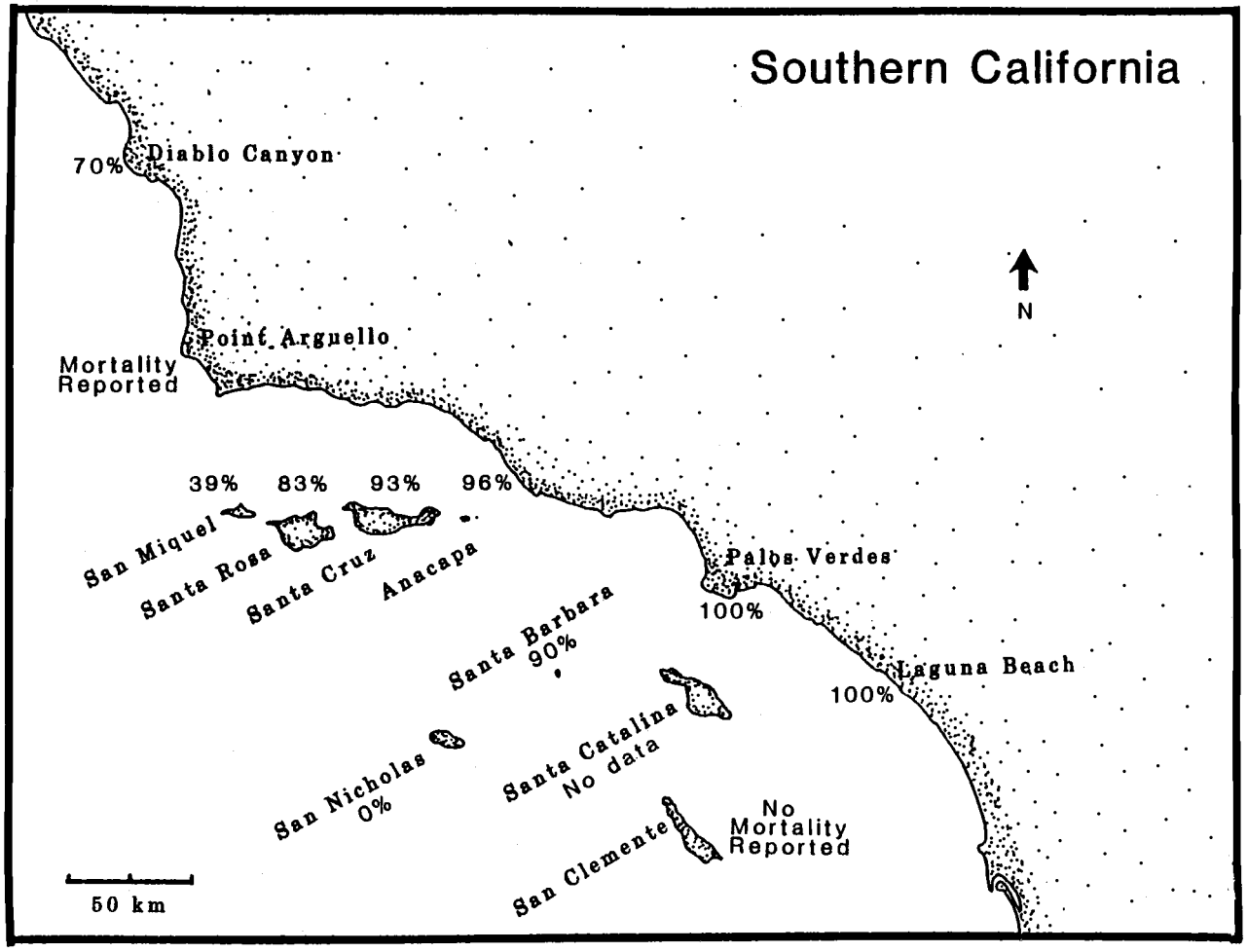

Southern California
70%
Diablo Canyon
N
Point Arguello
Mortality
Reported
39%
83%
93%
96%
San Miquel
Santa Rosa
Santa Cruz
Anacapa
Palos Verdes
100%
Santa Barbara
90%
Laguna Beach
100%
Santa Catalina
No data
San Nicholas
0%
No
Mortality
Reported
San Clemente
50 km

Figure 3.2

Figure 3.3. Location of exposed and protected intertidal study sites on the west end of Santa Cruz Island, California in relation to the 1987 kelp canopy. Subtidal study areas are denoted by stars.

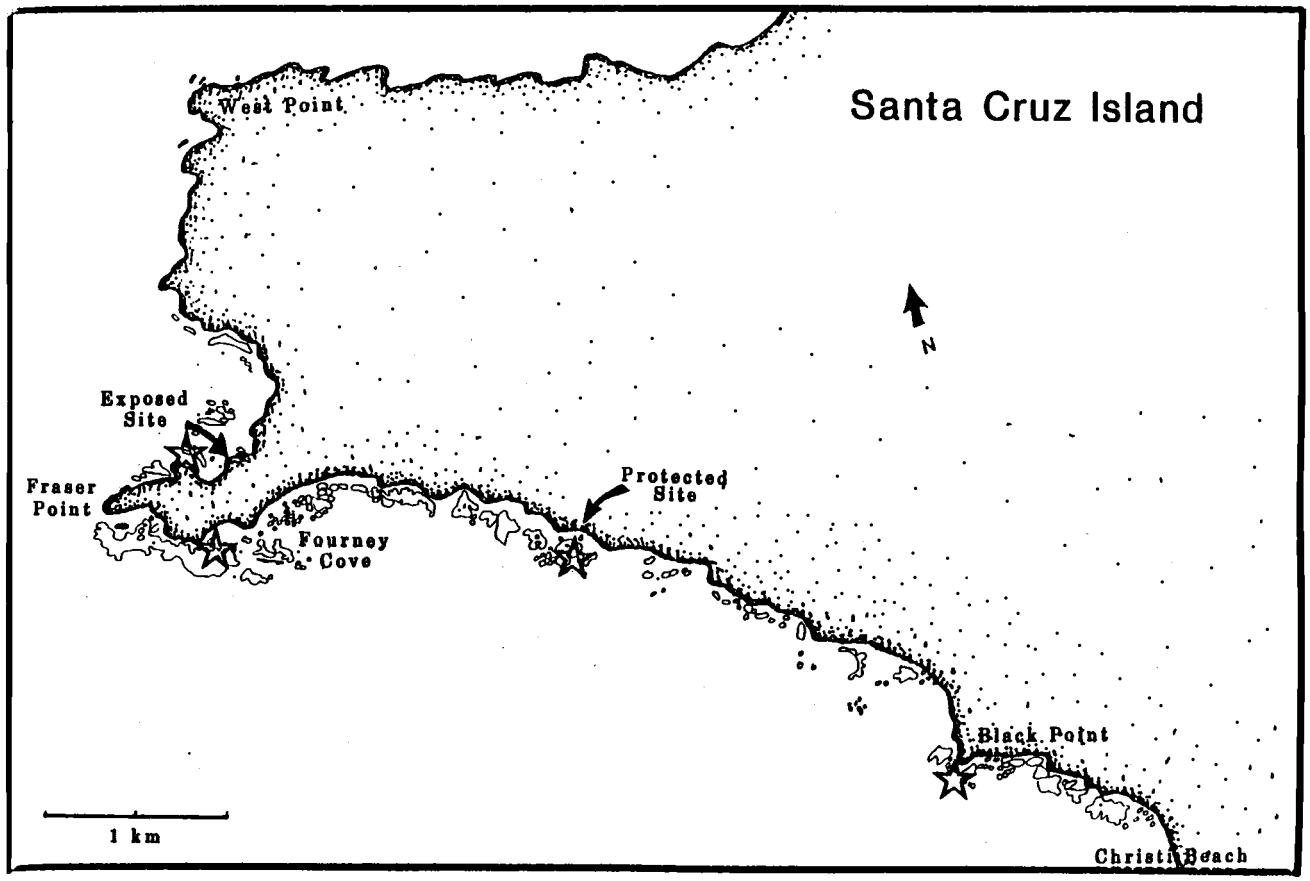

Santa Cruz Island
West Point
N
Exposed Site
Fraser Point
Fourney Cove
Protected Site
Black Point
Christi Beach
1 km

Figure 3.3

Figure 3.4. Photograph of black abalone on transect A before and after mass mortality. **A.** December. 30, 1986. **B.** June 21, 1988. **C.** Detail of June 21, 1988

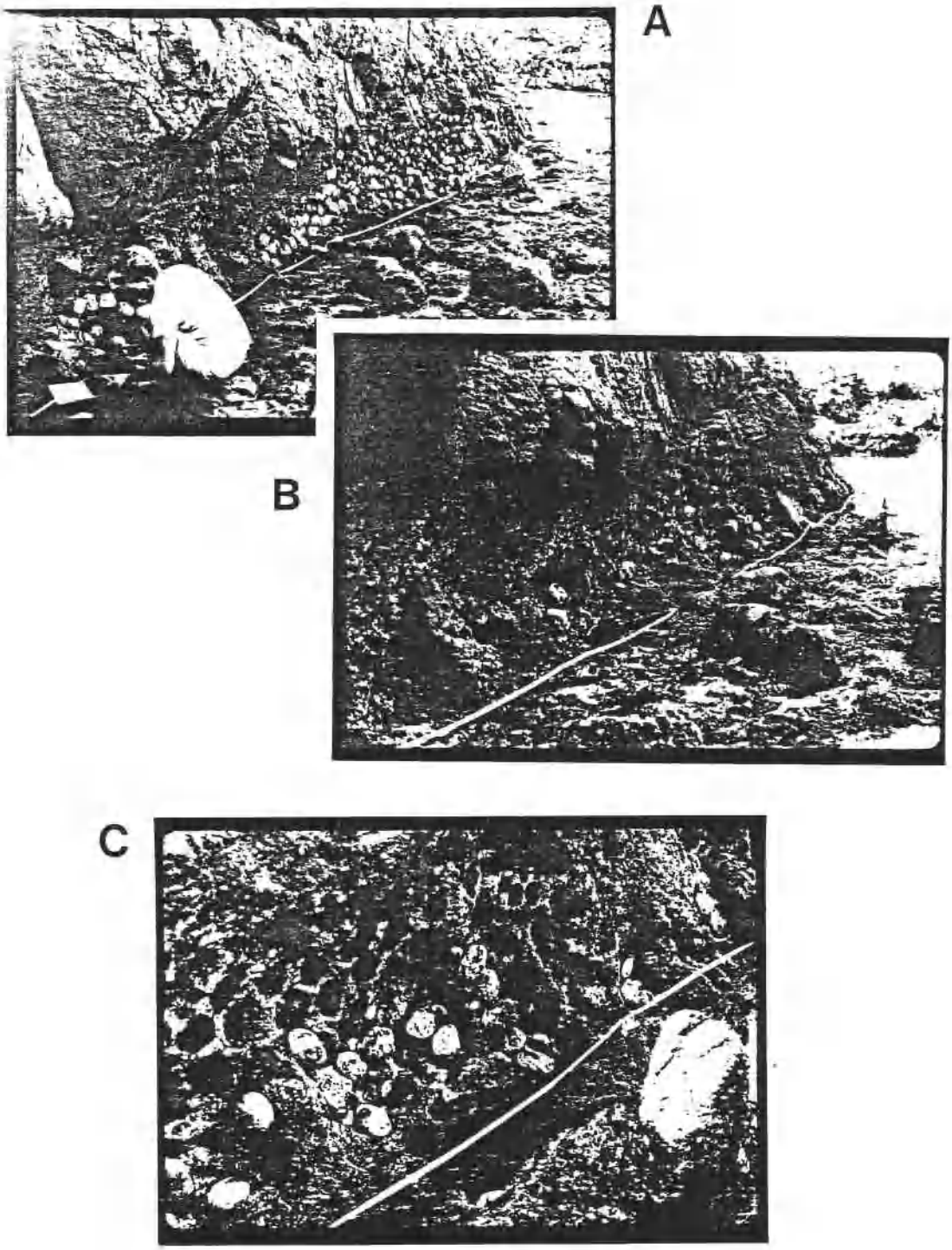


Figure 3.4

Figure 3.5. Mean density (± 1 SE) of black abalone along protected (A, B, E, F) and exposed (C, D, G) intertidal transects during the course of the study. The total percent decline in density between January-March 1987 and January 1990 is indicated for each transect.

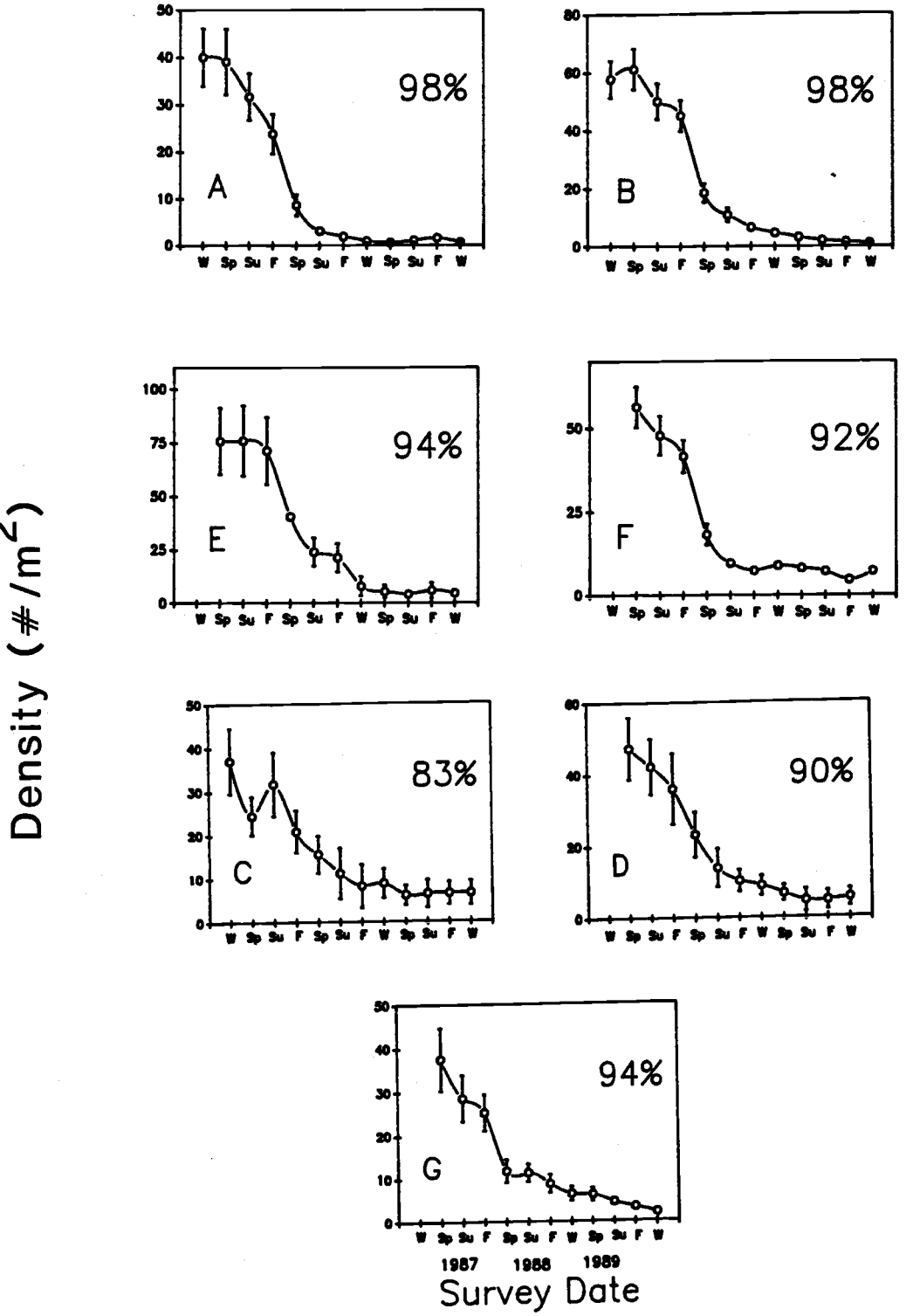

Density (#/m2)
A
98%
B
98%
E
94%
F
92%
C
83%
D
90%
G
94%
W Sp Su F Sp Su F W Sp Su F W
1987 1988 1989
Survey Date

Figure 3.5

Figure 3.6. Mean percent change in density (± 1 SE) of black abalone between surveys in exposed and protected intertidal areas during mass mortality in relation to densities in January 1987.

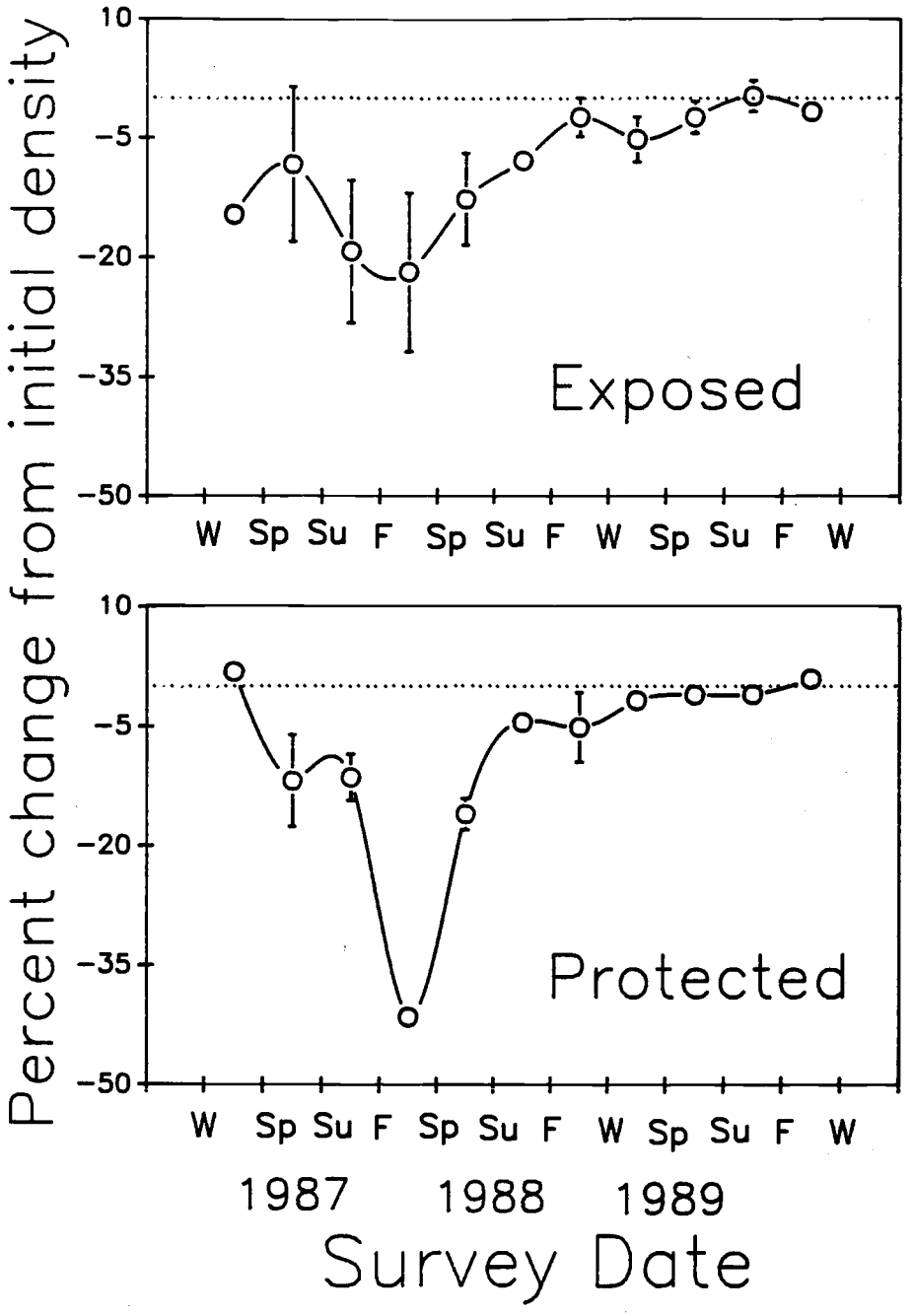

Percent change from initial density
10
-5
-20
-35
-50
Exposed
Protected
W Sp Su F Sp Su F W Sp Su F W
1987 1988 1989
Survey Date

Figure 3.6

Figure 3.7. Changes in the intertidal distribution of black abalone along protected (A-B) and exposed (C-D) intertidal transects before (January - March 1987) and after (January 1989) mass mortality. Transects were oriented perpendicular to the shore and extended from the high intertidal (2.0 m above MLLW, "upshore") to the low intertidal (-1.0 m above MLLW,"downshore").

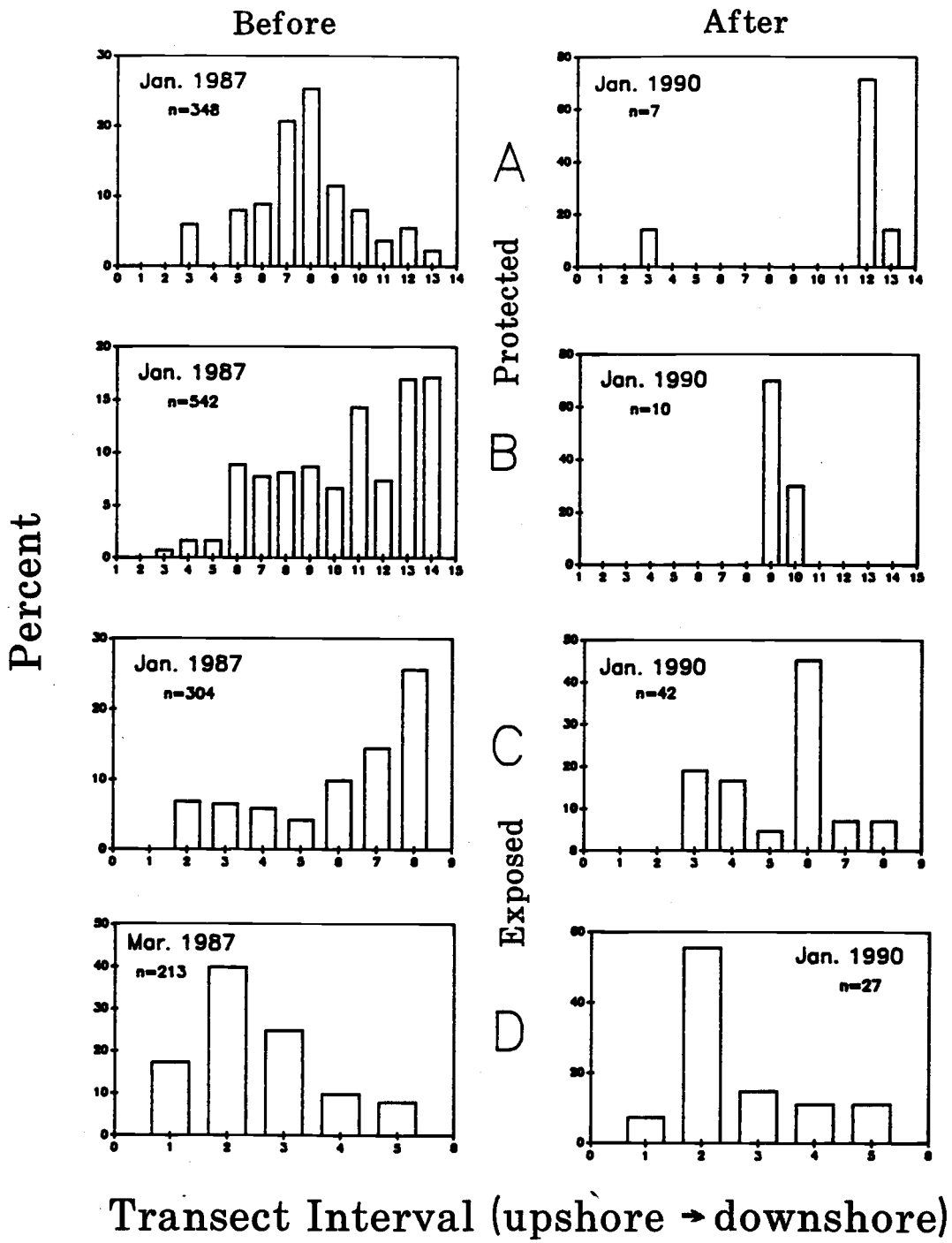

Before
After
Jan. 1987
n=348
Jan. 1990
n=7
A
Protected
Jan. 1987
n=542
Jan. 1990
n=10
B
Percent
Jan. 1987
n=304
Jan. 1990
n=42
C
Exposed
Mar. 1987
n=213
Jan. 1990
n=27
D
Transect Interval (upshore → downshore)

Figure 3.7

Figure 3.8. Size frequency distributions of recaptured tagged abalone (live), non-recaptured tagged abalone assumed dead (missing), and recovered dead shells (dead).

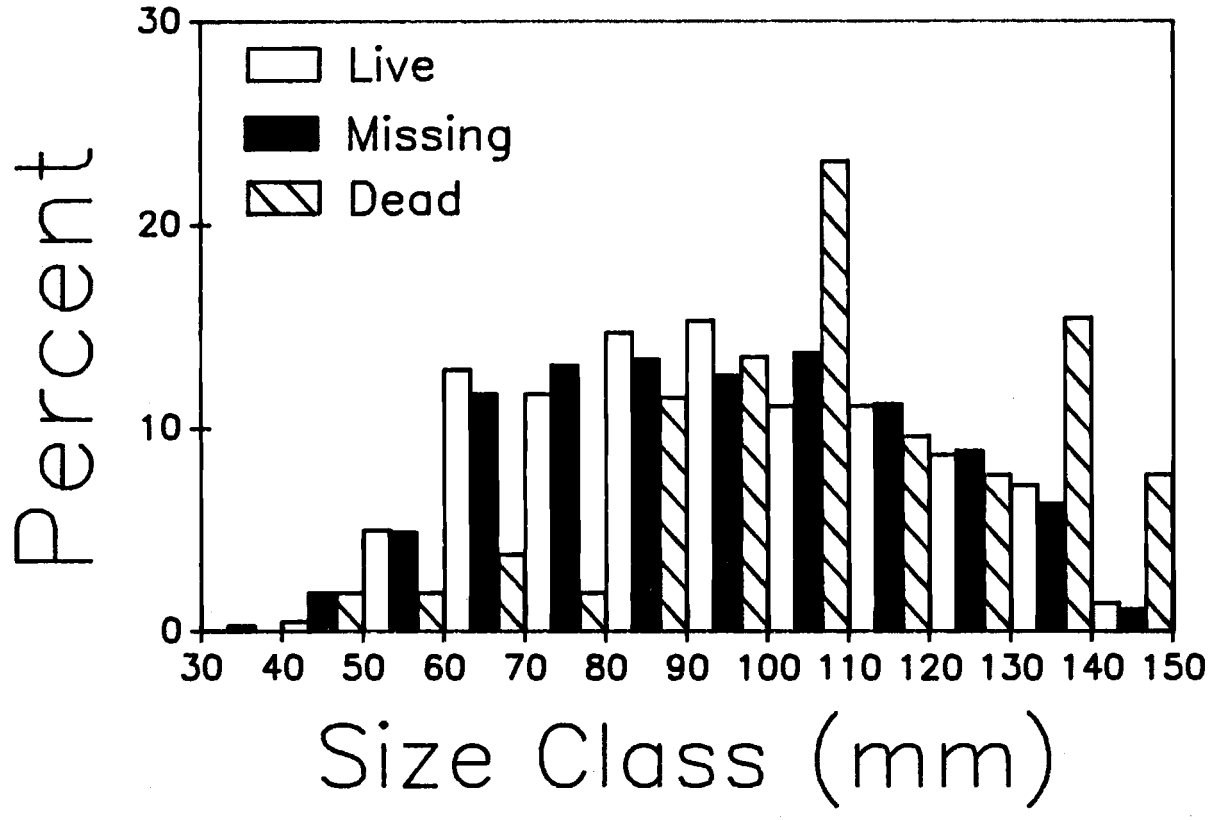

Live
Missing
Dead
Percent
0
10
20
30
30 40 50 60 70 80 90 100 110 120 130 140 150
Size Class (mm)

Figure 3.8

Figure 3.9. Jolly-Seber probability of survivorship (± 1 SE) of tagged black abalone between surveys in exposed and protected study areas.

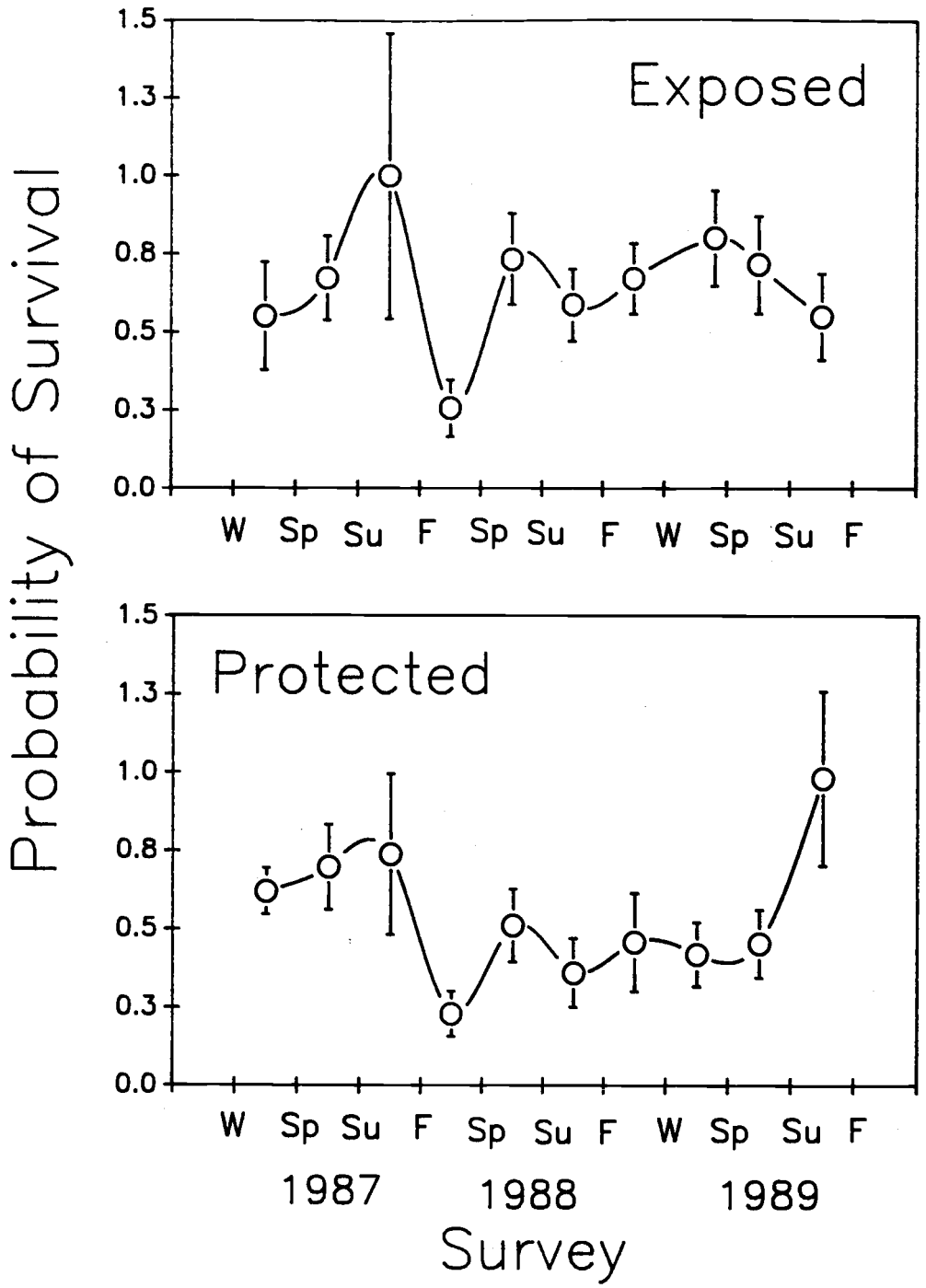

Probability of Survival
1.5
1.3
1.0
0.8
0.5
0.3
0.0
Exposed
Protected
W Sp Su F Sp Su F W Sp Su F
1987 1988 1989
Survey

Figure 3.9

Figure 3.10. Mean recapture rates (± 1 SE) of tagged black abalone in exposed and protected study areas. **A.** Mean recapture rate (± 1 SE) in relation to relative weight. **B.** Mean recapture rate (± 1 SE) in relation to intertidal distribution.

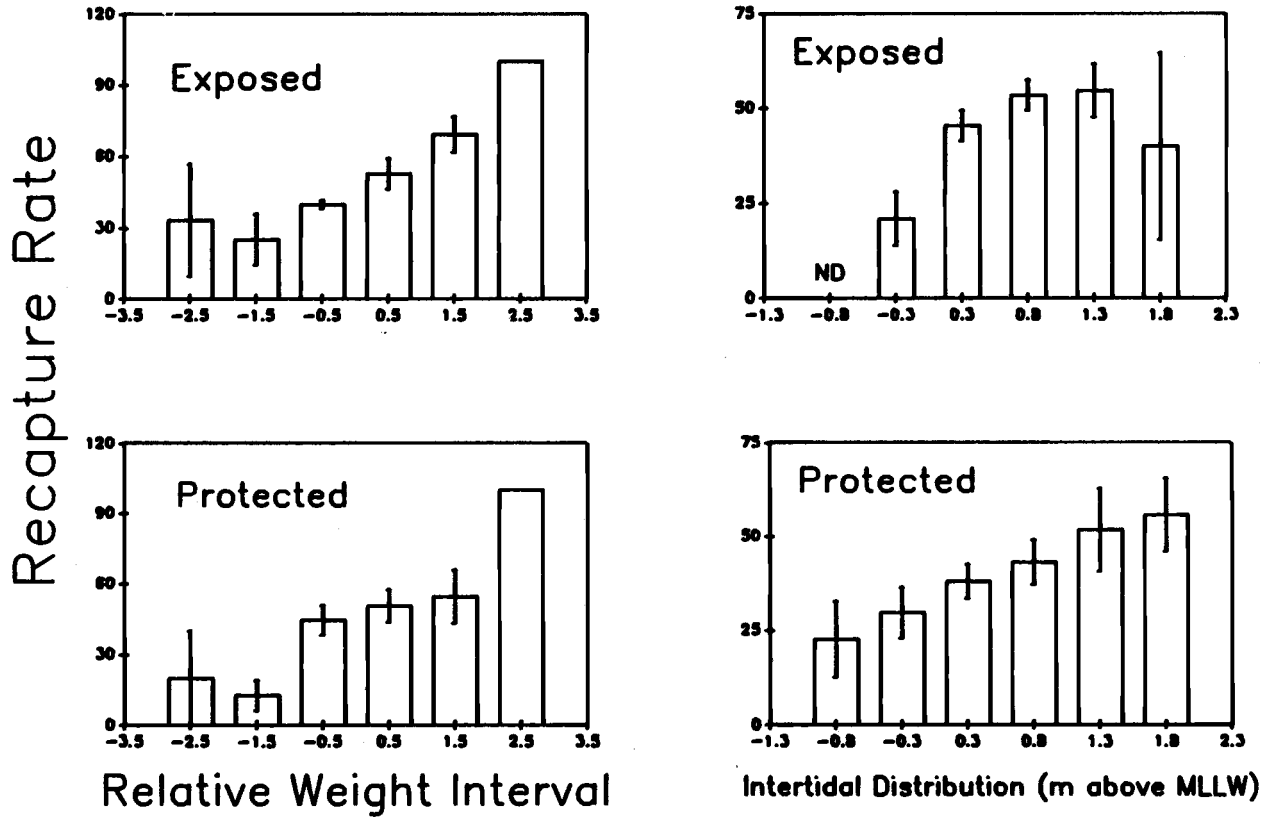

Recapture Rate
Exposed
Protected
ND
Relative Weight Interval
Intertidal Distribution (m above MLLW)

Figure 3.10

Figure 3.11. Mean total movement (+ 1 SE) of black abalone at exposed and protected study sites between surveys

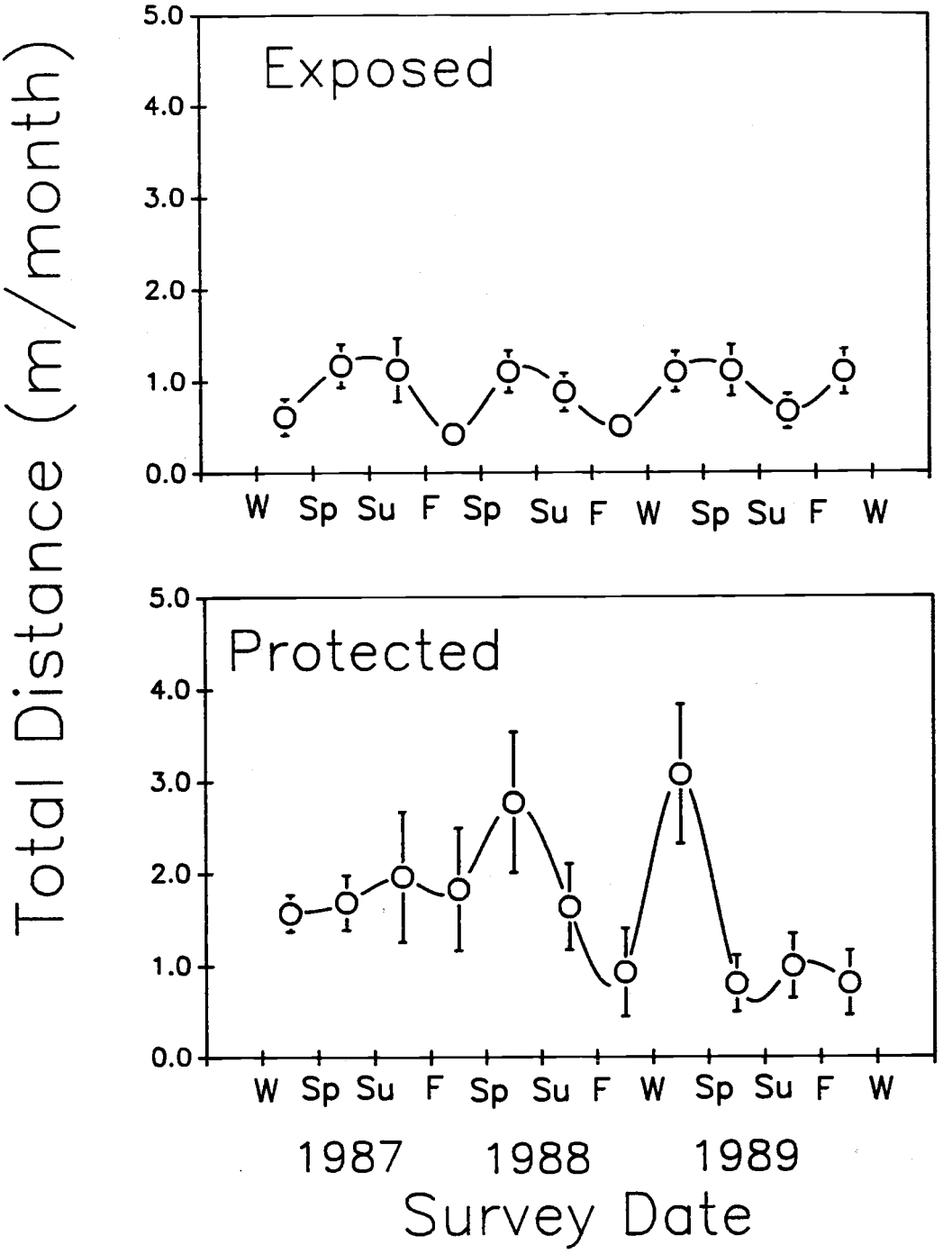

Total Distance (m/month)
Exposed
Protected
5.0
4.0
3.0
2.0
1.0
0.0
W Sp Su F Sp Su F W Sp Su F W
1987 1988 1989
Survey Date

Figure 3.11

Figure 3.12. Seasonal variation in black abalone growth and behavior in relation to environmental factors. **A.** Mean surface seawater temperatures (circles) in relation to the abundance of drift algae (histograms). **B.** Mean changes in the intertidal position of tagged abalone (triangles) relative to rates of movement (histograms). **C.** Relative rates of weight change (solid circles) and shell growth (open circles) of tagged abalone in relation to the probability of survival between surveys (histograms).

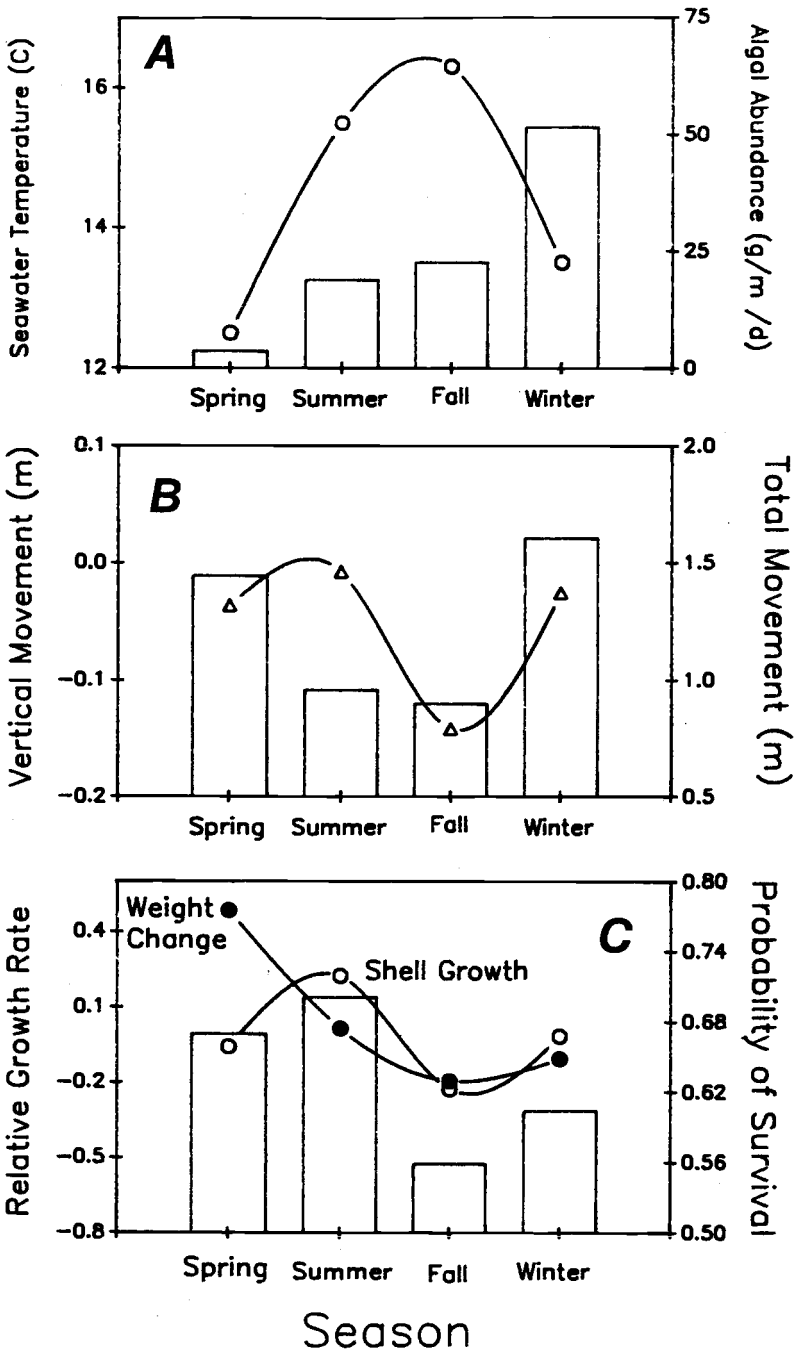

A
Seawater Temperature (C)
16
14
12
75
50
25
0
Algal Abundance (g/m /d)
Spring
Summer
Fall
Winter
B
Vertical Movement (m)
0.1
0.0
−0.1
−0.2
2.0
1.5
1.0
0.5
Total Movement (m)
Spring
Summer
Fall
Winter
C
Weight Change
Shell Growth
Relative Growth Rate
0.4
0.1
−0.2
−0.5
−0.8
0.80
0.74
0.68
0.62
0.56
0.50
Probability of Survival
Spring
Summer
Fall
Winter
Season

Figure 3.12

Figure 3.13. Mean vertical movement ($\pm$ 1 SE) of black abalone at exposed and protected study sites between surveys.

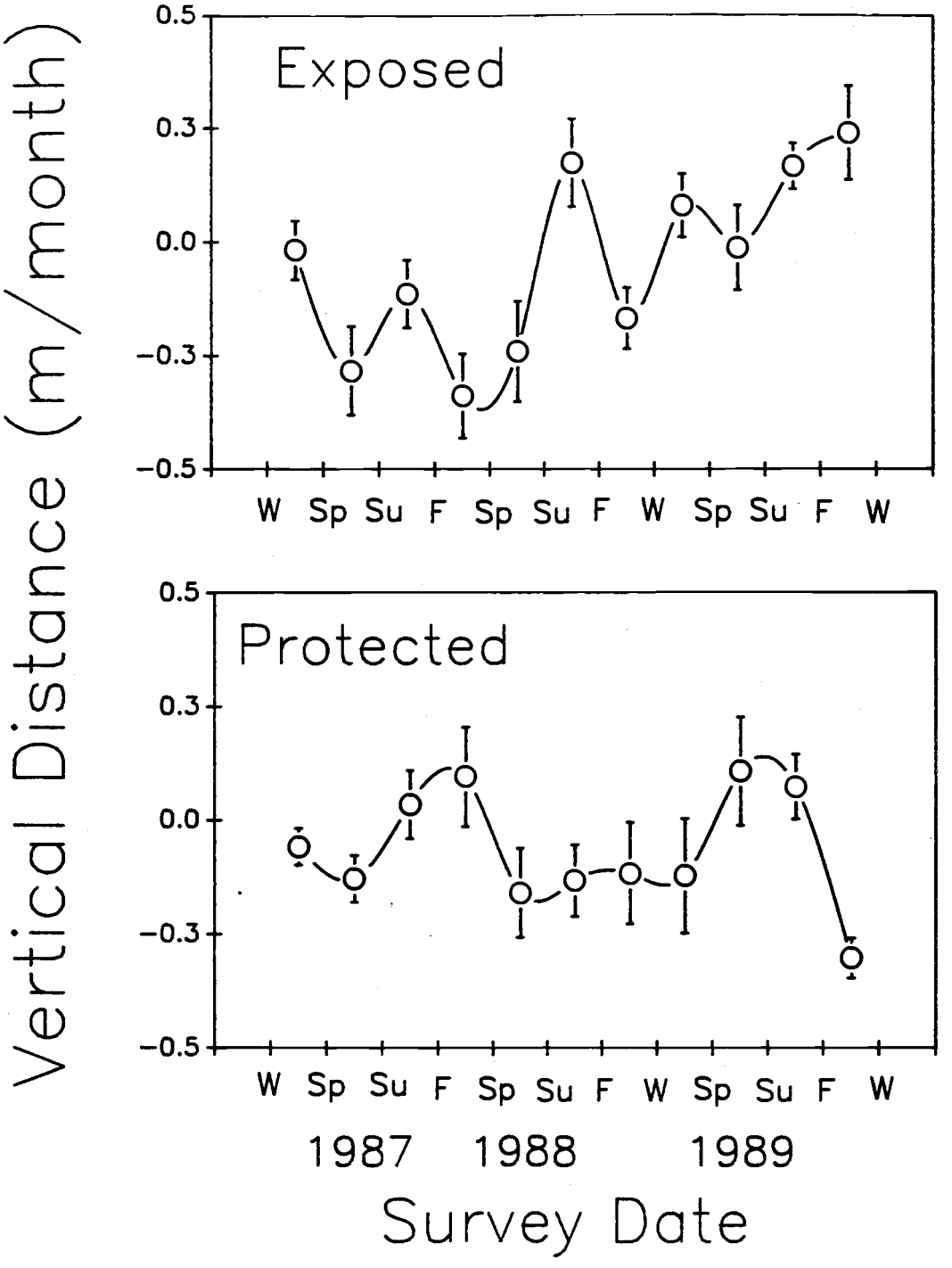

Vertical Distance (m/month)
Exposed
Protected
0.5
0.3
0.0
-0.3
-0.5
W Sp Su F Sp Su F W Sp Su F W
1987 1988 1989
Survey Date

Figure 3.13

Figure 3.14. Measures of shell growth among black abalone in exposed and protected study areas. Mean relative shell growth rates (see text), indicated by circles ($\pm$ 1 SE), are shown in relation to the percentage of individuals displaying shell growth, indicated by histograms.

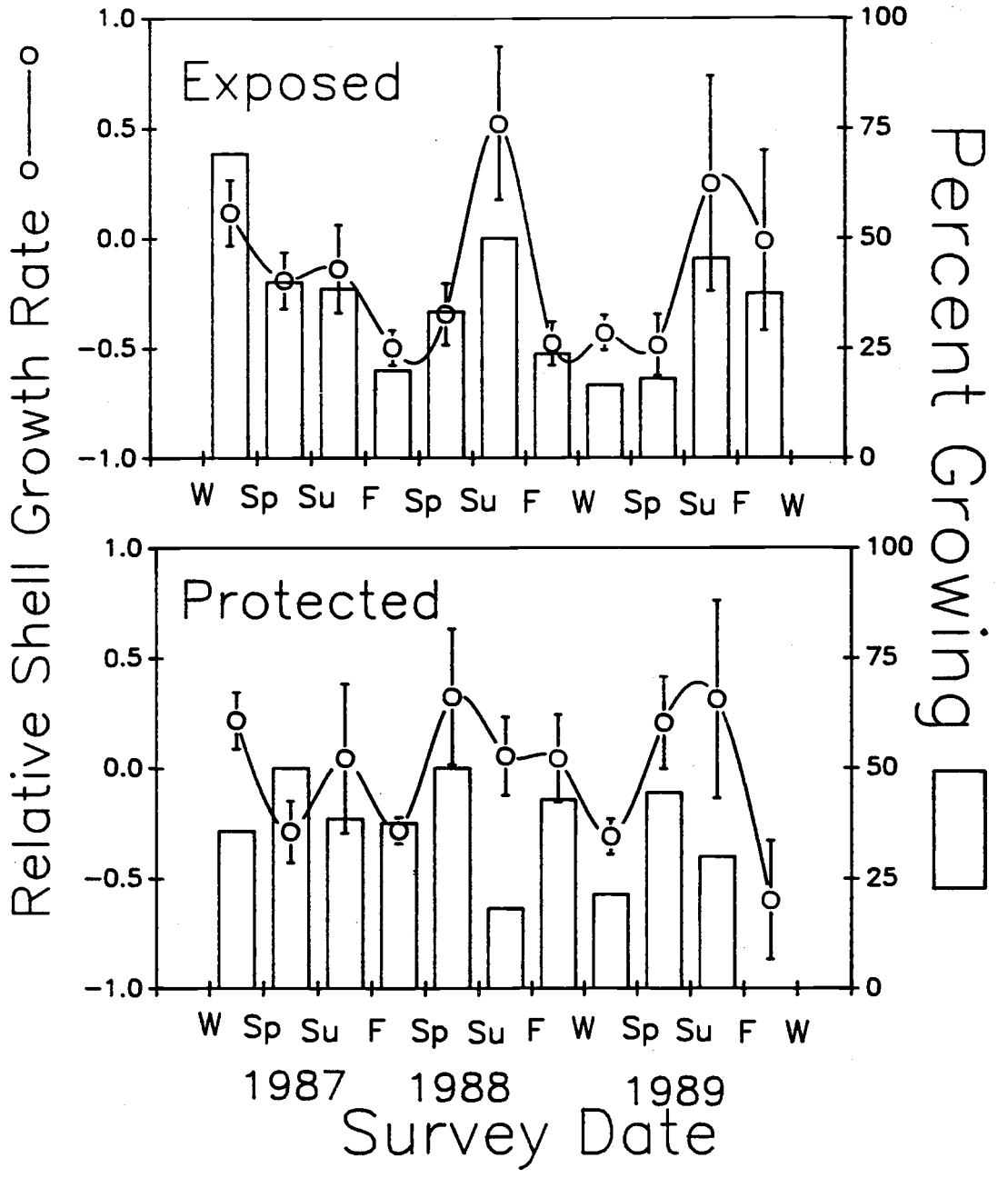

Exposed
Protected
Relative Shell Growth Rate o——o
Percent Growing □
1.0
0.5
0.0
−0.5
−1.0
100
75
50
25
0
W Sp Su F Sp Su F W Sp Su F W
1987 1988 1989
Survey Date

Figure 3.14

Figure 3.15. Comparisons of shell growth rates of black abalone among studies conducted on the west end of Santa Cruz Island by Wright (1975), Douros (1985) and this study.

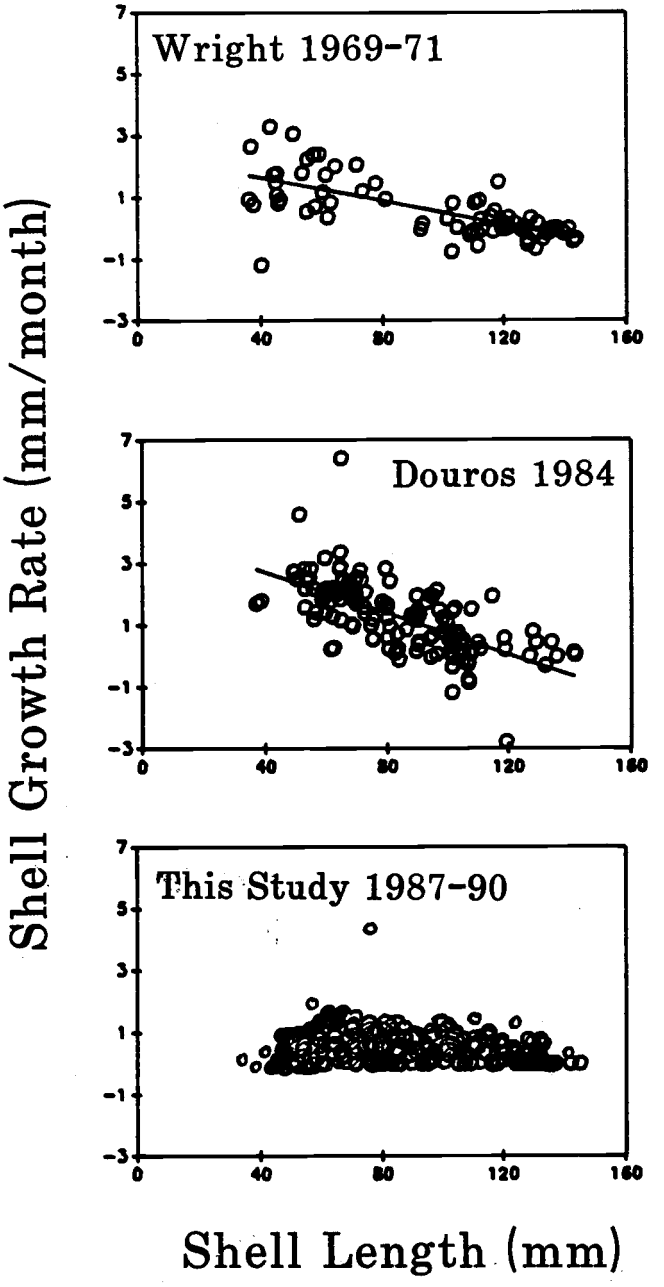

Wright 1969-71
Douros 1984
This Study 1987-90
Shell Growth Rate (mm/month)
Shell Length (mm)
7
5
3
1
-1
-3
0
40
80
120
160

Figure 3.15

Figure 3.16. Measures of weight gain of black abalone between surveys in exposed and protected study areas. Relative weight gain (see text), indicated by dots ($\pm$ 1 SE), are shown in relation to the percentage of individuals gaining weight, indicated by histograms.

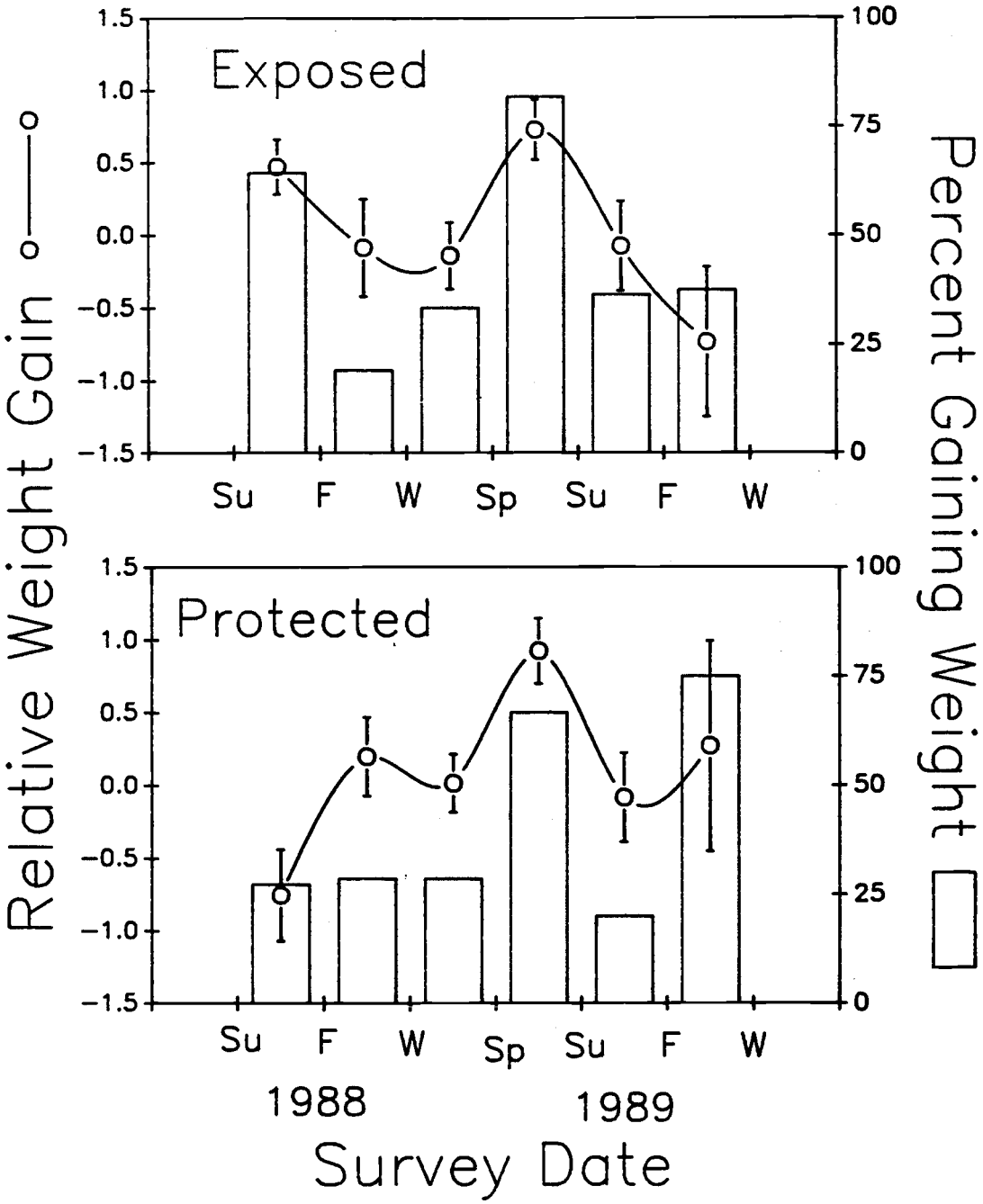

Exposed
Protected
Relative Weight Gain o—o
Percent Gaining Weight □
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
100
75
50
25
0
Su
F
W
Sp
Su
F
W
1988
1989
Survey Date

Figure 3.16

Figure 3.17. Measures of weight change and total weight among black abalone in relation to shell length. **A.** Relative total weight. **B.** Relative weight gain (g/90 d).

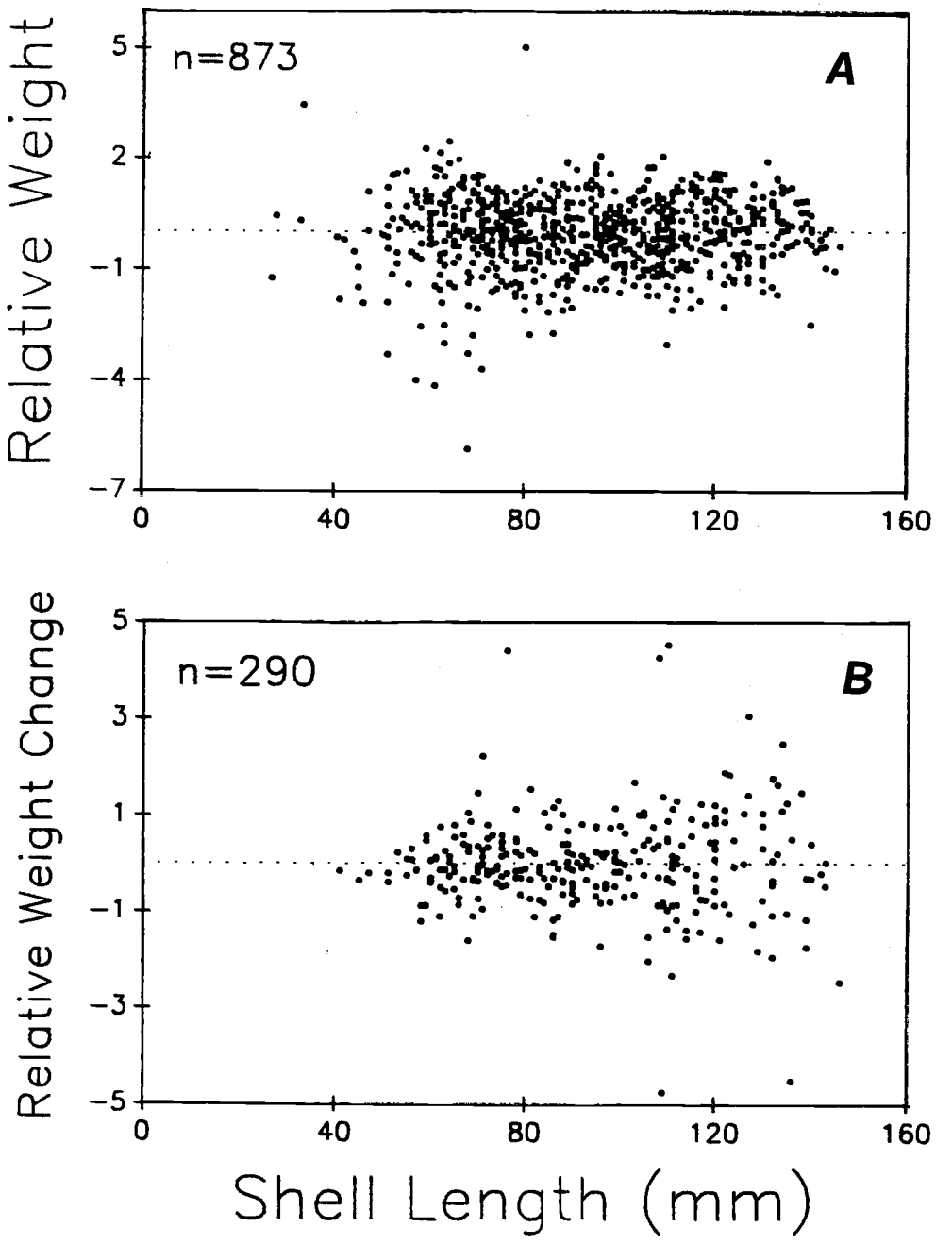

Relative Weight
n=873
A
5
2
-1
-4
-7
0
40
80
120
160
Relative Weight Change
n=290
B
5
3
1
-1
-3
-5
0
40
80
120
160
Shell Length (mm)

Figure 3.17

Figure 3.18. Relative weight of black abalone in exposed and protected study areas. Relative weights are standardized deviations of total abalone weight from the weight of "normal" abalone: individuals displaying both weight gain and shell growth (see text).

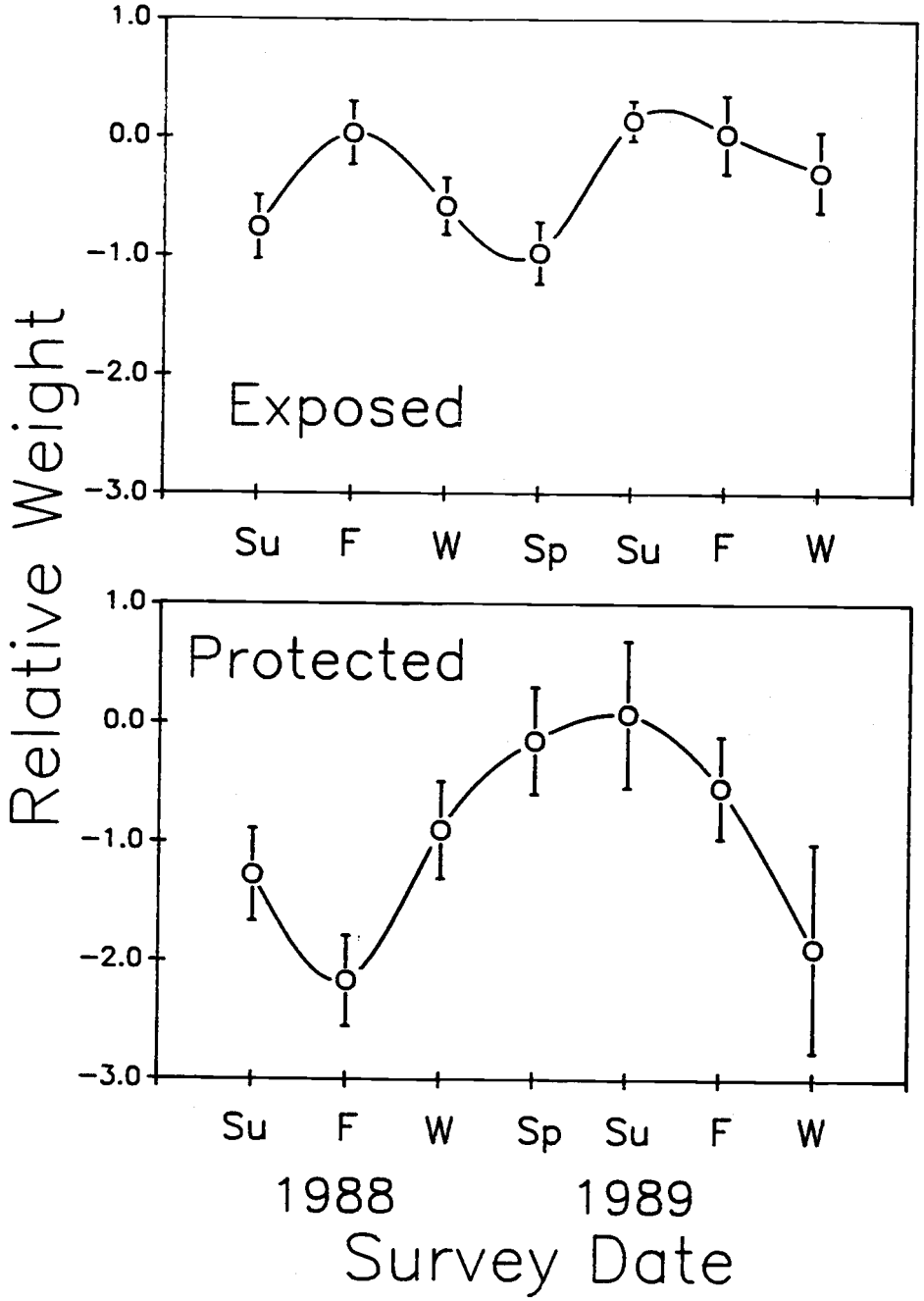

1.0
0.0
-1.0
-2.0
-3.0
Exposed
Su F W Sp Su F W
Protected
Relative Weight
1988
1989
Survey Date

Figure 3.18

Figure 3.19. Abalone weight in relation to the frequency of drift algae in exposed and protected study areas. The mean percentage ($\pm$ 1 SE) of abalone with weights above the weight predicted by "healthy" abalone (see text), and the mean frequency of occurence of drift macroalgae are presented in relation to intertidal distribution.

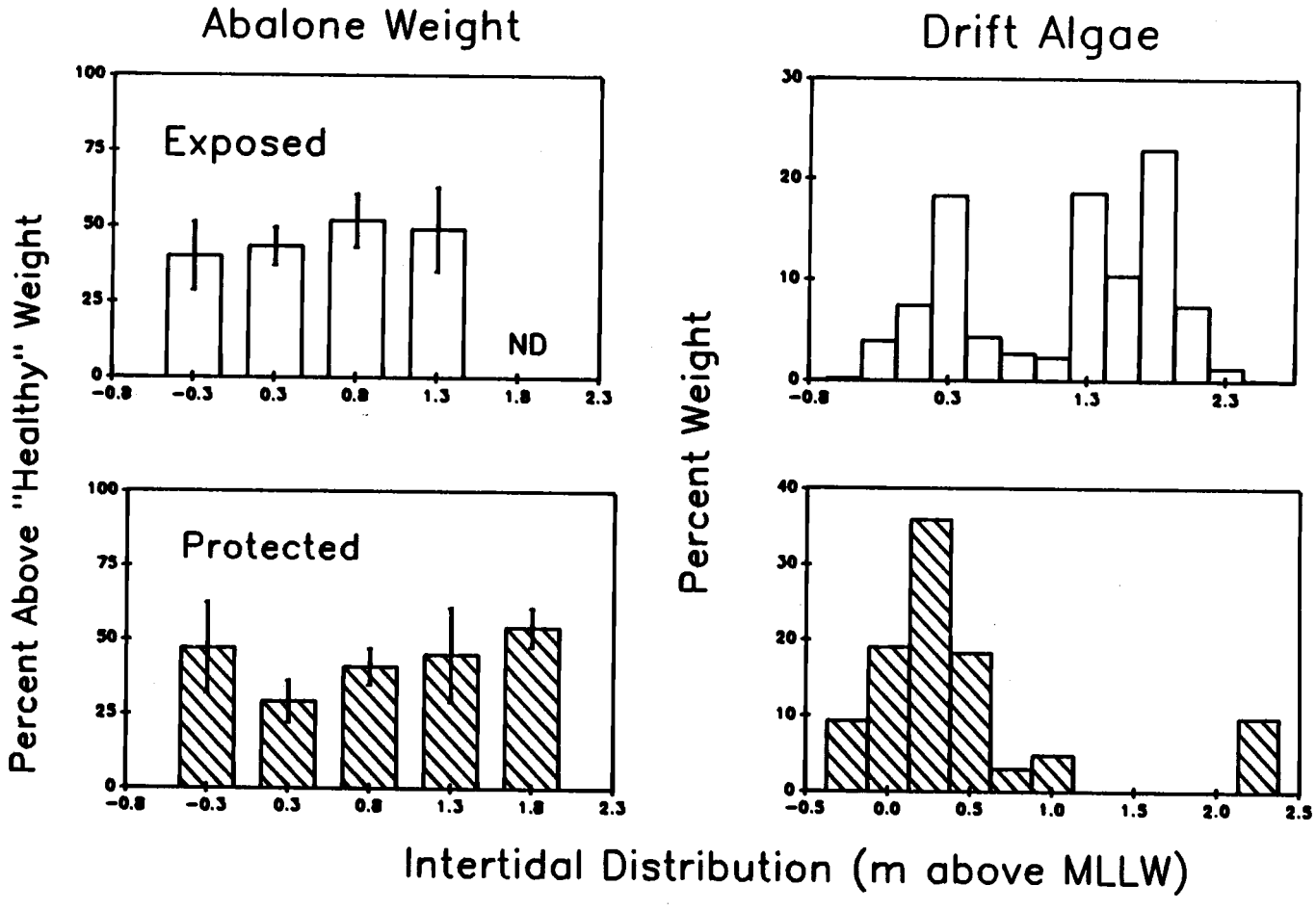

Abalone Weight
Drift Algae
Exposed
ND
Protected
Percent Above "Healthy" Weight
Percent Weight
Intertidal Distribution (m above MLLW)

Figure 3.19

Figure 3.20. Temporal variation of mean gonad indices ($\pm$ 1 SD) of male and female abalone collected at the protected study site.

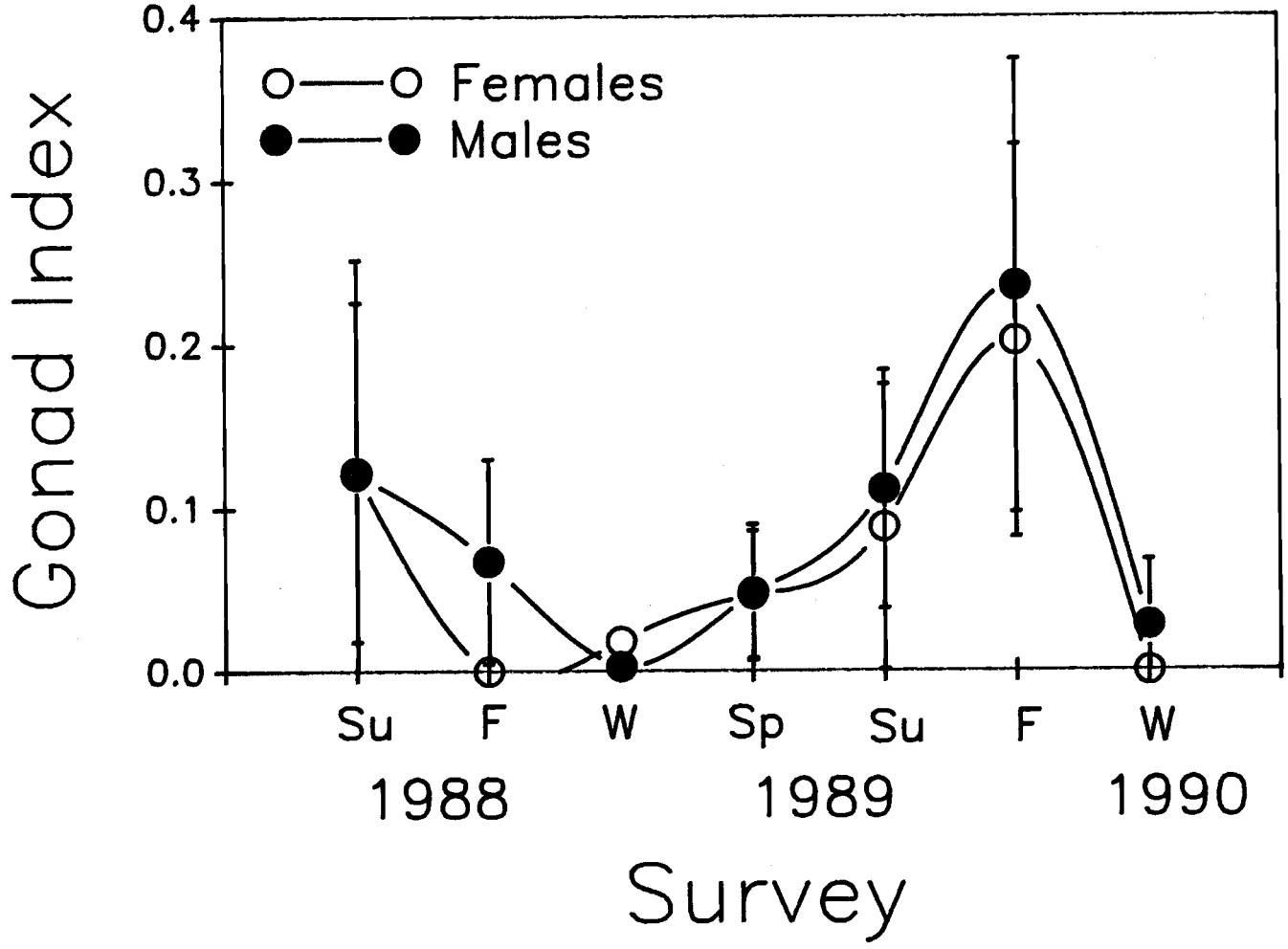

Gonad Index
0.4
0.3
0.2
0.1
0.0
Females
Males
Su
F
W
Sp
Su
F
W
1988
1989
1990
Survey

Figure 3.20

Figure 3.21. Gonad volume relative to size in June of 1988 and 1989 relative to June 1984 (Douros, 1985).

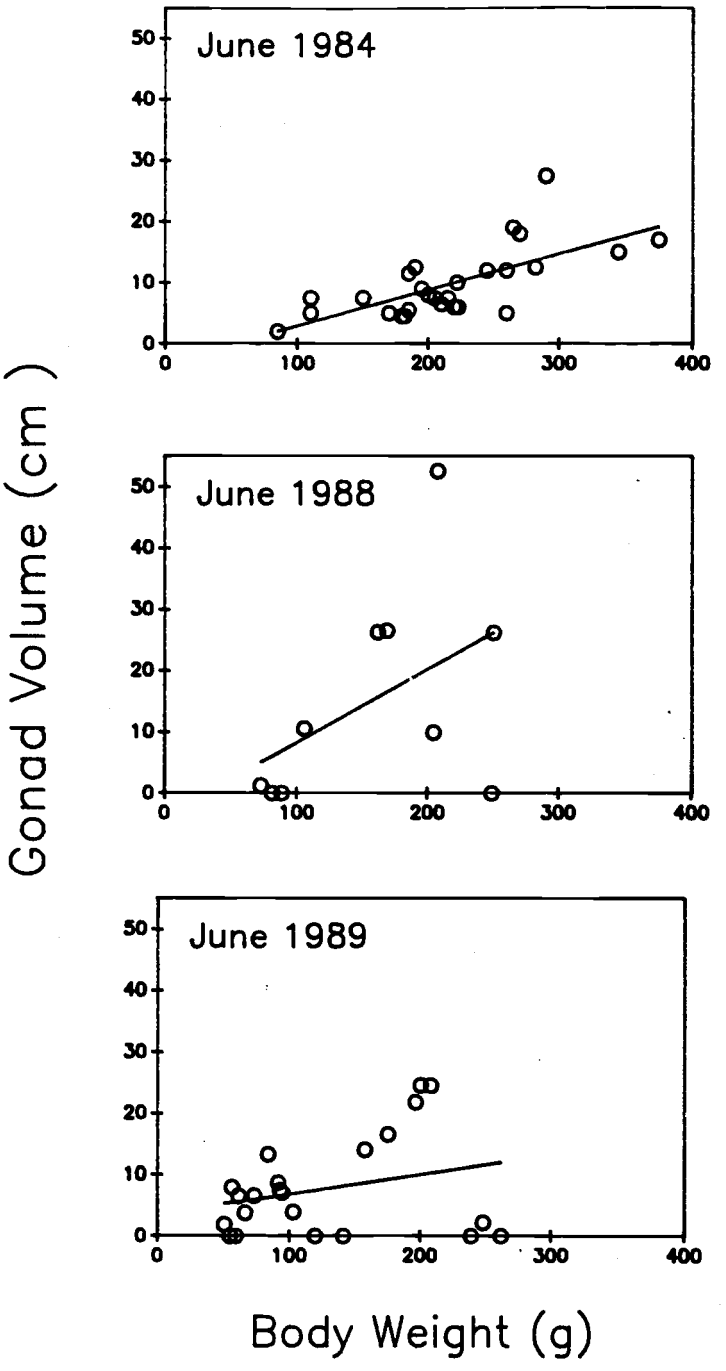

June 1984
June 1988
June 1989
Gonad Volume (cm)
Body Weight (g)
0
10
20
30
40
50
100
200
300
400

Figure 3.21

Figure 3.22. Spatial and temporal variation in the mean abundance of drift macroalgae ($\pm$ 1 SE) collected at wave-exposed and wave-protected study sites.

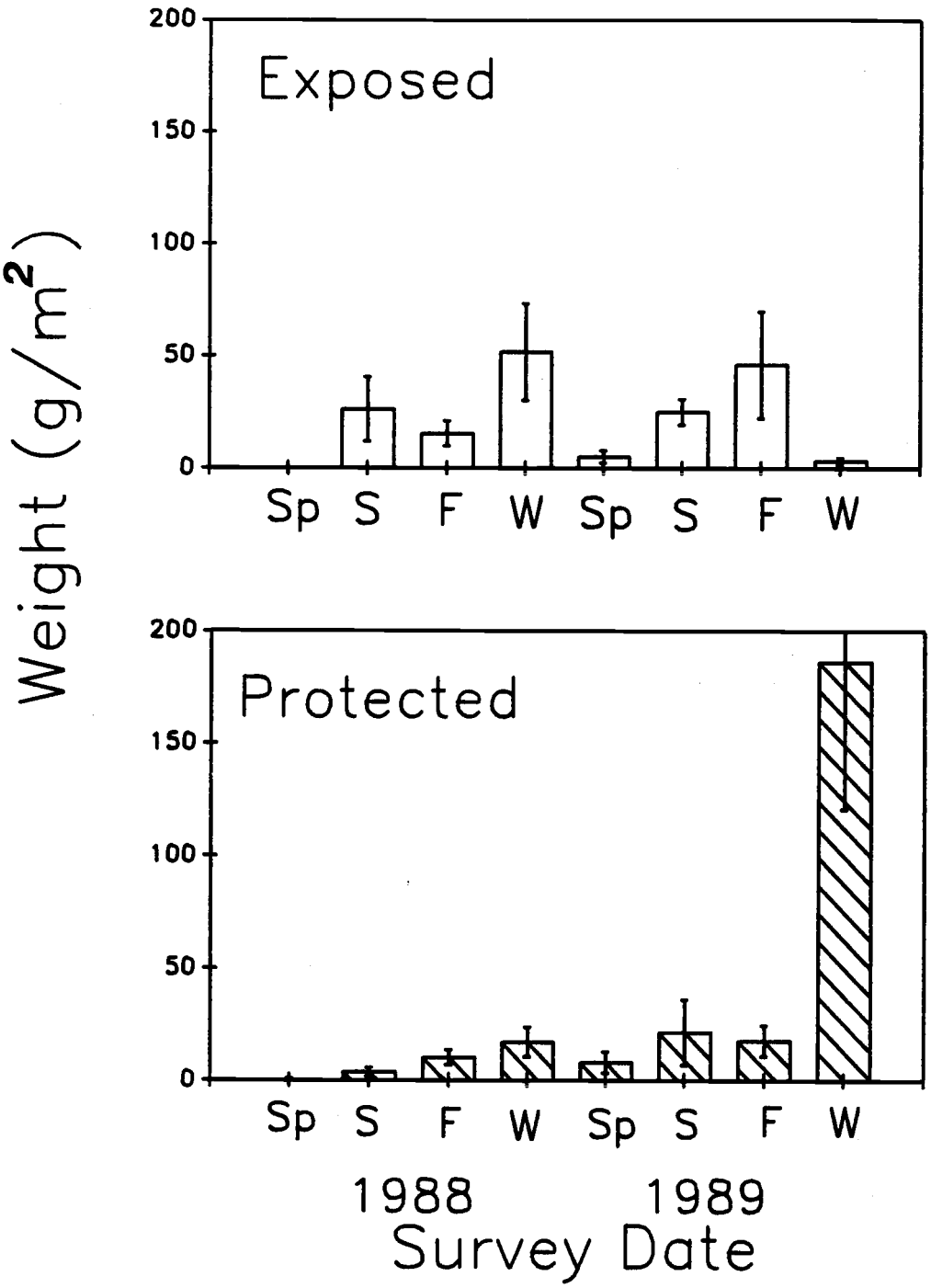

Exposed
Protected
Weight (g/m2)
200
150
100
50
0
Sp S F W Sp S F W
1988
1989
Survey Date

Figure 3.22

Figure 3.23. Changes in the canopy of *Macrocystis* at four areas along the west end of Santa Cruz Island prior to (1984-1985) and during (1987-88) mass mortality of black abalone. Canopy areas were derived from digitized images of aerial infared photographs (see text). Scale bar = 100 m.

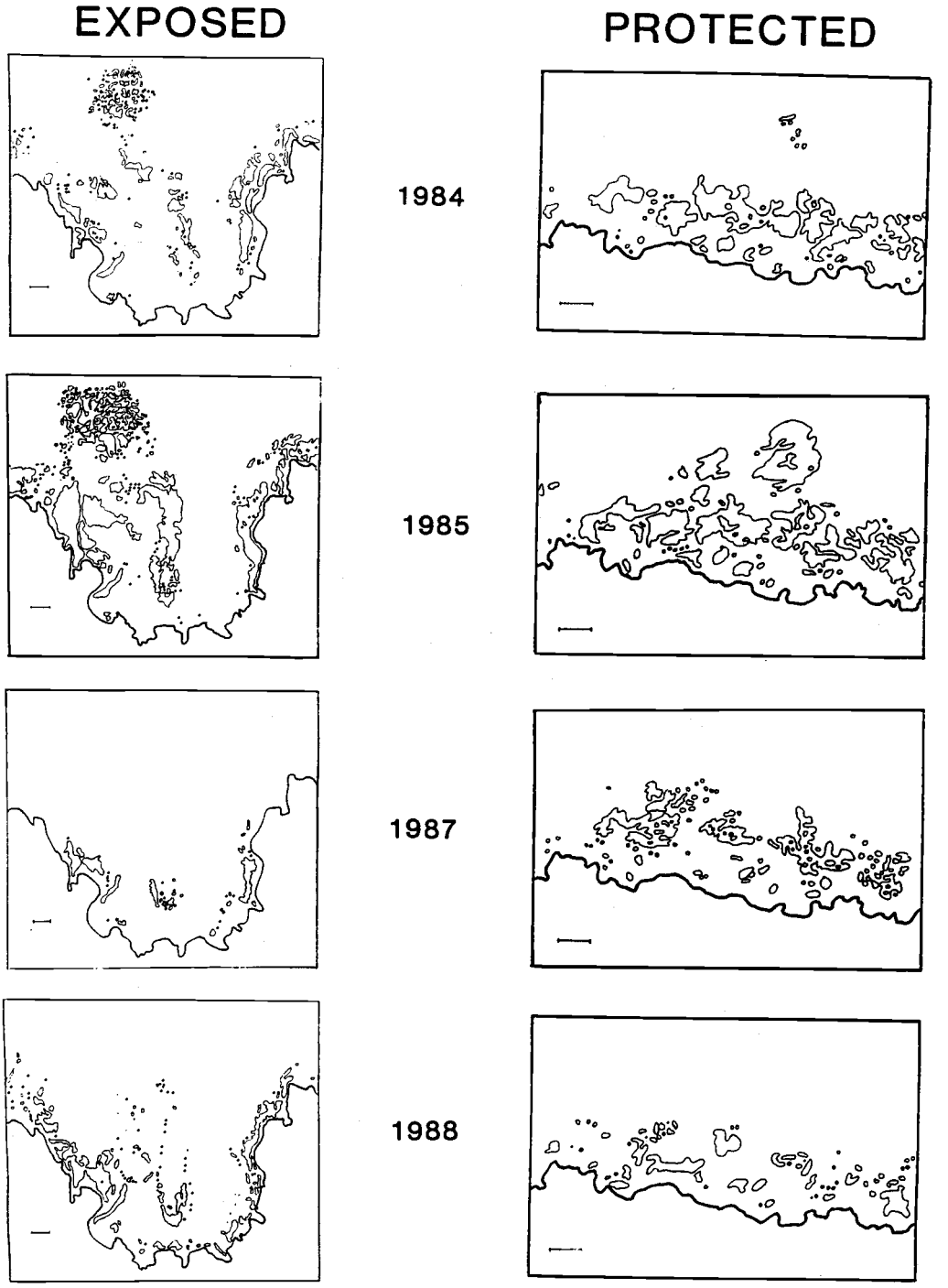


Figure 3.23

Figure 3.24. Surface seawater temperatures in the vicinity of Santa Cruz Island. Monthly mean surface seawater temperatures (open circles) for 1982-1989, derived from satellite imagery (NOAA, 1982-1989), are shown in relation to average surface seawater temperatures (solid circles) for the years 1942-1969 reported by Robinson (1976).

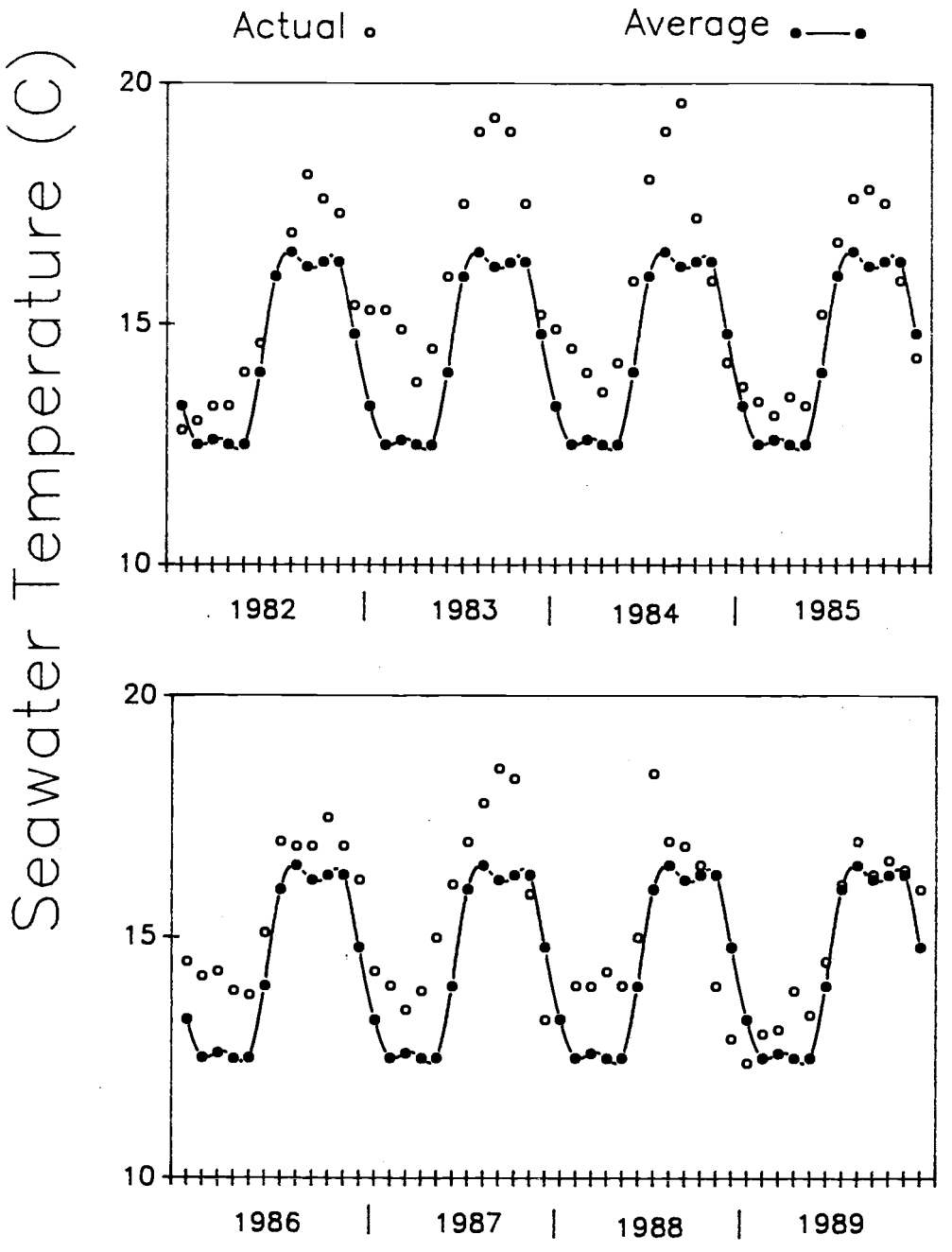

Actual
Average
Seawater Temperature (C)
20
15
10
1982
1983
1984
1985
20
15
10
1986
1987
1988
1989

Figure 3.24

Figure 3.25. Changes in relative weight (dots) and rates of algal consumption (histograms) for six abalone during Fall, 1988. For each abalone L indicates their shell length (in mm) and an X indicates mortality of that individual.

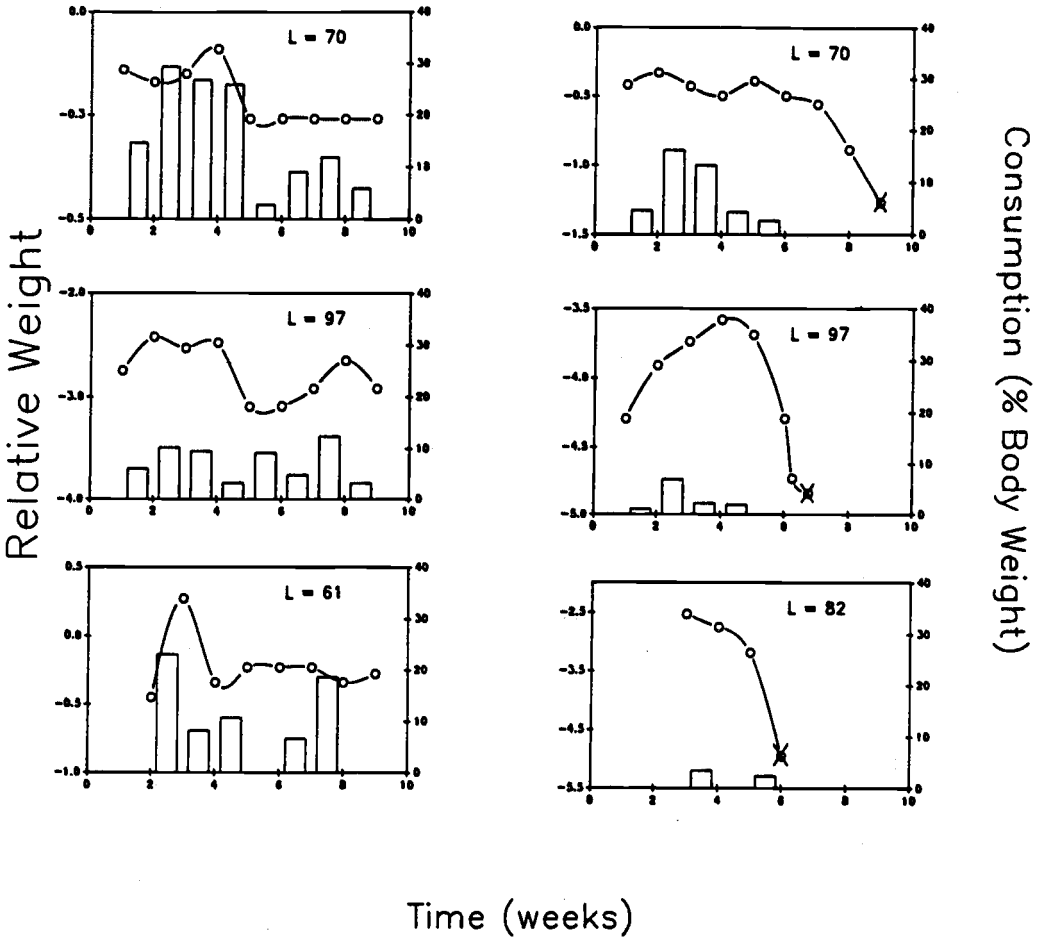

L = 70
L = 97
L = 61
L = 70
L = 97
L = 82
Relative Weight
Consumption (% Body Weight)
Time (weeks)

Figure 3.25

Figure 3.26. Relationship between shell length and time to mortality in abalone from Año Nuevo Island deprived of food.

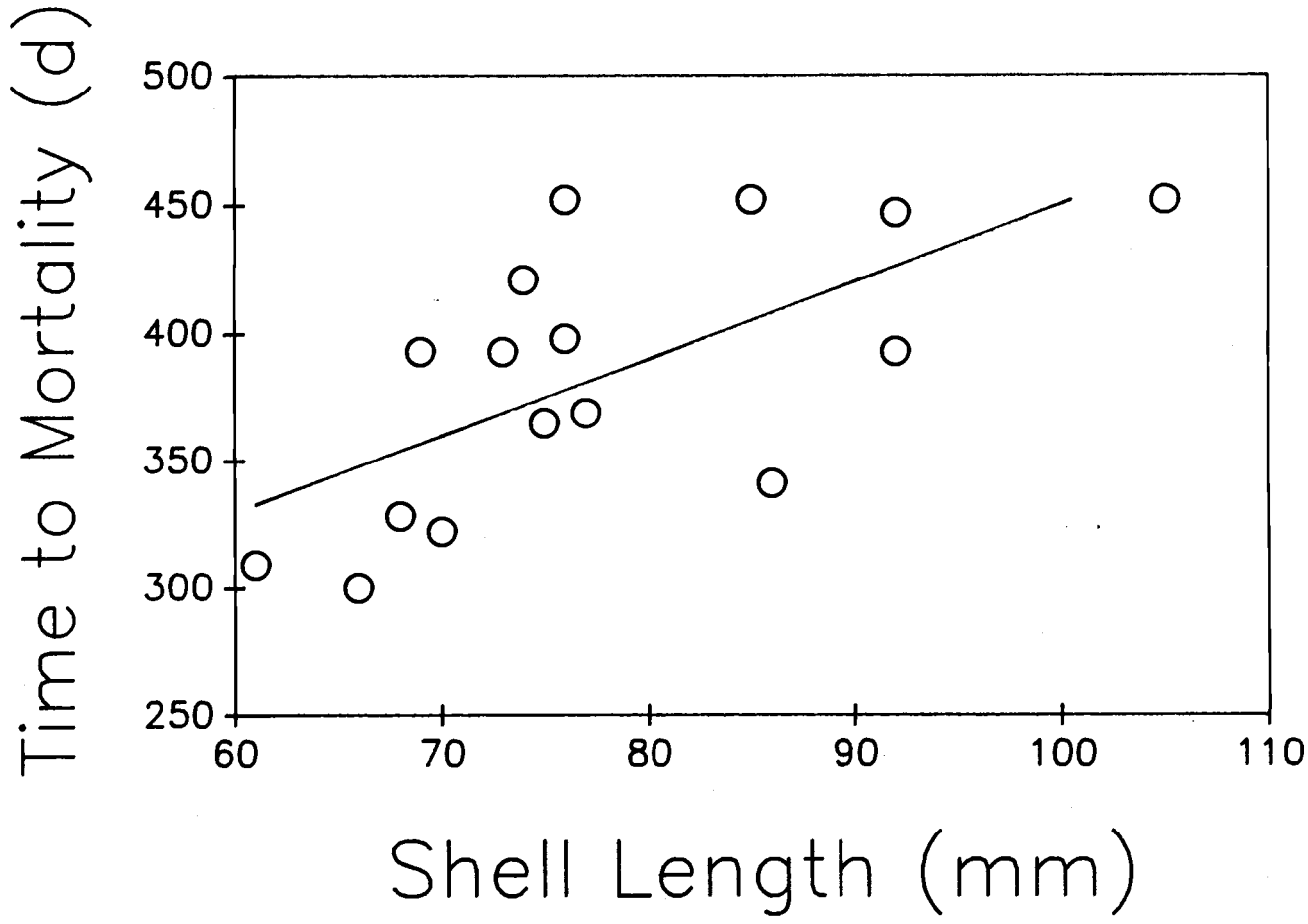

Time to Mortality (d)
500
450
400
350
300
250
60
70
80
90
100
110
Shell Length (mm)

Figure 3.26

Figure 3.27. Survivorship of black abalone from three populations cultured in the laboratory at three temperatures. Abalone were collected from Año Nuevo Island (ANI), Santa Cruz Island (SCI), and San Qunitin (SQ) (see Figure 1) and cultured together at 12, 15, and 18 C with *ad libitum* algal food.

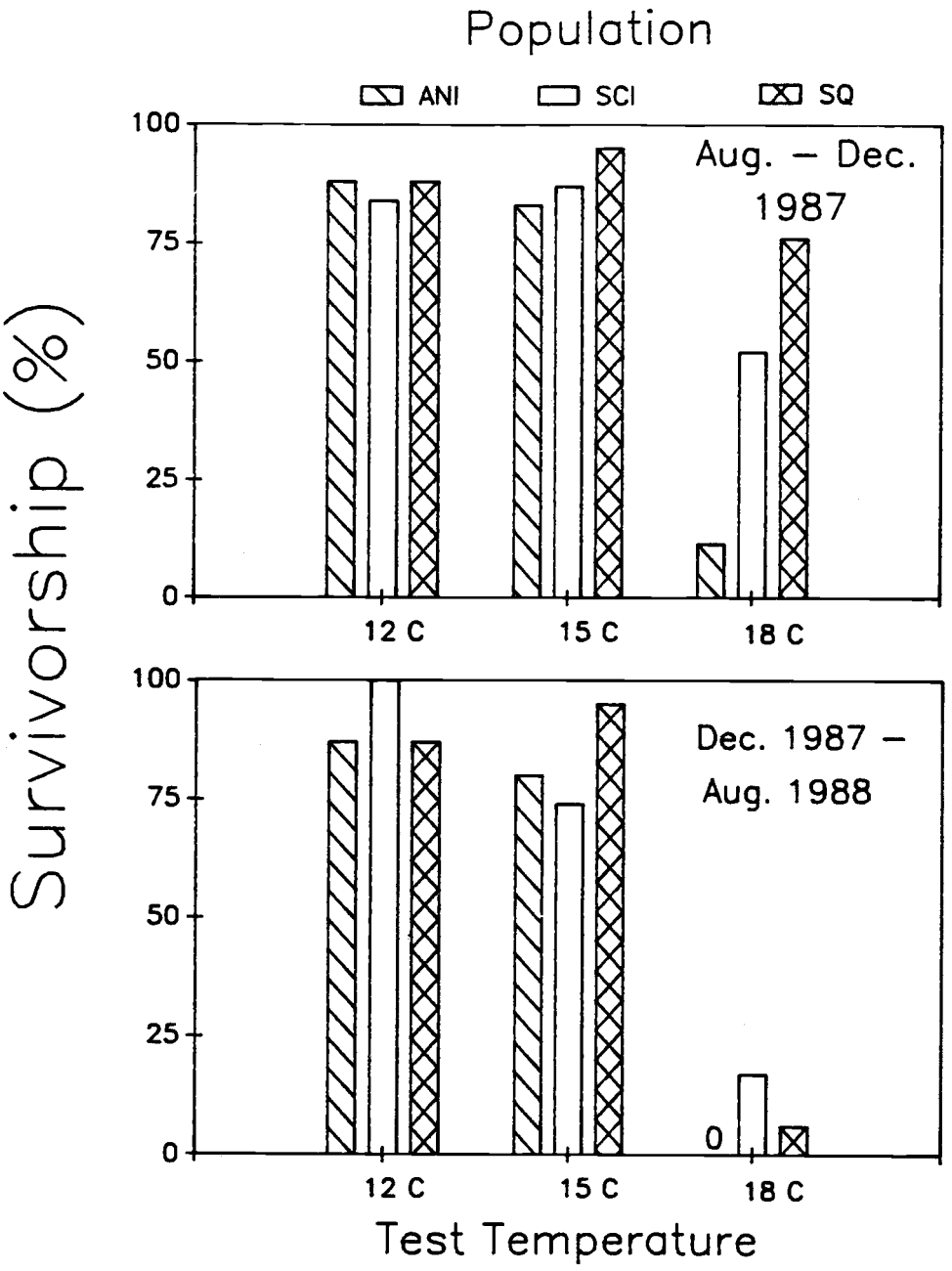

Population
ANI
SCI
SQ
Survivorship (%)
100
75
50
25
0
Aug. – Dec.
1987
12 C
15 C
18 C
Dec. 1987 –
Aug. 1988
0
Test Temperature

Figure 3.27

Figure 3.28. Relative total weight of black abalone in relation to shell length for three populations after culture in the laboratory for 120 days at three temperatures.

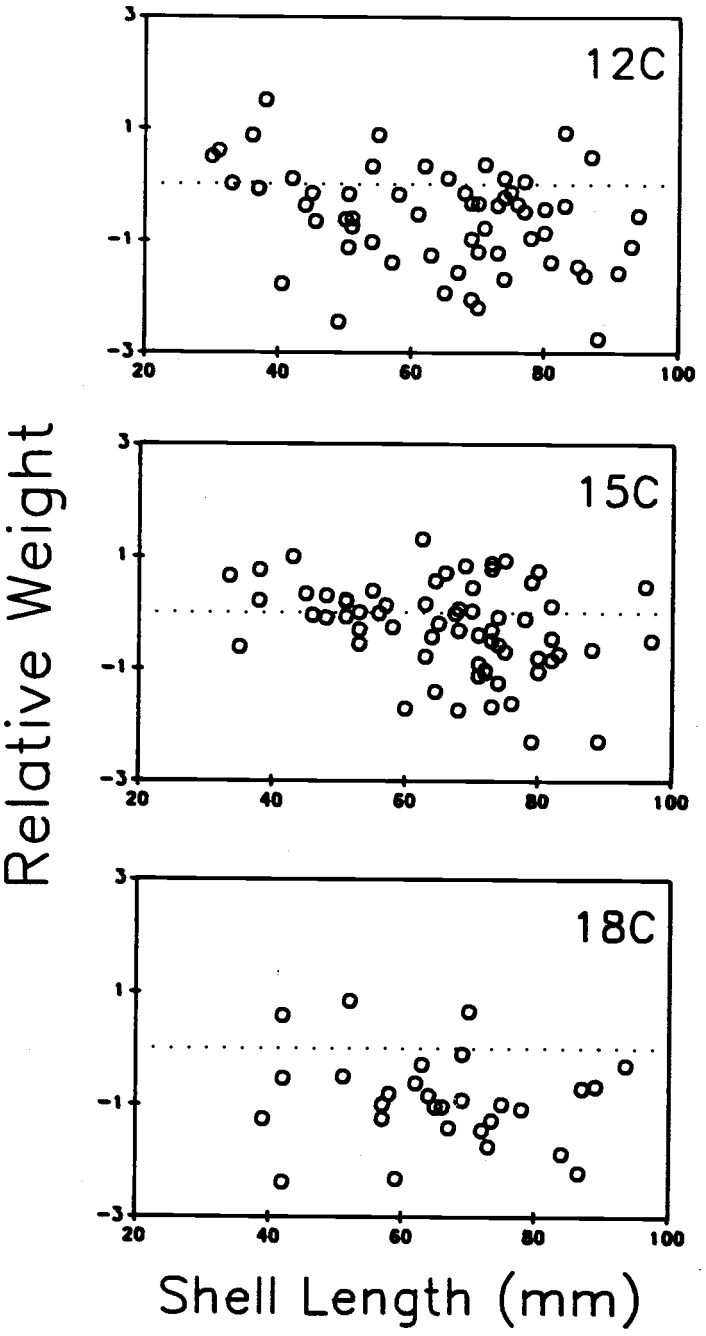

12C
15C
18C
Relative Weight
Shell Length (mm)
3
1
-1
-3
20
40
60
80
100

Figure 3.28

Figure 3.29. Ordinations of canonical correlation scores. **A.** Temperture-dependent declines in mortality among years. **B.** Seasonal variation in shell growth and movement. **C.** Density-dependent declines in abundance along exposed and protected transects.

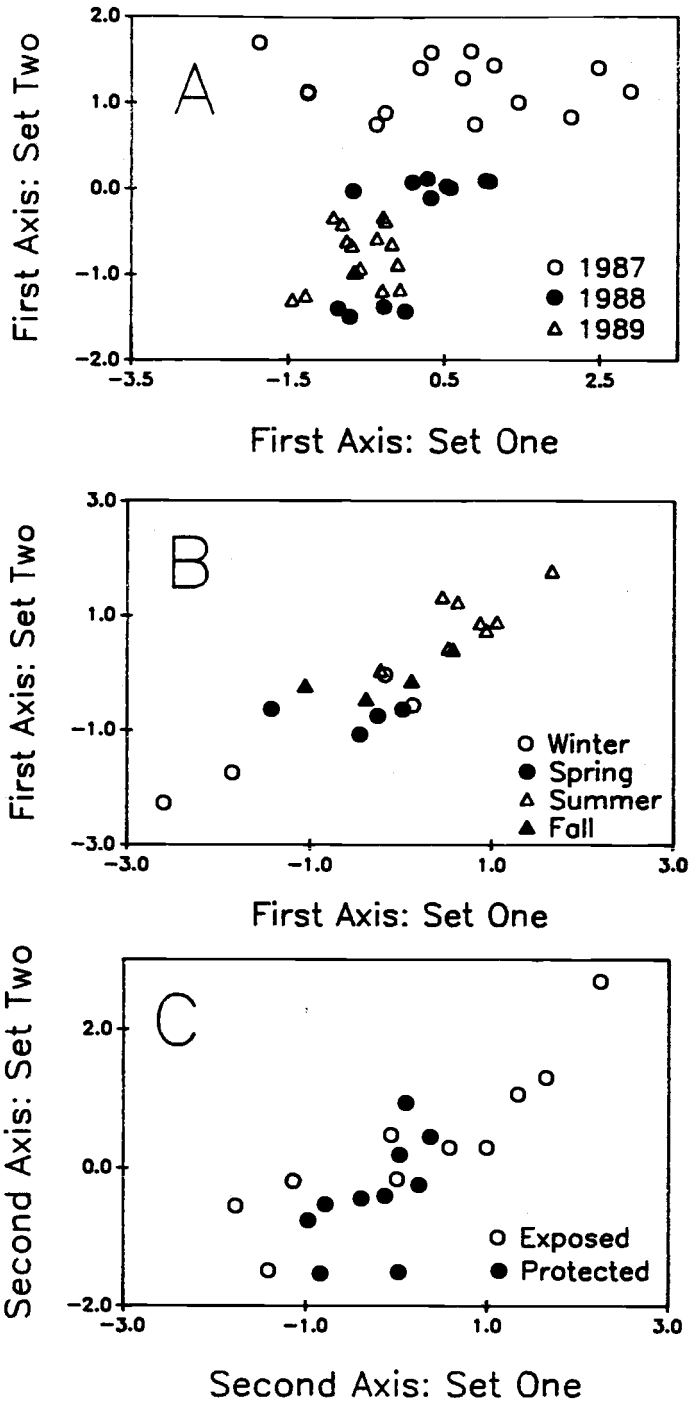

A
First Axis: Set Two
First Axis: Set One
2.0
1.0
0.0
−1.0
−2.0
−3.5
−1.5
0.5
2.5
1987
1988
1989
B
First Axis: Set Two
First Axis: Set One
3.0
1.0
−1.0
−3.0
−3.0
−1.0
1.0
3.0
Winter
Spring
Summer
Fall
C
Second Axis: Set Two
Second Axis: Set One
2.0
0.0
−2.0
−3.0
−1.0
1.0
3.0
Exposed
Protected

Figure 3.29

Chapter 4

GEOGRAPHIC VARIATION IN THE BLACK ABALONE: THE EFFECTS OF ECOLOGY ON DEVELOPMENT

Abstract

One major challenge of developmental studies, and a major focus of functional morphology, is to examine the effects of growth processes on whole-organism fitness under varying environments. The goal of this chapter is to describe the contribution of developmental and ecological processes to patterns of morphological variation in the shell of the black abalone, *Haliotis cracherodii*. I propose and test four hypotheses on the effects of ecology and development on morphological variation in trema (=respiratory pore) number and size: differential growth and/or differential survivorship due to either desiccation or water movement.

Multivariate ontogenetic trajectories revealed pronounced variation in allometric growth along shore-level, wave-exposure, and latitudinal gradients in several shell characteristics. Abalone from Año Nuevo Island were heavier, wider and deeper shelled, and displayed fewer, smaller and more distantly spaced tremata than individuals of similar sizes on Santa Cruz Island. These morphological patterns were largely due to differences in the underlying growth rate and subsequent allometry of their component variables.

Variability in trema number was an allometric consequence of variation in the rate of shell growth. Thus, I proposed that variation in trema number was a weak component of individual fitness. In contrast, shore-level gradients in trema number appeared to be maintained by abalone movement in combination with allometric growth and differential survivorship among individuals.

Variation in trema size was an additional morphological pattern which varied both geographically and along wave-exposure gradients. However, in contrast to trema number, trema size was associated with variation in external water velocity. These patterns indicated that variation in trema size was a functional response to the degree of respiratory efficiency.

The results of this study demonstrate the importance of assessing the contribution of developmental variation to morphological patterns. In instances where patterns of growth were not consistent with morphological differences, development served as a null model in which to evaluate selection as a cause of the patterns. Overall, results strongly indicate that morphological patterns, including both between- and within-population components, were the consequences of environmentally induced phenotypic plasticity.

Introduction

Ontogenetic development is a fundamental property of living organisms and represents large changes in many attributes, including an individual's size and shape. Among evolutionary biologists the importance of ontogenetic processes in evolutionary patterns has been apparent since Haeckel's days (1875). This interest remains strong today as evidenced by a proliferation of studies on heterochrony, or changes in developmental timing during evolution (Gould, 1977). These studies have documented the importance of ontogeny in evolutionary patterns (e.g., Goodwin, 1983; McKinney, 1988c). Among ecologists, however, interest in development has been primarily focused on phenotypic plasticity, or environmental modulation of development (Smith-Gill, 1983). Ecological studies, primarily conducted by botanists, have documented the strong influence of environmental factors on phenotypic characters (e.g., Bradshaw, 1965).

One major challenge of developmental studies, and a major focus of functional morphology, is to examine the effects of growth processes on whole-organism fitness under varying environments (Fisher, 1985; Maynard-Smith et al., 1985). While studies on heterochrony have been successful in documenting ontogenetic patterns in fossil and recent species (e.g, McKinney, 1988c), few studies have examined the interaction between ecological factors and development processes in natural populations. In contrast, studies of phenotypic plasticity have successfully documented population-level consequences of developmental variation in a wide-variety of organisms (e.g., Silander and Antonovics, 1979; Berven et al., 1979). A major challenge in evolutionary ecology is thus the integration of these two

themes: to examine the population-level consequences of developmental variation with respect to common evolutionary patterns.

The goal of this paper is to describe the contribution of developmental and ecological processes to patterns of geographic variation in a temperate, marine gastropod, the black abalone, *Haliotis cracherodii*. Studies of geographic variation are central to our understanding of evolutionary processes because: 1) distinguishing patterns of genetic versus phenotypic variation remains a major evolutionary problem (Mayr, 1982); 2) geographic variation compounds variation among species; and, 3) geographic variation may represent the earliest stage of speciation (Gould and Johnson, 1972).

Geographic Variation in the Black Abalone

The black abalone is a common inhabitant of rocky intertidal shores on the Pacific coast of North America and ranges from Point Arena, California, to southern Baja California, Mexico. Black abalone are herbivorous and sedentary and feed on drifting pieces of macroalgae, mostly kelps, that are captured by their large muscular foot (Cox, 1962; Leighton and Boolootian, 1963; Douros, 1985; Chapter 2).

Morphological variation in the shell of black abalone is pronounced and composed of three major components: 1) size variation; 2) variation in the number of tremata (=respiratory pores); and 3) variation in the diameter of the tremata (Tissot, 1988b,d). Within populations, these three components are correlated with variation in intertidal position resulting in morphological shore-level gradients (Tissot, 1988d). Among populations, clinal variation in the number, and spacing, of tremata on the shell is pronounced: tremata decrease in number and become more distantly spaced with increasing latitude (Tissot, 1988b). In a previous study I described this

clinal variation multivariately using principal components analysis of samples from four populations measured for seven shell characters (Tissot, 1988b). Using principal component scores -- independent, linear combinations of the original variables -- the ontogeny of individuals within populations was depicted by multivariate *ontogenetic trajectories* (Alberch et al. 1979) which measured covariation between variables of size and shape (see Figure 3 in Tissot 1988b). Using ontogenetic trajectories, geographic variation in the black abalone was described by variation in trajectory slope as a function of latitude.

Hypotheses

Previously documented morphological patterns suggest that tremata are a functional component of abalone morphology. Because black abalone occupy intertidal habitats, variation in trema size and number may be a response to two environmental gradients. First, during submerged periods, water flowing over tremata may enhance respiratory exchange by passively inducing mantle cavity flow rates (Voltzow, 1983). In this respect, individuals with fewer large tremata would be more efficient at promoting mantle cavity flow (Tissot, in press). Second, during low tides when individuals are emerged, a shell with fewer, smaller tremata may enable an abalone to avoid desiccation and occur higher on the shore where predators are less abundant (Tissot, 1988d).

This paper examines variation in individual growth trajectories in relation to the morphological patterns depicted by ontogenetic trajectories. Based on the previously documented morphological patterns I proposed and tested the following, not mutually exclusive, hypotheses:

H_0: Trema variation has no functional significance.

H_1: Trema variation is a response to desiccation stress.

H_2: Trema variation is a response to water movement.

I tested these hypotheses by: 1) documentation of morphological patterns along three natural spatial scales: shore-level, wave-exposure, and latitudinal gradients; 2) field experiments which manipulated morphology and habitat; and 3) laboratory experiments which manipulated physical factors.

Materials and Methods

A. Field Methods

The study populations were located on the west end of Santa Cruz Island (34° 00' N, 114° 50' W), 25 km south of Santa Barbara, and on Año Nuevo Island (ANI: 37° 6' N, 122° 20' W), 65 km south of San Francisco (Figure 4.1). Intertidal transects were located in two general locations on each island that differed in their exposure to ocean waves. On Santa Cruz Island (hereafter "SCI"), the "protected" site was located 1 km SE of Fourney Cove on the south side of the island; the "exposed" site was located 0.2 km NE of Fraser Point on the north side of the Island (Figure 4.1). On Año Nuevo island (hereafter "ANI") the exposed site was located on the SE corner of the island while the protected site was located on the NW side.

At each study site on each island two intertidal transects were established in areas inhabited by black abalone. Transects extended from the high (2.0 m above MLLW) to the low-intertidal (-0.5 m below MLLW), had varying slope, were 1 m wide, and were 5-25 m in length. On SCI, transects were located in surge channels bounded by vertical walls of irregular shape. Transects on ANI occurred on flat, layered mudstone with a 20 degree E-SE slope. Transects were monitored quarterly (winter, spring, summer, fall) at SCI and three times a year (winter, spring, fall) at ANI for periods of 5-14 d. The study period spanned three years: winter 1987 to winter 1990. One survey (SCI: January 1988) was missed due to bad weather.

I measured water movement using dynamometers similar to those described by Palumbi (1984). On each transect, 3-6 dynamometers were arrayed along the transect sampling high-, mid-, and low-intertidal areas. Dynamometers measured the maximal wave force exerted over a 24 hr

period which, assuming all forces were due to drag, were converted to maximal water velocities in m/s using the formula described in Vogel (1981).

I tagged 5-75 abalone on each transect during each survey. I found individual abalone for tagging by systematically sampling the entire length of the transect, haphazardly choosing individuals within any one transect area. Location was marked along each transect using three tape measures -- X (downshore), Y (vertical), and Z (alongshore) -- which were calibrated relative to mean lower low water (MLLW = 0.0 m) using a transit. Repeated measurements indicated that locations were accurate to within $\pm$ 0.1 m. Total net movement was measured as the minimum distance between tagging locations on sequential surveys. I measured changes in intertidal distribution, or net vertical movement, by calculating the change in position relative to MLLW between surveys.

For tagging, abalone were removed from the substrate, their shell was cleaned with a wire brush, and marine epoxy putty (Z-spar splash zone compound) was used to attach a numbered plastic tag from a Dymo label maker. For each individual the following characters were measured (Figure 4.2): 1) *Shell Length*: length of the longest dimension; 2) *Shell Width*: width of the shell perpendicular to length; 3) *Shell Height*: maximum height of the shell; 4) *Number of Tremata*: number of open holes on the shell; 5) *Trema Length*: the distance the tremata traverse on the shell; 6) *Trema Spacing*: distance between the two anterior-most trema; 7) *Trema Diameter*: maximum diameter of the anterior-most trema; and 8) *Total weight* (after June 1988): total weight of abalone after the removal of shell growths, measured using a Pesola spring scale; 9) *Degree of Sculpture*: a ranked index: 1 = no shell sculpture, 2 = slight sculpture, 3 = well defined sculpture, and, 4 = strong sculpture; 10) *Shell Growths*: proportion of the total shell surface initially

covered by shell growths; and 11) *Shell Erosion*: proportion of the total shell surface eroded to the nacreous layer.

During each survey, I intensively searched an area 10-30m around each transect for tagged abalone and dead tagged shells. As no tagged abalone were found further than 20m from their initial position this method was deemed sufficient. At the protected site of SCI I also searched the subtidal area adjacent to each transect using SCUBA.

I measured survivorship as the recapture rate of tagged individuals between successive surveys. I estimated relationships between measures of morphology, growth and behavior, and survivorship by calculating the product-moment correlation between variables and the number of recaptures of individual abalone, a method recommended by Endler (1986). Morphological differences between survivors and non-survivors (i.e., not recaptured) of field experiments were examined using one-way analysis of variance (ANOVA).

B. Description of Morphological Patterns

Scaling relationships between variables that described abalone shell shape were examined using the allometry equation:

$$Y = a\,Wb \qquad (1)$$

where, Y = the shape variable of interest, W = a measure of body mass, such as shell length, and a and b are the intercept and slope of the equation, respectively (Huxley, 1932; Peters, 1983). Allometry equations were calculated using reduced major axis regression of log transformed variables on shell length (Sokal and Rohlf, 1981). Differences between populations in allometry coefficients were examined using analysis of covariance (ANCOVA).

Multivariate patterns of covariation among variables were examined using multigroup principal components analysis (PCA). All PCAs in this study were R-mode analyses of the correlation matrix derived from z-score standardized data (see Tissot, 1988b). Multigroup PCA examines analyses of individual samples (i.e., SCI vs. ANI) in reference to a PCA of the pooled within-group dispersion matrix, which describes patterns of variation common to all samples. Principal component scores (PCs) on the subsequently derived axes serve as statistically independent multivariate traits, which are linear combinations of the original variables (Pimentel, 1979). These multivariate traits were assigned to size and/or shape variables and ontogenetic trajectories were calculated using the methods described in Tissot (1988a,b). Differences in the slope of ontogenetic trajectories derived from different samples were examined using ANCOVA.

Variation in abalone development was described by several univariate and multivariate measures. Shell growth rate (mm/month) was calculated by:

$$\textit{Shell Growth Rate} = dL/dt \qquad (2)$$

Where, dL = the change in shell length in mm between surveys divided by dt, the elapsed time in months.

Multivariate development was described by two independent metrics of growth. The *multivariate growth allometry* between two characters was calculated by the linear regression:

$$dY/dt = a + (b * dW/dt) \qquad (3)$$

where, dY/dt = rate of change in PC shape scores, dW/dt = rate of change in allometric size (PC1 scores), and a and b are the intercept and slope, respectively, of the regression. For example, if PC2 described variation in trema number, the linear equation describing the PC1-PC2 growth allometry

would depict variation in the number of tremata added during growth relative to increases in allometric size. The growth allometry between two characters examines the relationship between those characters during growth *independently* of time: it is not a measure of growth rate but a measure of allometry.

In contrast, the rate of change of multivariate characters was measured by the *multivariate growth rate*:

$$dY/dt = a + (b * W) \quad (4)$$

where, dY/dt = the rate of change of PC scores, and W = a measure of size (i.e., PC1 scores), and a and b are the intercept and slope, respectively, of the regression. The multivariate growth rate equation examines the scaling of shape changes, as measured by changes in PC scores per unit time, with allometric size. For example, if PC1 described variation in allometric size, the linear equation describing the multivariate growth rate of PC1 would depict the size-specific rate of increase in allometric size per unit time. Moreover, the multivariate growth rate of PC1 would be significantly correlated with measures of growth among its composite variables, such as shell growth rate (equation 2).

C. Tests of Hypotheses

I conducted a series of field and laboratory studies to test my hypotheses. For logistical reasons, all field studies were conducted on SCI. Abalone for laboratory studies were collected from three localities in 1987: on SCI, ANI, and at Punta San Quintin, Baja California (hereafter "SQ") (Figure 4.1). All abalone were transported in aerated ice chests to the Hatfield Marine Science Center, Newport, OR, and held in a partially recirculating seawater system. Mortality during transportation was generally

less than 1%. All experiments received an input of aerated fresh ambient seawater, which varied between 10-16 C and 29-34 ppt salinity. Abalone during all experiments were fed *ad libitum* on a diet of *Alaria marginata*, *Laminaria* spp., *Iridaea cordata* and/or *Hedophyllum setchelli*. Both prior to and after each experiment, abalone were measured for characters 1-8 described above (Figure 4.2).

Test of H_0: *trema variation has no functional significance*

I conducted a series of field experiments to test the prediction that individuals with no open tremata would exhibited no differences in growth and survivorship relative to normal individuals. Tremata were closed by covering all openings with marine epoxy putty (Z-Spar splash zone compound). Although splash zone compound is toxic while curing, which takes about one hour, fully cured putty is non-toxic, as evidenced by the variety of limpets, barnacles and algae which settled on it in the field. To control for this initial toxic effect, epoxy putty was momentarily applied to all tremata and subsequently removed on control individuals.

The effect of trema closure was assessed with three independent experiments located on separate transects at the protected site on SCI. In all experiments, individuals were chosen haphazardly and the treatment and control were applied to every other animal. Experiment #1 involved a total of 34 individuals and was monitored from Sep 1987 to Mar 1988. Fifty individuals were used in experiment #2 which ran from Mar 1988 to Mar 1989. Experiment #3 was conducted from Jan 1989 to Jan 1990 and involved 24 abalone.

A second prediction of the null hypothesis is that variation in trema size and number is a correlated response to variability in growth rate. Because temperature is known to influence shell growth in marine molluscs

(e.g., Frank, 1975) I assessed the effects of temperature on abalone growth in a "common garden" experiment on individuals from three populations. Between 15 and 25 abalone from each of three populations (ANI, SCI, and SQ) were cultured together in each of three seawater temperatures (12, 15, and 18C), which approximated the average ambient temperatures of the three populations. The 12C treatment was maintained by a Tecumseh refrigeration unit which held the temperature at 12.5C (SD = 0.5). The 15C and 18C treatments were maintained by submerged electrical heaters which held temperatures at 15.4C (SD = 0.9) and 19.2C (SD = 0.9). The experiment ran from Aug 1987 to Aug 1988.

Test of H_1: *trema variation is a response to desiccation stress*

To examine the contribution of open tremata to rates of desiccation, I measured abalone weight loss in a wind tunnel made of clear plexiglas (0.75 m long, 0.15 m wide, and 0.15 m high). Air was pulled through the tunnel at a rate of 1 m/s by an electric motor maintained at a constant velocity. A collimator was attached to the distal end of the tunnel to promote a laminar air flow (see Vogel, 1981). Abalone were held in the middle of the chamber on a plexiglas platform surrounded by vexar mesh. The platform rested on an electronic balance which provided a continuous display of abalone weight. Individuals were held in the wind tunnel for a period of three hours under two experimental conditions: 1) all tremata plugged with clay; and 2) controls (open tremata, no clay). A total of five individuals were tested under both conditions.

To measure the effects of intertidal desiccation gradients on abalone growth and survival, I reciprocally transplanted individuals between high and low intertidal areas at the protected site on SCI. A total of 24 abalone were randomly assigned to each of four treatments (7-9 per treatment): 1) low to

high transplants; 2) high to low transplants; 3) low controls; and 4) high controls. Transplanted individuals were removed from one area, moved vertically 1.5m, and placed at a new location adjacent to control abalone. Controls were removed from the substrate and displaced horizontally 1m, but maintained at the same vertical elevation. Shell measurements were taken before and after the experiment, which lasted from Jun 1989 to Jan 1990.

Test of H_2: ***trema variation is a response to water movement***

To examine the influence of variation in water movement on shell morphology, I cultured abalone in a flow tank. The flow tank consisted of a closed loop of PVC pipe, 3 m long by 2 m wide. One-half of the pipe was 6" in diameter and the rest was 8". Abalone were contained within 1.5 m sections of the pipe by vexar screens and fed algae through O-ring sealed lids. Water was recirculated through the flow tank by a propeller inserted through an O-ring at one end of the pipe and driven by an electric motor. The motor remained at a constant speed throughout the experiment and created flow regimes of 60 cm/s in the 6" pipe (high flow) and 30 cm/s in the 8" pipe (medium flow). The flow tank was connected by 0.75" PVC pipe to an adjacent 100 gallon holding tank in which abalone were cultured in 1.5 m lengths each of 6" and 8" pieces of PVC pipe enclosed by vexar screens. Water was recirculated between the flow tank and the holding tank with a partial input of fresh seawater. The abalone in the holding tanks experienced a water velocity of 5 cm/s (low flow) and were cultured in the dark in order to match conditions in the flow tank.

I conducted two different experiments in the flow tank. Experiment #1, which lasted from Oct 1987 to Mar 1988, involved 62 abalone from SCI (19-12 per treatment) which were grown under each of the four flow combinations: 1) high flow (6" flow tank); 2) medium flow (8" flow tank); 3)

8" low flow (8" holding tank); and 4) 6" low flow (6" holding tank). Experiment #2, which occurred between Mar and Dec 1988, involved 90 abalone from both ANI and SCI (19-10 per treatment) under all four flow conditions. Unfortunately, all the abalone in the low flow treatments were killed during a systems failure shortly after the start of the experiment. As a result, experiment #2 only examined variation between high and medium flow conditions.

To measure the influence of water movement on abalone growth and survival in the field, I reciprocally transplanted individuals between exposed and protected sites at SCI. Individuals from each of four transects were assigned to four treatments (n = 30 each): 1) exposed to protected transplants; 2) protected to exposed transplants; 3) protected controls; and 4) exposed controls. Transplants were removed from the substrate, wrapped in wet towels, transported to the opposite site, and placed at comparable intertidal elevations on the new transect (total elapsed time 1 hour). Control abalone were handled identically, except that they were transported to the opposite site then returned to their original exposure regime and placed on a new transect (total elapsed time 1.5 hours). To minimize transport time out of water, only shell length and number of tremata were measured. The experiment was initiated in Mar 1987 and monitored until Mar 1988.

D. Statistical Analysis of Patterns and Experiments

The statistical significance of differences among experimental treatments was examined using analysis of variance (ANOVA) and covariance (ANCOVA). In all ANCOVAs, either shell length or allometric size scores (PC1 scores) served as a covariate. Prior to these analyses, samples were examined using Bartlett's test for homogeneity of variances. In the few cases where variances were unequal, a transformation was chosen

that minimized differences among sample variances. Significant main effects in ANOVA were examined using Student-Newman-Keuls multiple range tests (Sokal and Rohlf, 1981). In many cases, measures of abalone growth and behavior (e.g., shell growth, movement) were derived from repeated recaptures of tagged abalone. Therefore, values obtained from multiple-recaptures were either averaged within individuals (i.e., all growth measures) or used only once. This method was used in order to maintain independence among samples. These analyses produced similar results to those obtained using repeated-measure ANOVAs (Winer, 1971), which were inapplicable in most cases due to unequal sample sizes among treatments.

Results

On Santa Cruz Island, I tagged 1000 individuals during 12 surveys. Repeated recaptures of tagged individuals resulted in 1805 observations. On Año Nuevo Island 423 individuals were tagged during 10 surveys and repeated recaptures resulted in 910 observations of tagged individuals (Table 4.1).

Morphological Patterns

There were strong differences among populations in the allometry of individual shell traits with increasing shell length (Table 4.2a). ANCOVA revealed significant differences among populations in all characters but trema length. Allometry coefficients indicated that abalone from ANI were heavier, wider and deeper shelled, and displayed fewer, smaller and more distantly spaced tremata than individuals at similar shell lengths on SCI.

Multigroup principal component analysis revealed multivariate patterns of character variation identical to those previously described (Tissot, 1988b; Table 4.3). For both populations PCA produced three axes that described 90% of the covariation among traits. These axes primarily described variation in allometric size (PC1); trema number and spacing (PC2); and trema diameter (PC3). The angle between group eigenvectors for PC1 was only 8.6°, indicating that allometric size variation was similar among populations. In contrast, the angular separation between eigenvectors for PC2 and PC3 were 24.1° and 21.8°, respectively, indicating moderate differences among populations in these multivariate patterns.

Multivariate ontogenetic trajectories derived from PC scores were significantly different among islands (Table 4.2b). The slope of the trajectory between allometric size (PC1) and trema number (PC2) was significantly

greater on SCI relative to ANI, indicating that abalone at comparable sizes possessed more numerous, closely spaced tremata on SCI relative to ANI. Ontogenetic patterns between allometric size and trema diameter (PC3) were similarly different in slope: abalone from SCI possessed larger trema at comparable sizes relative to ANI.

The growth allometry of multivariate characters paralleled morphological differences among populations (Table 4.2c). Increases in trema number (PC2) relative to increases in allometric size (PC1) were significantly higher at SCI than at ANI. The growth allometry of trema size (PC3) relative to allometric size, however, was not different among sites, although this rate was higher at SCI relative to ANI.

In contrast, the growth rate of multivariate characters exhibited few differences among populations (Table 4.2d). Rates of change in allometric size (PC1) were significantly higher on ANI relative to SCI, indicating that individuals grew in overall size at a faster rate on ANI relative to SCI. However, shell growth rates, or rates of change in shell length, were not significantly different among populations, nor was the rate of change of trema number, although individuals at SCI added more tremata at comparable sizes than individuals at ANI. Whereas differences in rates of change in trema size were also in the same direction as morphological differences between populations, these rates were not significantly different.

Ecological Patterns: *Shore-level gradients*

Overall there were significant correlations between multivariate measures of morphology and intertidal distribution (Table 4.4). On SCI, significant negative shore-level gradients in allometric size (PC1) occurred at both exposed and protected sites: smaller individuals occurred higher on the shore than larger individuals. In contrast, on ANI a positive shore-level size

gradient occurred at the exposed site, indicating that larger individuals occurred higher on the shore that smaller individuals. Shore-level gradients in the relative number of tremata (PC2) were significant at the exposed sites of both study areas but not on the protected sites. At these sites, individuals with fewer, more distantly spaced tremata, independent of size, occurred higher on the shore than individuals with more numerous, closely spaced tremata (Table 4.4).

There was additional intertidal variation in the relative size of tremata (PC3), but the patterns were opposite at each site. On SCI, there was a positive shore-level gradient in which trema size increased with tidal elevation. In contrast, on ANI, trema size decreased with increasing tidal elevation, indicating a negative shore-level gradient (Table 4.4).

Significant variation in rate and direction of abalone movement occurred along shore-level gradients (Figure 4.3). Overall, individuals on SCI moved three-times as far as individuals on ANI. At both sites, however, there was a relationship between position in the intertidal and the direction of movement: high intertidal individuals had a net downward movement and low intertidal individuals had a net upward movement (Figure 4.3).

Survivorship of tagged individuals also varied along vertical gradients (Figure 4.4). Survivorship, as measured by recapture rate, generally declined with decreasing vertical elevation at both sites.

Ecological Patterns: *Wave-exposure gradients*

There was marked variation in shell morphology along wave-exposure gradients, although the extent of differences varied between populations (Table 4.5a). On SCI, ontogenetic trajectories for trema number (PC2) and size (PC3) were not significantly different between exposed and protected sites. However, both trajectories varied significantly along exposure gradients

at ANI: individuals on protected transects had larger, more numerous tremata than individuals on exposed transects.

Differences in multivariate growth allometry were inversely related to the magnitude of morphological divergence along exposure gradients (Table 4.5b). The growth allometry of PC2 and PC3 varied significantly along exposure gradients on SCI but not on ANI. Individuals on protected transects at SCI produced more numerous, closely spaced tremata, and larger tremata, per increase in shell size than those on exposed transects. The same pattern of growth allometry occurred along exposure gradients at ANI but these differences were not significant. Changes in the growth allometry of trema size along exposure gradients were consistent with variation in average maximum water velocities along exposure gradients: individuals on low velocity protected shores added larger tremata than individuals on high velocity exposed shores (Figure 4.5). However, the correlation between average maximum water velocity and tremata size growth allometry was not significant ($r = 0.55$, $n = 8$, $p > 0.05$).

Morphological growth rates did not vary significantly along exposure gradients. At both sites there were no differences in rates of allometric size, trema addition, or trema expansion between exposed and protected sites (Table 4.5c). However, individuals on exposed transects generally displayed faster rates of size increase than individuals on protected transects at both islands.

Ecological Patterns: *Survivorship*

There were significant correlations between measures of survivorship and multivariate measures of morphology in both populations (Table 4.6). On ANI, there was a significant correlation between allometric size and the number of recaptures of tagged individuals: large individuals were more

frequently recaptured. At the exposed sites of both islands, recapture rate was also significantly correlated with relative trema number (PC2): individuals with fewer tremata were more frequently recaptured than individuals with more numerous tremata. At the protected site on ANI, a similar correlation between the number of recaptures and relative trema number (PC2 scores) was evident, indicating that individuals with relatively smaller tremata were more frequently recaptured. Furthermore, at the ANI protected site, high intertidal individuals were more frequently recaptured than low intertidal individuals.

In contrast, there were no significant correlations between recapture rate and growth rates of multivariate traits (Table 4.6). However, in three of the four study sites individuals with high rates of movement were more frequently recaptured than sedentary individuals, although this correlation was only marginally significant ($0.10 < p < 0.05$). On SCI, there was an additional correlation between recapture rate and movement in the intertidal zone: individuals that move upward had higher recapture rates than individuals moving downward (Table 4.6).

Along intertidal transects, there was variation in survivorship among individuals that varied in relative trema number (Figure 4.4). On SCI, individuals with fewer tremata (lower PC2 scores) were more frequently recaptured in the high and low intertidal than individuals with more numerous tremata (high PC2 scores), which were more frequently recaptured in the mid-intertidal. On ANI, abalone with many tremata were more frequently recaptured in the low intertidal, whereas those with few tremata were more frequently recaptured in the high intertidal.

Tests of Hypotheses

H_0: *trema variation has no functional significance*

A. Trema closure

Abalone with plugged tremata in the field generally displayed reduced survivorship and growth relative to control individuals (Table 4.7). In two of three experiments, control individuals had higher recapture rates than abalone with tremata closed with epoxy putty. Similarly, shell growth rate and the percent of individuals growing was generally higher in the control relative to the test group, although these differences were not statistically significant (all $p > 0.05$). There were no consistent changes between groups in the magnitude or direction of vertical movement between surveys. Because closure of tremata generally resulted in reduced survivorship and growth I rejected the null hypothesis.

B. Temperature-Induced Growth Variation

Varying temperature induced significant variation in abalone growth rate and growth allometry (Figure 4.6). However, in only one out of nine cases (3 samples x 3 temperatures) was the slope of multivariate ontogenetic trajectories (PC2 and PC3) altered during the experiment. Two-way analysis of covariance indicated that there were differences in rates of allometric size increase among temperatures and populations ($F = 3.0$, $df = 155$, $p < 0.05$). Samples from ANI and San Quintin (SQ), Mexico displayed the same pattern of growth: allometric size growth rate increased with increasing temperature (Figure 4.6a). In contrast, the sample from SCI displayed higher size growth rates at 15C relative to the 12C and 18C treatments. Rate of growth in trema number and spacing did not vary significantly among temperatures nor populations ($F = 0.8$, $n = 151$, $p > 0.10$), but there were significant differences in the rate of growth in trema size among treatments ($F = 4.9$, n

= 155, $p < 0.01$). Trema size growth rate was similar among samples from ANI and SCI: rate of increase in tremata size increased in proportion to temperature (Figure 4.6b). In contrast, the rate of growth in tremata size decreased with increasing temperature in the sample from SQ.

The growth allometry of trema number and allometric size varied among temperatures and populations ($F = 3.4$, $df = 151$, $p < 0.05$). Samples from each population displayed different patterns of growth allometry at different temperatures (Figure 4.6c). Individuals from SQ added fewer, more distantly spaced tremata per increase in allometric size at higher temperatures and more numerous, closely spaced tremata at lower temperatures. The ANI sample displayed the opposite pattern: fewer, more distantly spaced tremata were added at 12C relative to 15C and 18C. An intermediate pattern, in which the number of trema added per size increase was similar at 12C and 15C but lower at 18C, was displayed by the sample from SCI. There were no significant differences in the growth allometry of tremata size among temperatures or populations ($F = 1.8$, $n = 151$, $p > 0.10$). Although variation in trema number was associated with temperature-induced variation in growth rate, because there were significant statistical interactions among populations, I rejected the null hypothesis.

H_1: *trema variation is a response to desiccation stress*

Rates of weight loss among abalone in wind tunnels indicated that rates of desiccation were low and that a small proportion of desiccation occurred through open tremata (Figure 4.7). After three hours in the wind tunnel, control abalone with open tremata generally lost 2.8-3% of their total weight. Although the rate of water loss was not different among individuals with open tremata versus those without open tremata, the amount of water

lost was significantly lower by only 0.2% in plugged relative to normal abalone (ANCOVA, $F = 8.3$, $p < 0.01$).

Transplantation of abalone along vertical shore gradients indicated that survivorship, as measured by recapture rate, was reduced in the low relative to the high intertidal (Figure 4.8a). Recapture rates of control abalone were greater in both the high and low intertidal relative to abalone transplanted to those locations. The recapture rate of abalone transplanted upward was significantly higher (42.8%) than abalone transplanted downward (12.5%). In contrast, shell growth occurred only in high intertidal controls and in high intertidal abalone transplanted downward (Figure 4.8b). Moreover, transplanted individuals tended to return to their original intertidal position within the three month intersurvey period: abalone transplanted downward had a net upward movement and abalone transplanted upward had a net downward movement relative to controls (Figure 4.8c). Lack of shell growth in two treatments prevented tests of morphological change among transplants. However, there were no significant morphological differences between recaptured and non-recaptured individuals in any treatment (ANOVA, all $P > 0.05$). Because survivorship was greater in the high relative to the low intertidal, and open tremata were associated with a minor rates of desiccation, H_1 was rejected.

H_2: *trema variation is a response to water movement*

Variation in water velocity induced significant variation in shell morphology (Figure 4.9a). Individuals from SCI cultured for six months under low (5 cm/s), medium (30 cm/s), and high (60 cm/s) water velocities displayed significantly different rates of change in trema size (PC3). Individuals in the low flow regime added larger tremata at a faster rate than those in the medium or high flow regime (ANOVA, $F = 4.1$, $n = 58$, $p <$

0.01). In contrast, there were no significant differences among treatments in the rate of change in allometric size (PC1) or trema addition (PC2).

Water velocity also induced variation in growth rate among individuals from different populations (Figure 4.9b). Abalone from SCI and ANI cultured for nine months under high and medium flow regimes exhibited a significant interaction between water velocity and rate of change in allometric size. Individuals from ANI displayed elevated growth rates under the high flow relative to the low flow regime, while individuals from SCI displayed the opposite trend (Two-Way ANOVA, $F = 12.4$, $n = 23$, $p < 0.01$). The two samples did not, however, exhibit significant differences in rate of trema addition or trema expansion (both $p > 0.05$), although the rate of trema expansion was higher in the medium relative to low flow regime in both populations.

Reciprocal transplantation of abalone between sites that varied in wave exposure at SCI resulted in pronounced variation in growth, survivorship, and morphology (Table 4.8). Overall, the recapture rate of abalone on the exposed coast (both controls and transplants) was higher than on the protected coast. Recapture rate varied inversely with changes in density: abalone moved to higher density sites experienced decreased survivorship relative to abalone moved to lower density sites. In contrast, shell growth rates were not correlated with changes in density: individuals transplanted to a different exposure regime displayed significantly elevated shell growth rates relative to controls. Individuals at each site displayed significantly different patterns of vertical migration: abalone at the exposed site moved upward between surveys while protected site individuals moved downward. There were no significant differences in morphology among

recaptured vs. non-recaptured abalone in any treatments (ANOVA, all $P > 0.05$).

Transplantation of abalone had no significant effects on the growth allometry between trema number and shell length (ANCOVA, $F = 0.17$, $n = 44$, $p > 0.05$) (Table 4.8). However, the direction of morphological change in transplanted individuals was partially consistent with morphological differences along exposure gradients. Individuals on the protected-site control transect displayed a higher trema number growth allometry than those on the exposed-site control transect. Individuals at the protected site added more tremata per increase in shell length than those at the exposed site (Table 4.8). Protected abalone transplanted to the exposed site displayed a *decreased* trema growth allometry relative to protected site individuals: fewer tremata were added relative to changes in shell length (i.e., shell morphology became more "exposed-site"). In contrast, the trema growth allometry of exposed site abalone transplanted to the protected site did not change in the direction of a more "protected-site" morphology (i.e., develop more numerous tremata) (Table 4.8). Because variation in trema growth was clearly associated with variation in water movement, H_2 was not rejected.

Discussion

Multivariate ontogenetic trajectories revealed pronounced variation in allometric growth along shore-level, wave-exposure, and latitudinal gradients in several shell characteristics. The primary morphological pattern involved the relative number and size of tremata on the shell. Ontogenetic trajectories derived from principal components scores suggested that geographic variation in trema number represented clinal variation in the pattern of shell growth. Measurements derived from individual growth trajectories supported this hypothesis: morphological patterns were largely due to differences in the underlying growth rate and subsequent allometric variation among their component variables. The development of these variables, in turn, was influenced by a variety of environmental factors which varied both within and between populations.

Below I evaluate patterns of variation in trema number and size in relation to their functional role in black abalone biology. I then discuss the importance of measuring developmental patterns at the population level and the role of development as an evolutionary mechanism mediated by ecological processes in this system.

Functional Significance of Trema number

The primary pattern of morphological variation involved the relative number of tremata on the shell. Overall, experimental manipulation of morphology indicated that the number of open tremata was weakly associated with variation in growth and survivorship in the field. Although individuals with experimentally closed tremata exhibited generally lower survivorship and shell growth rates than those with open tremata, these differences were not consistently statistically significant. Moreover, rates of

desiccation in a wind tunnel indicated that open tremata accounted for only a small component of water loss during aerial exposure. Given that natural variation in trema number results in inter-individual variation of 2-5 open pores, variation in trema number is probably a weak component of individual fitness. For the most part, patterns of growth indicated that variability in trema number was an allometric consequence of variation in the rate of increase in size (hereafter referred to as "shell growth").

There were no significant differences along any spatial gradients in the *rate* of trema addition, indicating that tremata were added at a relatively constant rate in growing individuals. Given this constancy, variation in trema number would be produced as an in inevitable consequence of variation in shell growth rate: a faster rate of growth would result in fewer, more distantly spaced tremata on the shell. Thus, variation in trema number is indicated to be a correlated response of variation in overall growth rate.

Interestingly, patterns of variation in trema number were consistent in their association with intertidal position on all spatial gradients. Thus, individuals on Año Nuevo Island (ANI), individuals on wave-exposed transects, and individuals in the high intertidal, possessed fewer tremata than those individuals on Santa Cruz Island (SCI), on protected transects, and in the low intertidal. In all cases, individuals with fewer tremata occurred higher on the shore than those than those with more numerous tremata. If the trema number-growth rate hypothesis is true, these developmental patterns *predict* that the rate of shell growth is higher in areas where tremata are fewer.

Along latitudinal and wave-exposure gradients, associations between intertidal position and trema number were consistent with patterns of variation in rate of shell growth. Abalone on ANI grew faster than those at SCI, and growth was higher along exposed coasts relative to protected coasts

at each site. Thus, latitudinal variation in trema number, and variation along exposure gradients, was largely a response to variability in rates of growth in overall size.

Although numerous factors are known to influence the rate of abalone growth, the two most important factors are temperature and food supply (Hahn, 1988). Rates of size growth in the temperature experiment demonstrated that, when food is provided *ad libitum*, rate of shell growth increases in direct proportion to temperature. Similar temperature-dependent growth is a common pattern among marine organisms (Vernberg, 1962) and is responsible for a wide variety of geographic patterns (Frank, 1975; Vermeij, 1977; Graus, 1974; Kenny, 1983). However, if differences in shell growth rates between SCI and ANI are indicative of clinal patterns in the black abalone, then rate of shell growth is *inversely* related to temperature in the field, indicating that additional factors, such as variation in food abundance, are likely to be involved.

Because abalone are sedentary and feed on drift macroalgae, their growth is strongly dependent on the abundance of local algal stocks (Shepherd, 1973). Several studies have documented clinal variation in abalone shell growth that varies with the abundance of algal foods independently of temperature (Shepherd, in press; Hamer and Butcher, in press). The black abalone is a particularly sedentary species and its intertidal distribution is strongly correlated with the distribution of drift macroalgae (Chapter 3). Although measurements of drift algal abundance by Tissot (Chapter 3) showed no significant differences in the weight, density, or frequency of drift algal deposition between ANI and SCI, algae on ANI was generally less variable temporally (seasonally and interannually), and spatially. Moreover, drift algae at ANI was derived from twice as many

species on ANI compared to SCI. Although inconclusive, this more constant availability and greater diversity of food may be responsible for faster rates of growth in abalone from ANI relative to SCI. Along exposure gradients, however, drift algae was clearly more abundant on wave-exposed relative to wave-protected sites at both populations (Chapter 3). Thus, faster shell growth rates on exposed coasts, and the allometric response of fewer tremata on the shell, would be generated as a result of more abundant drift algae, which in turn was controlled by the intensity of water movement (Chapter 2).

In contrast, within each intertidal gradient, drift algae was generally more abundant in the low relative to the high intertidal (Chapter 2), opposite to the pattern of growth implied by shore-level gradients in trema number. In addition, there were no shore-level gradients in the rate of shell growth. However, significant variation in survivorship and movement patterns along the intertidal suggest another hypothesis: differential survivorship of morphotypes. Survivorship patterns along intertidal transects, and the results of the vertical transplant experiment, demonstrated that abalone in the low intertidal experience reduced survivorship relative to individuals in the high intertidal. Moreover, recovery of dead tagged abalone shells, positive evidence of mortality, indicate that this pattern is *not* due to a bias in recapturing tagged abalone: the frequency of recovery of dead shells was proportional to the frequency of non-recaptured individuals at all intertidal positions (Chapter 3).

Variation in physical and biological stresses along vertical gradients could have strong effects on survivorship. In general, disturbances due to burial by sand, and predation by crabs, fishes, and octopus appear to be greater in the low relative to the high intertidal (Frank, 1965; Ambrose, 1982; Markowitz, 1980; Fawcett, 1984; Tissot, 1988d). Wave forces, as measured by

dynamometers, vary irregularly along the intertidal (Chapter 2; see Denny, 1988). Because drift algal foods are more abundant in low relative to high positions, trade-offs are present along the intertidal gradient: high growth in the low intertidal and high survivorship in the high intertidal. Similar trade-offs between food and survivorship have been described for intertidal limpets by Sutherland (1970).

I hypothesize that variation in abalone movement combined with differential survivorship of individuals maintains shore-level gradients in morphology. In general, black abalone move upshore in the summer in response to abundant predators and burial by sand, and downshore in the spring and fall when they spawn (Tissot 1988d; Chapter 3). The vertical transplant experiment demonstrated that transplanted individuals tended to return to their original position in the intertidal. Furthermore, individuals transplanted along exposure gradients also displayed consistent patterns of vertical migration. Correlations between the rate and direction of movement, and the number of recaptures, indicated that abalone with high rates of movement, and those that moved upshore, had higher survivorship. Moreover, recapture rates of tagged abalone indicated that individuals variable in trema number experienced differential survivorship along the intertidal: abalone with fewer tremata were favored in the high intertidal while individuals with more numerous tremata were favored in the low and mid-intertidal. Therefore, shore-level gradients in trema number appear to be maintained by vertical migration combined with differential survivorship of morphological types. These patterns are similar to those proposed by Vermeij (1972) for a variety of intertidal molluscs.

Although the majority of geographic variation was due to environmentally-mediated growth, there was some evidence of genetic

differences among populations. The response of trema-number allometry to temperature differed among samples from three populations. The sample from San Quintin Mexico displayed a pattern consistent with the previously described effects of variation in growth rate on trema number: tremata were added inversely proportional to growth, which varied with temperature. Thus, at 18C when shell growth was high, few, widely-spaced tremata were produced. At 12C, when shell growth was low, more numerous, closely spaced tremata were added. In contrast, the sample from ANI displayed reduced rates of trema addition at 12C relative to 15C and 18C. This pattern suggests that compensation may be occurring which maintains limits on the number of tremata. Specifically, at temperatures above normal (> 15C) the ANI sample added *more* tremata relative to ambient-temperature patterns. Thus, individuals may be placing a lower limit on trema number, at which point they compensate by increasing the rate of trema addition. These patterns are similar to those described for altitudinal gradients in growth in the green frog, *Rana clamitans*. At similar temperatures, individuals from high altitudes had higher growth rates than individuals from low altitudes (Berven et al. 1979). Because growth rates varied inversely with altitude in nature, these patterns were interpreted as evidence of selection for increased rates of growth at high altitudes, or countergradient selection (Berven et al. 1979). In this study, increased rates of tremata addition at elevated temperatures is evidence in support of countergradient selection in black abalone.

Functional Significance of Trema Size

Variation in trema size was an additional morphological pattern which varied both geographically and along exposure gradients. However, in contrast to trema number, trema size was not associated with variation in the

rate of shell growth, but instead with a clearly defined environmental gradient: variation in external water velocity. In the field, there were strong associations between the rate of increase in trema size and average maximum water velocities measured with dynamometers. Moreover, abalone cultured under varying flow regimes in the laboratory added tremata whose size was inversely proportional to flow regime: larger pores were added at lower velocities. In the temperature experiment, abalone also added larger pores at higher temperatures.

These patterns indicate that variation in trema size is a functional response to variation in respiratory efficiency: larger tremata enhance respiration under low flow, or low oxygen, conditions. Consistent associations between morphology and habitat among many species of abalone suggest that trema size and shape is functionally important (Tissot, in press). Species of abalone which live in low-flow subtidal habitats possess large, elevated tremata that are efficient at inducing a passive, mantle cavity flow. The advantage of utilizing passive mantle cavity flow does not appear to be directly related to increased respiratory pumping rates *per se*, as only a small percentage of the total energy budget is devoted to ciliary pumping (e.g., keyhole limpets: Hughes, 1971). Rather, increased flow likely decreases the volume fraction of oxygen which must be removed from mantle cavity water for aerobic metabolism and allows a decrease in respiratory surface area (Murdock and Vogel, 1978). Thus, black abalone respond to external variation in water movement through phenotypic plasticity: trema size is influenced by flow regime.

A mass mortality of black abalone, which occurred on Santa Cruz Island in 1986-1989 (Chapter 2), could have had additional strong effects on these morphological patterns. Evidence indicates that a disease, in

combination with marked interannual variation in giant kelp abundance (*Macrocystis pyrifera*) during the 1986-87 El Niño, was responsible for the mortality. As a result, the density of black abalone on SCI declined about 90% from $50/m^2$ in 1987 to $6/m^2$ in 1989 (Chapter 3). Although the disease may also have been present at ANI, the density of abalone on ANI remained relatively constant at $8/m^2$ during the same study period (Tissot, unpublished data). During the mass mortality, however, there were few instances of selection on morphological characters (Tissot, manuscript in prep). Therefore, the effect of the mortality episode on morphological patterns remains unknown.

The Importance of Development

The results of this study demonstrate the importance of assessing the contribution of developmental variation to morphological patterns. The majority of the morphological variation described here occurred in response in underlying developmental variation in rates of change and allometry between component variables. In instances where patterns of growth were not consistent with morphological differences, development served as a null model in which to evaluate selection as a cause of the patterns.

Overall, my results strongly indicate that morphological patterns, including both between- and within-population components, were largely the consequences of environmentally induced variation. Clinal variation in trema number was due to phenotypic plasticity: environmentally-modified development (Smith-Gill, 1983). These patterns were not due to heterochrony as they did not represent shifts between the timing of developmental processes (Gould, 1977). Instead, plasticity resulted from the allometric consequences of variation in growth rate and the rate of tremata addition.

These patterns demonstrate the importance of including *time* as a causal component of morphological divergence. Without measuring rates of morphological change, it is impossible to distinguish between timing or allometry as a cause of shape change (Shea, 1983). Moreover, evaluation of heterochrony as a causal mechanism in any morphological pattern requires measurement of time because heterochrony, by definition, represents changes in timing (McKinney, 1988a). As such, multivariate ontogenetic trajectories are a useful tool for examining developmental rates in relation to patterns of morphological variation. In this study they were sufficient in distinguishing environmentally-induced variation from evolutionary meaningful patterns.

Table 4.1. Descriptions of black abalone transects on exposed and protected areas of Santa Cruz and Año Nuevo Islands.

Transect Average	*Santa Cruz Island* Exposed	Protected	*Año Nuevo Island* Exposed	Protected
Density (#/m_2)	38.4*	58.4*	8.4	5.6
Intertidal Position (m above MLLW)	0.52	0.33	0.90	0.57
Shell length (mm)	92	101	120	127
Number Tagged	340	660	178	223
Recapture Rates	45%	40%	59%	5%
Transect Area (m2)	14	27	54	20
Total Survey time (d)	32**	52**	17	23

* - in March 1987
** - includes all field experiments

Table 4.2. Univariate and multivariate metrics of allometric growth for black abalone derived from field surveys on Santa Cruz Island (SCI) and Año Nuevo Island (ANI). Results of analysis of covariance (ANCOVA) of slopes and intercepts between populations is presented for each metric. Multivariate metrics reflected allometric size (PC1), trema number and spacing (PC2), and trema size (PC3) (see Table 4.3).

	Slope		Intercept		
	SCI	ANI	SCI	ANI	ANCOVA
A. *Allometric Equations*					
Width	1.10	1.14	-0.75	-0.89	slopes**
Height	1.29	1.46	-2.82	-3.56	slopes**
Trema number	0.27	0.32	0.66	0.37	intercepts**
Trema Length	1.12	1.15	1.12	-1.05	ns
Trema Spacing	0.93	0.98	0.93	-2.31	slopes**
Trema Diameter	0.64	0.47	-1.79	-0.94	slopes**
Total Weight	3.24	3.30	-9.78	-9.87	intercepts**
B. *Ontogenetic Trajectories*					
PC2 (x 10^2)	0.60	-0.30	4.15	4.98	slopes**
PC3	-0.18	-0.19	0.83	1.80	slopes**
C. *Growth Allometry*					
PC2	0.64	-0.16	0	0	slopes**
PC3	0.35	0.21	0	0	ns
D. *Growth Rates*					
Length (x 10^2)	-0.10	-0.20	0.49	0.61	ns
PC1 (x 10^1)	0.10	-0.07	0.04	-0.01	slopes**
PC2 (x 10^2)	0.10	-0.01	-0.02	-0.01	ns
PC3 (x 10^1)	0.17	-0.03	0.02	0	ns

Significance levels: ns - not significant ($p > 0.05$); * - $p < 0.05$; ** - $p < 0.01$

Table 4.3. Results of multigroup PCA on black abalone from Santa Cruz and Año Nuevo Islands. High variable loadings are indicated in boldface ($p < 0.05$). Measured variables are diagrammed in Figure 4.2.

	EIGENVECTORS								
	Santa Cruz Island			*Año Nuevo Island*			*Pooled Dispersion*		
Variable	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Length	**0.44**	0.03	-0.07	**0.46**	-0.01	-0.08	**0.45**	0.00	-0.06
Width	**0.44**	0.00	-0.09	**0.46**	-0.02	-0.10	**0.45**	0.08	-0.08
Height	**0.41**	-0.04	-0.11	**0.44**	-0.08	-0.12	**0.43**	0.06	-0.09
Trema Number	0.22	**0.83**	-0.02	0.24	**0.68**	-0.20	0.23	**0.75**	-0.19
Trema Length	**0.43**	0.12	-0.10	**0.46**	-0.07	-0.08	**0.45**	0.09	-0.09
Trema Spacing	**0.32**	**-0.51**	0.40	0.22	**-0.72**	-0.11	0.26	**-0.64**	-0.33
Trema Diameter	**0.32**	-0.19	**0.90**	**0.26**	0.05	**0.95**	**0.30**	-0.07	**0.91**
Eigenvalues	5.02	1.01	0.52	4.33	1.11	0.76	4.63	1.07	0.65
Percent Variation	71.70	14.50	7.40	61.90	15.90	10.80	66.20	15.30	9.30

Table 4.4. Correlations between multivariate metrics of morphology and vertical distribution along wave-exposure gradients at the two study islands. PC1 measures variation in allometric size; PC2 in the relative number and spacing of tremata; PC3 in relative tremata size (see Table 4.3).

Morphological Metric	*Santa Cruz Island* Exposed	Protected	*Año Nuevo Island* Exposed	Protected
PC1	-0.31**	-0.16**	0.14**	0.07
PC2	-0.16**	0.03	-0.20**	0.10*
PC3	0.23**	0.05	-0.16**	0.02
N	451	581	424	490
PC1 Growth	-0.08	-0.02	0.05	-0.01
PC2 Growth	-0.04	-0.05	-0.05	-0.01
PC3 Growth	0.19**	0.07	-0.03	-0.02
N	202	234	249	268

Significance levels: * - $p < 0.05$, ** - $p < 0.01$

Table 4.5. Differences between populations in multivariate measures of morphology along exposure gradients: Exp = Exposed, Pro = Protected. Results of analysis of covariance (ANCOVA) testing for differences among exposed and protected sites are shown.

	Slope		*Intercept*		
	Exp	Pro	Exp	Pro	ANCOVA
A. Static Allometry					
Santa Cruz Island					
PC2 ($\times 10^1$)	0.18	0.13	-0.80	-1.20	ns
PC3 ($\times 10^1$)	-0.95	-0.79	1.50	1.00	ns
Año Nuevo Island					
PC2 ($\times 10^1$)	-0.80	0.05	-4.99	2.50	slopes**
PC3 ($\times 10^1$)	-0.78	-0.33	-2.10	2.40	intercepts**
B. Growth Allometry					
Santa Cruz Island					
PC2	-0.17	1.00	0	0	slopes**
PC3	-0.03	0.52	0	0	slopes**
Año Nuevo Island					
PC2	-0.18	0.20	0	0	ns
PC3	0.20	0.54	-0.01	-0.02	ns
C. Growth Rates					
Santa Cruz Island					
PC1 ($\times 10^1$)	-0.13	-0.04	0.20	0.30	ns
PC2 ($\times 10^2$)	-0.70	0.50	0	3.00	ns
PC3 ($\times 10^2$)	0.01	0.60	0	0	ns
Año Nuevo Island					
PC1 ($\times 10^2$)	-0.60	-0.16	4.00	2.00	ns
PC2 ($\times 10^2$)	-0.10	0.01	-2.00	0	ns
PC3 ($\times 10^2$)	-0.30	-0.60	-1.00	-1.00	ns

Significance levels: ns - not significant ($P > 0.05$); * - $p < 0.05$; ** - $p < 0.01$

Table 4.6. Measures of survivorship: correlations between the number of recaptures of individual abalone and variables describing abalone morphology, growth, and movement. Multivariate metrics reflected allometric size (PC1), trema number and spacing (PC2), and tremata size (PC3; see Table 4.3).

	Santa Cruz Island		*Año Nuevo Island*	
Trait	Exposed	Protected	Exposed	Protected
PC1	0.01	0.07	0.20**	0.24**
PC2	-0.17**	-0.02	-0.13**	-0.02
PC3	0.01	0.05	-0.01	-0.11**
Vertical Location	0.05	0.02	0.08	0.54**
N	448	555	424	489
PC1 Growth	0.02	0.07	-0.08	-0.09
PC2 Growth	0.01	-0.03	0.10	0.01
PC3 Growth	0.01	-0.03	0.06	0.01
Total Movement	0.05	0.13$	0.13$	0.14$
Vertical Movement	0.18**	0.14*	-0.11	-0.04
N	200	226	249	268

Significance Levels: $ - $p < 0.10$, * - $p < 0.05$, ** - $p < 0.01$

Table 4.7. Results of trema closure experiments: differences between abalone with tremata closed by marine epoxy putty versus control abalone (putty applied then removed). Results of analysis of variance (ANOVA) testing differences between control and test individuals are presented. ns = not significant. Growth rate is reported in mm/month; movement in m/month

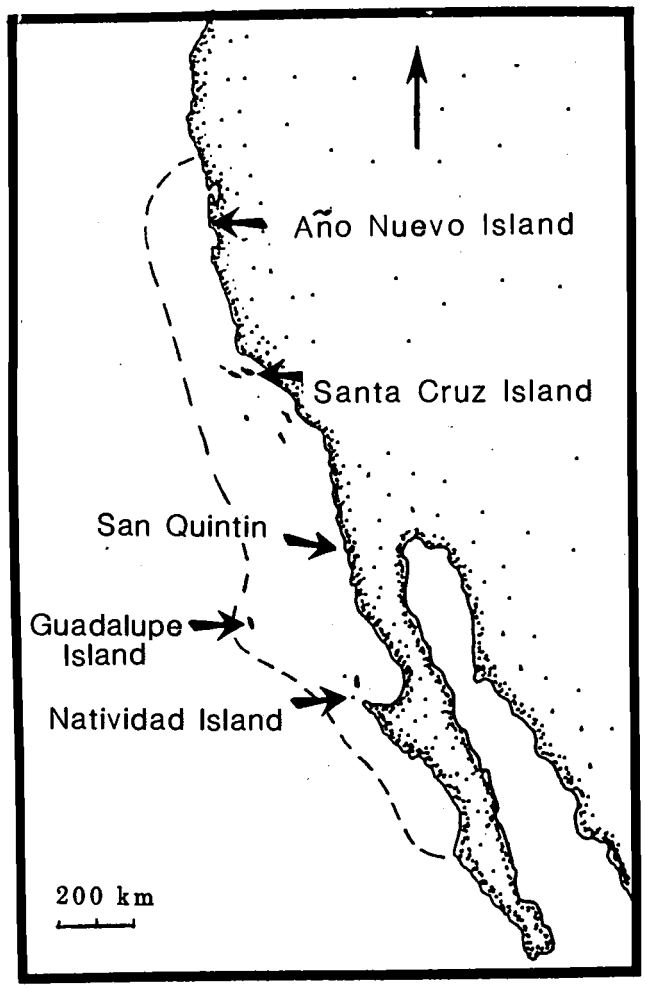
Treatment	N	Recapture Rate	Percent Growing	Growth Rate	Movement Total	Movement Vertical
A. *Experiment #1*: Sep 1987-Mar 1988						
Control	14	21.4%	14.3%	0.19	0.58	-0.08
Ablation	20	25.0%	15.0%	0.15	0.43	+0.06
ANOVA				ns	ns	ns
B. *Experiment #2*: Mar 1988-Mar 1989						
Control	25	37.6%	42.7%	0.22	0.90	---
Ablation	25	31.2%	28.7%	0.23	0.27	---
ANOVA				ns	ns	no data
C. *Experiment #3*: Jan 1989-Jun 1989						
Control	12	83.0%	60.0%	0.22	0.93	+0.10
Abaltion	12	50.0%	16.7%	0.11	0.97	-0.01
ANOVA				ns	ns	ns

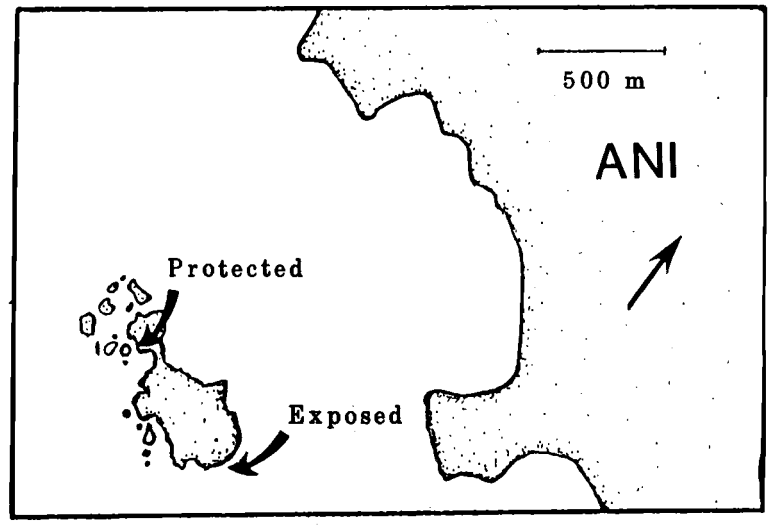
Table 4.8. Results of transplantation of abalone between wave-exposure gradients on Santa Cruz Island, Mar 1987 - Mar 1988. Density changes occurring during transplantation and results of analysis of variance (ANOVA) testing differences among all groups are indicated.

	Exposed		*Protected*		
	Control	Transplant	Control	Transplant	ANOVA
Density Changes ($no./m^2$)	20 » 37	76 » 37	56 » 76	37 » 56	--
Recapture Rate	63.3%	53.3%	33.3%	43.3%	--
Shell Growth (mm/month)	0.33	0.50	0.25	0.39	**
Percent Growing	84.2%	81.2%	40.0%	84.6%	--
Total Movement (m/month)	0.33	0.20	0.40	0.71	ns
Vertical Movement (m/month)	+0.10	+0.09	-0.16	-0.10	**
Trema Number Growth Allometry	0.15	0.30	0.42	0.12	ns

Significance Levels: ns - not significant ($p > 0.05$); ** - $p < 0.01$

Figure 4.1. Geographic range of the black abalone (dashed line) in reference to three study areas, and wave-exposed vs. wave-protected study sites at Santa Cruz Island (SCI) and Año Nuevo Island (ANI).


Año Nuevo Island
Santa Cruz Island
San Quintin
Guadalupe Island
Natividad Island
200 km


500 m
ANI
Protected
Exposed

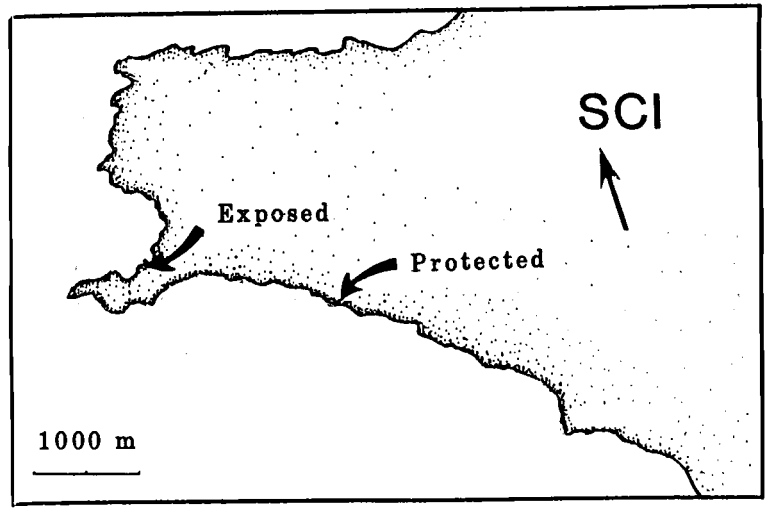

SCI
Exposed
Protected
1000 m

Figure 4.1

Figure 4.2. Shell characters used to describe the morphology of black abalone.

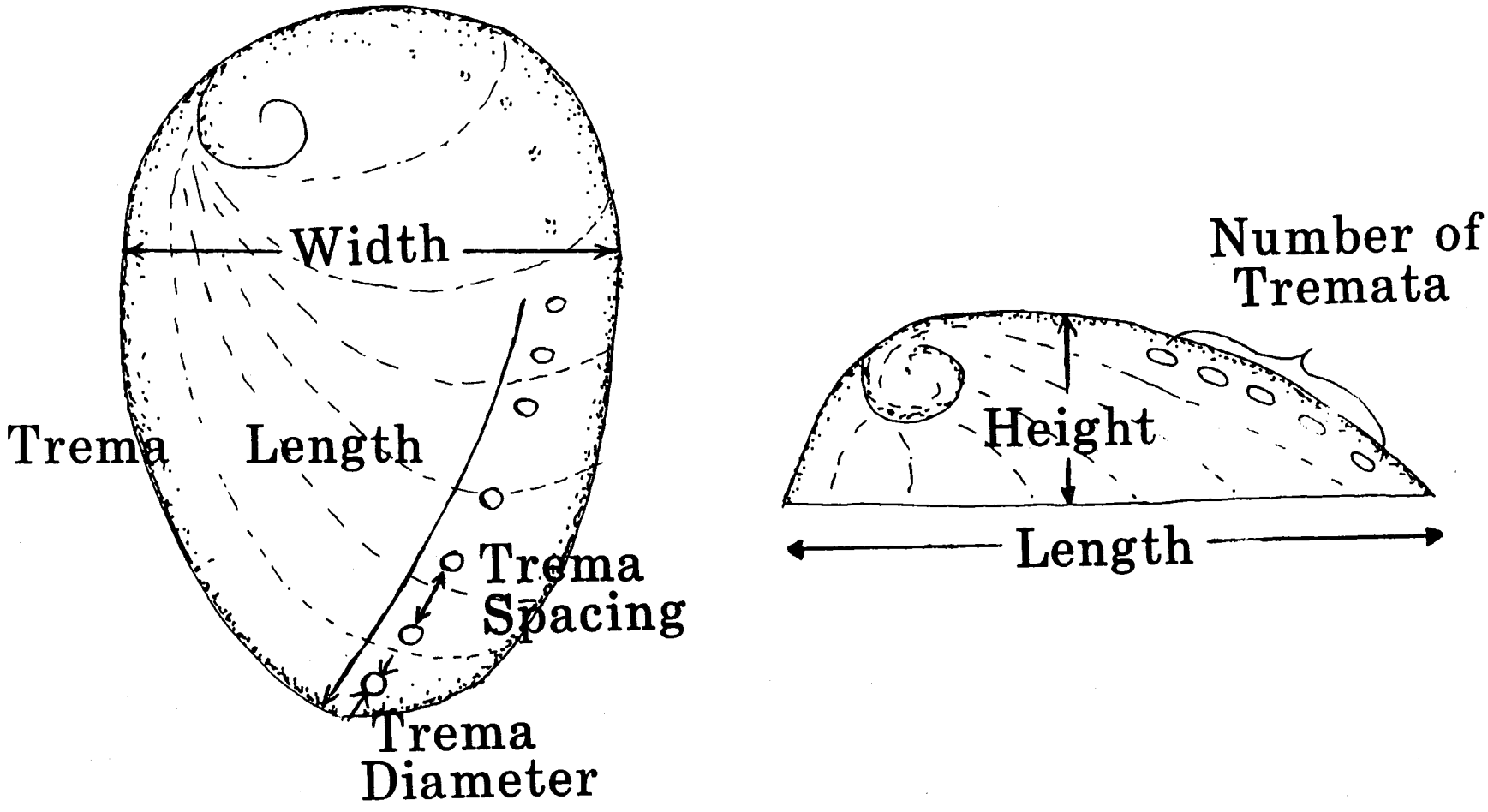

Width
Trema Length
Trema Spacing
Trema Diameter
Number of Tremata
Height
Length

Figure 4.2

Figure 4.3. Patterns of movement along intertidal transects at Santa Cruz and Año Nuevo Islands. For four intervals of tidal level, the average total distance moved by individuals between surveys (± 1 SE) is presented with histograms. The average vertical movement occurring between surveys (± 1 SE) is depicted by curves.

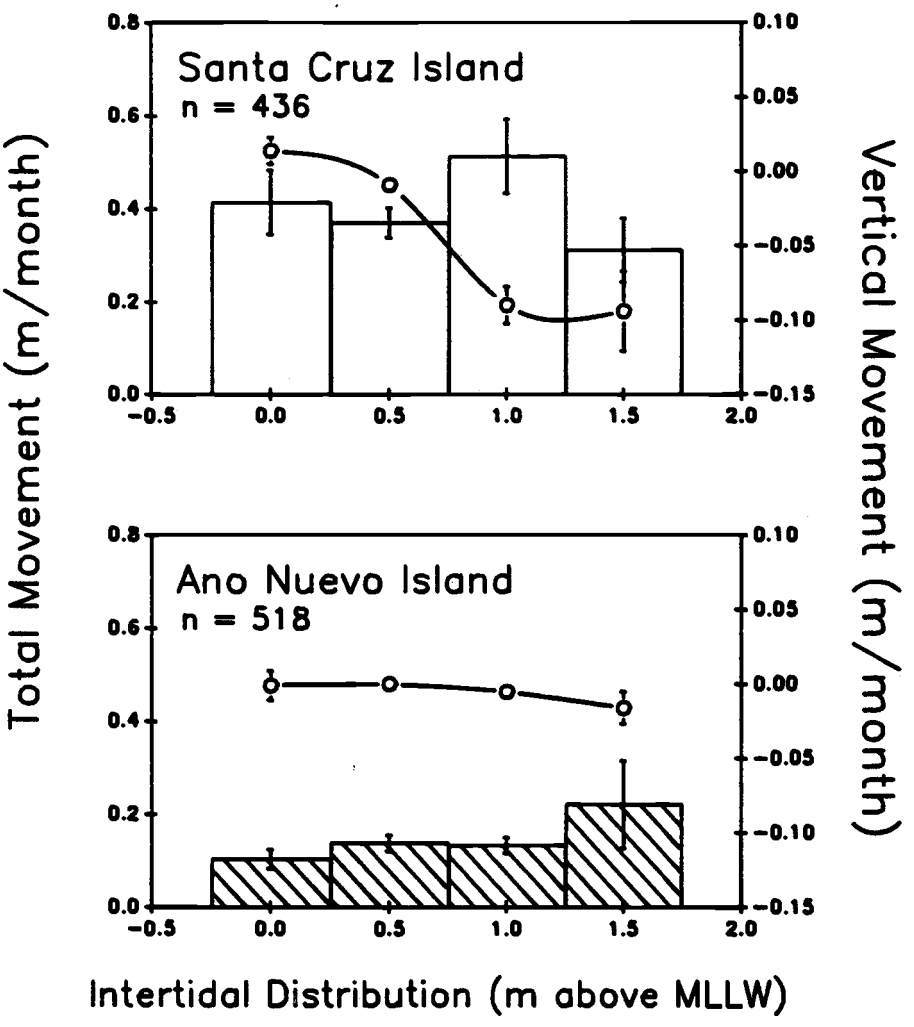

Santa Cruz Island
n = 436
Ano Nuevo Island
n = 518
Total Movement (m/month)
Vertical Movement (m/month)
Intertidal Distribution (m above MLLW)
0.8
0.6
0.4
0.2
0.0
0.10
0.05
0.00
−0.05
−0.10
−0.15
−0.5
0.0
0.5
1.0
1.5
2.0

Figure 4.3

Figure 4.4. Variation in survivorship along intertidal gradients. The recapture rate of individuals varying in the relative number of tremata (=respiratory pores) on the shell, measured by PC2 scores, is presented for four tidal-level intervals along transects at both study sites. PC scores are scaled in standard deviation units.

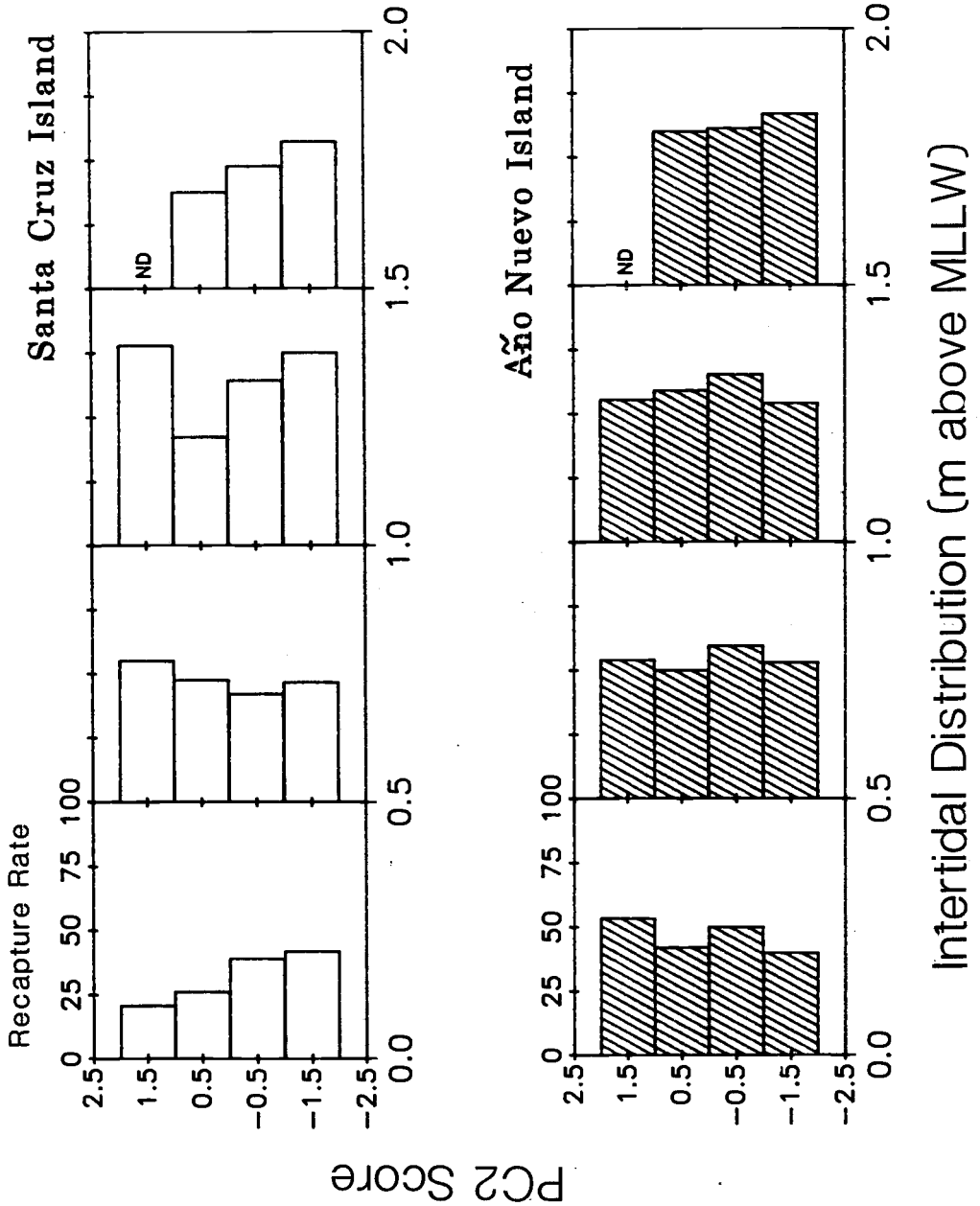

Santa Cruz Island
Año Nuevo Island
Recapture Rate
0
25
50
75
100
ND
2.5
1.5
0.5
−0.5
−1.5
−2.5
0.0
0.5
1.0
1.5
2.0
PC2 Score
Intertidal Distribution (m above MLLW)

Figure 4.4

Figure 4.5. Variation in the rate of trema expansion during growth, measured by PC3 growth rates, in relation to average maximum water velocities along exposure gradients at each site ($\pm$ 1 SE). The correlation between the two variables is not significant at $P = 0.05$.

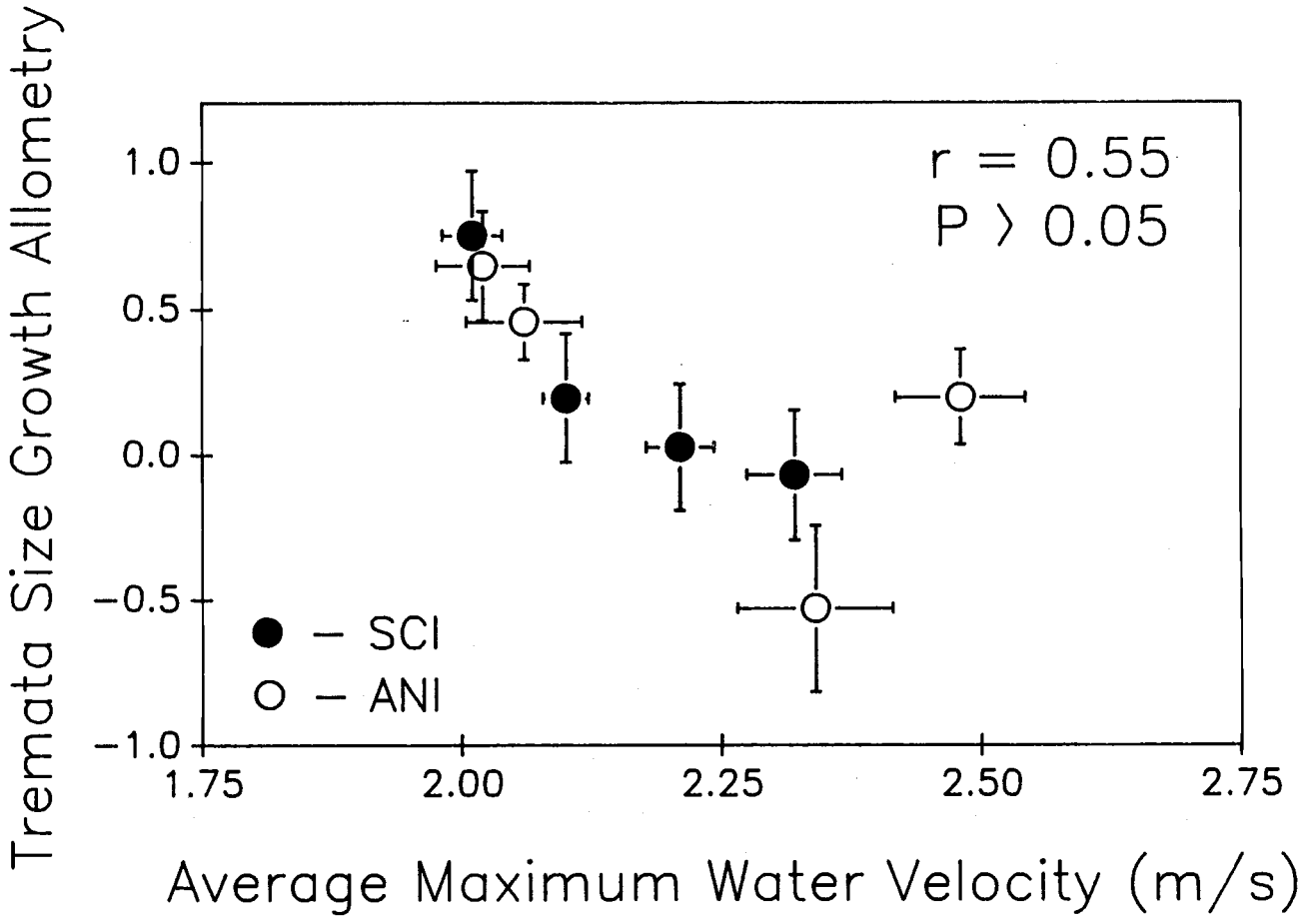

Tremata Size Growth Allometry
1.0
0.5
0.0
−0.5
−1.0
1.75
2.00
2.25
2.50
2.75
r = 0.55
P > 0.05
● – SCI
○ – ANI
Average Maximum Water Velocity (m/s)

Figure 4.5

Figure 4.6. Effects of temperature on abalone growth and morphology in samples from three populations: ANI = Año Nuevo Island, SCI = Santa Cruz Island, and SQ = San Quintin, Baja California. **A.** Differences among samples in the effects of temperature on allometric increases in size (PC1). **B.** Interactions among samples in the rate of tremata expansion (PC3). **C.** Interactions among samples in the growth allometry of trema number (PC2). See text for a description of multivariate variables.

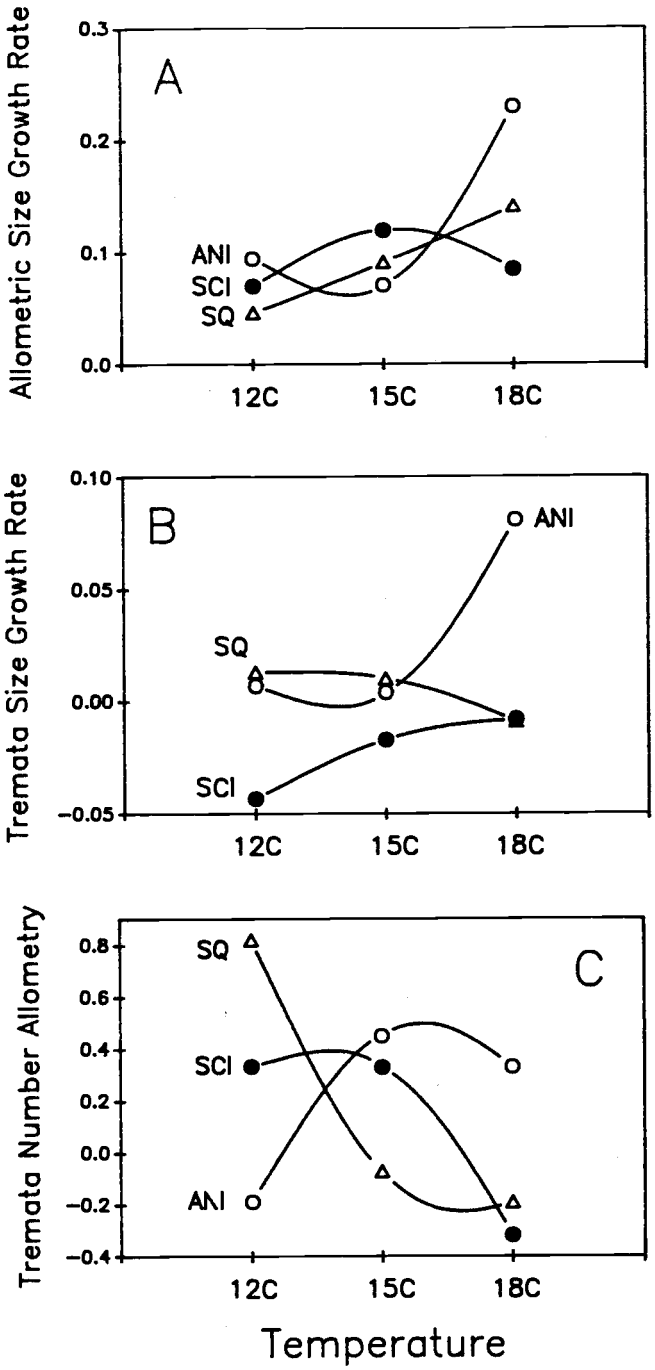

Allometric Size Growth Rate
0.3
0.2
0.1
0.0
A
ANI
SCI
SQ
12C
15C
18C
Tremata Size Growth Rate
0.10
0.05
0.00
−0.05
B
ANI
SQ
SCI
12C
15C
18C
Tremata Number Allometry
0.8
0.6
0.4
0.2
0.0
−0.2
−0.4
C
SQ
SCI
ANI
12C
15C
18C
Temperature

Figure 4.6

Figure 4.7. Desiccation rates of abalone in a wind tunnel with open and closed tremata. Linear regressions measuring the average rate of weight loss of abalone with open tremata (upper line) versus those with tremata closed with clay (lower line) are presented. Analysis of covariance indicated that the y-intercepts of the lines were significantly different ($P < 0.05$).

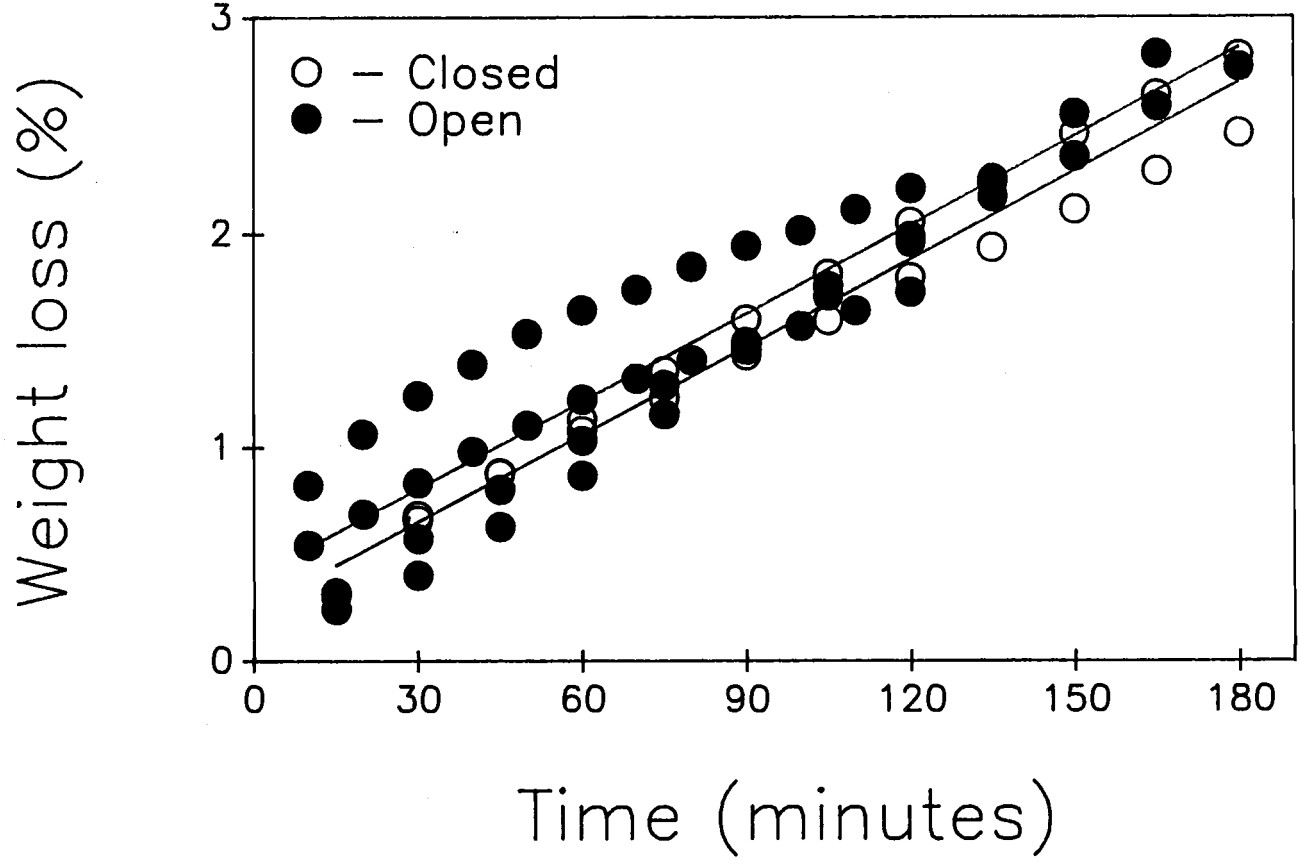

Weight loss (%)
3
2
1
0
○ – Closed
● – Open
0
30
60
90
120
150
180
Time (minutes)

Figure 4.7

Figure 4.8. Results of transplantation of abalone along intertidal transects. "L -> H" = low-to-high treatment; "H -> L" = high-to-low treatment. Each bar gives the mean and standard deviation for each treatment. **A.** Recapture rates of transplanted individuals relative to controls, which were moved horizontally. **B.** Shell growth rates of transplanted individuals relative to controls. **C.** Vertical movement patterns of transplanted individuals relative to controls.

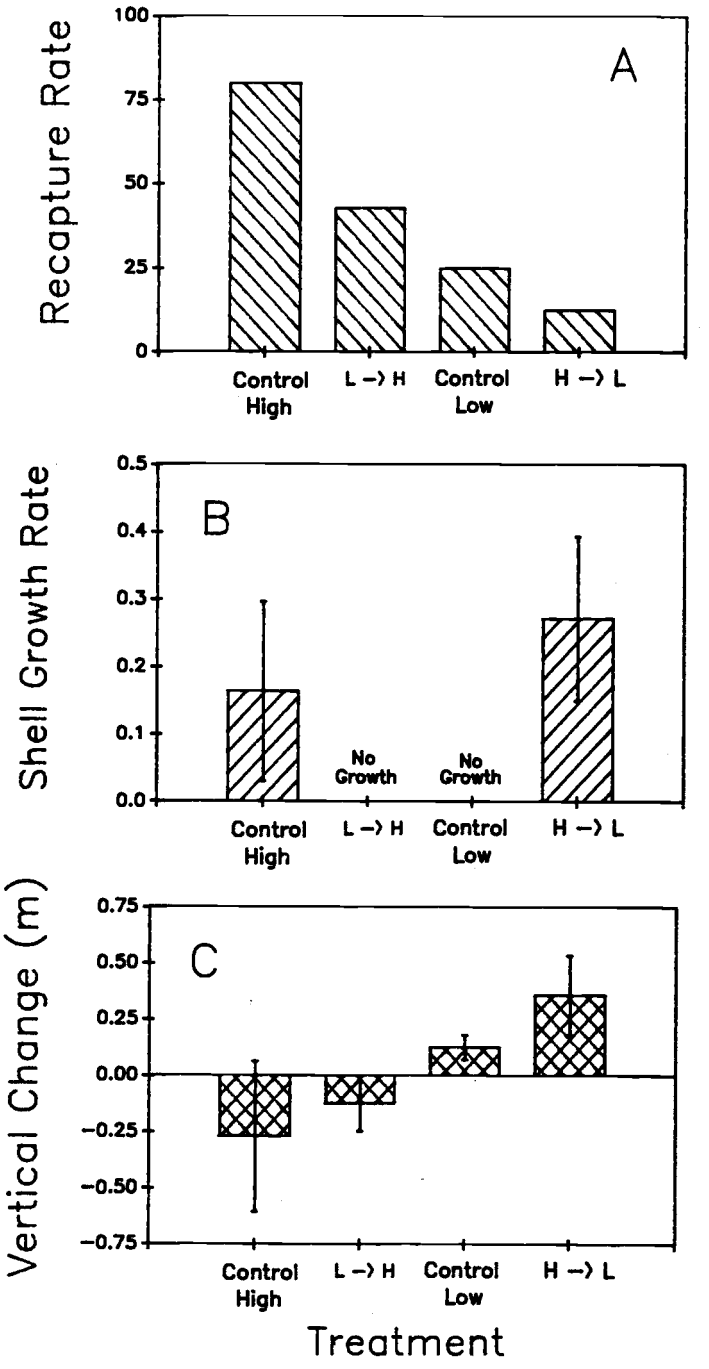

Recapture Rate
100
75
50
25
0
A
Control High
L -> H
Control Low
H -> L
Shell Growth Rate
0.5
0.4
0.3
0.2
0.1
0.0
B
No Growth
No Growth
Control High
L -> H
Control Low
H -> L
Vertical Change (m)
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
C
Control High
L -> H
Control Low
H -> L
Treatment

Figure 4.8

Figure 4.9. Effects of variation in water velocity on abalone growth and morphology. Abalone were cultured in a flow tank which created external velocities of 60 cm/s (high), 30 cm/s (medium), and 5 cm/s (low). **A.** Effects of flow regime on the rate of trema expansion in abalone from Santa Cruz Island. **B.** Interactions between samples in the effects of flow regime on allometric increases in size. ANI = Año Nuevo Island, SCI = Santa Cruz Island.

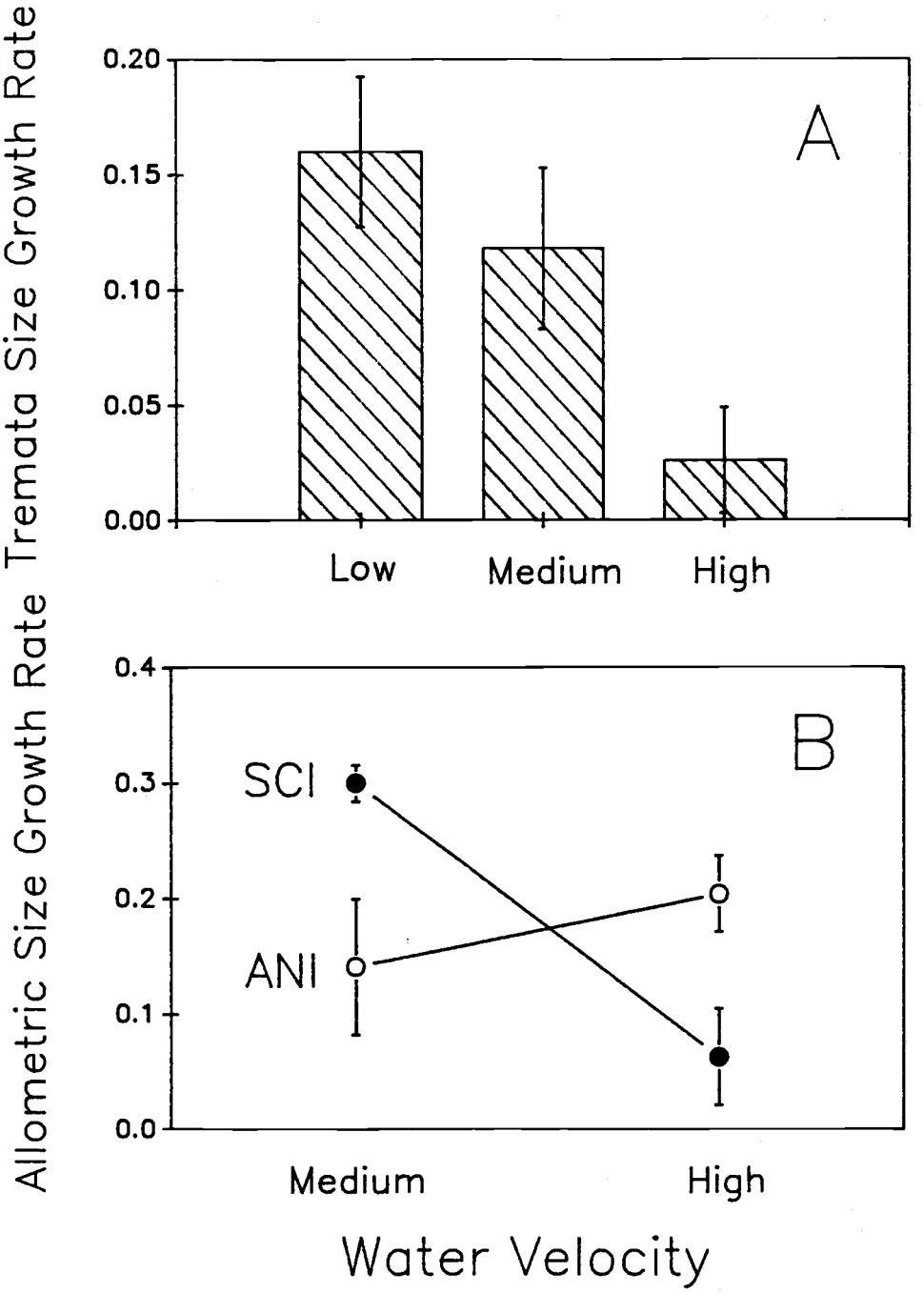

Allometric Size Growth Rate Tremata Size Growth Rate
0.20
0.15
0.10
0.05
0.00
A
Low
Medium
High
0.4
0.3
0.2
0.1
0.0
B
SCI
ANI
Medium
High
Water Velocity

Figure 4.9

CONCLUSIONS

Geographic variation in the shell morphology of black abalone was pronounced and occurred in response to a wide variety of ecological factors. In Chapter 1, the statistical methods I developed were used to quantify organismal ontogeny using ontogenetic trajectories. Variation among abalone populations in the slope of ontogenetic trajectories was evidence of marked developmental variation in tremata number. I proposed that these patterns resulted from heterochrony, or changes in the timing of developmental events, which occurred in response to latitudinal variation in intertidal habitat.

In chapter 2 I examined the availability of drift algae to abalone, which was proposed to have a strong influence on abundance, distribution, and feeding preference. I found that spatial and temporal variation in the abundance of drift algae was high and had a strong effect on abalone distribution and diet. Moreover, associations between the vertical distribution of abalone and drift algal abundance were consistent with observed latitudinal variation in intertidal habitat. Thus, it was concluded that one component of geographic variation, a vertical habitat shift, occurred in response to geographic variation in their food source. This study demonstrated the strong links that often exist between herbivores and their food sources. However, because abalone consume detached pieces of drifting macroalgae, in contrast to the majority of plant-herbivore interactions (reviewed by Lubchenco and Gaines, 1980), abalone do not exert a strong effect on the algal community.

Mass mortality of abalone on Santa Cruz Island, examined in Chapter 2, had strong effects on abalone population dynamics. This chapter demonstrated that abalone abundance, growth, behavior, and survivorship was influenced by a wide variety of factors, several unique to warm-temperate, shallow-water marine communities. Overall, I found that the environmental perturbations associated with El Nino, and their subsequent devastation of nearshore kelp forests, promoted starvation of intertidal abalone and induced a disease. However, there were several additional factors, such as elevated seawater temperatures, high abalone densities, and abundant sea urchins which may have contributed to the population decline. Because mass mortality was limited to southern California, and hence varied geographically, this chapter elucidated factors that have important effects on geographic variation in population structure and dynamics.

In chapter 4 I found that ecological factors had marked effects on ontogenetic trajectories of tremata number and size. A combination of laboratory and field studies indicated that morphological variation was not significantly associated with desiccation stress, but that variation in water movement, growth rate, and survivorship had marked effects on development and subsequent morphological patterns. Ontogenetic trajectories in tremata number varied in response to the rate of shell growth, which was largely controlled by the abundance of drift algae. I concluded that geographic variation in morphology occurred primarily in response to spatial variation in ecological factors that influenced shell growth rates. Thus, geographic variation in morphology was not a result of heterochrony, but from environmentally-induced developmental variation, or phenotypic plasticity.

Overall, this dissertation demonstrated the importance of examining developmental processes in relation to ecological factors when evaluating morphological variation. To understand morphological *pattern* we must evaluate the underlying developmental *mechanisms* in relation to their population-level ecological *causes*. Because studies of geographic variation are central to our understanding of evolutionary processes (Mayr, 1982), this dissertation exemplifies the link between ecology and the process of evolution.

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