AN ABSTRACT OF THE THESIS OF

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Title: Effects of Interactions Between Predators, Variable Predation Regimes, and Species Body Size on Rocky Intertidal Communities: Comparative and Experimental Approaches

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The body size (W) of animal species is one of the best predictors of population density (D) when large assemblages are considered. It has been shown that theoretically the D-W relationship can be the consequence of two other distributions: the log-normal distribution of body sizes of the species and of their abundances. We show in Chapter II (Navarrete and Menge) that the D-W relation is independent of other community patterns and that its expression can be under the control of ecological forces. In Chapter III I show that within assemblages of gastropods the D-W patterns are similar to those observed in entire local communities, suggesting that processes controlling the D-W expression operate at the community level, regardless of taxonomic affiliation.

In Chapter IV (Navarrete and Menge) the strength of predation on mussels by the keystone seastar *Pisaster ochraceus* and whelks of the genus *Nucella* was studied under different environmental conditions. Predation intensity by the keystone predator was strong under all site x wave exposure

combinations and was unaffected by the presence of whelks. On the other hand, whelks had ecologically important effects on mussel survival in the absence, but not in the presence of seastars. These results support the idea that in keystone-dominated systems other species have only minor, if any effects on the rest of the community. However, after the loss of the keystone these species can adopt a major role in the altered system.

In Chapter V I conducted two cage experiments to evaluate the impact of constant and temporally variable predation by different densities of whelks on a mid intertidal successional community. Direct and indirect effects of the exclusion of predators led to several changes in the abundance of sessile species, notably a rapid increase in the cover of the bay mussel *Mytilus trossulus*. Variable predation produced community compositions different from those observed under constant predation regimes or predator exclusions. Community composition in unmanipulated control plots resembled closer the composition observed under variable predation treatment. Temporal variability in predation by whelks can increase spatial variability in the sessile community and create distinctive community compositions.

Effects of Interactions Between Predators, Variable Predation Regimes, and Species Body Size on Rocky Intertidal Communities: Comparative and Experimental Approaches

by

Sergio A. Navarrete

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Typed by author for Sergio A. Navarrete

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This thesis is dediacted to my father and the loving memory of my mother

Effects of Interactions Between Predators, Variable Predation Regimes, and Species Body Size on Rocky Intertidal Communities: Comparative and Experimental Approaches

CHAPTER I

GENERAL INTRODUCTION

The profound effects of human activities on the Earth's ecological systems is now evident in all terrestrial, aquatic and oceanic environments (IGBP 1986, 1990). The possibility of rapid climate change and the reality of unprecedented rates of habitat destruction and species extinctions are now threatening the stability of most ecological systems (Watt, E. F. 1972, Ehrlich and Ehrlich 1981, Ehrlich and Wilson 1991, Lubchenco et al. 1991). In the midst of these discouraging presages, ecologists are being challenged to provide the basis for understanding and predicting the potential consequences of both natural and human-induced changes on the Earth's life support systems (Davis 1989, Lubchenco et al. 1991, 1993, Navarrete et al. 1993). Predicting the consequences of such large scale transformations is an immense task. It requires not only the identification of many human activities that can have 'invisible' effects on ecosystems for many years before they become apparent (Lubchenco et al. in prep.), but also a deep understanding of the patterns and causes of natural (non-human related) variation in these ecosystems (Lubchenco et al. 1991, Levin 1992, Navarrete et al. 1993).

Variability is probably the one feature that characterizes most natural communities. Large spatial and temporal variation in population abundance or species composition has always impressed and fueled the investigations of field ecologists (Watt, A. S. 1947, Andrewartha and Birch 1954, Hutchinson 1959). Since variability can be observed at all scales of space and time (Haury et al. 1978, Marquet et al. 1993), quantification of patterns of variation as well as identification of their causes and consequences requires the use of different approaches and techniques suited to address similar questions at different scales (Levin 1989, 1992). Correlational and comparative correlational approaches can be used over large spatial and temporal scales and are the primary tools for the detection and characterization of patterns of variation, but they are in general weak approaches in terms of determining the causes of this variation (Diamond 1986, Lubchenco and Real 1991). On the other hand, field experiments are the most powerful tool ecologists have to determine the causes of variation in natural communities, but they are usually limited in space and temporal extension (Diamond 1986, Lubchenco and Real 1991, Underwood and Petraitis 1993). The use of a 'comparative experimental approach' (Lubchenco 1986, Menge 1992) substantially expands the domain of applicability of experimental results (e.g. Berlow and Navarrete in prep.) and can help bridge the gap between the typically small-scale experimental and large-scale correlational approaches. Both approaches, the experimental and correlational are used here to address questions related to the patterns and causes of variability in community structure and population density over different scales.

The abundances or population densities of animal species inhabiting extensive geographic regions or entire continents vary over several orders of magnitude; many species are rare or uncommon while others are extremely abundant (Preston 1962, May 1988). When these large animal assemblages are considered, the mean body size of the species (W) is a good, and so far perhaps the best, predictor of the density (D = number of organisms per unit area) that species achieve in different habitats within their distribution ranges (Damuth

1981, 1987, Carrascal and Tillería 1991). The idea that species density could be predicted from an easily measurable attribute of the species such as body size sparked much interest among ecologists. Further research has shown, however, that the body size-population density relationship itself is not simple, but it depends on a number of biological and methodological factors and on the ecosystem type and taxonomic group under consideration (Morse et al. 1988, Blackburn et al. 1990, 1993a, Cotgreave 1993, and see Lawton 1989, Cotgreave 1993 for reviews). Moreover, despite the existence of strong negative correlation between body size and population density in many systems, the evolutionary and proximate causes for such a correlation are still unclear. Explanations vary from the action of ecological processes such as competition or predation acting over evolutionary time (e.g. (Damuth 1981, Peters and Wassenberg 1983), to sampling artifacts (Morse et al. 1988, Gaston et al. 1993), to the statistical consequence of way both body sizes and species abundances are distributed in most animal assemblages (Lawton 1989, Blackburn et al. 1993a, b). In Chapter II (Navarrete and Menge) we studied the relationship between body size and population density within local communities of intertidal invertebrates on the Pacific coast of Panama and addressed the question of statistical versus biological control of the expression of this relationship. Previous detailed experimental studies have shown important differences in patterns of species abundance and community organization between this tropical system and those observed in other temperate intertidal communities around the world (Menge and Lubchenco 1981, Lubchenco et al. 1984, Menge et al. 1985, 1986a, b). In general, low recruitment and strong, seasonally invariant predation pressure combine to produce a weak zonation pattern and overall low abundances of all sessile and mobile species on the shores of Panama (Menge and Lubchenco 1981, Lubchenco et al. 1984). Unlike temperate intertidal zones in which predation by fish appears to have only minor effects on prey communities (Castilla and Paine 1987, Stepien 1990), a diverse assemblage of herbivorous, carnivorous and omnivorous fishes feed throughout the intertidal zone at Panama. In this community, we determined the pattern of distribution of body sizes (the frequency of species of different body sizes) and of species population densities (the frequency of species of different population densities) to then make predictions about the relation between body size and population density. We then contrasted these patterns with those previously reported for temperate intertidal zones (Marquet et al. 1990, in press) and tested predictions about the effect of fish predators on the expression of the body size-population density relationship.

Besides the studies on rocky intertidal communities of temperate central Chile (Marquet et al. 1990, in press), tropical Panama (Chapter II) and one study on the freshwater macro-invertebrates found in tanks of Bromeliad plants (which did not distinguish among species, Cotgreave et al. 1993), all the rich literature on body size patterns (see (Cotgreave 1993) is based on a taxonomically-restricted definition of 'communities' (e.g. "bird" or "insect" communities). This taxonomic bias to the study of 'real' communities -- all organisms that coexist in a given area, regardless of taxonomic affiliation (Menge and Sutherland 1976, Begon et al. 1990) -- is pervasive in most areas of ecology, yet it can be one of the causes of the relatively modest success community ecology has enjoyed in the past few decades (Drake 1990, Oksanen 1991). How dependent are the patterns and explanations of the body size-population density relation on whether a taxonomically-restricted animal assemblage or a 'real' community is examined has not been addressed. In Chapter III I present the relation between body size and density within local "communities" of intertidal gastropods -- a taxonomically restricted animal assemblage -- from two tropical and two temperate regions. I then compared these patterns with those found for the entire communities (all coexisting animal species) and explored the effect of taxonomic affiliation on the relationship.

Large variability is not only observed at large scales and large animal assemblages, but also at local scales among sets of coexisting species within communities. At these scales, experimental determination of causes of variation is not only possible but necessary if community ecology is going to become a predictive science (Dayton 1973, Lubchenco et al. 1993, Berlow and Navarrete in prep., but see Peters 1991). In many ecosystems predation plays an important role in the maintenance and variation of community structure, however, demonstration of predation effects has usually been limited to the removal of a single species or of all predator species together (see references in Sih et al. 1985, Menge and Farrell 1989). This makes it difficult or sometimes impossible (e.g. Elner and Vadas 1990) to determine the pattern of predation and to quantify the relative importance of different predator species on the community (see Bond 1993, Robles and Robb 1993, for a similar argument). With these limitations, the experimental evidence gathered so far suggest that both 'keystone' (one or few strong and numerous weak interactions) and 'diffuse' (a number of equally weak interactions) kinds of predation patterns occur in natural systems (e.g. Paine 1966, 1992, Dayton 1971, Lubchenco 1978, Peterson 1979, Morin 1981, Hixon and Brostoff 1983, Quammen 1984, Castilla and Durán 1985, Menge et al. 1986a, Robles 1987, Brown and Heske 1990, Posey and Hines 1991, Heske et al. 1993, Robles and Robb 1993, reviewed by Menge et al. 1994). The relative importance of a keystone and weak predators in natural communities have rarely been quantified, however (but see Fauth and Resetarits 1991). With few exceptions we know little about the pattern of interactions between a keystone and a weak predator, about the effects of this interaction for lower trophic levels (indirect effects on prey), and about the relative dependency of strong (keystone) and weak interactions on environmental conditions and on the presence of other species in the system. In Chapter IV (Navarrete and Menge) we studied the interactive effects of predators on prey communities in a well studied system , the rocky intertidal zone of the Northwest coast of USA. There, the first keystone species ever identified, the seastar *Pisaster ochraceus* (Paine 1966, 1969) overlaps in distribution and diet with a number of other vertebrate and invertebrate predators (Castilla and Paine 1987). In this system we asked the questions: Is the effect of a keystone affected by the presence of other predator species (see also Fauth and Resetarits 1991)? Is the effect of other species dependent on the presence of a keystone? Is the effect of non-keystone species (weak interactors) more variable across environmental gradients than that of the keystone (strong interactor)? And is the *per capita* effect of a keystone species less variable across environmental gradients than that of a non-keystone? Our experiments showed that predation intensity by the keystone predator was strong under all site x wave exposure combinations and was unaffected by the presence of whelks. On the other hand, whelks had ecologically important effects on the survival of mussels in the absence, but not in the presence of the keystone. We suggest that this pattern of interactive effects between keystone and weak predators may be general to all keystone predator-dominated systems, but currently there are limited data to test this proposition. The total (population) interaction strength between seastars and mussels was stronger and less variable across sites and wave exposures than that of whelks and the *per capita* interaction strength of seastars was two orders of magnitude larger than that of whelks. However, *per capita* effects of seastars were much more variable between sites and wave exposures, probably because simple density values grossly underestimate the ability of keystone predators to localize prey. In general, our results support the idea that in keystone-dominated systems, species other than the keystone have only minor, if any effects on the rest of the community and may be an example of 'redundant species'. However, they also suggest that after the loss of the keystone species previously 'redundant' species can compensate for the reduced predation and adopt a major role in the altered system. Such responses are potentially and important force in stabilizing communities.

Much empirical information on the effects of predators has accumulated since the pioneering field studies of Paine (1966) and Connell (1961) and the vast majority comes from an insightful albeit simple approach, the short- or long-term deletion of predators from a system and monitoring of prey responses to this perturbation (see Sih et al. 1985, Hixon 1986, 1991, Kerfoot and Sih 1987, Menge et al. 1994 for reviews). Nevertheless, predation as other disturbance agents is not invariable but it usually fluctuates widely over time. With the notable exception of Butler's (1989) study on the effects of sunfish predation in lakes, few studies have experimentally evaluated the consequences of temporally variable predation on prey species composition and variation (Fairweather 1988, Butler 1989). The effects of temporally variable predation by the whelks *Nucella emarginata* on a successional mid intertidal community were experimentally investigated in Chapter V. The experimental design allowed me to distinguish between the effects of frequency and intensity of predation and test the hypotheses that 1) temporally persistent exclusion of whelks lead to changes in prey abundance and prey composition, 2) variable predation creates prey communities different to those resulting from a constant predation regime, 3) variable predation contributes to the temporal and spatial variability in prey populations, 4) variable predation increases local species richness and diversity, 5) variable predation creates communities that resemble more closely the natural predation regimes than the constant predation treatments. The results test these propositions and shed light into the importance of temporally variable predation in natural ecosystems. In summary, the permanent exclusion of whelks had direct and indirect effects on the sessile community, notably a rapid increase in the cover of the bay mussel *Mytilus trossulus* and a slow and small increase in the cover of gooseneck barnacles and the California mussel *Mytilus californianus*. Variable predation produced community composition different from those observed under a constant predation regime or predator exclusions. Community composition in the unmanipulated control plots resembled closer the composition observed under the low and medium frequency treatment (variable predation) and least that one observed under a constant predation regime, regardless of the intensity. Temporal variability in predation by whelks can increase spatial variability in the sessile community and create distinctive community compositions, even though the overall effects of whelks in this successional communities are rather mild. Variability in predation in probably an important, yet poorly understood cause of spatial heterogeneity in most ecosystems.

CHAPTER II

PREDATORS SUPPRESS THE BODY SIZE-POPULATION DENSITY RELATIONSHIP IN TROPICAL ROCKY INTERTIDAL COMMUNITIES

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Abstract

Body size is the best predictor of animal population density when large assemblages of species occurring over regional or continental scales are considered (Damuth 1981, 1987, Peters 1983). Within local communities of interacting organisms the relationship varies from weakly negative or absent in some terrestrial and freshwater systems (Tokeshi 1990, Cotgreave and Harvey 1992, Cotgreave et al. 1993), to strongly negative in temperate rocky intertidal communities (Marquet et al. 1990). Postulated explanations for the relationship include ecological-evolutionary mechanisms (Peters 1983, Damuth 1987, Gaston and Lawton 1988), sampling artifacts when data are compiled from the literature (Morse et al. 1988, Cotgreave 1993), and the unessential consequence of two other general distribution patterns: the log-normal distribution of body sizes of the species and of their population abundances (Blackburn et al. 1990, 1993b). We show here that tropical intertidal communities exhibit log-normal distributions of body sizes and of species abundance, but unlike their temperate counterparts, there is no correlation between population density and body size.

The inverse relationship between these variables did appear when a diverse guild of subtidal fish predators was experimentally excluded. These results demonstrate that in intertidal communities the body size-population density scaling is independent of other community patterns and suggest that its expression can be under the control of ecological forces.

Introduction

On the temperate rocky coast of Chile, density of intertidal invertebrates in local communities was tightly and negatively correlated with body size (Marquet et al. 1990). Moreover, the slope of the relationship when both variables are measured in logarithms was not affected by differences in predation pressure exerted by benthic intertidal predators, as revealed by large-scale exclusions from marine preserves of humans, who remove benthic predators (Marquet et al. 1990). To test the significance of the body size-population density relationship over similar local scales in an intertidal ecosystem assembled by the same major taxa but different species and structured by different ecological processes, we studied the tropical rocky intertidal communities on the Pacific coast of Panama. Community structure and regulation on these shores are strikingly different from those on temperate shores. Panamanian and Chilean communities share some genera and most families and higher order taxa, but no species. Intertidal 'zonation', typical of high latitude communities around the world (Stephenson and Stephenson 1972), is less evident in Panama. Local population abundance of the many invertebrates and the few erect algae are far lower than those of comparable species in temperate zones (Menge and Lubchenco 1981, Lubchenco et al. 1984).

Overall, the seascape is dominated by bare rock, coralline and fleshy crustose algae with sparse sessile invertebrate populations and a species-rich assemblage of mobile invertebrates. These patterns are persistent over time and exhibit almost no seasonal variation (Menge and Lubchenco 1981, Lubchenco et al. 1984). Field experiments have demonstrated that the general scarcity of intertidal species results from a combination of low recruitment and intense, seasonally and spatially constant predation (Menge et al. 1985, 1986, Menge 1991). Unlike temperate zones, where fish predation is relatively less important (Castilla and Paine 1987), diverse and highly mobile subtidal fishes are a dominant component of the severe predation regime in Panama.

Methods

To determine the body size-population density relationship, we directly quantified population densities and body masses of all macroscopic invertebrate species found in the entire rocky intertidal zone at sites on Taboguilla Island, on the Pacific coast of Panama. The field methods used to estimate densities and body masses were identical to those used previously in temperate zones, allowing for straight comparisons.

Results and Discussion

The distribution of body sizes - the number of species belonging to different body size classes measured in logarithmic scale - of Panamanian invertebrate species was log-normal (Fig. 1a). A log-normal distribution of body sizes was also observed in temperate intertidal communities (Marquet et al. in

Figure II.1. a) Distribution of body sizes of rocky intertidal invertebrates found in the entire rocky intertidal zone at sites on Taboguilla Island, on the Pacific coast of Panama, b) distribution of population abundances of the same species (X-axis in octaves to facilitate comparison with literature), c) regression of log population density (D) on log body size (W). The regression equation using ordinary least squares to facilitate comparison with published values is: $\log(D)= 0.29\ (\ 0.12) - 0.11(\ 0.12) \log(W)$, n= 56. The species used for the general regression belong to 6 Phyla and 12 major Orders. Densities of all species were estimated along 30-50 m transects parallel to the coastline in the high, mid, low and very low intertidal zones of four rocky reefs in Taboguilla Island, Bay of Panama in January, February, March and July 1977, January 1978, February and March 1979 and March 1980. Direct counts of invertebrates were taken in 10 to 15 permanently marked 0.25 m^2 quadrats randomly located along each transect. Rare species were counted on 1 m^2 quadrats or by searches on the entire reefs. Mean length was determined in samples of 10 to >200 individuals of each species found in the quadrats. Body mass was estimated from regressions of length versus wet weight for each species. When a regression for a species was not available we used the closest relative for which we had that information. The field methods used to estimate densities and body masses were identical to those used previously in temperate zones, allowing for comparisons uncomplicated by differences in methods. Data were treated as in previous studies.

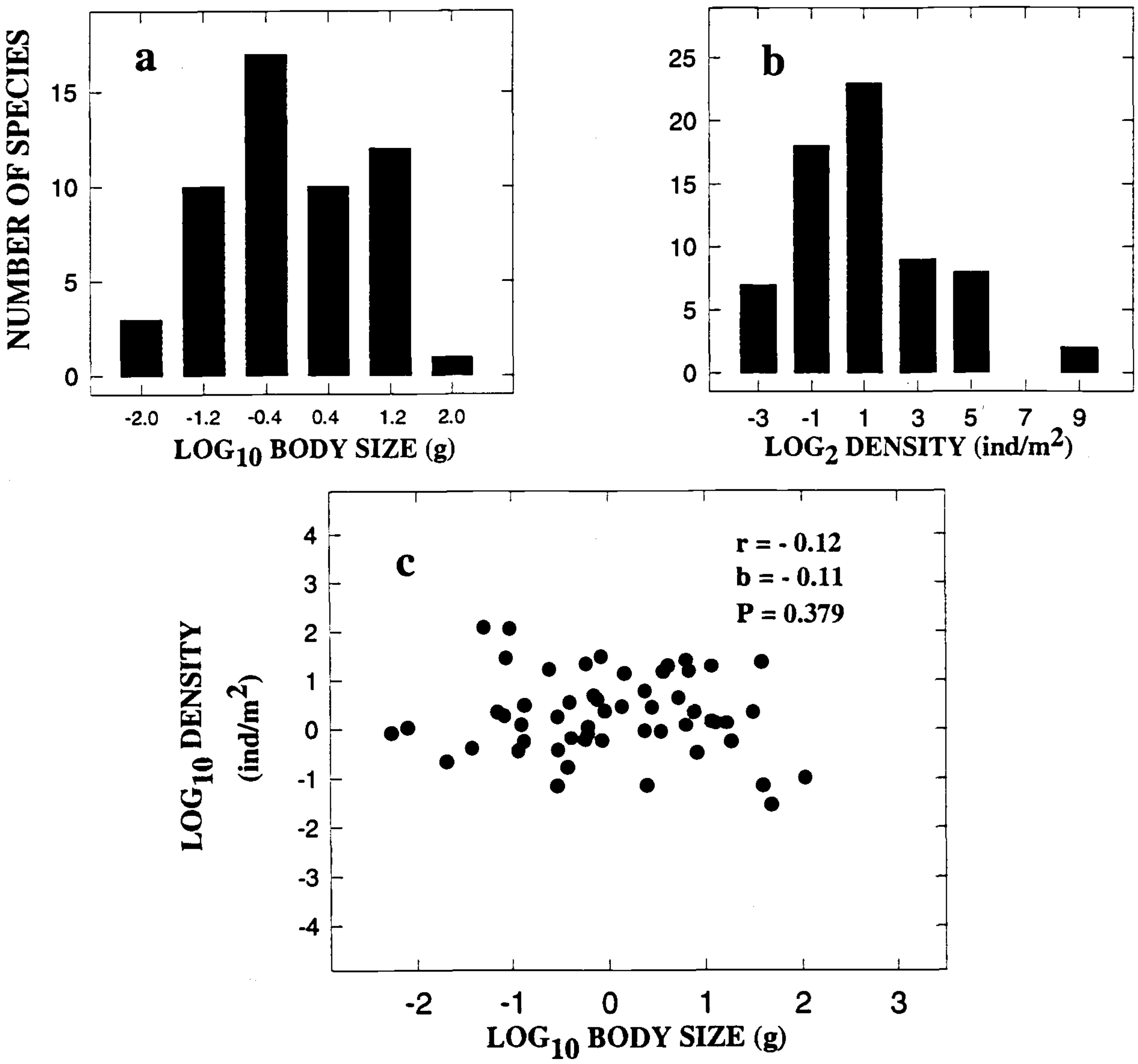

a
NUMBER OF SPECIES
0
5
10
15
-2.0
-1.2
-0.4
0.4
1.2
2.0
LOG10 BODY SIZE (g)
b
0
5
10
15
20
25
-3
-1
1
3
5
7
9
LOG2 DENSITY (ind/m2)
c
r = - 0.12
b = - 0.11
P = 0.379
LOG10 DENSITY (ind/m2)
4
3
2
1
0
-1
-2
-3
-4
-2
-1
0
1
2
3
LOG10 BODY SIZE (g)

Figure II.1.

press) and the pattern characterizes most taxa ranging from bacteria to mammals (May 1988, Brown and Nicoletto 1991, Brown et al. 1993). Similarly, a log-normal frequency distribution of the abundance of species - the number of species belonging to different abundance classes measured in a logarithmic scale - was also observed in the tropical invertebrates of Panama (Fig 1b). This latter pattern (also called species abundance curve) is commonly found in assemblages of animal taxa (Preston 1962, Sugihara 1980), but it is not universal (Morse et al. 1988, Lawton 1993). It has been demonstrated that these two independent and general distribution patterns are sufficient to produce a negative relationship between body size and population density (Blackburn et al. 1990, 1993b, Lawton 1990). In fact, knowledge of the distribution of body sizes and of species abundances within a particular assemblage allows to theoretically predict the slope of the log body size- log population density relationship (Blackburn et al. 1993b). Since several explanations exist for the former two patterns (Sugihara 1980, Brown et al. 1993, Lawton 1993), specific ecological or evolutionary explanations for the latter are not essential (Blackburn et al. 1993b). However, in Panamanian communities, despite log-normal distributions of body size and population densities, the slope of the log body size- log density relationship was not significantly different from 0 (Fig. 1c). Considering the very high correlation (r= -0.73) observed in temperate intertidal communities with the same major taxa, the lack of correlation between body size and density is particularly striking and deserves explanation.

We hypothesized that the failure of body size to explain variation in population density among Panama species is a consequence of the strong and constant predation, exerted by the herbivorous, omnivorous, and carnivorous subtidal fish that feed throughout the intertidal zone (Menge et al. 1986). Unlike temperate systems in which recruitment of most benthic species is high and predation is mostly exerted by one or a few dominant benthic predators (Menge et al. 1994), in Panama, the coupling of low recruitment of benthic species and a highly diversified subtidal fish assemblage can control the abundance of all or most intertidal invertebrates. Assuming that fishes as a group feed selectively on the more abundant intertidal species, with no restrictions on prey morphology, size, or mobility, then exclusion of fish should produce an increase in the density of species as predicted by the allometric body size relationship.

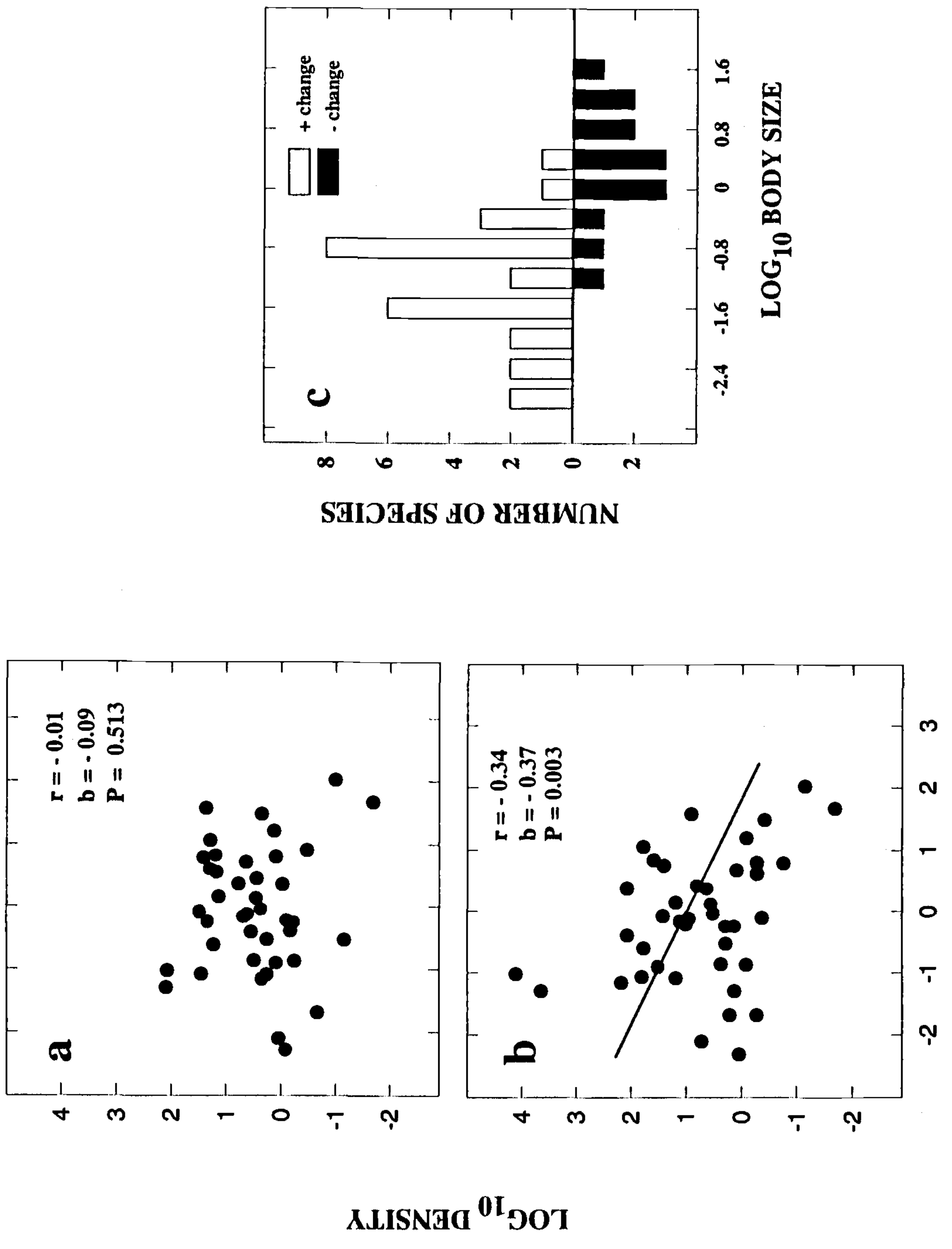
Exclusion of fishes led to the development of a significant inverse body size- population density relationship (Fig. 2). Densities of species in the experimental areas before manipulation are not different from a subset of those presented in Fig. 1 for the entire intertidal zone. In barrier-free controls (+fish) body size did not explain variation in population density (Fig 2a), a pattern which persisted throughout the study (Menge et al. 1986). In fish exclosures, however, the slope of the body size-population density regression changed. Before manipulation, the slope was not significantly different from zero ($b = -0.09$; $p = 0.51$) while two years after manipulation was begun, the slope was significantly less than zero ($b = -0.37$; $p < 0.05$)(Fig. 2b). A similar response was observed for the upper boundary slope (Blackburn et al. 1992, 1993a, Marquet et al. in press). Most intermediate and small sized species increased in density in the absence of fish (Fig. 2c). These results represent the first experimental evidence that the body size-population density relationship can be influenced by ecological processes.

The suppression of the body size-population density pattern under normal, non-experimental conditions by subtidal fish may be a consequence of the relative independence of fishes from the intertidal prey as an energetic source. Benthic intertidal predators are usually restricted in the range of prey species they can consume at sufficiently high rates to control their abundances and they also depend energetically on the intertidal prey they consume. Consequently, benthic intertidal predators are probably subjected to the same general ecological and evolutionary processes affecting the rest of the species in the community. In contrast, all the fish species observed preying in the intertidal in Panama are also active foragers in the nearby subtidal areas (Menge et al. 1985, 1986), where they spend most of their time and likely get most of their energy. While fish have strong effects on the intertidal zone, their occurrence in both subtidal and intertidal habitats uncouples them from strict dependence on intertidal food sources, and as a group they are probably little affected by variation in intertidal prey populations. The horizontal, longshore distribution ranges of many intertidal species in Panama encompasses areas where fish predation is lower or non-existent (Ortega 1986, Sutherland 1990), which together with the high dispersal abilities of most marine invertebrates might prevent community-wide evolutionary responses to fish predation. We predict that in tropical or subtropical intertidal zones that share a large portion of the species included in Fig. 1c, but where fish predators are absent, body size will be correlated with population density as strongly as in temperate communities.

The data presented here do not support a particular ecological-evolutionary explanation for the body size-population density pattern, but suggest that this general relationship is not just a consequence of the way body sizes and species abundances are distributed in natural animal assemblages and that its expression, although not necessarily its shape, can be under the control of ecological processes.

Figure II.2. Regression of body size on population density for invertebrate species found in fish exclusion cages a) before and b) after 19 mo of fish exclusion. The statistics for the regression of log density on log body size after fish exclusions are: intercept = 0.702 (0.172), slope = -0.366 (0.164), r = -0.336, p= 0.032. The densities of species in the experimental areas before manipulation (a) are not different from a subset of those presented in figure 1 for the entire intertidal zone. The upper boundary slopes[20,29] of the body size-population density distribution for organisms larger than 0.1 g before and after fish exclusions are: -0.55 ($p = 0.162$, $r^2 = 0.35$, n=7) and -0.99 ($p = 0.043$, $r^2 = 0.59$, n=7), respectively. Panel c shows the number of species by body size whose density either increased (open bars) or decreased (closed bars) as a result of fish exclusions. The distributions of positive changes as well as the number of positive and negative changes were significantly different form the control plots (X^2 tests $p< 0.0001$, 11 df; $p= 0.016$, 1 df, respectively). The same species are presented in all panels (n = 41). Fish exclusions were conducted by installing twenty-four large stainless steel mesh exclosures (0.5 x 0.5 x 0.05 m) in the high, mid, low, and very low intertidal zones of the study sites in Panama for 2 years. These barriers excluded fish from experimental areas while allowing access to most benthic predators. Densities of the crabs *Eriphides hispida* and *Eriphia squamata*, large and rare predators that were not manipulated and did not seem to be affected by the fish exclusions, were assumed to remain unchanged during the experiments. Prey abundance and size under the barriers was quantified before, during, and after predator manipulation.

Figure II.2.


a
r = - 0.01
b = - 0.09
P = 0.513
b
r = - 0.34
b = - 0.37
P = 0.003
LOG$_{10}$ DENSITY
4
3
2
1
0
-1
-2
-2
-1
0
1
2
3
LOG$_{10}$ BODY SIZE
c
+ change
- change
NUMBER OF SPECIES
8
6
4
2
0
2
-2.4
-1.6
-0.8
0
0.8
1.6
LOG$_{10}$ BODY SIZE

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CHAPTER III

BODY SIZE AND POPULATION DENSITY IN ROCKY INTERTIDAL GASTROPODS OF THE TEMPERATE AND TROPICAL PACIFIC

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Abstract

A common pattern in natural communities is a negative relationship among species between body size (W) and population density (D). This relationship has been studied at different spatial and taxonomic levels and using different methodologies, so that it is difficult the determine the causes of variability in the relationship as well as to make comparisons across different ecosystems and across different groups of animals. Within local assemblages of intertidal gastropods, mean population density was not correlated with body size in two tropical regions (Panama and Costa Rica) and in the temperate zone of San Juan Island, Washington, but it was significantly and negatively correlated with body size in the temperate coast of central Chile. The degree of taxonomic affiliation within Gastropoda, a correlate of phylogenetic relatedness, did not have effect on the DW relationship. The patterns observed within orders and families did not differ from those expected from a random sample taken from the next higher taxonomic level. Similarly, the patterns observed in

two of the four regions studied here correspond well with previous community-wide studies which included all intertidal organisms, regardless of taxonomic affiliation. These results suggest that among these organisms the ecological units subjected to the evolutionary processes determining the DW relationship are, to some extent, independent of phylogenetic relatedness.

Introduction

One striking feature of natural communities is the large variability in population density observed among species within a community or taxonomic assemblage and within the same species across space and time. Consequently, much ecological research and modeling efforts have been dedicated to understanding the processes and mechanisms determining or regulating population densities (Andrewartha and Birch 1954, Begon et al. 1990). A complementary approach has been the search for an easily measurable attribute of a species which can predict the density of that species under natural conditions, although such a relationship need not imply causality (Peters 1983). In recent years, the body size of species (W) has been identified as a good, and so far perhaps the best, predictor of species density (D) (Damuth 1981, 1987, Carrascal and Tillería 1991). Further research has shown, however, that the body size-population density relationship (DW) itself is not simple, but it depends on a number of biological and methodological factors and on the ecosystem type and taxonomic group under consideration (Morse et al. 1988, Blackburn et al. 1990, 1993a, Cotgreave 1993, and see Lawton 1989, Cotgreave 1993 for reviews). In general, when large taxonomic assemblages (e.g. mammals) are considered over large spatial scales (e.g. continents) ecological density decreases with body size to a power between -0.66 to -1.0. (e.g. (Damuth 1981, 1987, Brown and Maurer 1986, but see Juanes 1986, Morse et al. 1988, Cotgreave and Harvey 1992). The significance of the power relating body and density is controversial. Some argue that the true slope should be centered around -0.75, reflecting the operation of an 'energetic equivalence rule' that keeps the total energy used by different species independent of body size (Damuth 1981, 1987, 1991, Carrascal and Tillería 1991). However, the empirical and theoretical basis of such a rule have been strongly criticized (Lawton 1989, Blackburn et al. 1993a, b, Marquet et al. in press). Other explanations have been proposed, but by large remain untested (see Blackburn et al. 1993b, Cotgreave 1993 for review).

Recently Nee et al. (1991) suggested that phylogenetic relatedness can constraint and determine the actual power relation between ecological density and body size. They examined the DW relation within phylogenetically related bird species in Great Britain and Sweden and found significantly more positive correlations within these groups than expected from random samples of all bird species (Nee et al. 1991). When all bird species were considered together, density declined with body size to the -0.75 power. Nee et al. (1991) reasoned that phylogenetically related tribes of birds with no close relatives were more likely to constitute entire guilds of interacting species and that a positive correlation should characterize guilds of birds (see also Damuth 1991). However, these provocative results are based on analyses of entire biotas at geographical scales over which it is difficult to visualize a tight association between species and their resources (see also Tillería and Carrascal 1994). Before generalizations about the effect of phylogeny on the DW relation are possible, Nee at al.'s (1991) results must be corroborated by analysis at local scale within local communities (see Tillería and Carrascal 1991).

Here I study the effect of phylogenetic relatedness (using taxonomic affiliation as a correlate) on the DW relationship within local assemblages of tropical and temperate intertidal gastropods, separating the geographic patterns from the patterns observed among those species inhabiting the same local community. I emphasize the difference between a true community, defined as all the organisms that inhabit a given area (Menge and Sutherland 1976, Begon et al. 1990), from the taxonomically-restricted definition used by most authors ("bird" or "insect" communities), probably due to logistic limitations and biases. Indeed, taking subsets of species arbitrarily defined by taxonomic affiliation can substantially affect the interpretation and explanation given to any ecological pattern (Drake 1990, Marquet et al. 1990, Oksanen 1991), since it is precisely at the community level that the effects of biological interactions can be maximally realized. Among the few "real" communities (broadly defined) from which the DW relationship is known are the temperate rocky intertidal communities of central Chile and Panama (Marquet et al. 1990, in press, Navarrete and Menge in prep.). The existence of these previous studies allowed me to compare the patterns found in two assemblages of gastropods with those observed in the entire community, regardless of taxonomic affiliation. If the processes determining the DW relationship are distinctive and characteristic of specific taxonomic groups one would expect differences between the patterns within gastropods and entire communities.

Methods

Data Collection

Data on density and size (usually shell length) were obtained both from the literature and *de novo* (Appendix 1). In all cases the sampling involved quadrats along transects laid down on rocky substratum at different tidal heights. Size of the quadrat varied between 0.01 and 2 m^2, depending on the sizes and abundances of the organisms being sampled. Densities thus correspond to the "ecological density" of species in the habitat they actually occupy (Damuth 1987, Carrascal and Tillería 1991). Details of the field methods can be found in the original sources. When provided, the modal or the mean size was used. If only a range was given, the median point was calculated. Wet weights were obtained from length data by using regressions published for the species at the site of collection or my own regressions for the same or a closely similar species in the same site or elsewhere.

Four regions were considered: Costa Rica and Panama in the tropical Pacific, San Juan Islands in the temperate north Pacific, and central Chile in the temperate south Pacific. In each, extensive samples of all intertidal gastropod species were taken, including density and a measure of body size. Two of these sites, Chile and Panama, have previously been studied to determine the relationship between body size and population density in the entire community, across taxonomic affiliation (Marquet et al. 1990, Navarrete and Menge in review).

Data Analysis

I used ordinary least squares regressions (OLS) to determine the relationship between the mean population density and body size (Sokal and

Rohlf 1981). Griffiths (1992) and others have argued that a type II regression model (e.g. reduced major axis, RMA) is more appropriate for these kind of data because the OLS's assumption of no error variance associated with the independent variable (body size) is violated . However, OLS still provides a faithful representation of the functional relation between the two variables when the variance associated to population density estimates is many times larger than that associated with body size (see McArdle 1988, Damuth 1993, and references therein); certainly, this is the case with the gastropod data.

In order to characterize the shape of the DW relationship and determine whether maximum densities (i.e. densities of those species that form the 'upper bound' of the DW distribution) are correlated with body size (Blackburn et al. 1993a, Marquet et al. in press), I selectively sub-sampled species with the highest density along intervals of the body size-axis using the method proposed by (Blackburn et al. 1992). Both linear and second order polynomial least square regressions were fit to the new data sets obtained using a body size interval of 0.4 logarithmic units, which has provided good estimates of the upper boundary DW slope with similar kinds of data (Marquet et al., in press).

Whenever phylogenetic comparisons are made and two or more attributes of the species are correlated across taxonomic units, problems of statistical independence arise (Felsenstein 1985). There are no simple solutions to this problem. The best approximation is the construction of independent contrasts assuming a Brownian-like evolution of species attributes (Felsenstein, 1985). Construction of these contrasts requires a fairly detailed evolutionary model of actual phylogenetic distances among the species (e.g. (Cotgreave and Harvey 1992, Tillería and Carrascal 1994). In the absence of such a model for the group of species analyzed here, I determined the magnitude of variance components within different taxonomic groups using a nested analysis of variance (Harvey and Mace 1982) and the MIVQUE0 maximum likelihood method in SAS statistical software (SAS Institute Inc. 1989). The taxon with a disproportionately large share of the total variance can then be used as the unit of analysis (Harvey and Mace 1982). For taxonomic categories at the family and order levels I followed (Keen 1971). To determine if the DW relationship within orders and families of gastropods differed from that for the total species pool I selected 1000 random bootstrapped samples of the same number of species from the taxon immediately above (order for family or all gastropods for orders). In each of these samples I regressed population density over body size and then estimated the 95th percentile of the distribution of regression parameters from the 1000 samples, which correspond to the 95% confidence interval for that parameter (Dixon 1993).

Results

Family, genus and species, contributed approximately the same to the total variance in population density observed among gastropod species, while for body size, progressively higher taxa accounted for progressively less variance in body size (Table 1). The taxon Order contributed little or nothing to the total variance. This latter pattern suggest that the species level is a relative independent sampling unit for analyses of body size patterns. The pattern of relatively uniform contributions by several taxonomic levels to the total variance of population density implies that taxa above the species level make important (though not significant at =0.05) contributions to the total variance in species attributes, the use of species as the unit of analysis in comparative studies probably tends to over-estimate the real number of degrees of freedom (see Felsenstein 1985)). However, without one taxon capturing disproportionately more variance and without detailed knowledge of the phylogenetic relations among the species, I conducted my analyses assuming species as independent samples. Results presented here should thus be regarded with caution.

Body size was significantly and negatively correlated with population density when all gastropod species from all regions were pooled (Fig. 1). However, body size explained only 7 % of the total variance in population density, and the slope of the log-log relationship between these variables was significantly higher (-0.29) than the -0.75 value observed for other animal taxa (t-student test, $P < 0.0001$). The upper boundary slope of the DW distribution presented in figure 1 was steeper (-0.63, Table 2) than the slope for all data and did not differ significantly from -0.75 ($P > 0.05$).

Table III.1. Components of variance (percentage of total variance) within taxa of intertidal gastropods. Pooled data from all regions (see text for details).

SOURCE	log Body Size %	log Population Density %
Order	0.0	4.4
Family	15.2	35.2
Genus	38.3	22.5
Species	46.5	37.9

The DW relationship for gastropods was however distinctly different between temperate and tropical gastropods (Table 2). When only tropical gastropods from local communities in Panama and Costa Rica were considered, no significant relationship between body size and population density was observed (Table 2). Densities of tropical species in the upper boundary of the distribution (maximum densities) were also uncorrelated with body size (Table 3). On the contrary, body size alone explained a significant portion of the variance (32%) in the population density of temperate gastropods. Both mean density as well as maximum density slopes for temperate species did not differ significantly from -0.75 (Tables 1 and 2). The higher order terms of the polynomial regression on the DW upper boundary were not significant but negative, suggesting that this upper boundary is convex in shape.

Table III. 2. Parameters of ordinary least squares regressions of the logarithm of mean population density (ind./m^2) over the logarithm of body size (g) for intertidal gastropods. a: intercept; b: slope; r^2: variance explained by body size; P: probability of F-test for the hypothesis of b= 0; n: number of species.

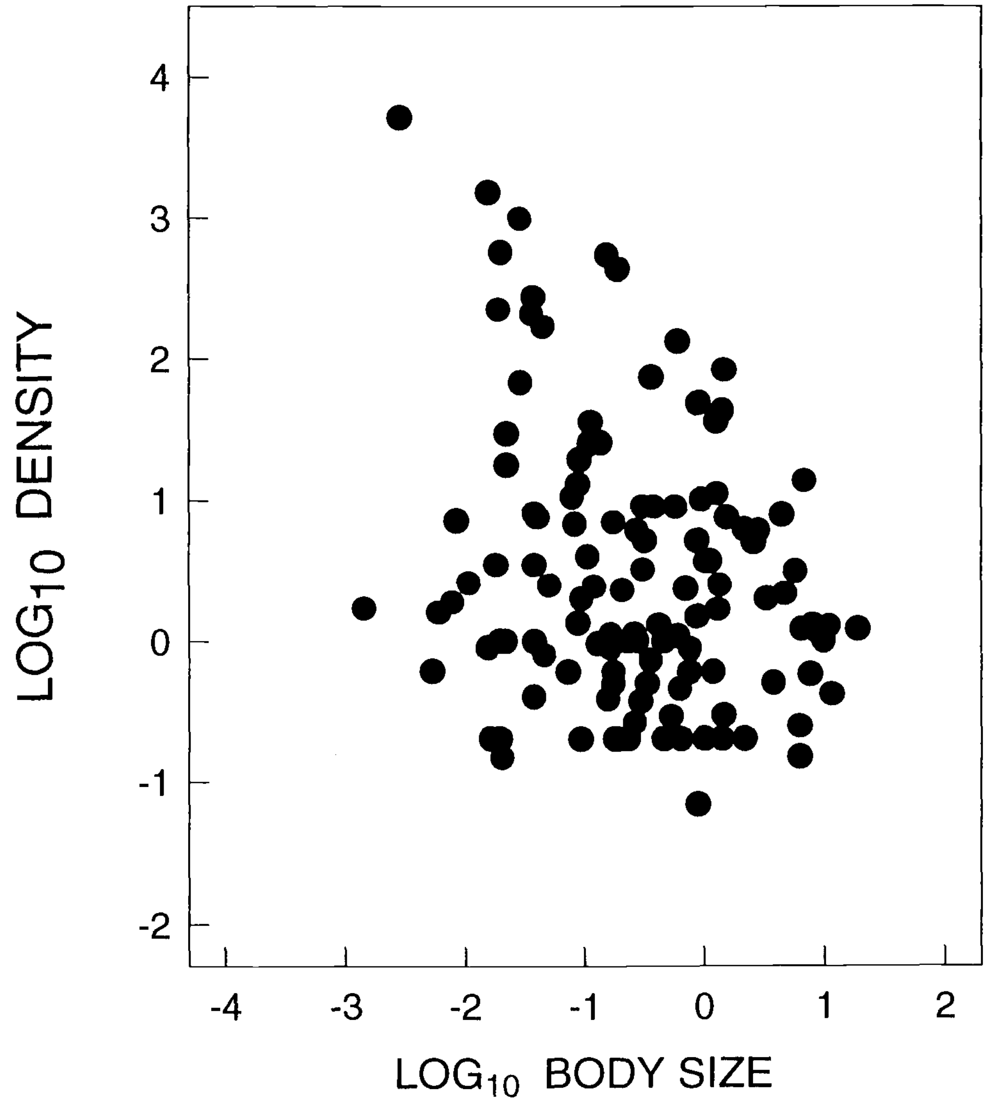
	intercept (a)	slope (b)	r^2	P	n
All gastropods	0.315	-0.286	0.07	0.0034	123
Latitude:					
Temperate	0.826	-0.655	0.32	0.0001	40
Tropical	0.094	-0.121	0.02	0.1857	83
Region:					
Chile	0.689	-1.116	0.74	0.0001	20
San Juan Island	0.981	-0.161	0.03	0.4931	20
Panama	-0.02	0.090	0.01	0.5443	29
Costa Rica	0.229	-0.122	0.02	0.2509	76

When the DW relationship was further broken into regions, body size appeared uncorrelated to mean population density in the two tropical regions, and particularly in Panama, where the slope of the relationship was slightly positive (Table 1). The maximum population densities were not correlated to body size in Panama, but were negatively correlated with body size in Costa Rica (Table 2). The pattern in the two temperate regions was different. In Chile, both mean and maximum population densities were tightly ($r^2 > 0.75$) correlated with body size, while on San Juan Island, only the maximum density of the species (upper boundary) showed a significant association with body size (Tables 2 and 3).

Table III.3. Parameters of linear least squares regressions on the upper boundary of the population density-body size distribution of intertidal gastropods. The 1st, 2nd, and 3rd coefficients of a polynomial regression and the total variance explained (r^2 poly) are also given. Significance of polynomial coefficients at the 0.05 level is indicated by *. Other symbols as in Table III.2.

	a	b	r^2	P	1st	2nd	3rd	r^2 poly	n
All gastropods	1.52	-0.63	0.50	0.0152	-0.59	-1.21	-0.95	0.54	11
Latitude:									
Temperate	1.58	-0.87	0.86	0.0001	-0.83*	-0.22	-0.08	0.88	10
Tropical	0.94	-0.26	0.15	0.2449	-0.62	-0.25	0.04	0.34	11
Region:									
Chile	1.14	-0.99	0.95	0.0010	-1.07*	-0.29	-0.09	0.96	6
San Juan Is.	1.56	-0.86	0.65	0.0290	-0.58*	-0.43	-0.03	0.34	11
Panama	0.61	0.30	0.24	0.1853	0.29	-0.77	-0.27	0.62	9
Costa Rica	1.11	-0.44	0.35	0.0959	-1.15*	-0.26	0.21	0.81	9

Figure III.1. The relationship between log mean population density (ind/m^2) and log body size (g) in rocky intertidal gastropods from temperate and tropical regions of the Pacific coast of America.



Taxonomic affiliation within the class Gastropoda had no clear effects on the overall DW relationship presented in figure 1. Population density was negatively correlated with body size in all four orders of intertidal gastropods represented in the data, but significantly so only in Archaeogastropoda (Fig. 3, Table 4). However, none of the slopes or the amount of variance explained by body size was significantly different to those expected from a random sample of species taken from the total pool of species or from the pool stratified by latitude (Table 4). The pattern within families of Gastropoda was similar in that all the regression parameters were within the 95% confidence interval for random samples taken from the respective order above. Of the 13 families represented by at least 4 species (families with less than 4 species were not included), only 1 regression was significant and two more were marginally significant (P around 0.05). Seven slopes (54 %) were positive (non significant) and six were negative. The proportion of positive and negative slopes did not differ from random (binomial test, $P > 0.05$). A positive and marginally significant correlation among families between the magnitude of the slope and the mean body size of the species in that family was observed (Fig 4). However, this correlation disappeared when data for temperate and tropical latitudes were treated separately.

Figure III.2. Relationship between log mean population density (ind/m^2) and log body size (g) in rocky intertidal gastropods from temperate (San Juan Island and central Chile) and tropical (Panama and Costa Rica) regions.

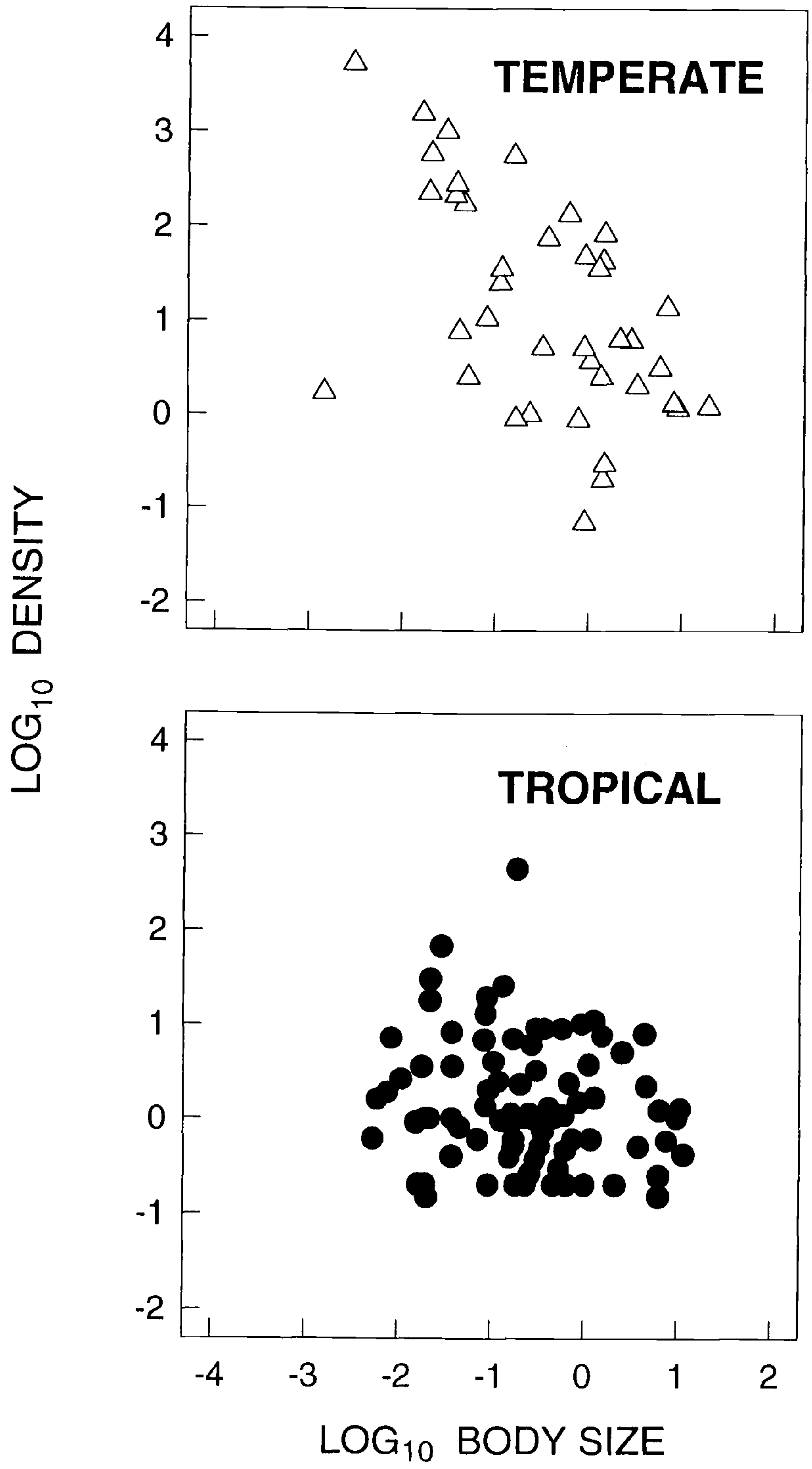


Table III.4. Parameters of linear least square regressions of log mean population density over log body size within orders of intertidal gastropods. All regions pooled. b-95% is the 95% percentiles of 1000 random samples taken from the total pool of species; r^2-95% is the upper 95% percentile of the same random samples (see text). Other symbols as in Table III.2.

ORDER	a	b	r^2	P	n	b-95%	r^2-95%
Archaeogastropoda	0.53	-0.46	0.13	0.0257	39	-0.53, +0.03	0.198
Bassomatophora	0.76	-0.49	0.20	0.4523	5	-1.45, +0.65	0.809
Mesogastropoda	0.43	-0.12	0.01	0.6750	23	-0.67, +0.14	0.282
Neogastropoda	0.11	-0.18	0.06	0.0806	55	-0.47, -0.01	0.165

Figure III.3. Relationship between log mean population density (ind/m^2) and log body size (g) within the major orders of intertidal gastropods.

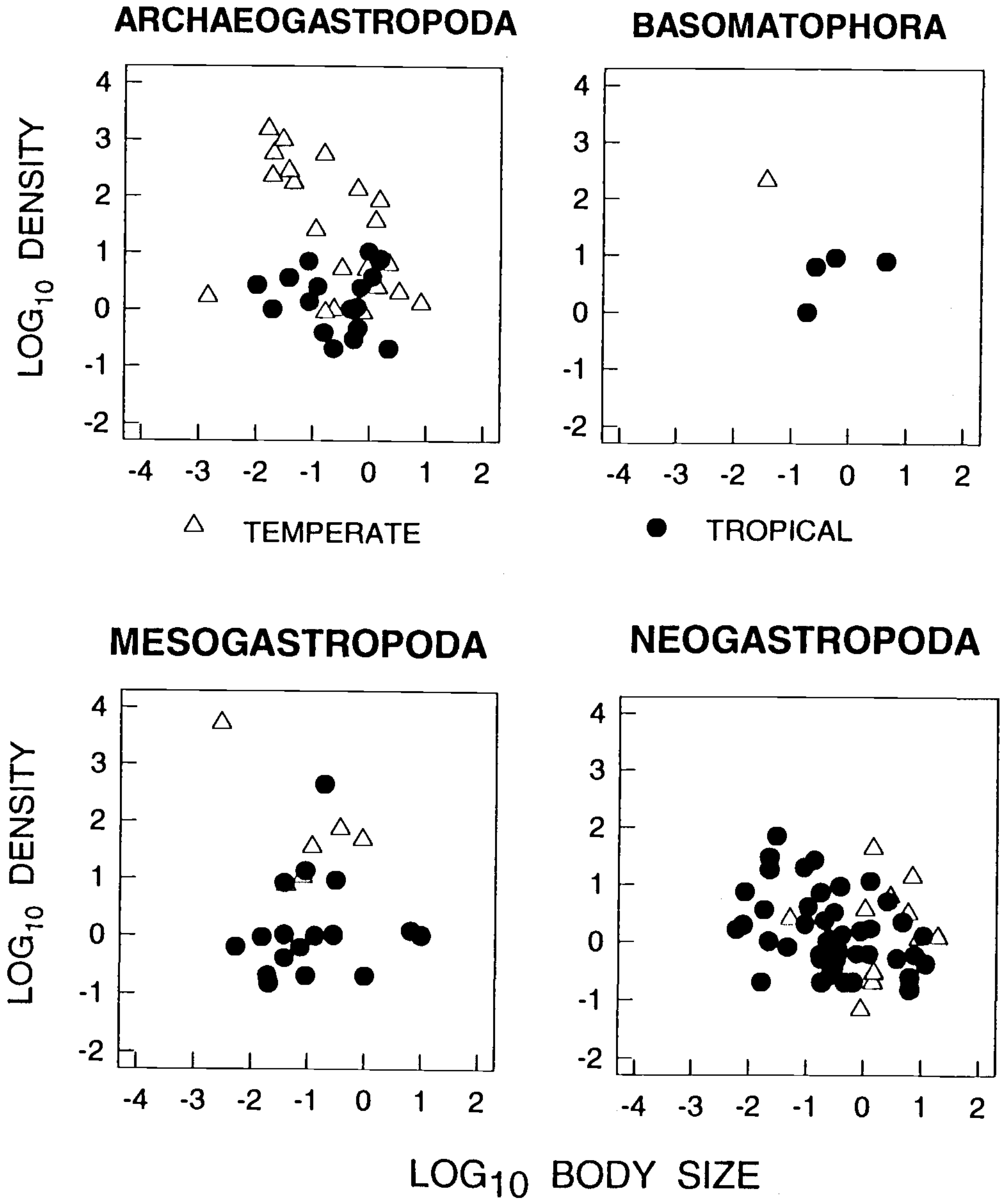
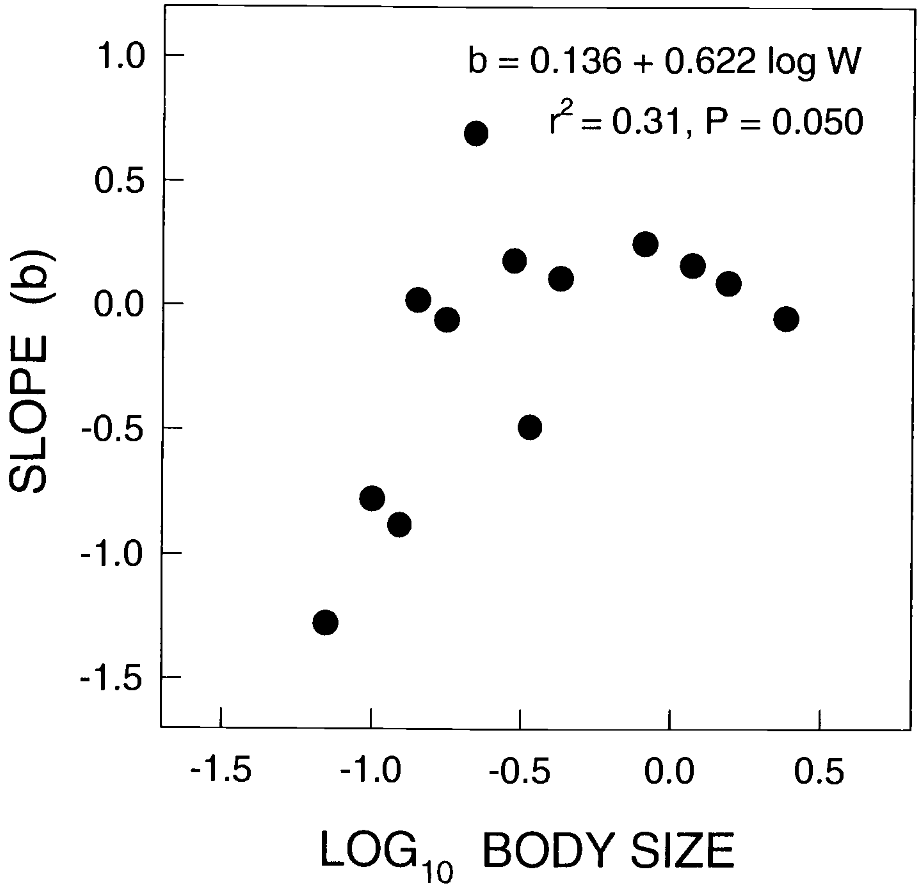


Table III.5. Parameters of linear least squares regressions of log mean population density over log body size within families of intertidal gastropods. Only families represented by at least 4 species are included. Symbols as in table III.2.

FAMILY	a	b	r^2	P	n
Acmaeidae	0.63	-0.88	0.21	0.0562	18
Buccinidae	0.30	+0.02	<0.01	0.9255	6
Calyptraidae	-0.49	-0.06	0.01	0.8939	4
Cerithidae	0.71	+0.11	0.02	0.8709	4
Collumbelidae	-0.15	-0.78	0.32	0.0344	14
Conidae	-0.35	+0.15	0.25	0.5020	4
Fissurellidae	0.05	+0.09	<0.01	0.8217	9
Littorinidae	0.06	-1.28	0.54	0.0945	6
Mitridae	0.16	+0.69	0.11	0.5900	5
Muricidae	-0.18	-0.05	0.01	0.8050	12
Siphonaridae	0.77	-0.49	0.20	0.4523	5
Thaiididae	0.47	+0.25	0.09	0.3963	10
Trochidae	0.67	+0.18	0.15	0.4545	6

Figure III.4. Relationship between the slope (b) of the body size-population density relationship within families of gastropods and the mean body size of the species within those families.



Discussion

The relationship between mean population density and body size of gastropod species pooling all regions for which data are available showed a significant, though weak negative association between these variables. However, pooling data from all regions obscured important differences in the DW pattern between latitudes and among regions. On the one hand, body size was not correlated with mean population density in the species-rich assemblage of gastropods of the rocky intertidal zones of both tropical regions, Panama and Costa Rica. Generalizing from these to the entire tropical Pacific is complicated by the large proportion of species shared by the two regions (Spight 1976, Lubchenco et al. 1984, Navarrete and Menge in prep.). However, a large number of gastropod species are found throughout the tropical Pacific (Keen 1971) and thus it is likely that lack of correlation between body size and mean population density within gastropod assemblages characterize all tropical intertidal zones in the Pacific. On the other hand, body size appeared tightly correlated to mean population density in one of the temperate regions (Chile), but not the other (San Juan Island). These two regions share no species and differ appreciably in physical conditions. While heat and desiccation stresses appear higher at San Juan Island, wave forces are higher in Chile, even in protected sites (Connell 1970, Castilla and Paine 1987, Navarrete and Castilla 1990, Berlow and Navarrete in prep., and personal observations). To what extent differences in the DW pattern between temperate regions reflect differences in physical conditions is unknown and at present difficult to test, but research in other temperate regions can shed light into the causes of these differences.

Does phylogenetic relatedness affect the DW pattern within Gastropoda? Results using taxonomic affiliation as a correlate for phylogenetic relatedness showed that the DW patterns within orders and families of gastropods were not different from those observed in the entire assemblage at either regional or local scales. This contrasts with results of Nee et al. (1991) study in which they showed that phylogenetically related tribes of birds inhabiting geographic regions exhibited a distinctive relationship between body size and population density. Nee et al. (1991) suggested that this effect was due to the inclusion of entire guilds of species in these phylogenetically close tribes, although their data represented averages over large geographic regions over which phylogenetically close species might never form part of the same local guild. Indeed, a study over more restricted spatial scales on North American and European birds showed no effect of phylogeny and suggested that more autoecological information should be collected to interpret the DW patterns (Tillería and Carrascal 1994). My results with intertidal gastropods support this idea and suggest that among these organisms the ecological units subjected to the evolutionary processes determining the DW relationship are, to some extent, independent of phylogenetic relatedness.

Do patterns within taxonomically restricted species assemblages correspond with the patterns observed in entire communities? Comprehensive studies including all intertidal animal species have been conducted only in some areas of Chile and Panama (Marquet et al. 1990, Navarrete and Menge in prep.). However the DW patterns in these two regions correspond well with those within gastropods: in Panamanian intertidal communities as well as within gastropods, the mean and maximum density of organisms of different species is not correlated with body size. In the temperate central coast of Chile body size explains a large portion of the variance in population density in entire communities as well as within gastropods. The slopes characterizing the DW relationship are also similar. It is important to note that, to a great extent, the data sets for gastropods and for entire communities are independent (see Appendix 1) and densities for gastropods correspond to averages over several sites taken from the literature and amended with my own unpublished data. Community-wide studies in Costa Rica and Panama are necessary to further evaluate the extent to which processes operating within restricted taxonomic assemblages and shaping the DW relationship are similar to those operating in the entire community. The results presented here suggest that they are.

Comparisons of slopes of the DW relation among families of gastropods showed a weak positive correlation between the mean body size of the species within a family and the magnitude of the slope: shallower slopes with larger mean body size. A similar pattern has been observed within local assemblages of birds (Tillería and Carrascal 1994) and dietary groups of mammals (Damuth 1993) and has been interpreted as the result of different relative advantages of body size within guilds of small and large animals. However, the extent to which this pattern and its explanation depend on the spatial scale and taxonomic resolution is unclear. Among gastropods, the pattern disappears when only local assemblages are considered.

The results presented here highlight the need for more detailed studies on the DW relationship within taxonomic assemblages and communities. It is clear that many explanations for the DW pattern within regional or local taxonomic assemblages (e.g. birds, insects, gastropods) make assumptions about the operation of ecological processes that would fit better within the context of true community-wide studies.

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CHAPTER IV

KEYSTONE PREDATION: INTERACTIVE EFFECTS OF TWO PREDATORS ON THEIR MAIN PREY

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Abstract

The strength of predation on mussels by the keystone seastar *Pisaster ochraceus* and by the predatory whelks *Nucella emarginata* and *N. canaliculata* was studied under different environmental conditions on the intertidal zone of the Oregon coast. We attempted to determine: a) the robustness of keystone predation to the presence of other predators in the system, b) the role of other predators in the presence and in the absence of a keystone species, and c) the population and per capita variability in the interaction strengths of strong (keystone) versus weak interactors.

Predation intensity was measured by recording the survival of mussels transplanted to areas from which seastars or whelks, or both had been either manually removed or left undisturbed at natural densities. Whelk experimental units were nested within those for the seastar treatment to account for large

differences in body size and mobility of these predators (seastars being much larger and faster). Each combination of seastar and whelk treatments was replicated four times in both wave exposed and wave protected habitats of two sites differing in primary productivity and community structure. The effect of seastars on whelk size structure and density was also recorded. Predation intensity by the keystone predator was strong under all site x wave exposure combinations and was unaffected by the presence of whelks. On the other hand, whelks had ecologically important effects on the survival of mussels in the absence, but not in the presence of the keystone. We suggest that this pattern of interactive effects between keystone and weak predators may be general to all keystone predator-dominated systems, but currently there are limited data to test this proposition. The total (population) interaction strength between seastars and mussels was stronger and less variable across sites and wave exposures than that of between whelks and mussels, and the *per capita* interaction strength of seastars was two orders of magnitude larger than that of whelks. However, *per capita* effects of seastars were much more variable between sites and wave exposures, probably because simple density values grossly underestimate the ability of keystone predators to localize prey.

Negative effects of seastars on whelk density were observed within less than 4 months following *Pisaster* removals. Seastars also had a negative effect on whelk sizes, but the effect was evident only after more than 6 mo. of continuous *Pisaster* removal. Negative effects of seastars on whelks appeared to be stronger in places with higher densities of predators and can explain, in part, the reduced predation intensity of whelks observed in the presence of seastars.

Our results support the idea that in keystone-dominated systems, species other than the keystone have only minor, if any effects on the rest of the community and may be an example of 'redundant species'. However, they also suggest that after the loss of the keystone species previously 'redundant' species can compensate for the reduced predation and adopt a major role in the altered system. Such responses are potentially and important force in stabilizing communities.

Introduction

The idea that communities and ecosystems are dominated by the actions of a few important species embedded in a web of species with little or no effects (weak interactions) has become a central point of debate in ecology and conservation biology in recent years (Lawton 1992, Bond 1993, Lawton and Brown 1993, Mills et al. 1993, Tilman and Downing 1994). Some argue that if communities and ecosystems exhibit a high proportion of species with no measurable effect on the rest of the community ("redundant species", *sensu* Lawton & Brown 1993), then research and conservation efforts should be directed at identifying and protecting those species with disproportionately large effects (Rohlf 1991, Walker 1991, Bond 1993). The term 'keystone species' has been used for those species that play a dominant role in the functioning and structure of an ecological system (Paine 1966, 1969, Lawton and Brown 1993). Alternatively, all species might play a similarly small, but significant role within their communities and ecosystems (Ehrlich and Ehrlich 1981, McNaughton 1993, Tilman and Downing 1994) as a sort of 'diffuse' or more equally shared impact on the rest of the species (Menge and Lubchenco 1981, Lubchenco et al. 1984, Robles and Robb 1993). Prevalence of this latter pattern in natural systems would further stress the need for the conservation of biodiversity *per se* (Ehrlich and Wilson 1991, Lawton and Brown 1993, Mills et al. 1993). Knowledge of the relative importance of species within a community is not only critical for conservation biology and our ability to predict the consequences of species loss, but it also has important consequences for the development of theoretical models. For instance, models about the dynamics of food webs (Pimm 1982) or about the relation between species diversity and stability (May 1973, Pimm 1991) make specific assumptions about the way interaction strengths (or relative importance of species) are distributed among the species that form the community.

In many ecosystems predation plays an important role in the maintenance and variation of community structure, however, demonstration of predation effects has usually been limited to the removal of a single species or of all predator species together (see references in Sih et al. 1985, Menge and Farrell 1989), making it difficult or sometimes impossible (e.g. Elner and Vadas 1990) to determine the pattern of predation and to quantify the relative importance of species (see Bond 1993, Robles and Robb 1993, for a similar argument). With these limitations, the experimental evidence gathered so far suggest that both 'keystone' (one or few strong and numerous weak interactions) and 'diffuse' (a number of equally weak interactions) kinds of predation pattern occur in natural systems (e.g. Paine 1966, 1992, Dayton 1971, Lubchenco 1978, Peterson 1979, Morin 1981, Hixon and Brostoff 1983, Quammen 1984, Castilla and Durán 1985, Menge et al. 1986, Robles 1987, Brown and Heske 1990, Posey and Hines 1991, Heske et al. 1993, Robles and Robb 1993), reviewed by (Menge et al. 1994). When the effects of several predator species have been investigated, the results have generally but not always shown important interactive effects between predators (indirect effects) on the rest of the community (e.g. Menge et al. 1986, Van Buskirk 1988, Martin et al. 1989, Resetarits 1991, Robles and Robb 1993). Thus, the relative importance of predator species within a community, as well as the consequences of interactions between predators on lower trophic levels appear to vary among ecosystems and among habitats within a given system (Robles and Robb 1993, Menge et al. 1994). Field experiments remain as a the only means to determine which predation pattern occurs and what is the relative importance of different species.

Quantification of the relative importance and interactive effects of predators in systems in which a keystone pattern of predation seems prevalent, has rarely been done (see exceptions below). When testing for the existence of a keystone, the effects of other predators in the system are usually assumed rather than experimentally demonstrated to have only minor effects, if any, on the rest of the community. This assumption is usually well justified by the lack of compensatory responses from other predators following the removal of the keystone, an extensive knowledge of natural history of the system under study, and by the logistic limitations of performing manipulations on all the potentially important species. However, failing to perform manipulations of other predators has prevented us from developing a more comprehensive understanding of the actual role of these species in the system and the nature of the interactions between them and the keystone (see also Dayton 1971, Fauth and Resetarits 1991). In this study, we test the assumption that in the presence of a keystone, other predators in the system have no ecologically significant effects and quantify the interaction strengths of the keystone and the 'weak predators' under different environmental conditions. We selected a well studied system , the rocky intertidal zone of the Northwest coast of USA where the first keystone species ever identified, the seastar *Pisaster ochraceus* (Paine 1966, 1969) overlaps in distribution and diet with a number of other vertebrate and invertebrate predators (Castilla and Paine 1987). In this system we sought to answer the questions: Is the effect of a keystone affected by the presence of other predator species (see also Fauth and Resetarits 1991)? Is the effect of other species dependent on the presence of a keystone? Is the effect of non-keystone species (weak interactors) more variable across environmental gradients than that of the keystone (strong interactor)? And is the *per capita* effect of a keystone species less variable across environmental gradients than that of a non-keystone?

Background

Paine's (1966) landmark studies on the structure of rocky intertidal communities of the outer coast of Washington, demonstrated that predators can keep the abundance of competitively dominant prey at low levels and by doing so increase the local diversity of species (see Lubchenco and Real 1991, for an historical perspective). Paine observed a dramatic increase in the lower distribution limits of the competitively dominant mussel *Mytilus californianus* after the removal of a single predator species, the starfish *Pisaster ochraceus* (see also Paine 1974), while other predators in the system were not manipulated. He later termed *Pisaster* a "keystone" predator species (Paine 1969).

Recently, (Menge et al. 1994) studied the variation over time, space, and environmental conditions in the interaction strength between *Pisaster* and mussels on the coast of Oregon. They manipulated *Pisaster* in wave-exposed and wave-protected habitats of two localities with different productivities, Strawberry Hill (hereafter SH) and Boiler Bay (hereafter BB); (see Menge 1992, Menge et al. 1994). Separate experiments in two consecutive years (1991, 1992) estimated the intensity of predation on transplanted adult (4-7 cm long) mussels, *M. californianus*. Results showed that *Pisaster* predation was strong in all localities and exposures but the low zone of SH protected, where sand burial accounted for most mussel mortality. They also found that *Pisaster* predation was stronger at exposed than at protected habitats, and stronger at the more productive site (SH) where seastars (and other benthic predators) were more abundant.

The Pacific coast of North America and most intertidal communities around the world have many species of predators (e.g. Menge 1983, Lubchenco et al. 1984, Castilla and Paine 1987, Navarrete and Castilla 1993). Coexisting with *Pisaster ochraceus* in the open coast of Washington and Oregon states there is a number of other vertebrate and invertebrate species also prey on intertidal organisms (see Castilla and Paine 1987 for review). Among these, the most abundant and potentially most important for the sessile prey community are two species of whelks of the genus *Nucella, N. emarginata* and *N. canaliculata* (Menge et al. 1994). Other whelk species are known to have important effects on the abundance of sessile prey and community organization in places where other predators are absent or scarce (Menge 1976, Fairweather et al. 1984, Hughes and Burrows 1993). Similarly, in the wave-protected habitats of the San Juan Islands, Washington, where *Pisaster* were scarce and large mussels were nearly absent, *Nucella* played a key role in the barnacle-dominated community (Connell 1970, Dayton 1971), although their effects might be limited in spatial scale and microhabitat conditions (Berlow and Navarrete in prep.). The role of these species in the mid-low zone of the exposed coast of the Pacific Northwest, where they coexist with relatively high densities of *Pisaster*, has not been investigated in detail. At semi-protected habitats of Washington (areas with low mussel cover and dominated by barnacles), Dayton (1971) removed whelks from areas in which *Pisaster* had been manually removed and suggested that whelks could compensate for the seastar removal, but he could not evaluate the interaction between these predators (see discussion). We do not know if whelks affect the intensity of predation by seastars on mussels, or if seastars have effects on whelk populations, although preliminary evidence suggests that seastars can have negative effects on whelk sizes and densities (Menge et al. 1994). Here we perform manipulations to determine primarily the separate and combined predation intensity of seastars and whelks on mussels and, secondarily, the effect of seastars on whelk populations.

Methods

Study Sites

The study was carried out at two sites along the central coast of Oregon, Boiler Bay (BB, 44°50'N, 124°03'W) and Strawberry Hill (SH, 44°15'N, 124°07'W). These sites have been described in detail by Menge et al. (1994), Farrell (1988) and D'Antonio (1985). Briefly, classic zonation patterns are observed in Boiler Bay, with a high intertidal zone dominated by fucoid algae and barnacles, a mid intertidal zone dominated by mussels (*Mytilus californianus*), and a low zone dominated by a mosaic of seaweeds and surfgrass species. A striking wave exposure gradient occurs along three rocky benches running northwest to southeast, which served as the main experimental area. Another nearby platform (ca. 200 m apart), with the same orientation, wave exposure, zonation pattern, and species composition as the most protected platform of the main experimental area was also used in the experiments.

Strawberry Hill, 65 km south of BB, also exhibited a wave exposure gradient between wave exposed rocky benches and outcrops on the seaward edge of the site and those wave protected on the landward edge about 200 m distant. Zonation patterns were clear at SH as well, but there were differences in community structure, particularly in the low zone. Unlike BB, where algae dominate the low zone and bare space was scarce, filter feeders (mostly barnacles) and abundant bare rock space dominated the low zone at SH exposed. The low zone of the protected habitat of SH was usually covered by sand for a few months each year, beginning mid to late summer, and as a consequence the rock was mostly bare. The mussel *Mytilus trossulus*, a common species in both exposed and protected habitats on the coast of Oregon and Washington (Suchanek 1978), recruits heavily in the low zone of SH exposed. By late spring, *M. trossulus* beds cover much (> 70 %) of the substratum in extensive areas (hundreds of square meters) from the lower edge of the larger *M. californianus*, down into the zone. By late spring to early summer the effects of predators were apparent in *M. trossulus* beds, and usually by mid summer these mussels are completely exterminated from the low zone (Menge et al. 1994, pers. obs.). Differences in community structure were also observed for mobile species. Herbivores and carnivores, including seastars and whelks were more abundant at SH than BB, particularly in wave-exposed habitats (Menge et al. 1994).

Associated with differences in community structure, were differences in the productivity of the two sites. Both abundance and productivity of phytoplankton in the water column were higher at Strawberry Hill than Boiler Bay (Menge et al. in press). Growth rates of mussels and barnacles, as well as recruitment of mussels were also higher in the former site (Menge 1992, Menge et al. 1994).

Predation Intensity

To estimate the effects of seastars and whelks on prey, we measured the separate and combined intensity or rate of predation by both predators on a common prey, mussels. Since the goal was to compare predator-prey interaction strengths between predator species, exposures, and sites, we transplanted a fixed number of mussels to areas with or without predators (see below). This transplanting technique has the advantage of providing a standardized measure of interaction strength, while avoiding the potentially confounding effects of spatial and temporal variability in prey colonization rates (e.g. Menge 1978, Garrity and Levings 1981, Aronson 1989). Because results of such experiments do not incorporate rates of prey supply (recruitment and growth), they can be viewed as an estimate of "potential" interaction strength (Menge et al. 1994).

Mussels *Mytilus trossulus* were transplanted in clumps of 50 small (2.5-5.0 cm shell length) individuals to the experimental areas. The small mussel size ensured that both seastars and whelks could easily prey on them. To mimic their orientation in the natural beds, individual mussels were placed in overlapping rows with their ventral side against the substratum. Mussel clumps were held against the rock with cages of Vexar® plastic mesh (Fig. 1) to allow them to reattach to the rock. After about 4 weeks, when mussels were firmly attached to the rock, the mesh was removed and screws were used to mark the original position of the clumps. This method has been successfully used before with the California mussel (*M. californianus*) in Washington State (Paine 1976) and in Oregon (Menge et al. 1994).

The main experiment was conducted between June-September 1993. The design included two sites (SH and BB) x two wave exposures (exposed and protected) x four predator treatments (-P-N: removal of seastars [P= *Pisaster*] and whelks [N= *Nucella*]; -P+N : seastars removed, natural densities of whelks; +P-N: natural densities seastars, whelks removed; +P+N: natural densities of both seastars and whelks) x four replicates (Fig. 1). Seastars were manually removed (-P) from large areas ranging from 60-140 m^2 at BB and from 69-170

m^2 at SH. Adjacent areas (ca. 10 m apart) of similar size, in which seastar densities were left undisturbed (+P), were used as controls in this manipulation. Within each of these seastar experimental areas (-P and +P), whelks (*Nucella emarginata* and *N. canaliculata*) were either manually removed (-N) or left undisturbed (+N, controls for whelk removal). These smaller areas ranged in size from 8-15 m^2 at BB and 8-20 m^2 at SH. The different sizes of experimental areas used for seastar and whelk treatments make this a split-plot design, in which the larger and more mobile predators (seastars) were removed from larger areas than the smaller and slower whelk species. The actual size of each replicate varied as a function of natural substratum discontinuities, but all of them were large enough for 3 transplant clumps and marked plots (see below). All experimental areas had a bed of the California mussel (*M. californianus*) at the upper edge. All removed predators were placed in appropriate habitat at some distance from our plots.

Three mussel clumps (50 mussels each) were transplanted to the center of each replicate of all predator treatments (ca. 1-1.5 m above MLLW), right below the edge of California mussel beds. Each clump covered approximately 400 cm^2 of rock surface previously cleared of all organisms. After the transplanted mussels re-attached to the rock and the plastic mesh holding them down had been removed, a cage of the same plastic material, in the form of a dome, was placed over two of the transplants in all seastar removal areas (-P), and a roof (cage with open sides) was placed over the transplants in the seastar control areas (+P). This aspect of the design was a modification forced by the failure of a preliminary experiment in 1992, which demonstrated that denying access to the *M. trossulus* clumps strictly using manual removals was insufficient. Seastars were able to invade -P plots and decimate mussels during high tides when sites are inaccessible by foot. Further, diving is too hazardous at these open coastal sites to permit working at high tides. The dome cages helped keep seastars away from the transplanted clumps in seastar removals, while roofs served as controls for potential cage effects due to shading. Although cages impeded their movements, whelks could still access the mussels in the +N treatments by crawling under the dome cages, through the open corners, or if small enough, through the mesh. To ensure that the cages did not completely prevent access by whelks in +N treatments, medium size individuals of *N. canaliculata* were placed inside these cages at the beginning of the experiment. The number of snails inside these cages varied among replicates so as to match the natural density of whelks observed in the replicates at the time the experiment was begun. Small and medium size seastars can also work their way inside the cages if not removed periodically (pers. obs). On the other hand, the roofs provided shade, but did not stop seastars or whelks from preying on the mussels.

The experiment was monitored every two to four days for the first 14 days and approximately every 7-10 days for the next 60 days, until some treatments had no mussels left. Each time, the number of live and dead mussels remaining in the clumps was counted, and predators in removal areas were removed and counted. Mussel shells still attached to the rock were inspected for the presence of holes drilled by whelks. Predator removals continued at lower frequency (ca. monthly) for several months after the transplant experiment was terminated.

Pisaster Densities and Diet

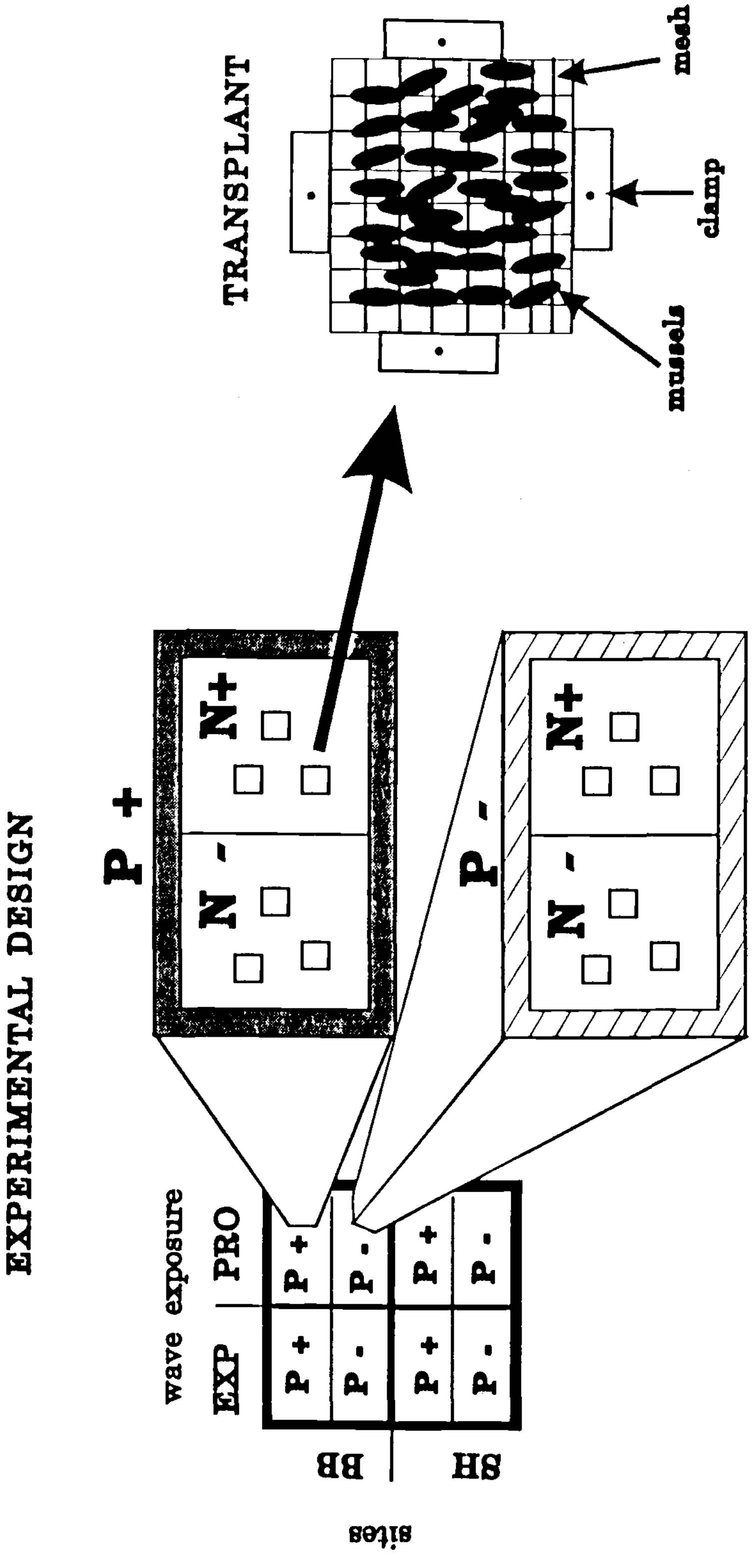
Seastar densities were estimated in May, July, and November 1993 in the four replicates used in the transplant experiment as controls (+P). At each wave exposure and site combination, the number of seastars found in these areas was divided by the total area of that replicate (see Menge et al. 1994 for details). The diet of seastars was studied at SH exposed in November 1993 and April 1994. Low numbers of seastars in BB did not allow diet characterization. Sizes of seastars (ray length) were measured in 1990 and results are presented in Menge et al. (1994).

Nucella Population Structure: Effects of *Pisaster*

To determine the potential effects of seastars on the population of *Nucella,* the density and sizes of whelks were measured in areas with and without seastars (P), before and after the experiment was begun. Estimates of densities and sizes in June 5 1993, before the predator removals, came from two sources. First, the number of whelks removed from the *Nucella* removal areas (-N) was divided by the total area of each replicate, thus providing four estimates of density for each wave exposure and site combination. Secondly, density of whelks in the *Nucella* control areas (+N) was estimated by counting individuals in 8 20 x 20 cm quadrats haphazardly placed in each replicated area. The mean of all 8 quadrats was used as an estimate for each replicate in the analysis. Using the same quadrat positions, densities of whelks in +N areas were estimated again in September 27 1993. The shell length of all individuals removed from -N areas and of the ones found in the quadrats in +N areas were measured with vernier calipers to the nearest 0.5 mm. At Strawberry Hill, shell lengths were measured again in December 1993.

Figure IV.1. Diagram of the design of mussel transplant experiments. Seastars *Pisaster ochraceus* were either manually removed (P-) or left undisturbed (P+, natural density) in large areas of the low intertidal zone. Within each of these areas, two smaller areas were selected and whelks (*Nucella canaliculata* and *N. emarginata*) were manually removed (N-) from one and left undisturbed (N+) in the other. Three clumps of 50 small (2.5-3 cm long) mussels (*Mytilus trossulus*) were transplanted to each of the smaller areas using a plastic mesh to hold them down until they re-attached to the rock. This basic design was replicated four times under each wave exposure (EXP, PRO) and site (SH, BB) combination.

Figure V.1.


EXPERIMENTAL DESIGN
wave exposure
EXP
PRO
sites
BB
SH
P +
P -
P +
P -
P +
P -
P +
P -
P +
N -
N+
P -
N -
N+
TRANSPLANT
mussels
clamp
mesh

Interaction Strengths

Interaction strengths are a measure of the magnitude of the effect one species has on another (MacArthur 1972) and constitute the building blocks of many theoretical models (e.g. food web dynamics, species-stability, Lawton 1992). The interaction strengths (IS) between seastars and mussels and between whelks and mussels under each wave exposure and site combination were estimated using the index proposed by (Paine 1992). This index measures the effect of predators in isolation (i.e. seastars in the absence of whelks and whelks in the absence of seastars), by comparing the survival of a prey species (e.g. mussels) in the absence of all predators (*C*, reference state) and in the presence of one predator species (*T*). Thus, for each predator species (i), the interaction strength was calculated as:

$$IS_i = \frac{(T_i - C)}{C}$$

where T_i is the survival of mussels in the presence of *either* seastars or whelks, and C is the survival of mussels in the absence of *both* seastars and whelks. The index varies from -1 for complete extermination of the prey, to 0, when there is no predator effect, to an unlimited positive value when the predator actually increases survival of the prey. The mean survival of all transplanted clumps within a replicate was used as an estimate of survival for that replicate. A single estimate of C was then obtained for each wave exposure and exposure combination by averaging the mussel survival of the four -N-P replicates. The survival of mussels in the presence of predators (T_i) in each replicate was used in combination with the single estimate of survival in the absence of predators (C) to give four values of IS_i, the mean of which was considered the 'observed' interaction strength. The entire data set was then bootstrapped (Dixon 1993) to obtain estimates of standard errors and confidence intervals (see 'Data Analysis' below). Per capita interaction strengths for seastars and whelks (pcIS_i) were obtained by dividing IS_i of each replicate by the observed density of predators in that replicate (see Paine 1992).

Data Analysis

Data analysis was done using SAS v. 6.04 (SAS Institute Inc. 1989) statistical package for DOS system in IBM-compatible PC's. Assumptions of normality and variance homogeneity were checked by visual inspection of residual plots and normal probability plots (Sokal and Rohlf 1981). In all cases, arcsin-transformed mussel survival data exhibited better distribution and homogeneity than raw data and thus all statistical analysis were done on transformed data. Density data were transformed to logarithms when so indicated. A Cochran's C test for variance homogeneity was conducted after transformation of data to verify this assumption.

The experimental design for the mussel transplant experiment (Fig. 1) corresponded to a split-plot design (Miliken and Johnson 1984, Mead 1988), in which site (BB, SH), wave exposure (exposed, protected), seastars (P) and the interaction terms among them formed the 'main plot' factors, and whelks (N) and the interaction terms with all the main plot factors formed the 'sub-plot' sources of variance. The following basic model (without the repeated observations, see below) was fitted to the data:

$$\begin{gathered} y_{ijklm} = \mu + S_i + W_j + P_k + a_{ij} + b_{ik} + c_{jk} + d_{ijk} + \xi_{i(jkl)} \\ + N_m + (N_m * B_{ijk}) + \gamma_{i(jkml)} \end{gathered}$$

where ξ and γ are error terms. All factors (S: site, W: wave exposure, P: *Pisaster*, N: *Nucella*) and their interactions (a, b, c, d, N*B: interaction between *Nucella* with all main plot factors) were considered to be fixed effects. The appropriate error terms used to test the different hypotheses are indicated in the tables of the Results section. To simplify the analysis, the mean of the clumps within replicates was used as an estimate of survival for each replicate. Variances among clumps within a replicate were used for other analysis (see below). Because mussel survival data are serially correlated over time (the same transplanted clumps were sampled over time), a repeated measures split-plot analysis of variance (RM-ANOVA) was used (von Ende 1993). In all cases survival data did not meet the assumption of circularity among the levels of the within subjects factor (homogeneity of treatment differences variance (von Ende 1993, Miliken and Johnson 1984) as indicated by the Mauchly's sphericity test criterion applied to the ortho-normalized components of the variance co-variance matrix (Crowder and Hand 1990). Thus, results for the univariate (split-plot) approach to the within subjects factors of the repeated measures analysis are presented with Huynh-Feldt (H-F) adjusted probability values (H-F-epsilon correction factors are given in the tables of results). Further, results of the multivariate (MANOVA) approach, which is less constrained by assumptions, are presented for comparison to the univariate analysis (Miliken and Johnson 1984, Crowder and Hand 1990, von Ende 1993). Correspondence between univariate and multivariate results lends confidence to interpretation.

Two types of contrasts for the within subjects factor (time) were performed. Contrasts between adjacent weeks were generated using the 'profile' options in the Repeated statement of SAS (SAS Institute Inc. 1989) to determine when treatments became significantly different. Time trends were examined using orthogonal polynomial contrasts with the 'polynomial' option in the Repeated statement of SAS (Freund et al. 1986).

Considering "site" as a fixed effect requires further explanation. As stated in the Introduction, the two sites (BB and SH) were selected because they exhibited clear differences in community structure, seemingly produced by differences in productivity levels (Menge et al. in press). They were clearly not selected at random from a set of potential study sites along the Oregon coast and we make no general statistical inferences about "sites" in Oregon.

In addition to the repeated measures approach, a curve fitting approach (Potvin et al. 1990) was also used to determine differences in mussel mortality rates at the beginning of the experiment. Both linear and quadratic (polynomial) least squares regression models were fitted to the survival data of the first 5 dates (up to day 24) for each replicate under each predator, site, and wave exposure combination. Clumps within replicates were not averaged in this case, to provide more degrees of freedom for the estimation of slopes. The four slopes for the linear regressions (one for each replicate) were compared using a split-plot ANOVA, with seastars (P) as main factor and whelks (N) as a nested factor, for each site and wave exposure combination. The first and second order coefficients of the polynomial regression provided a multivariate data set for each predator combination and thus they were compared using a split-plot MANOVA for each site and wave exposure combination.

To estimate the relative contributions of spatial scales (clumps = meters, replicates = tens of meters), wave exposure, and site to the total variation in predation intensity by whelks and seastars, the variance components of the mussel survival data were calculated. Considering only the experimental areas in which a particular predator was left undisturbed while the other was removed, and assuming that mussel survival did not significantly change among factors in the absence of predators (see results), a two-way (site x wave exposure) analysis of variance with two nested levels (replicates, clumps within replicates) was fitted to the data. Note that these analyses considered only mussel survival data in the presence of predators and do not involve hypothesis testing. Variance components were estimated using SAS 'varcomp' procedure and the restricted maximum-likelihood (REML) method (SAS Institute Inc. 1989). The method generates maximum-likelihood estimates of variance for a part of the model that contains the fixed effects and a part that does not, using the W-transformation developed by Hemmerle and Hartley (1973, in SAS Institute Inc., 1989; see Goodnight and Hemmerle 1978, for details). A reduced model, including only variation due to exposure, replicates, and clumps was used to estimate variance components for each site separately.

The effects of site, wave exposure, and seastars on the densities of *N. emarginata* and *N. canaliculata* in the +N areas were tested before (June 5) and after (September 27) the removal the seastars. Two analyses were conducted over log-transformed density data. First, a three-way factorial ANOVA (site, exposure, *Pisaster*) was used to compare the total density of whelks without distinguishing between species (pooled). Secondly, a similar factorial design was used in a MANOVA to compare the densities of both whelk species simultaneously.

Comparison of sizes of whelks was done separately for the two species of *Nucella*. Low numbers of whelks in BB precluded statistical analysis of sizes in this site (some replicates were represented by less than 3 individuals). The generally low numbers of *N. emarginata* in the exposed areas, and of *N. canaliculata* in protected areas did not allow a comparison of all wave exposure conditions. Thus, analyses for *N. emarginata* were restricted to protected habitats, and those of *N. canaliculata* to exposed habitats of Strawberry Hill. A one-way nested analysis of variance (ANOVA) was used to compare areas with and without seastars (P). Individual measures within each replicated area were considered as nested observations.

Results

Predation Intensity

Overall, removals of predators were successfully maintained during the mussel transplant experiment. However, despite the frequency of removals (3-5 days), some re-invasions occurred, particularly in wave exposed habitats of Strawberry Hill, where seastars and whelks reach highest densities. When whelks invaded and ate mussels in the clumps of the -N areas, the number of dead mussels with valves drilled by whelks was added to the total number of live mussels before data analysis. On the rare occasions (3 of 128 clumps) that seastars invaded the transplants of the -P areas and were found inside the protective dome cage, the whole clump was dropped from the analysis.

Figure IV.2. Results of the mussel transplant experiment of summer 1993. Data are the mean proportion of live mussels (± 1 SE) found in four replicates under each predator, site, and wave exposure treatment (see text for details). The experiment was begun 3 June 1993 by removing the plastic mesh from mussel clumps (50 individual mussels in each clump) transplanted to areas where seastars or whelks or both were either manually removed or left undisturbed at natural densities.

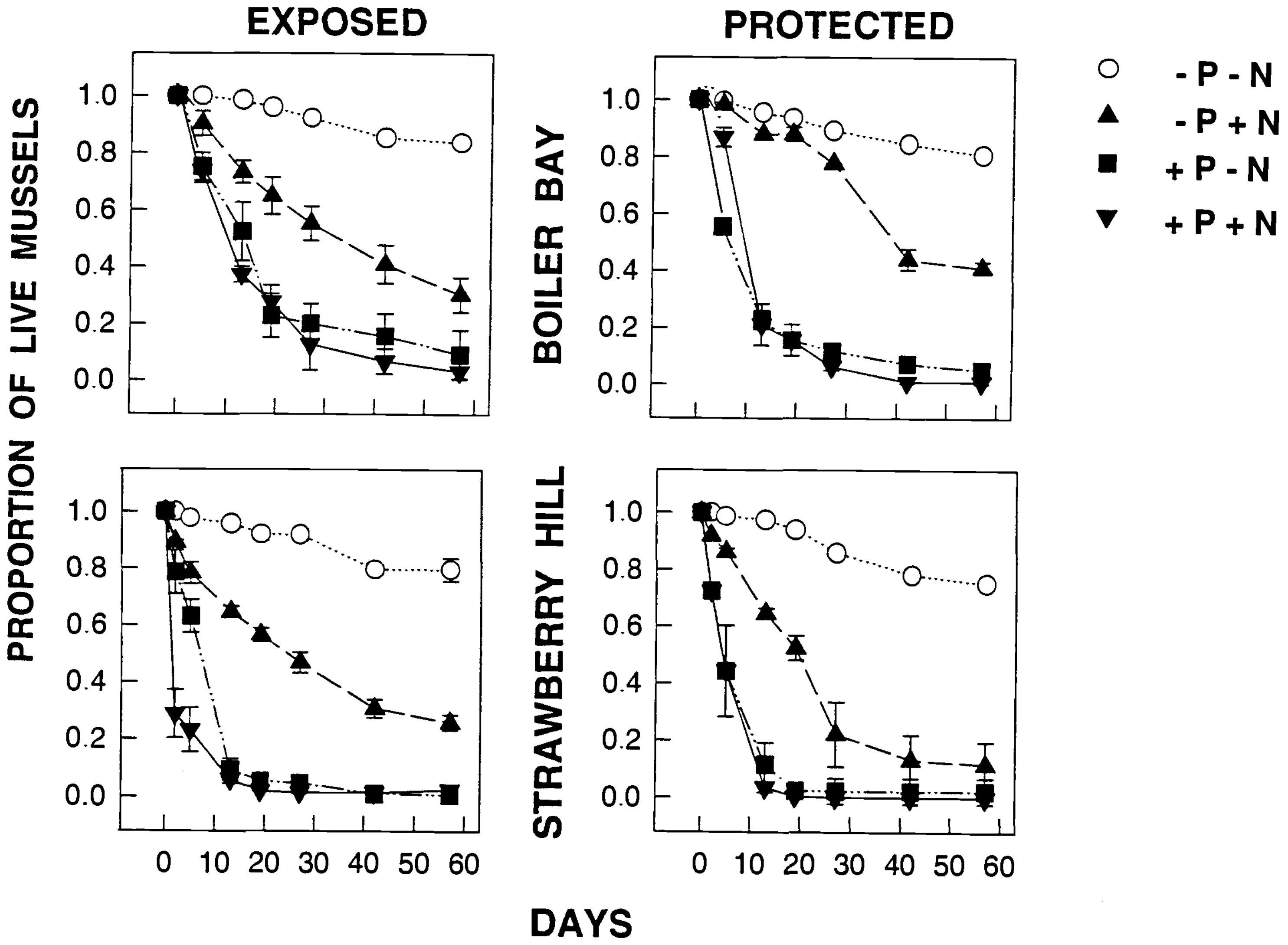
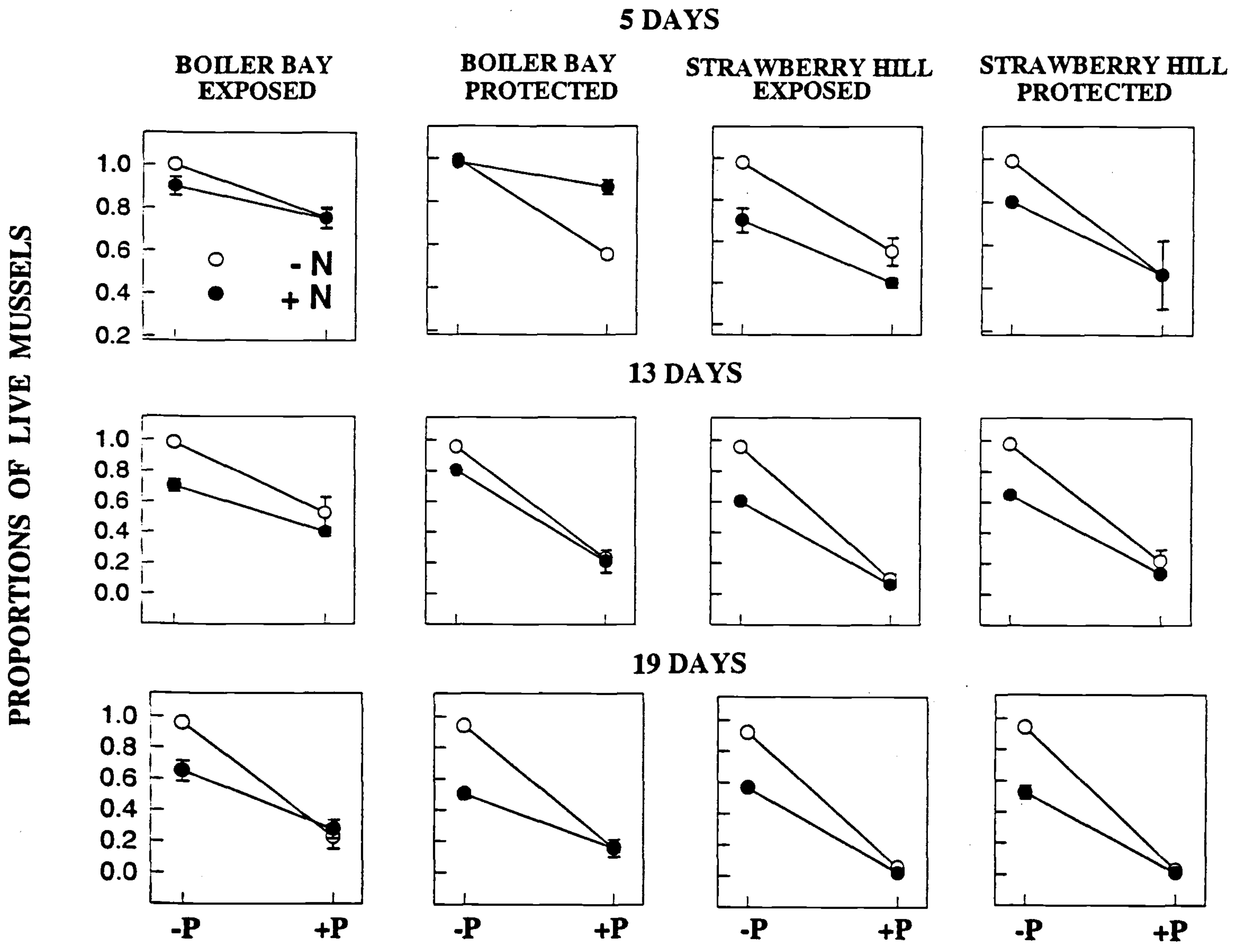

EXPOSED
PROTECTED
PROPORTION OF LIVE MUSSELS
BOILER BAY
STRAWBERRY HILL
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
60
DAYS
○ - P - N
▲ - P + N
■ + P - N
▼ + P + N

Figure V.2.

Figure IV.3. Interactive diagrams of the effects of predator treatments on the mean proportion of live mussels (± SE) during the first 19 days of mussel transplant experiment. Note that mussel survival was consistently higher when seastars were removed (left pair of points in each panel) and that whelks negatively affected survival of mussels only in the absence of seastars (compare lines with open and solid symbols).

Figure V.3.


5 DAYS
13 DAYS
19 DAYS
BOILER BAY EXPOSED
BOILER BAY PROTECTED
STRAWBERRY HILL EXPOSED
STRAWBERRY HILL PROTECTED
PROPORTIONS OF LIVE MUSSELS
1.0
0.8
0.6
0.4
0.2
0.0
○ - N
● + N
-P
+P

Transplanted mussels survived well in the absence of seastars and whelks (-P-N), under all site and wave exposure conditions (Fig. 2). Seven months after the beginning of the experiments, transplanted mussels were still attached to the rock in the -P-N areas and had grown significantly (pers. obs.). Overall (across wave exposure and predator treatments), there was a significantly higher survival of mussels at BB than at SH (Table 1, between subjects effect of 'site' was significant), probably due to the steeper mortality suffered at SH in the presence of predators. These differences between sites seemed to change over time and with wave exposure (Table 1, within subjects effect of 'time x site x exposure' for MANOVA, but not univariate tests), and they became apparent only toward the end of the experiment (Table 2, successive times contrast for site at 'day27-day42'). On the other hand, wave exposure did not have an overall effect on mussel mortality. Significant differences were observed among replicates for the seastar treatment (Table 1, between subjects effect of 'rep(site exposure *Pisaster*)'), reflecting the patchy distribution of predators (see below).

Seastars had a strong negative (main) effect on mussel survival (Table 1, between subjects effect of '*Pisaster*') under all wave exposure-site combinations (Fig. 2). At Strawberry Hill exposed, seastars attacked the transplanted clumps of mussels immediately (next tide) after removal of the plastic mesh, aggregating around the clumps and removing most of the mussels in a matter of days (pers. obs.). In other site x exposure combinations with lower predator densities, seastars did not become visible on or around the clumps for the first 2-3 days, but by the time of the second monitoring (5 days) they had found the clumps and their effects were apparent (pers. obs). Sites with lower seastar densities also had greater variability in mussel mortality rates among clumps (see below). Thus, in all site and exposure combinations, seastar effects were significant from the beginning of the experiment (Table 2, successive times contrast for *Pisaster*

Table IV.1. Repeated measures analysis of variance of the effects of predation by *Nucella* and *Pisaster* on mussel survival. Comparisons include all combinations of predators present (natural densities) or absent (manually removed) in two sites (Strawberry Hill and Boiler Bay) and two wave exposures (exposed and protected). The experimental units for *Nucella* were nested within those for *Pisaster* in a split-plot design (see text). Data did not show homogeneity of treatment differences variances (Sphericity test, P = 0.0004). Huynh-Feldt corrected probabilities (P H-F) are given for the univariate within subjects analysis (H-F epsilon = 1.968). df: degrees of freedom; MS: mean squares. Bold face P values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
site	1	3.66	12.10	**0.0019**
exposure	1	0.14	0.46	0.5026
Pisaster	1	37.94	125.47	**0.0001**
site x exposure	1	0.04	0.12	0.7271
site x *Pisaster*	1	0.16	0.55	0.4664
exposure x *Pisaster*	1	0.08	0.27	0.6082
site x exposure x *Pisaster*	1	0.27	0.89	0.3554
rep (site x exposure x *Pisaster*)	24	0.30	3.18	**0.0036**
Nucella	1	3.58	37.67	**0.0001**
site x *Nucella*	1	0.31	3.38	0.0789
exposure x *Nucella*	1	0.13	1.34	0.2582
site x exposure x *Nucella*	1	0.08	0.82	0.3752
Pisaster x *Nucella*	1	1.74	18.24	**0.0003**
site x *Pisaster* x *Nucella*	1	0.01	0.07	0.7900
exposure x *Pisaster* x *Nucella*	1	0.39	0.42	0.5230
site x exposure x *Pisaster* x *Nucella*	1	0.05	0.49	0.4912
Error	23	0.09		

Table IV.1. (continued).

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F H-F	P H-F	num df	den df	Wilk λ	p λ
time	4	3.33	124.0	**0.0001**	4	20	0.07	**0.0001**
time x site	4	0.02	0.5	0.6781	4	20	0.81	0.3032
time x exposure	4	0.03	1.1	0.3592	4	20	0.86	0.5061
time x *Pisaster*	4	0.28	10.4	**0.0001**	4	20	0.55	**0.0115**
time x site x exp.	4	0.04	1.4	0.2239	4	20	0.59	**0.0224**
time x site x *Pisaster*	4	0.05	1.8	0.1336	4	20	0.84	0.4317
time x exp. x *Pisaster*	4	0.02	0.8	0.5030	4	20	0.90	0.6967
time x site x exposure x *Pisaster*	4	0.01	0.3	0.8245	4	20	0.93	0.8015
time x rep	96	0.03	1.1	0.2431	96	81.7	0.06	0.6598
time x *Nucella*	4	0.07	2.7	**0.0350**	4	20	0.70	0.1155
time x site x *Nucella*	4	0.02	0.9	0.4542	4	20	0.79	0.2901
time x exp. x *Nucella*	4	0.07	2.6	**0.0365**	4	20	0.72	0.1442
time x site x exposure x *Nucella*	4	0.01	0.2	0.9263	4	20	0.96	0.9146
time x *Pisaster* x *Nucella*	4	0.03	1.0	0.4329	4	20	0.85	0.4782
time x site x *Pisaster* x *Nucella*	4	0.03	1.2	0.3036	4	20	0.86	0.5356
time x exposure x *Pisaster* x *Nucella*	4	0.03	1.1	0.3714	4	20	0.90	0.6876
time x site x exp. x *Pisaster* x *Nucella*	4	0.01	0.2	0.9205	4	20	0.93	0.8108
Error	92	0.03						

at 'day4-day13'). Whelks also had an overall significant negative effect on mussel survival (Table 1, between subjects effect of '*Nucella*') and the effect varied between wave exposures and over time (Table 1, within subjects effect of 'time x exposure x *Nucella*'). While whelks produced a rather linear decline on mussel survival, seastars caused a steeper, exponential reduction in mussel survival (Fig. 2, Table 2, polynomial contrasts: *Pisaster* effect, $P < 0.001$ for quadratic trend and $P = 0.09$ for linear trend; *Nucella* effect, $P < 0.05$ for linear trend and $P = 0.59$ for quadratic trend).

More informative than the main effects of predators is their interactive effects on mussel survival. While the effect of seastars on mussels was strong regardless of whether whelks were present or not (Fig. 2), whelks had ecologically significant effects on mussels only in the absence of seastars (Fig. 3). In all but one case, fewer mussels survived in -P plots in the presence than in the absence of whelks. The only exception occurred at the beginning of the experiment (day4) in Boiler Bay protected, where whelks actually had an initially positive effect on mussel survival in the presence of seastars (Fig 4). It is not clear what mechanism produced this positive indirect effect of whelks on mussels, but the effect had disappeared by day 13. Throughout the course of the experiment, the interaction between seastars and whelks was highly significant (Table 1, between subjects effect of '*Pisaster* x *Nucella*'). Univariate analyses of variance (not reported here) on each date suggested that the interaction became significant before the third monitoring date (< day 13). This means that the effect of whelks in the absence of seastars was different than in their presence from the beginning of the experiment, which was reflected in different mussel survival rates (slopes of mussel survival over time) during the first 24 days of experiment (Fig. 4, Table 3, significant interaction '*Pisaster* x *Nucella*' for both linear and quadratic fits to survival data).

Table IV.2. Contrasts between A) successive dates (days) and B) polynomial (linear and quadratic) time trends for the repeated measures analysis of variance of the effects of predation by *Nucella* and *Pisaster* on mussel survival (see Table 1). Significance levels have not been adjusted for time correlations. See Table 1 for explanations of labels.

A. SUCCESSIVE DATES

		day4-day13		day13-day19		day19-day27		day27-day42	
SOURCE	df	F	P	F	P	F	P	F	P
site	1	0.0	0.86	0.2	0.68	0.2	0.64	4.0	**0.05**
exposure	1	1.3	0.25	0.4	0.55	1.3	0.26	0.1	0.81
Pisaster	1	17.5	**0.00**	2.4	0.13	1.3	0.27	8.6	**0.01**
site x exposure	1	0.4	0.54	3.6	0.07	1.8	0.19	4.9	**0.03**
site x *Pisaster*	1	0.3	0.59	0.9	0.36	2.7	0.12	0.4	0.55
exposure x *Pisaster*	1	0.3	0.48	0.0	0.84	2.1	0.16	0.1	0.75
site x exposure x *Pisaster*	1	0.5	0.41	0.2	0.64	0.4	0.52	0.5	0.49
rep (site x exposure x *Pisaster*)	24	0.6	0.43	0.6	0.88	1.3	0.26	1.0	0.47
Nucella	1	0.9	0.57	0.6	0.47	2.7	0.11	2.3	0.14
site x *Nucella*	1	2.3	0.14	0.4	0.54	0.0	0.97	4.9	**0.03**
exposure x *Nucella*	1	1.2	0.29	0.0	0.98	0.2	0.66	4.8	**0.03**
site x exposure x *Nucella*	1	2.2	0.14	0.3	0.61	0.0	0.99	0.3	0.60
Pisaster x *Nucella*	1	0.6	0.46	0.3	0.57	0.0	0.86	2.8	0.10
site x *Pisaster* x *Nucella*	1	0.1	0.71	0.1	0.75	0.4	0.53	0.1	0.81
exposure x *Pisaster* x *Nucella*	1	2.1	0.15	0.2	0.69	0.0	0.99	0.4	0.52
site x exposure x *Pisaster* x *Nucella*	1	1.4	0.24	0.9	0.36	0.1	0.79	1.2	0.28
Error	23								

Table 2 (continued).

B. POLYNOMIAL

SOURCE	df	linear F	linear P	quadratic F	quadratic P
site	1	0.9	0.36	0.2	0.61
exposure	1	1.4	0.25	0.5	0.47
Pisaster	1	3.0	0.09	18.9	**0.00**
site x exposure	1	0.8	0.39	0.5	0.48
site x *Pisaster*	1	2.6	0.11	0.1	0.80
exposure x *Pisaster*	1	0.7	0.41	0.3	0.27
site x exposure x *Pisaster*	1	0.3	0.62	0.4	0.59
rep (site x exposure x *Pisaster*)	24	1.4	0.20	1.3	0.53
Nucella	1	6.2	**0.02**	0.3	0.59
site x *Nucella*	1	1.6	0.21	0.0	0.99
exposure x *Nucella*	1	6.2	0.02	0.5	0.50
site x exposure x *Nucella*	1	0.0	0.94	0.3	0.57
Pisaster x *Nucella*	1	2.6	0.12	0.0	0.91
site x *Pisaster* x *Nucella*	1	1.6	0.21	1.4	0.24
exposure x *Pisaster* x *Nucella*	1	1.1	0.31	2.0	0.17
site x exposure x *Pisaster* x *Nucella*	1	0.0	0.98	0.3	0.56
Error	23				

The effects of the interaction between the two predators on mussel survival rates did not significantly vary between sites and wave exposures (Table 3, no significant second order interactions).

Spatial Variation in Predation Intensity

Most of the spatial variation in predation intensity by both seastars and whelks was due to differences between sites, which accounted for 59.3 % and 71.0 % of the total variance in mussel survival due to predation by whelks and seastars, respectively (Fig 5). Wave exposure alone did not contribute to variation in predation by seastars, but in Boiler Bay explained 11.8% of the total variance in predation by whelks. Spatial variation due to both replicates (tens of meters) and clumps (< 4 m) explained different portions of the total variance in whelks and seastars. Overall, predation by seastars varied more among replicates separated by tens of meters than among clumps, which were only few meters apart. On the other hand, predation intensity by whelks varied more among clumps (25.7 % of total variance) than among replicates (3.2 %). Analyses of variance components by sites showed that variation over the smallest spatial scale (among clumps) was proportionally higher at Boiler Bay than Strawberry Hill, for both seastars and whelks (Fig. 5). At Boiler Bay, where lower densities of whelks and seastars were observed, almost all variation in predation by whelks occurred over a scale of few meters. In the case of seastars, there was a shift between the relative contribution of clumps and replicates from Strawberry Hill, where high seastar densities and low variation over few meters (clumps) were observed, to Boiler Bay, where low seastar densities and high variation over few meters were recorded.

Figure IV.4. Mussel survival rates (mean proportion of live mussels/day ± SE, n = 4) for the first 24 days of the transplant experiments under the different predator, site, and wave exposure treatments. Data are the mean slopes of the regression between the proportion of live mussels versus time (days) for the 4 replicates.

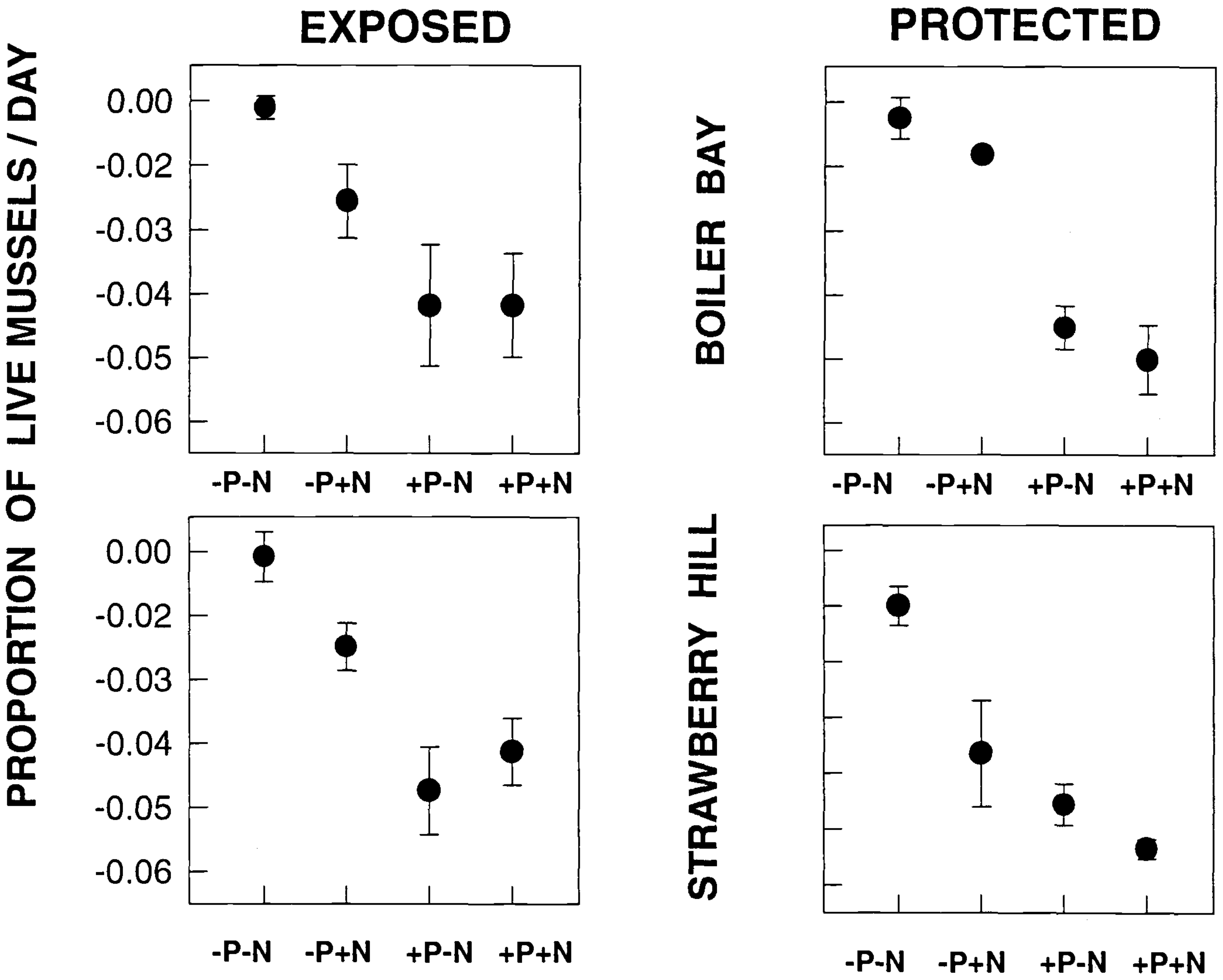

EXPOSED
PROTECTED
PROPORTION OF LIVE MUSSELS / DAY
BOILER BAY
STRAWBERRY HILL
0.00
-0.02
-0.03
-0.04
-0.05
-0.06
-P-N
-P+N
+P-N
+P+N

Figure IV.4.

Figure IV.5. Percentage of the total variance in predation intensity (survival of mussels in the transplant experiment) of either *Pisaster* or *Nucella* that is explained by differences between sites (S), wave exposures (W), the interaction site x wave exposure (S*W), or among replicates (R, tens of meters apart), and clumps (C, few meters apart). The panels on the right show the variance due to replicates and clumps for each site and predator species. Estimates of variance were based on the treatments in which the other predator species had been manually removed and thus do not reflect changes due to interspecific interactions.

Figure IV.5.

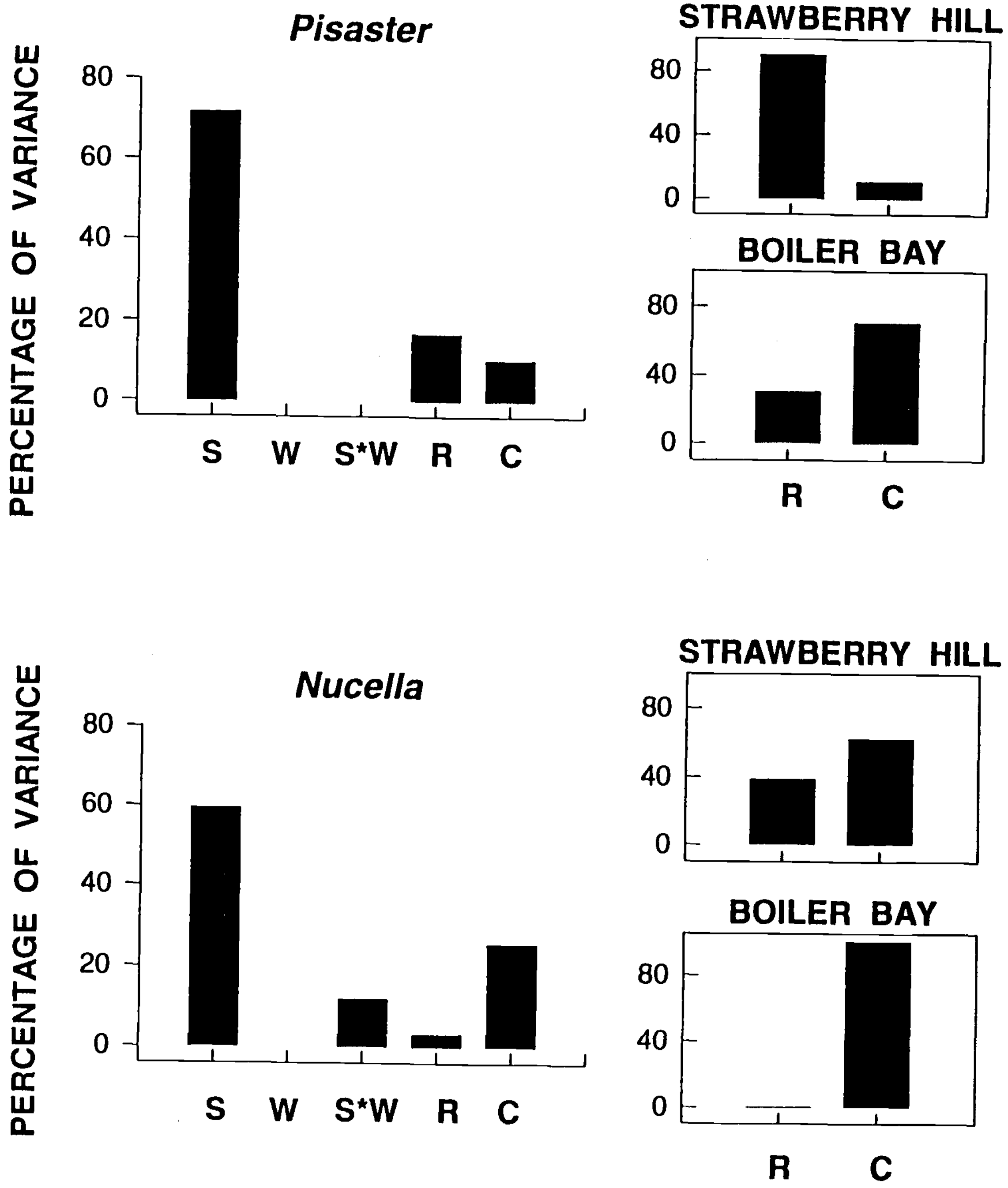
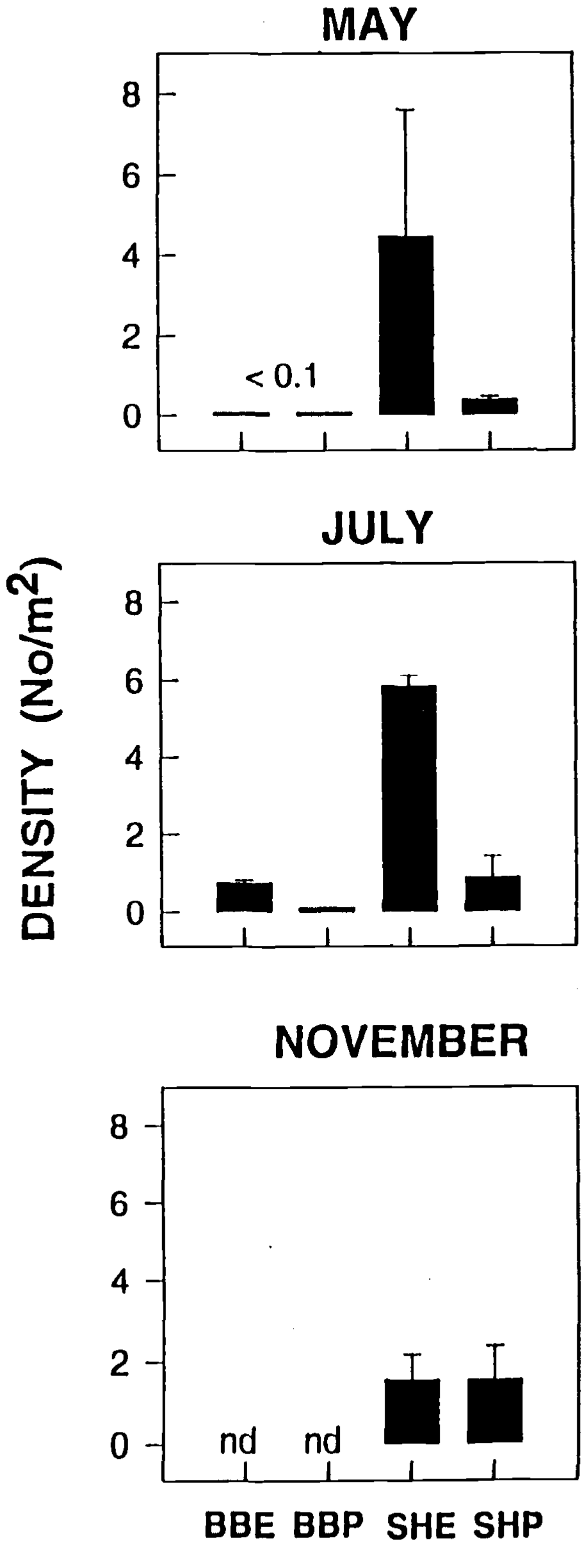

Pisaster
PERCENTAGE OF VARIANCE
80
60
40
20
0
S
W
S*W
R
C
STRAWBERRY HILL
80
40
0
BOILER BAY
80
40
0
R
C
Nucella
PERCENTAGE OF VARIANCE
80
60
40
20
0
S
W
S*W
R
C
STRAWBERRY HILL
80
40
0
BOILER BAY
80
40
0
R
C

Figure IV.6. Density of *Pisaster ochraceus* in seastar control areas (P+) of Strawberry Hill (SH) and Boiler Bay (BB) in both exposed (E) and protected (P) habitats for May, July, and November of 1993.



Pisaster Densities and Diet

As suggested by our previous observations (Menge et al. 1994) seastar densities were higher at Strawberry Hill than Boiler Bay and higher at exposed than protected habitats (Fig. 6). Maximum aggregation of seastars (highest density) was observed at the beginning of the summer, declining by fall. Toward the beginning of fall, sand accumulated in the wave protected habitat of Strawberry Hill (see Menge et al. 1994), causing aggregation of seastars in a small strip of rock right below the California mussel beds (personal observations). This might have inflated density estimates during these months.

The diet of seastars was studied in November 1993 and April 1994 in Strawberry Hill exposed (Fig. 7). The mussel *Mytilus trossulus* was the most frequent item in the diet of seastars in April, when small (< 1 cm long) mussels start to dominate the low intertidal zone. Barnacles (*Balanus glandula* and *Pollicipes polymerus*) and the California mussel, *Mytilus californianus*, were also frequent in the diet, particularly in November. Seastars also consumed whelks (*N. emarginata*), but at very low frequencies (Fig. 7).

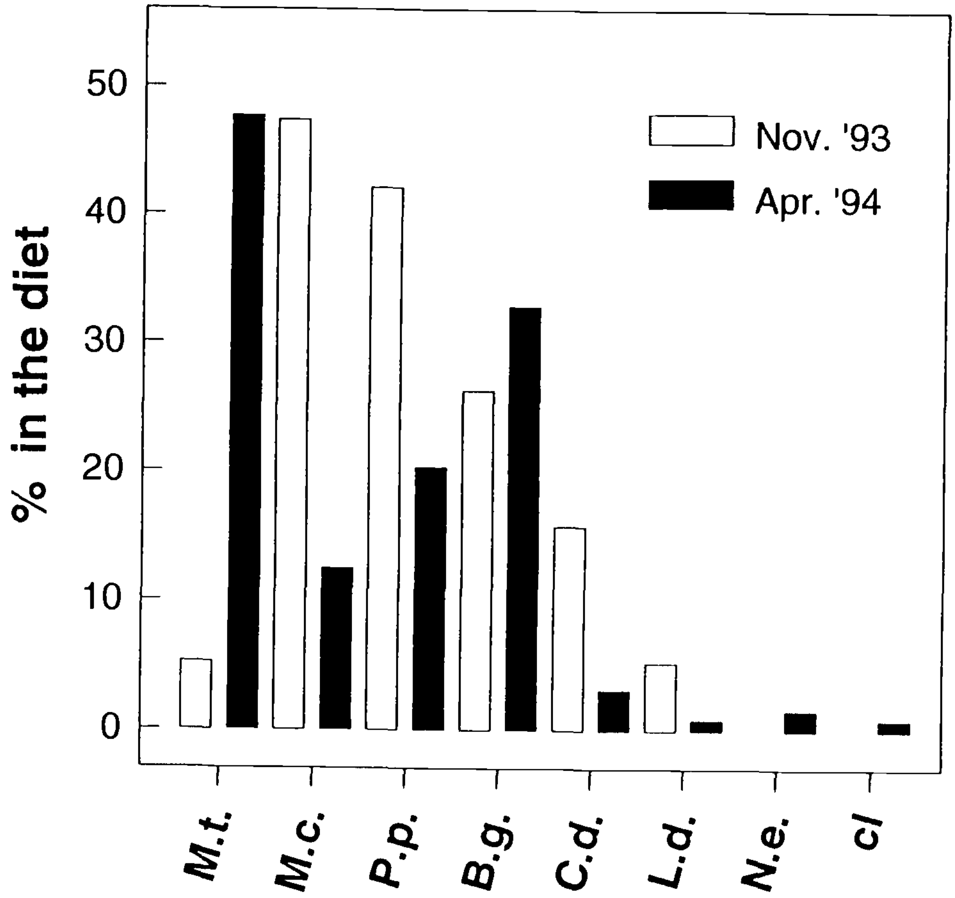
Nucella Population Structure: Effects of *Pisaster*

Under unmanipulated (control) conditions, the highest densities of whelks (*Nucella canaliculata* and *N. emarginata* pooled) were observed at SH exposed (45.9 and 32.3 Ind./m^2 in June and September, respectively) and the lowest at BB protected (7.9 and 15.1 Ind./m^2 in June and September, respectively, Fig 8), a pattern consistent with previous results (Menge et al. 1994). Whelks (both species pooled) were also significantly more abundant in wave exposed (June 47.9 Ind./m^2, September 25.5) than in wave protected habitats (June 6.1 Ind./m^2, September 21.6), but the effect of wave exposure varied with site (Table 4, significant 'site x exposure' interaction for June 5). Before seastars were removed from the experimental areas, there were no significant differences in whelk densities between the areas chosen for seastars removals (-P) and controls (+P), although significant differences were observed among replicates (Table 4, significant effect of 'rep (site exposure *Pisaster*)' for June 5).

After only 4 months of seastar removal, it became apparent that seastars had a significantly negative effect on the total density of whelks (both species pooled) under all wave exposure x site combinations (Table 4, significant main effect of '*Pisaster*' and no significant interaction between *Pisaster* and other factors for September 27). Similar results were obtained when the densities of *Nucella* were considered by species as dependent variables. Results of MANOVA showed that before the experiment (June 5), densities of whelks varied with site and wave exposure condition, but not between areas chosen for the seastar removals and controls (Table 4). After roughly 4 months, the negative effect of seastars on whelk densities was significant (Table 4).

Figure IV.7. Diet of *Pisaster ochraceus* in Strawberry Hill during fall (November 1993, open bars) and spring (April 1994, solid bars). The % in the diet is the number of seastars that were found eating a particular prey out of the total number of individuals eating. In all, 19 out of 42 and 128 out of 207 individuals sampled were observed in fall and spring, respectively. The cumulative percentage exceeds 100 because many seastars were observed eating more than one prey species at the time. M.t.= *Mytilus trossulus*, M.c.= *M. californianus*, P.p.= *Pollicipes polymerus*, B.g.= *Balanus glandula*, C.d.= *Chthamalus dalli*, L.d.= *Lottia digitalis*, N.e.= *Nucella emarginata*, cl= clam.

Figure IV.7.



Comparison of sizes of *Nucella* was restricted to single exposures of Strawberry Hill because low numbers of individuals rendered the analysis impossible in Boiler Bay. Although the statistical analysis was based on the mean size of whelks of each species found within each replicated area, figure 9 presents the pooled sample of all individuals collected from all replicates to facilitate graphical representation. At the beginning of the experiment in June 7, as well as roughly 4 months after (Sept. 23), no significant differences in the sizes of *N. canaliculata* were observed between the areas with and without seastars. However by December, roughly 7 months after the removal of seastars, significantly larger *N. canaliculata* were observed in areas without seastars (Fig 9, Table 5). These results are consistent with those of Menge et al. (1994). In wave protected habitats of Strawberry Hill, a slight, non significant tendency toward larger sizes of *N. emarginata* was also observed after 7 months of seastar removals (Table 5). High and significant variation in *Nucella* sizes among replicates, particularly in the case of *N. emarginata,* made detection of seastar effects difficult.

Table IV.3. Analysis of the linear and quadratic trends of mussel survival rates during the first 24 days of experiment. Slopes of the linear trends were compared among treatments using ANOVA. Linear and quadratic polynomial coefficients were compared using MANOVA. See Table IV.1 for explanations of experimental design and labels.

SOURCE	**linear (ANOVA)** df	F	P	**quadratic (MANOVA)** num df	den df	Wilks λ	P
site	1	1.39	0.2508	2	23	0.71	**0.0184**
exposure	1	0.89	0.3556	2	23	0.95	0.5655
Pisaster	1	79.25	**0.0001**	2	23	0.17	**0.0001**
site x exposure	1	0.69	0.4144	2	23	0.88	0.2381
site x *Pisaster*	1	0.01	0.9329	2	23	0.85	0.1561
exposure x *Pisaster*	1	0.31	0.5836	2	23	0.91	0.3217
site x exposure x *Pisaster*	1	0.33	0.5686	2	23	0.99	0.8799
rep (site x exposure x *Pisaster*)	24	1.61	0.1254	48	46	0.15	0.0872
Nucella	1	14.41	**0.0009**	2	23	0.59	**0.0024**
site x *Nucella*	1	0.49	0.4886	2	23	0.97	0.7268
exposure x *Nucella*	1	1.96	0.1743	2	23	0.88	0.2396
site x exposure x *Nucella*	1	1.95	0.1752	2	23	0.89	0.2348
Pisaster x *Nucella*	1	7.00	**0.0141**	2	23	0.72	**0.0248**
site x *Pisaster* x *Nucella*	1	2.14	0.1560	2	23	0.90	0.3097
exposure x *Pisaster* x *Nucella*	1	1.08	0.3099	2	23	0.95	0.5575
site x exposure x *Pisaster* x *Nucella*	1	0.76	0.3934	2	23	0.97	0.7509
Error	24						

Table IV.4. Analysis of the effects of *Pisaster*, site, and wave exposure on the total density of whelks (both species of *Nucella* pooled) using ANOVA and on the densities by species using MANOVA both before (A) and after (B) the removal of seastars. See table IV.1 for explanation of experimental design and labels.

	ANOVA				MANOVA			
SOURCE	df	MS	F	P	num df	den df	Wilks λ	P
A. Before (June 5)								
site	1	82.89	11.34	**0.0026**	2	23	0.69	**0.0162**
exposure	1	135.22	18.49	**0.0002**	2	23	0.55	**0.0010**
site x exposure	1	73.04	9.99	**0.0042**	2	23	0.73	**0.0260**
Pisaster	1	7.04	0.96	0.3361	2	23	0.96	0.5983
Pisaster x site	1	6.22	0.85	0.3655	2	23	0.98	0.8122
Pisaster x exposure	1	0.75	0.10	0.7509	2	23	0.99	0.9076
Pisaster x site x exp.	1	1.10	0.15	0.7010	2	23	0.97	0.6912
rep(site exp. *Pisaster*)	24	175.51	3.26	**0.0001**	48	522	0.51	**0.0001**
Error	224	3.86						
B. After (September 27)								
site	1	81.32	11.74	**0.0022**	2	23	0.47	**0.0002**
exposure	1	14.82	2.14	0.1564	2	23	0.22	**0.0001**
site x exposure	1	6.13	0.89	0.3561	2	23	0.45	**0.0001**
Pisaster	1	86.23	12.45	**0.0017**	2	23	0.71	**0.0199**
Pisaster x site	1	5.59	0.81	0.3779	2	23	0.90	0.2993
Pisaster x exposure	1	19.93	2.88	0.1027	2	23	0.82	0.0986
Pisaster x site x exposure	1	11.70	1.69	0.2059	2	23	0.86	0.1828
rep(site exposure *Pisaster*)	24	166.22	2.24	**0.0012**	48	446	0.60	**0.0001**
Error	224	4.86						

Table IV.5. Nested analysis of variance of the effect of *Pisaster ochraceus* on the size (shell length) of *Nucella emarginata* and *N. canaliculata* at Strawberry Hill before (June) and after (September, December) the removal of seastars.

	N. canaliculata **(exposed)**				***N. emarginata*** **(protected)**			
SOURCE	df	MS	F	P	df	MS	F	P
A. June								
Pisaster	1	0.6	0.01	0.9199	1	3.9	0.29	0.6066
rep(*Pisaster*)	4	520.4	10.58	**0.0001**	3	57.4	2.73	0.0558
Error	659	12.3			42	7.0		
B. September								
Pisaster	1	2.0	0.26	0.6169	1	42.0	1.41	0.2960
rep(*Pisaster*)	6	32.4	0.64	0.6720	4	148.5	6.78	**0.0001**
Error	206	10.19			121	5.5		
C. December								
Pisaster	1	167.1	7.84	**0.0257**	1	2.4	0.20	0.6945
rep(*Pisaster*)	2	49.5	1.34	0.2671	2	23.2	0.85	0.4372
Error	97	18.5			31	5.8		

Interaction Strengths

The interaction strength between seastars and mussels and between whelks and mussels was estimated for the predators in isolation using Paine's (1992) index. Using this index it was not possible to estimate the interaction strength of each predator when together since then we could not unequivocally attribute mussel mortality to whelks or seastars. The general pattern presented here for day 19 (Fig. 10) varied little over the course of the experiment. Overall, the population (total) interaction strength between seastars and mussels was stronger than that of whelks in all site and wave exposure combination, but only slightly so at Boiler Bay exposed (Fig. 10, notice overlap in the 95% confidence intervals around the mean interaction strength of whelks and seastars at Boiler Bay exposed, BBE). Both seastar and whelk interaction strengths were stronger at Strawberry Hill than at Boiler Bay. The weakest interaction between seastars and mussels was observed at Boiler Bay exposed and the strongest at Strawberry Hill exposed, but these differences tended to decrease toward the end of the experiment. On the other hand, the weakest interaction between whelks and mussels was observed at Boiler Bay protected, with considerably stronger interactions under all the other site and wave exposure conditions. The *per capita* interaction strength of whelks and seastars showed a different pattern (Fig. 10). *Per capita* interaction strengths of whelks were two orders of magnitude lower than those of seastars. They also showed much less variation across site and wave exposure conditions than those of seastars. The pattern observed for *per capita* interactions of seastars was almost opposite to the population interaction strengths; weaker *per capita* values were observed at Strawberry Hill than at Boiler Bay and a large variability between sites and wave exposures characterized the pattern.

Figure IV.8. Mean densities (individuals/m^2 ± SE) of *Nucella* spp (*N. canaliculata* plus *N. emarginata*) in areas of *Pisaster* removal (P-, open bars) and controls (P+, solid bars). Densities for both before (3 June 1993) and 4 months after (23 September 1993) the seastar removals are shown.

Figure IV.8.

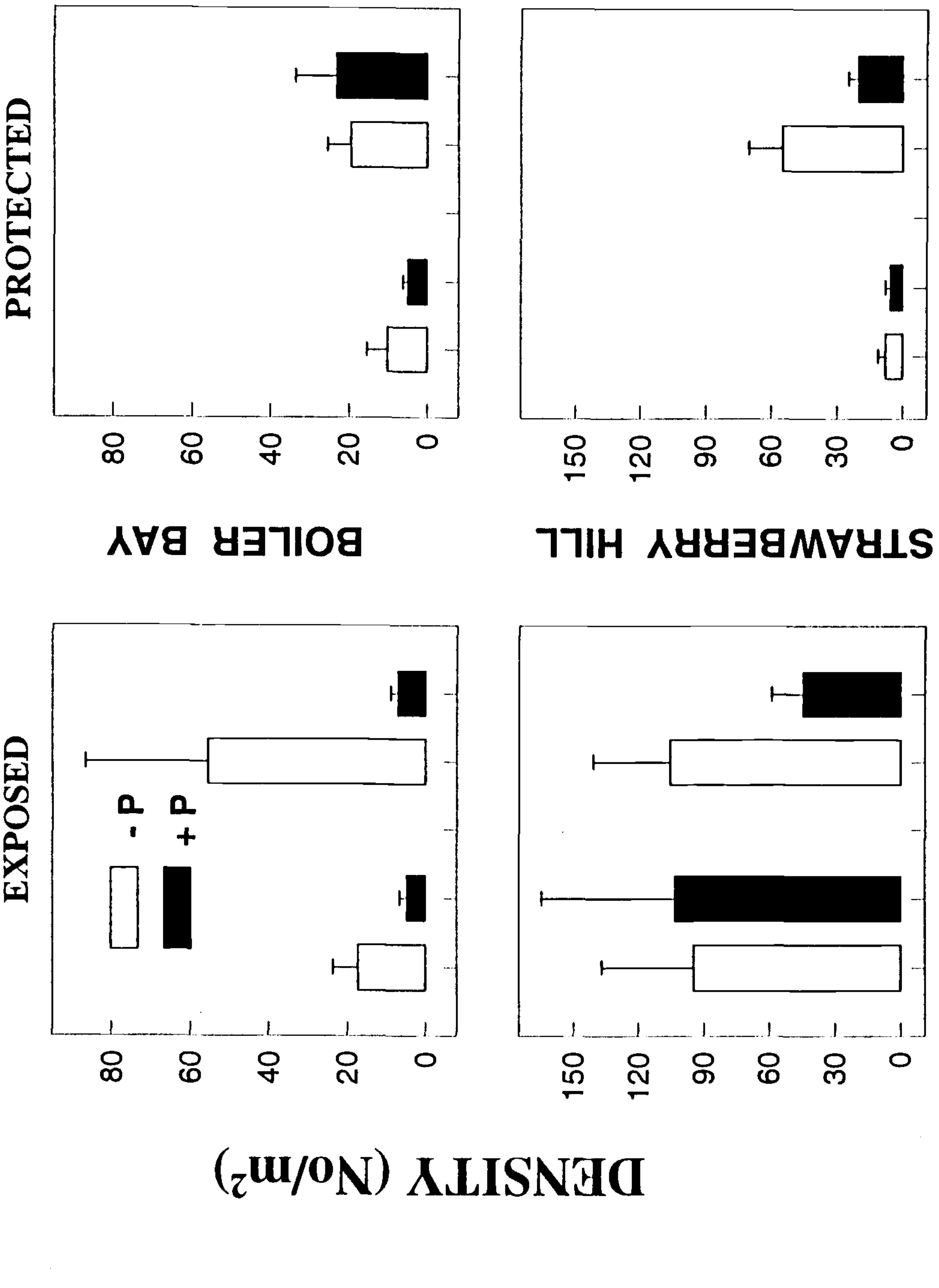

DENSITY (No/m²)
EXPOSED
PROTECTED
BOILER BAY
STRAWBERRY HILL
- P
+ P
80
60
40
20
0
150
120
90
60
30
0
BEFORE
(june)
AFTER
(sept.)

Figure IV.9. Shell length (mm) of whelks in areas with natural densities of seastars (P+, solid bars) or with seastars removed (P-, open bars) for June, September, and December 1993. Data are the pooled sample from the four replicates in Strawberry exposed for *Nucella canaliculata* and from Strawberry Hill protected for *N. emarginata*.

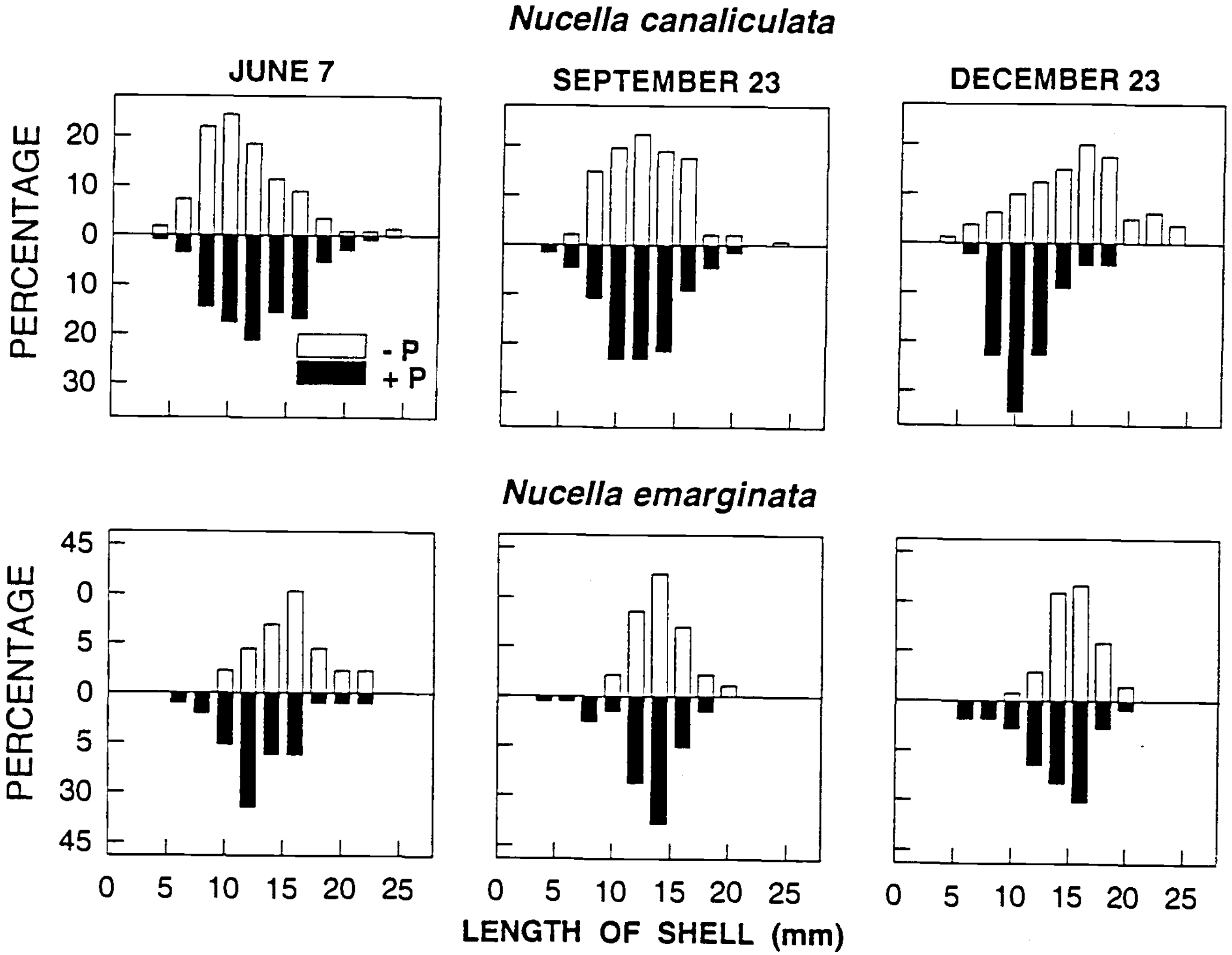
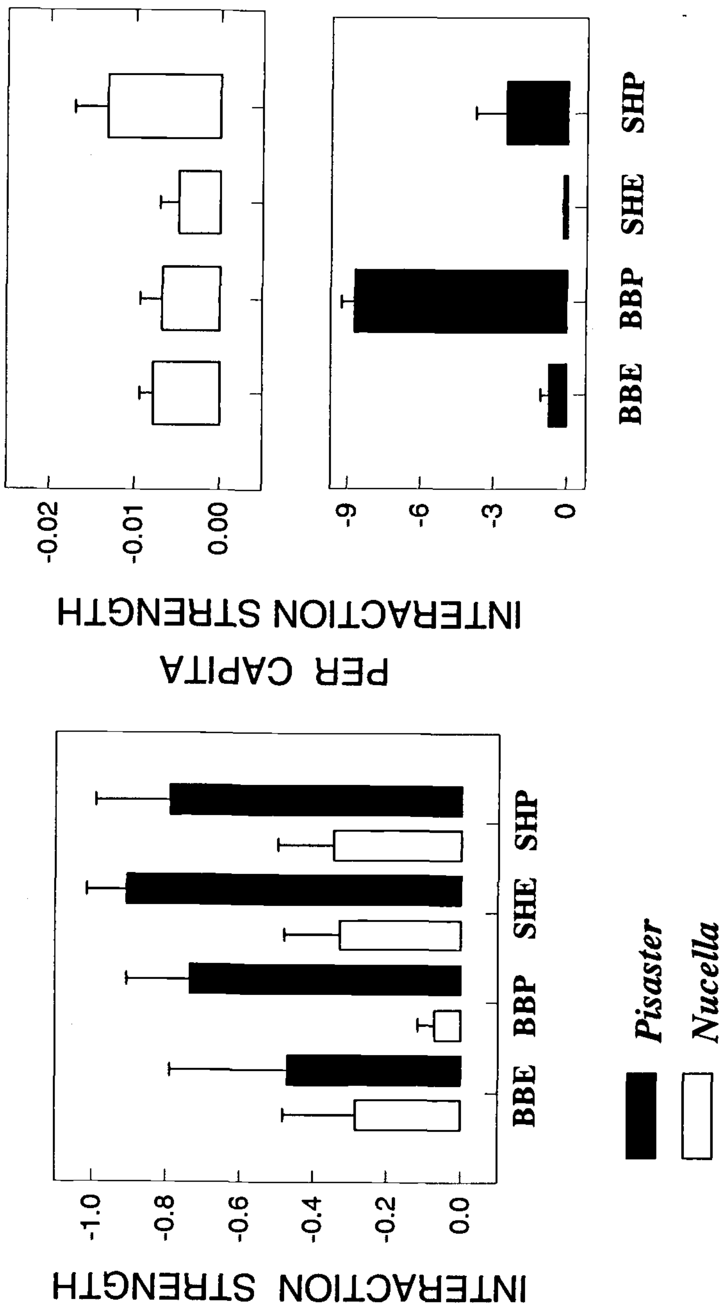

Nucella canaliculata
JUNE 7
SEPTEMBER 23
DECEMBER 23
PERCENTAGE
20
10
0
10
20
30
- P
+ P
Nucella emarginata
PERCENTAGE
45
0
5
0
5
30
45
0
5
10
15
20
25
0
5
10
15
20
25
0
5
10
15
20
25
LENGTH OF SHELL (mm)

Figure IV.9.

Figure IV.10. Mean interaction strengths (± SE) of seastars (solid bars) and whelks (open bars) when in the absence of each other (separate effects) using Paine's (1992) index. The error bars are the 95% confidence intervals obtained from 1000 bootstrap samples (see text for details). Left panels: population or total interaction strength. Right panels: *per capita* interaction strengths calculated by dividing each individual value of population interaction strength by the density of predators (see codes in Figure 6).

Figure IV.10


INTERACTION STRENGTH
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
BBE
BBP
SHE
SHP
Pisaster
Nucella
PER CAPITA
INTERACTION STRENGTH
-0.02
-0.01
0.00
-9
-6
-3
0
BBE
BBP
SHE
SHP

Discussion

Tests of Keystone Predation

Our results show that the intensity of predation by the keystone predator *Pisaster ochraceus* was strong in all site x wave exposure conditions and was not affected by the presence of whelks. On the other hand, predation by whelks was ecologically significant in the absence, but not in the presence of the keystone predator. We suggest that this pattern of interactive effects, where predation by a keystone is robust to the presence of other predators and other predators have weak or insignificant effects in the presence of the keystone is a characteristic of keystone dominated systems. At present, there are no comparable data to test this proposition in other intertidal systems (discussed below), but experiments in freshwater pond communities lend support to the idea that keystone predation is unaffected by the presence of other species in the guild.

In temporary pond communities the newt *Nothophthalmus viridescens dorsalis* acts as a keystone predator; by preying on competitively dominant tadpoles the newt facilitates the coexistence of species that would otherwise be excluded by competition (Morin 1981). Using artificial ponds, (Fauth and Resetarits 1991) tested the robustness of *Nothophthalmus* predation to the presence of the salamander *Siren intermedia,* one of the several other species of predatory salamanders and insects that coexist with *Nothophthalmus* in these communities (Van Buskirk 1988, Fauth et al. 1990). They found that *Nothophthalmus* predation was not affected by the presence or absence of *Siren,* despite the existence of strong competitive effects between the predators (see also Fauth et al., 1990). In their experiments, the salamander preyed unselectively on tadpoles and its effect did not appear to be affected by two different density levels of *Nothophthalmus*. However, their design was incomplete and did not allow for determination of the effect of the salamander in the absence of the keystone.

In intertidal systems, the removal of the starfish *Stichaster australis* from the intertidal zone of New Zealand led to an expansion of the lower limit of the mussel *Perna canaliculus*, despite the presence of the whelk *Neothais scalaris* (Paine 1971), much in the same way as the removal of *Pisaster ochraceus* from the coast of Oregon and Washington led to downward expansions of the mussel *Mytilus californianus*, despite the presence of *Nucella* spp (Paine 1966, 1974, Menge et al. 1994). In New Zealand, Paine (1971) manually removed *Neothais* and *Stichaster* simultaneously, but evaluation of the role of *Neothais* was not possible because mussels did not settle in the experimental rock (Paine 1971, pg. 1103). However, Paine noted that after about a year of *Stichaster* exclusion the density of *Neothais* had increased in the two experimental areas and there was the potential for this whelk species to have important community effects.

In wave protected areas of the outer coast of Washington State, manual removals of *Nucella* spp (= *Thais*) in the absence of *Pisaster* showed that whelk predation can have important effects on barnacle populations, killing most barnacles by the end of each summer (Dayton 1971). However, evaluation of the degree to which *Nucella* predation is affected by *Pisaster* was not possible because the appropriate controlled experiments to measure predation by whelks in the presence of seastars, and by seastars in the absence of whelks could not be conducted (Dayton 1971, pg. 382).

Mechanisms of Interactive Effects

The pattern of interactive effects between whelks and seastars was clear at the beginning of the experiment well before mussels were exterminated by seastars (Figs. 4, 5). The causes for this interaction are not completely understood, but are at least partly related to the fast (few weeks) changes in whelk densities following the removal of seastars. Whelks reached higher densities in areas from which seastars were removed, than in control areas with natural seastar densities, corroborating previous, independent experiments (Menge et al. 1994). The effect of *Pisaster* on the local density of *Nucella* was proportional to the overall density of predators: strong in Strawberry Hill, where predators reach the highest densities, low in boiler Bay exposed, and non existent in Boiler Bay protected, where both seastars and whelks are scarce (Fig. 8). Changes in density of *Nucella* over a few weeks are most likely due to a tendency of whelks to avoid areas with seastars or to aggregate in areas without them (either as a direct response to the seastars or to the local depletion of food), rather than the result of a population buildup (e.g. through increased reproductive rates), or increased mortality due to direct predation by seastars. Although seastars consume whelks, they do so at very low frequencies (Fig. 7), and it seems unlikely that predation has direct consequences on the whelk population. Although the original increase in density might be produced by behavioral aggregation, once a locally dense population of whelks has been established it can be maintained for a long (>2 years) period of time, as long as seastar densities are reduced (Menge et al. 1994). This ability to exploit very localized favorable conditions over few square meters is related to the direct development (lack of a free larval stage) exhibited by species of *Nucella* (Spight

1974), allowing them to maintain locally increased reproductive and/or survival rates (Spight 1974, Spight and Emlen 1976).

Short term interactive effects between seastars and whelks could also (in addition to density changes) be produced by changes in feeding preferences of whelks in the presence of seastars. This kind of indirect effect of a top carnivore predator affecting the feeding or habitat choices of a prey species, which in turn has effects on the rest of the community seems common in lake or estuarine ecosystems (Werner and Hall 1988, Posey and Hines 1991, Osenberg et al. 1992, Werner 1992), but it has been documented rarely in intertidal systems. Preliminary studies performed in protected areas of Strawberry Hill and Boiler Bay suggest that, at least during winter time, seastars do not affect the feeding preferences of whelks, although some differences between sites do occur (E. Wieters, unpublished data). Whether or not seastars affect whelk feeding choices during peaks of foraging activity and/or at high densities has not yet been addressed, however.

Over a period of about 7 months, removal of *Pisaster* from large areas of Strawberry Hill also led to significantly larger sizes of *Nucella canaliculata* in comparison to control areas with normal densities of seastars, although no significant effect on the sizes of *N. emarginata* were observed. The difference between *Nucella* species may be related to the distribution of whelks between wave exposures and to our ability to test for the significance of the seastar effect. While *N. canaliculata* is more abundant in wave exposed habitats, where seastars reach high densities, *N. emarginata* is more abundant in wave protected areas where they might be less affected by the generally lower densities of seastars. However, it is very difficult to demonstrate the effect of seastars on the sizes of whelks because of the high variation over small spatial scales (few meters) in both whelk densities and sizes (see also Dayton 1971, Spight 1974), which probably reflects the recent local history of prey and seastar abundances in the site. Our experiments were designed to test primarily the separate and combined effects of predators on mussels, and only secondarily the effect of seastars on whelk populations. A more powerful experimental design would include increased replicate number and/or the initial manipulation of the sizes of whelks in each replicate. Thus, given the limitations in experimental design, the significance of the seastar effect on *Nucella* sizes is remarkable and supports previous independent observations (Menge et al. 1994). Interspecific competition for food between seastars and whelks is a likely explanation for this. In areas where seastars deplete the mussel *M. trossulus*, one of the preferred prey of *Nucella* species (Palmer 1984), the whelks might have to revert to less preferred prey (e.g. *Chthamalus dalli, Semibalanus cariosus, Pollicipes polymerus;* pers. obs.). Indeed, both *N. emarginata* and *N. canaliculata* feeding on small to medium size *M. trossulus* or medium size *Balanus glandula* can reach higher growth rates than when feeding on a number of other, less preferred prey (Palmer 1983). Direct size selective predation by seastars on large whelks seems an unlikely cause of the shift in *Nucella* sizes because of the seemingly low seastar predation rates on whelks, but at present this alternative cannot be ruled out.

Our experimental design did not allow us to determine the potential effects of whelks on seastar population structure (e.g. size, density). Because of the large differences in body size and mobility, evaluation of the effects of whelks on seastar populations requires removal of whelks over areas well beyond what can be realistically maintained in the field. These same differences in body size, mobility, and predation rates lead us to believe that whelks have little, if any effect on populations of *Pisaster*.

The interactive effects of seastars and whelks on mussels is thus the result of two factors: a) the ability of seastars to exterminate mussels from the mid-low intertidal zone under both experimental and natural conditions, regardless of the presence of whelks, and b) the negative effect of seastars on predation by whelks when mussel prey are still abundant. The short-term (few weeks) effect of seastars on whelk predation intensity is at least partly produced by the negative effect of seastars on local whelk densities, which in turn seems to result from behavioral responses of whelks to the presence of seastars (or the local depletion of food by the seastars). Besides this 'interaction chain' kind of indirect effect of seastars on mussels (sensu Wootton 1993), a higher-order interaction (Abrams 1983) or "interaction modification" (*sensu* Wootton 1993), in which seastars modify whelk feeding preferences might also be involved in areas of high predator densities. These possibilities are currently being explored.

Interaction Strength

Estimates of interaction strengths between predators and prey using Paine's (1992) index, measured the separate effects of seastars and whelks in the absence of each other. Because whelk predation intensity is reduced in the presence of seastars, the separate interaction strengths cannot provide good estimates of the combined interaction strength of these predators (non-additivity of predators effects, Navarrete and Menge in prep.). Nevertheless, these estimates show the potential for predators to control prey and allow comparisons of the variability in strong (keystone) versus weak interactions. Across sites and wave exposures the interaction strength between the keystone (*Pisaster*) and mussels was stronger than that between whelks and mussels. However, the difference was slight at Boiler Bay exposed, reflecting the potential for whelks to compensate for *Pisaster* predation on small mussels after the removal of the keystone. Overall, total population interaction strength of *Pisaster* was less variable than that of whelks, which varied greatly between wave exposures in Boiler Bay. This is also reflected in the relative contributions of wave exposure to the total variance in predation intensity of whelks and seastars. Within a given site and exposure, predation intensity of the larger and more mobile *Pisaster* varied more over scales of several tens of meters (among replicates) than over few meters (among clumps), while most variation in whelk predation occurred over just few meters. Increased density of predators changes the pattern of spatial variation, however. At higher densities, the variation over the smallest spatial scales tends to decrease, presumably as both whelks and seastars encounter prey more frequently.

The *per capita* interaction strengths of seastars and whelks were very different; the effect of each individual seastar was over two orders of magnitude larger than that of an average individual of *Nucella* spp (Fig. 10). This is not surprising given their widely different individual rates and modes of predation on mussels. *Pisaster* can dislodge an entire clump of mussels in a single foraging bout while *Nucella* eats mussels individually, usually drilling a hole through the valves (Dayton 1971, Menge 1982, Palmer 1984, Hughes and Burrows 1993). However, the *per capita* effect of *Pisaster* was much more variable across sites and wave exposures than that of *Nucella*, contrasting with their comparatively homogeneous population effects. Mean *per capita* effect of seastars at Boiler Bay protected was over 9 times larger than at Strawberry Hill exposed. Large differences in per capita effects among sites and wave exposures occurred because, in general, simple measures of density grossly under-estimate the ability of large and mobile predators to localize prey.

How important is predation by *Nucella* on the rest of the intertidal community? In the absence of *Pisaster*, predation by *Nucella* can have important consequences for the rest of the mid-low intertidal community since they are capable of controlling the abundance of the mussel *Mytilus trossulus;* otherwise, the mussels dominate the space and, temporarily, exclude other sessile species by smothering them (pers. obs.). However, the competitive dominant species for space in this habitat is the California mussel *M. californianus* (Paine 1966, 1974) and although *Nucella* can eat small individuals of this species in the low zone, they cannot prevent the downward expansion of the mussel bed following the removal of *Pisaster* (Menge et al. 1994). When patches of *M. trossulus* remain in the substratum, in the absence of whelks and seastars, *M. californianus* recruits among these mussels and after about a year start to dominate the mussel clumps and take over the space (Menge et al. 1994, Navarrete, in prep.). In contrast, when *M. trossulus* are preyed upon, *M. californianus* does not recruit on the barnacle- and bare rock-dominated substratum of the low zone. Thus, in the areas where *Nucella* reach high densities, the whelks can probably delay the establishment of *M. californianus* for an indefinite time.

Although these results give support to the idea that in systems with keystone species other coexisting species have minor effects on the rest of the community, the use of the keystone concept in conservation biology should be carefully evaluated. After the loss of a keystone from a particular system, the rest of the community can rearrange and previously 'redundant' species (sensu Lawton & Brown) can play major role in the new scenario. Certainly, Paine(1971) and others (e.g. Dayton 1971) have recognized the potential of other predators following the removal of a keystone species. Before decisions about conservation efforts can be made, evaluation of the potentially interactive effects of the main species in a community is necessary.

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CHAPTER V

VARIABLE PREDATION: EFFECTS OF WHELKS ON A MID INTERTIDAL SUCCESSIONAL COMMUNITY

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Abstract

I studied the impact of variable predation by whelks on a mid intertidal successional community at a wave exposed environment in the coast of Oregon. Monitoring of the density of whelks over time and space for a period of 34 months permitted an estimation of the spatial variation in both predation intensity and predation frequency. Two simultaneous cage experiments were then conducted for a period of 25 months. One experiment evaluated the effect of exclusion of invertebrate predators on the sessile community by using permanent exclusion cages and comparing the results against unmanipulated control plots and 'roofs' that controlled for cage shading and predation by birds. The other experiment evaluated the effects of variable predation in a factorial design that permitted the separation of the effects of predation intensity from variation in predation frequency (temporal pattern of predation events). I contrasted the patterns observed under a constant versus two variable predation regimes.

The densities of the two whelk species present in the study site, *Nucella canaliculata* and *N. emarginata,* were highly correlated over time and varied greatly within and among years. Spatial variation in whelk density and frequency also occurred. Some areas of the site were exposed to whelks most of the time, while others rarely had predators. Areas of high whelk frequency were spatially uncorrelated with the mean density of whelks. The size and the intensity of whelk aggregations also varied over time, becoming more patchy in summer when the highest densities were observed. These factors contributed to within habitat variability in predation regimes by whelks. Direct and indirect effects of the exclusion of invertebrate predators led to several changes in the abundance of sessile species, notably a rapid increase in the cover of the bay mussel *Mytilus trossulus* and a slow and small increase in the cover of gooseneck barnacles and the California mussel *Mytilus californianus.* With one exception, cage shading and bird predation had no effect on the sessile species assemblage. Variable predation produced community composition different from those observed under a constant predation regime or predator exclusions. In general, the individual species responses to the different predation regimes could not be predicted from the results of the exclusion experiment. Non-linearities and indirect effects could be magnified by a variable predation regime. Community composition in the unmanipulated control plots resembled the composition observed under the low and medium frequency treatment (variable predation) more closely than that observed under a constant predation regime for all levels of predation intensities. However, none of the predation regimes used in the experiment completely matched the community observed in the controls.

Temporal variability in predation by whelks can increase spatial variability in the sessile community and create distinctive community compositions, even though the overall effects of whelks in this successional community was rather weak. Variability in predation is probably an important, yet poorly understood cause of spatial heterogeneity in most ecosystems.

Introduction

Probably the one feature that characterizes most natural communities is variability. Large spatial and temporal variation in population abundance or species composition has always impressed field ecologists (Watt 1947, Andrewartha and Birch 1954, Hutchinson 1959). Physical and biological, deterministic and stochastic processes can contribute significantly to the total variability in communities, and theoretical models make predictions about the way these processes might interact and vary over environmental gradients (Huston 1979, Oksanen et al. 1981, Menge and Sutherland 1987, Schoener 1989, Menge and Olson 1990). Predation has long been recognized as an important cause of variability in prey populations and communities (Darwin 1859, Lubchenco and Real 1991). Early experiments showed how predators can affect prey abundance, body size distributions, or species composition (Brooks and Dodson 1965, Paine 1966, Peterson 1979), and simple theoretical models helped explain this process and made predictions about its consequences (Roughgarden and Feldman 1975, Caswell 1978, Chesson and Case 1986). Much empirical information on the effects of predators has since accumulated and the vast majority comes from an insightful albeit simple approach, the short- or long-term deletion of predators from a system and monitoring of prey responses to this perturbation (see Sih et al. 1985, Hixon 1986, 1991, Kerfoot and Sih 1987, Menge et al. 1994, for reviews). Nevertheless, predation as many other disturbance agents is not invariable but it usually fluctuates widely over time.

This realization led to the incorporation of temporal variability into theoretical models (Chesson 1978, Abugov 1982, Anderson et al. 1982, Pickett and White 1985, Petraitis et al. 1989) and to the prediction that temporal variability in predation can increase the spatial and temporal variability in prey populations and promote diversity and persistence and stability (Chesson and Case 1986, Woolhouse and Harmsen 1987). Despite these theoretical insights, few studies have experimentally evaluated the consequences of temporally variable predation (Fairweather 1988b, Butler 1989).

Both within year (seasonal) and between year fluctuations in predation regimes are apparent in many ecosystems and their effects are manifested in prey species composition, abundance or size structure (Dayton 1971, Menge 1976, 1983, Gutierrez et al. 1980, Marsh 1986, Fairweather 1988b, Hairston 1988). However, experimental manipulation of the pattern of temporal variation is rare. In many cases prey variability could easily be attributable to variation in the intensity of predation between seasons or years. Indeed, much experimental evidence obtained through repetition of exclusion experiments in different areas or times shows that the intensity of predation, as measured by prey mortality or by the total biomass removed by predators from a given habitat, vary significantly over space and time and can produce significant variation in prey community structure (Hixon and Brostoff 1983, Menge 1983, Fairweather et al. 1984, Fawcett 1984, Berlow and Navarrete in prep., Menge et al. 1994, Navarrete and Menge in prep.).

The extent of the effects of variable predation on community structure cannot be evaluated unless the correlated variation in predation intensity is experimentally isolated from the frequency at which predation events occur. Of course, it is possible that within natural communities temporally variable predation has no distinctive effects from those of a constant predation regime that produces the same total mortality of prey when a period of time longer than the interval of time between predation events is considered. At some simplified theoretical level the community-level consequences of predation (or disturbance) frequency are the same as those produced by varying predation intensities (Huston 1979, Malanson 1984).

A number of mechanisms suggest that variable predation can create distinctive community patterns, however. For instance, if predators are limited by the size of prey they can handle (e.g. Paine 1976, Palmer 1984, Navarrete and Castilla 1988), the removal and subsequent reintroduction of predators to a patch of habitat may or may not lead to the recovery of the original prey community structure (Paine et al. 1985, Farrell 1988). Whether or not temporally variable predation creates prey communities that are different from those produced by constant predation and whether or not it contributes to the temporal or spatial variation of prey remain open questions in most ecosystems.

To my knowledge the only experimental approach to directly answer these questions in a natural system is Butler's (1989) elegant study of the effects of variable predation by the bluegill sunfish, *Lepomis macrochirus* on the invertebrate community of a small in Florida, USA. His results showed that a variable predation regime produced distinctive prey compositions, resembled closer the species composition and variability of natural (unmanipulated) mid-depth areas of the lake than a constant predation regime, and increased the mean body size and body size variance of some prey species over those observed under the constant predation regime or a constant exclusion treatment. Bluegill sunfish exhibited aggregating behavior and the degree of aggregation changed among habitats and between seasons. This produced a variable pattern of predation and spatial variation in the frequency at which patches of habitat were visited by the fish schools (Butler 1989, see also Werner et al. 1983). Although

Butler's experimental design did not allow him to separate the effects of frequency and intensity of predation (in the variable predation treatment both the frequency and the number of fish per cage were manipulated in an effort to emulate the natural regime in control areas; Butler 1990, pp. 325), his results highlight the importance of variable predation for this ecosystem.

It is important to emphasize that seasonal or year to year variation is not the only or necessarily the most important scale of temporal variability in predation. Since most predator species exhibit aggregated distributions at some spatial scale (Taylor 1961, 1984, Titmus 1983), and since these aggregations typically move over a larger space, patches of prey species within the same habitat will be affected by different levels of intensity and frequency of visits by predators. This phenomenon is obvious in highly mobile and large predators that move as a discrete unit such as a flock of birds or a school of fish (Marsh 1986, Butler 1989), but it is also observed in less discrete aggregations of less mobile predators such as intertidal whelks (Spight 1974, Fairweather 1988a).

Whelks are ubiquitous predators in mid and mid-low zones of rocky intertidal communities (Fairweather et al. 1984, Palmer 1984, Hughes and Burrows 1993) where they can have from very minor to very dramatic effects on their prey (Wootton 1994, Berlow and Navarrete in prep.) . On the wave exposed coast of Oregon, the whelks, *Nucella emarginata* and *N. canaliculata*, are found in dense aggregations in the mid-low zone below the mussel beds of the California mussel *Mytilus californianus*, or in the patches within the mussel bed at mid-zones (Menge et al. 1994, Navarrete and Menge in prep.). Both species are limited by the size of mussel or barnacle prey they can handle (Dayton 1971, Palmer 1984), yet in the lower zone they can have important negative effects on mussel mortality over small spatial scales if the keystone predator *Pisaster ochraceus* is removed (Navarrete and Menge in prep.). These characteristics and comparatively slow mobility and size of whelks make them a good model to study the effects of variable predation in rocky intertidal communities.

In this study I document the small-scale spatial distribution and persistence of whelks at a mid-zone habitat on the Oregon coast and experimentally evaluate the effects of 1) long-term (3 years) predator exclusions and 2) variable predation by whelk on the successional sessile prey community that occupy patches within the California mussel beds. The experimental design allowed me to distinguish between the effects of frequency and intensity of predation and test the hypotheses that 1) temporally persistent exclusion of whelks lead to changes in prey abundance and prey composition, 2) variable predation creates prey communities different from those resulting from a constant predation regime, 3) variable predation contributes to the temporal and spatial variability in prey populations, 4) variable predation increases local species richness and diversity, 5) variable predation creates communities that resemble more closely the natural predation regimes than the constant predation treatments.

Site and Study Organisms

The study was conducted at the mid intertidal zone of Fogarty Creek Point (44°51'N, 124°03'W), about 2 Km north of Boiler Bay State Park, on the central coast of Oregon. Tides in Oregon are of the mixed semidiurnal type with a range of ≈ 2.5 m. Zonation of intertidal organisms at Fogarty Creek Point was clear and similar to that described for Boiler Bay by (Menge et al. 1994). The high intertidal zone was dominated by acorn barnacles, *Balanus glandula* and *Chthamalus dalli*, fucoid algae *Pelvetiopsis limitata* and *Fucus distichus*, and the red filamentous algae *Endocladia muricata* (see Farrell 1991 for detailed description of this high intertidal assemblage). The mid zone was dominated by beds of the California mussel, *Mytilus californianus*. Patches of bare rock or varying sizes are continually created either by waves dislodging the mussels (Paine and Levin 1981) or the combination of winter freezes and wave dislodgment (D. Brosnan, personal communication). The sea-palm kelp, *Postelsia palmaeformis* also contributes to patch formation in the lower end of the mussel bed at highly wave exposed areas at the north end of the site by settling on mussel shells (S. Navarrete, personal observations). Species composition and the relative abundance of species in the patches varied widely over space and within a patch as succession progressed (see also Paine and Levin 1981, Wootton 1993). The barnacles *Semibalanus cariosus* and *Pollicipes polymerus* were common and sometimes dominant in the older patches; the smaller mussel *Mytilus trossulus* (= *M. edulis*) usually appeared in the patches in early spring (settlement occurs in fall) and it also dominated some of the patches for long time (> 3 years). Several algae, mostly filamentous reds (*Polysiphonia, Pterosiphonia, Odonthalia*), were common but overall not very abundant, although some patches were temporarily (few months) covered with an algal turf. The low intertidal zone at Fogarty Creek was dominated by coralline calcareous algae, mostly *Corallina* spp., surfgrass, *Phyllospadix* spp. and the kelps *Lessoniopsis littoralis, Hedophyllum sessile*, and *Laminaria setchellii.* The gooseneck barnacle *P. polymerus* and the acorn barnacles *S. cariosus* and *Balanus nubilus* were also common in the low zone.

Herbivores, mostly limpets and littorines, were abundant in the high zone and moderately abundant in the patches among the mussel bed in the mid zone (see Farrell 1988, 1991). Other grazers, such chitons and urchins were scarce and restricted to the low zone, below the California mussel beds. Densities of the predatory starfish *Pisaster ochraceus* were similar to those observed in Boiler Bay and other rocky sites (Menge et al. 1994, and S. Navarrete, personal observations). The most abundant invertebrate predators in the mid zone were the whelks *Nucella canaliculata* and *N. emarginata*. Birds, mostly oystercatchers, *Hematopus bachmani*, and gulls, *Larus* spp., were also present at these sites.

Experiments were conducted in the mid zone of two horizontal (slope≈ 0) benches moderately exposed to waves in the South end of Fogarty Creek Point. Benches were about 10-15 m long and 5-6 m wide and about 20 m apart. The lower end of the benches ended abruptly in a steep, almost vertical wall. Mussel beds of *M. californianus* occupy roughly between 50-60% of the substratum. Whelks were abundant, particularly in spring and summer (see results) and adults of the starfish *P. ochraceus* were naturally absent from the benches, although recruits and juveniles (< 3 cm total diameter) were common. The brooding starfish *Leptasterias hexactis* was also common in the edge of patches in the mussel bed.

Methods

Abundance and Distribution of Whelks

In order to estimate the temporal and spatial variation in the abundance of whelks, fixed quadrats were monitored on an approximately bimonthly basis from February 1991 through December 1993. It was not always possible to monitor densities with this frequency. Sampling in rough winter condition was very slow and the time available for work during the low tides was dedicated to monitoring the cage experiments (see below). In all, densities were monitored

13 times in a period of 34 months. Three 10-14 m long transects 1 m apart were laid along each of the two benches. The position and orientation of the transects was permanently marked with marine putty (Z-spar) and each time a tape measure was extended from the marked positions. Ten to twelve 50 x 50 cm quadrats were placed every 50 cm along the transects. All whelks found in the quadrats were identified, counted and every 4-6 mo. their shell lengths were also recorded. Percent cover of *M. californianus* was visually estimated in each quadrat. Special care was placed to collect whelks from amongst the mussels without damaging the mussel bed. The resulting difficulty of sampling snails among the mussels might have resulted in underestimates of whelk abundance. However, a destructive sampling taken in June 1991, in which snails were first sampled from a 20 x 20 cm area and then all mussel removed to look for all snails in the area showed that only 1 small recruits (< 5 mm shell length) had escaped the sampling. Similar results have been obtained nearby with larger sample sizes (E.L. Berlow, personal communication).

To characterize the spatial pattern of variation in more detail, three additional transects, with 10-12 quadrats each, were added in between the previously marked transects in April and May 1992. Quadrats sampled about 40-60% of the entire flat surface of the benches. Time constraints did not allow me to monitor all these quadrats on a regular basis however.

Data Analysis. Correlation coefficients were calculated to determine the degree of association between species of *Nucella* over time and over space. Similar analysis was used to determine the correlation of densities with the cover of mussel beds over space. In all cases, the Pearson product-moment correlation coefficient was used when data exhibited normal distribution and the Spearman

Rank correlation when data could not be transformed to conform with normality.

The frequency at which whelks were observed in different areas of the study site was calculated by recording the number of times at least 2 whelks were observed in a fixed quadrat position out of a total of 13 observations in 34 months. In this case, both species were pooled (despite the spatial correlation between species, see Results) since the interest was on the total (potential) predation by whelks. To determine the size of aggregation and if the aggregation level changed between seasons, the paired-quadrat variance method (Ludwig and Goodall 1978) and plots of variance versus quadrat spacing were used as recommended by Ludwig and Reynolds (1988) for each *Nucella* species.

Predation by Whelks: Exclusion Experiments

To determine the effects of predation by *Nucella emarginata* and *N. canaliculata* on the sessile successional community that occupy the patches within the mussel bed zone, I conducted a cage exclusion experiment that permanently removed the whelks for the duration of the experiment. Cages 20 x 20 x 5 cm in size were made of stainless steel mesh and had 5 cm wide outward flaps in the bottom rim. The flaps helped affix the cages to the rock with stainless steel screws and prevented invasion by unwanted invertebrates. A piece of silicone tubing was attached around the rim of the cages to provide a better fit to the irregular rock. The cages excluded whelks and most other mobile macro invertebrates. Limpets and other herbivores (e.g. small chitons, gammarus amphipods) were present inside the exclusion cages and no attempt was made to regulate their densities. Monitoring showed that the cages did not affect the densities of limpets, although they might have reduced the density of large chitons (personal observations). Four replicates were randomly assigned to 52 20 x 20 cm plots that were selected in January 1991, marked with 4 stainless steel screws in the corners, and inspected periodically until the experiment began by installing the cages in April 1991. Three plots (out of 55) originally marked with screws were not used in this or the variable predation experiment (see below) because their species composition differed from the rest by the time the experiment was begun. The rock surface of the plots was dominated by adults and recruits (<2 mm diameter) of the barnacle *Balanus glandula* (>70 % combined cover), and *Chthamalus dalli* (10% cover). Natural variation of the community in the presence of predators ('controls') was monitored in 11, randomly assigned marked plots that were left undisturbed, except for 4 screws in the corners. The greater number of control than treatment replicates was considered necessary to encompass the expected natural spatial variation in the community. All controls were used in the statistical analyses.

To evaluate 'cage effects' or artifacts introduced by the cages themselves, separate from the exclusion of invertebrate predators, I set up 4 replicates of 'roofs' made of the same mesh as the cages. Roofs were 20 x 20 cm squares of mesh held 5 cm off the rock surface with four pieces of PVC tubes. Roofs provided shading similar to the full cages while allowing the free movement of whelks and other invertebrates under them (Connell 1961, Dayton 1971, Menge 1976). However, the roofs were also effective barriers against predation by birds (Marsh 1984, Wootton 1992, S. Navarrete, personal observations). Thus, comparisons of roofs versus the marked control plots showed the magnitude of the effects of cage shading and bird predation, but these two factors could not be separated.

Besides the shading introduced by the cage mesh, the cage rims attached to the rock potentially introduced another artifact. Nereis polychaetes were attracted under the flaps, as were small individuals (< 1.5 cm total diameter) of the brooding starfish *Leptasterias hexactis*. However, most of these were retained outside the plot by the silicone tubing. Efforts were made to reduce the number of *Leptasterias* inside the cages to levels similar to those observed in the control plots. Plots were monitored every month and photographed every 2 months (2 pictures of a 20 x 10 cm area per plot) from April 1991 through May 1993. Two remaining exclusion cages, one roof and the marked control plots were again visited and photographed in November 1993 and June 1994, but these data were not included in the analyses. During the regular monitoring, re-invading snails were counted and removed and cages and roofs were brushed with a metal brush to remove algae and barnacles that settle on the mesh. The presence of species was recorded in the field to help in the identification when analyzing the pictures. Percent cover of sessile species was estimated from the pictures by the intersection-point method using a transparent quadrat with 100 regularly spaced points. In February 1991, before the experiment was begun, direct estimates of percent cover were taken in the field with a 20 x 20 cm quadrat with 81 intersection points and compared to estimates obtained from pictures. Picture estimates of percent cover did not differ appreciably from field estimates (see also Foster et al. 1991), but it was difficult to identify algae at the species level from the pictures. Field notes listing all species present in each plot helped with this part of the analysis.

Data Analysis. A one-way repeated measures analysis of variance (RM-ANOVA) was used to analyze the results of the exclusion experiment. Repeated measures were necessary to take into account the time correlation of the experimental units (von Ende 1993). Assumptions of normality and variance homogeneity (Sokal and Rohlf 1981) were checked by visual inspection of residual plots and Cochran's C test for variance homogeneity. In all cases arcsin, square root transformed cover data exhibited better distribution and homogeneity. The assumption of homogeneity of treatment differences variance (circularity) required to approach repeated measures as a univariate split-plot design was tested using the Mauchly's sphericity test applied to the ortho-normalized components of the variance co-variance matrix (Crowder and Hand 1990) . When this assumption was not met, I present results of 1) the univariate (split-plot) approach with Huynh-Feldt (H-F) adjusted probability values (H-F Epsilon correction factors are given in the tables of Results), which makes the tests more conservative (Crowder and Hand 1990, von Ende 1993), and 2) the multivariate (MANOVA) approach to repeated measures, which avoids problems of inflated Type I errors (concluding there is a difference when there is not) due to time correlations, but in general gives less powerful tests of hypotheses than the univariate approach (Mead 1988, von Ende 1993). Two *a priori* planned contrasts were performed on the between (means over time) and within subjects factors (time and its interaction with treatment). The first contrast compared control plots versus exclusion cages; a test for the effects of exclusion of predators (*Nucella* spp.). The second contrast compared control plots versus the roof (cage control) plots; a test for the effect of cages and predation by birds (see above).

The analyses were conducted separately for the most abundant sessile species in the plots. This procedure is not always desirable since correlations among species might affect the Type I error rate and a multivariate analysis of variance (MANOVA) considering all species simultaneously is recommended by some authors (Tabachnick and Fidell 1989, Scheiner 1993). In this study a repeated measures MANOVA could not be used because it did not have enough degrees of freedom to test for treatment effects. Pooling of data over time (e.g. years) is an alternative to increase the degrees of freedom (e.g. Butler 1989), but in this case the temporal pattern of variation and its interaction with treatments was an important component of the study. While the single species-based approach described above has the advantage of providing probability values for each species, which can be of much help when interpreting the results (e.g. test effects of predation on the competitive dominant species), these probabilities might be affected by correlations. Because of these constraints, I also conducted a MANOVA on the six most abundant sessile species by considering the year averages as one factor (3 levels: 1991, 1992, 1993) and the treatment (control, exclusion) as another in a two-way factorial design. Yearly means can also be correlated, however, and results of this analysis should also be taken with caution. Correspondence between the species-based approach and the MANOVA lends confidence to interpretation. Calculation of standardized canonical coefficients of canonical variates (Scheiner 1993) followed the MANOVA to determine the relative contribution of the different species to the differences among treatments.

The predator exclusion experiment and statistical analyses tested the following specific hypotheses:

1) Whelks have no effect (direct or indirect) on the abundance (cover) of sessile species. Tested by the repeated measures analysis on the cover of different species (contrast between control and exclusion plots).

2) Whelks have no effect on the relative abundances of the sessile species. Tested by the species-based analysis (evaluating all results together) and by MANOVA on most abundant species.

3) Whelks have no effects on species richness (number of species) or species diversity (relative abundances of species, regardless of species identity). Tested by repeated measures analysis of variance on rank transformed species richness data and by ANOVA on bootstrapped species diversity indices (see below for details).

Variable Predation: Frequency and Intensity of Predation

To determine the effects of variable predation and separate the effects of frequency of predation events from the intensity of predation, a cage inclusion experiment was conducted simultaneously with the exclusion experiment described above. Using the same kind of cages used for the exclusion experiment, the intensity of predation was regulated by manipulating the number of whelks allowed inside the cages. Three levels of intensity were chosen, low (2 individuals of *Nucella emarginata* per cage), medium, (4 whelks), and high (8 whelks). These numbers of whelks were chosen to correspond to 50, 100, and 200 whelks/m^2, which are within the range of mean densities observed in the field (see Results). Lower mean densities ($< 50/m^2$) were observed in the study site during winter months, but I could not reproduce them in the cages without having to include 1 single individual and increase the cage size.

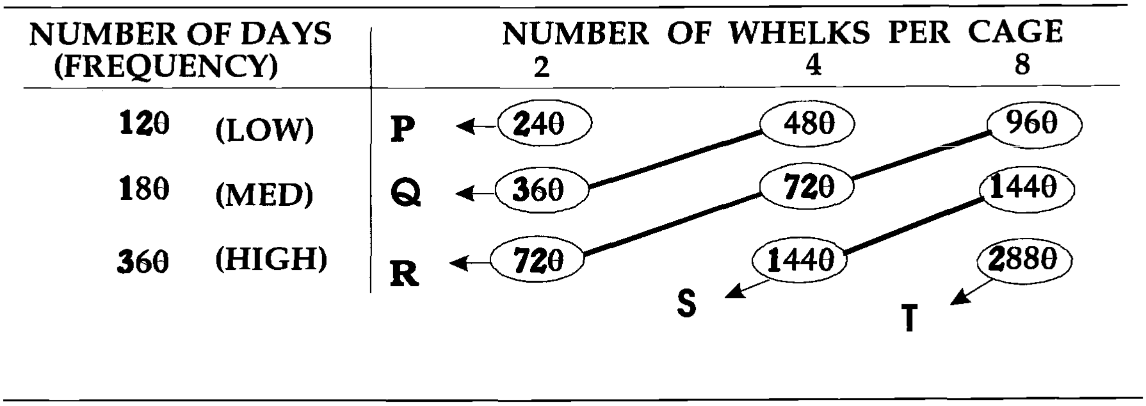
The three levels of intensity (number of snails per cage) were combined with 3 levels of frequency in an orthogonal manner, so that 9 different treatments, each replicated 4 times, were randomly assigned to previously marked plots in the field. In the low frequency treatment whelks were allowed inside the cages for a period of 2 months and then removed for the following 4 months, when they were re-introduced to the cages again. The cycle was repeated from April 1991 until the end of the experiment in May 1993. In the intermediate frequency treatment whelks were allowed inside the cages for 4 months and then removed for 2 months to allow the sessile community to recover, then they were re-introduced to the plot and the cycle repeated as with the low frequency treatment. The high frequency treatment corresponded to a 'constant predation' regime in which predators were left in the cages throughout the experiment.

Selection of the temporal variation treatments (frequency) was somewhat arbitrary but not random. The natural pattern of temporal variation in predation was not known before the experiment and it really is difficult to determine without some sort of continuous monitoring of an area of the coast. Diving during high tides or installation of video cameras is not safe in this rough environment. Preliminary observations suggested, however, that a minimum of 1 to 2 months was necessary to observe significant changes in whelk density (see Results and also Navarrete and Menge Chapter 2), which might translate into varying frequencies. A frequency of 4 months seemed necessary to allow many sessile species to recruit and grow and was close to the longer term variation in whelk densities in the site (see Results and Discussion).

To ascribe differences in the treatments to variability and not intensity of predation (total mortality over a time scale longer than the interval between predation events), I calculated the number of 'predation days' by simply multiplying the number of whelks per cage by the total number of days predators were in the cages in a year (Table 1). The frequency and intensity treatments overlapped in the number of predation days per year, forming at least 5 distinct 'predation days' groups (letters P to T in Table 1). This grouping was used in the multivariate ordination analysis (see below) to determine if they discerned among different species compositions better than frequency and intensity.

Cages were monitored in the same manner and regularity as the exclusion experiment. Medium sized (14-18 mm shell length) whelks used in the treatments were collected in nearby areas. When the plots were photographed, whelks of all treatments were temporarily removed, which helped to control for the inevitable manipulation of animals in the variable predation treatments. Also, every 4 to 6 months all whelks in the constant predation treatment were replaced by new individuals. This procedure helped to standardized among treatments the inter-individual variability in prey preferences typical of *Nucella* species (West 1986), which probably increased the within cages variability.

Table V.1. Number of 'predation days' in the different treatments of variable and constant predation by *Nucella*. Predation days were calculated by multiplying the total number of days whelks were inside the cages in a year (frequency) by the number of snails per cage (intensity). The capital letters in the table refer to grouping used in multivariate ordination comparisons.



NUMBER OF DAYS (FREQUENCY)			NUMBER OF WHELKS PER CAGE 2	4	8
120	(LOW)	**P** ←	240	480	960
180	(MED)	**Q** ←	360	720	1440
360	(HIGH)	**R** ←	720	1440	2880

Data Analysis. A two-way factorial repeated measures analysis of variance was used to analyze the results of this experiment. Intensity and frequency were considered fixed factors because they were chosen to represent specific values of density and frequency as suggested by field observations (see above). The procedure for the treatment of data and analyses was identical as that described above for the exclusion experiment.

Besides the univariate RM-ANOVA and multivariate three-way MANOVA (frequency, intensity and years as factors), two other analyses were performed to test the hypothesis that the different treatments produced distinct prey communities. First, species richness, the total number of species present per plot and sampling date, and species diversity as measured by the Shannon (H') diversity index (Magurran 1988) were calculated for each treatment in the exclusion and variable predation experiment. A modification of Margalef's index of species richness, which standardizes the number of species by the number of individuals in the sample (Magurran 1988), was calculated by replacing the total number of individuals by the total cover of all sessile species (1- cover of bare rock) in each plot. Species diversity (H') was calculated on the mean covers across time for each sampling unit (plot). Confidence intervals were obtained by bootstrapping the data considering replicates and not species within a cages as the independent source of variability in H' (Dixon 1993). After testing for normality and variance homogeneity, the bootstrapped indices were used in 2-way ANOVA to compare the effects of predation frequency and intensity. Second, a principal components analysis (PCA) was performed using the program PC-Ord (McCune 1991) to obtain a representation of all plots (sampling units under different predation regimes) in the species space. Species with a mean cover of less than 1 % were not included in this analysis. Data were arcsin transformed and standardized by the maximum variance among species within sampling units.

The variable predation experiment and statistical analyses tested the following specific hypotheses:

1) The cover of sessile species changes in a predictable manner by changes in either the intensity (density of whelks at each frequency level) or frequency (variable or constant predation at each density level) of predation by whelks. If a species increased in abundance in the absence of predators, it was expected to progressively decrease in abundance as the intensity or frequency of predation increases. This hypothesis was tested by examination of mean covers and the main effects of the repeated measures analyses of variance on each species.

2) Predation regime (variable, constant) has no effect on the relative abundances of species. This hypothesis was tested by the significance of the frequency treatment and its interaction with intensity in the individual repeated measures analyses (combination of results) and MANOVA on most abundant species, and by the position of variable and constant predation treatments in the multivariate ordination.

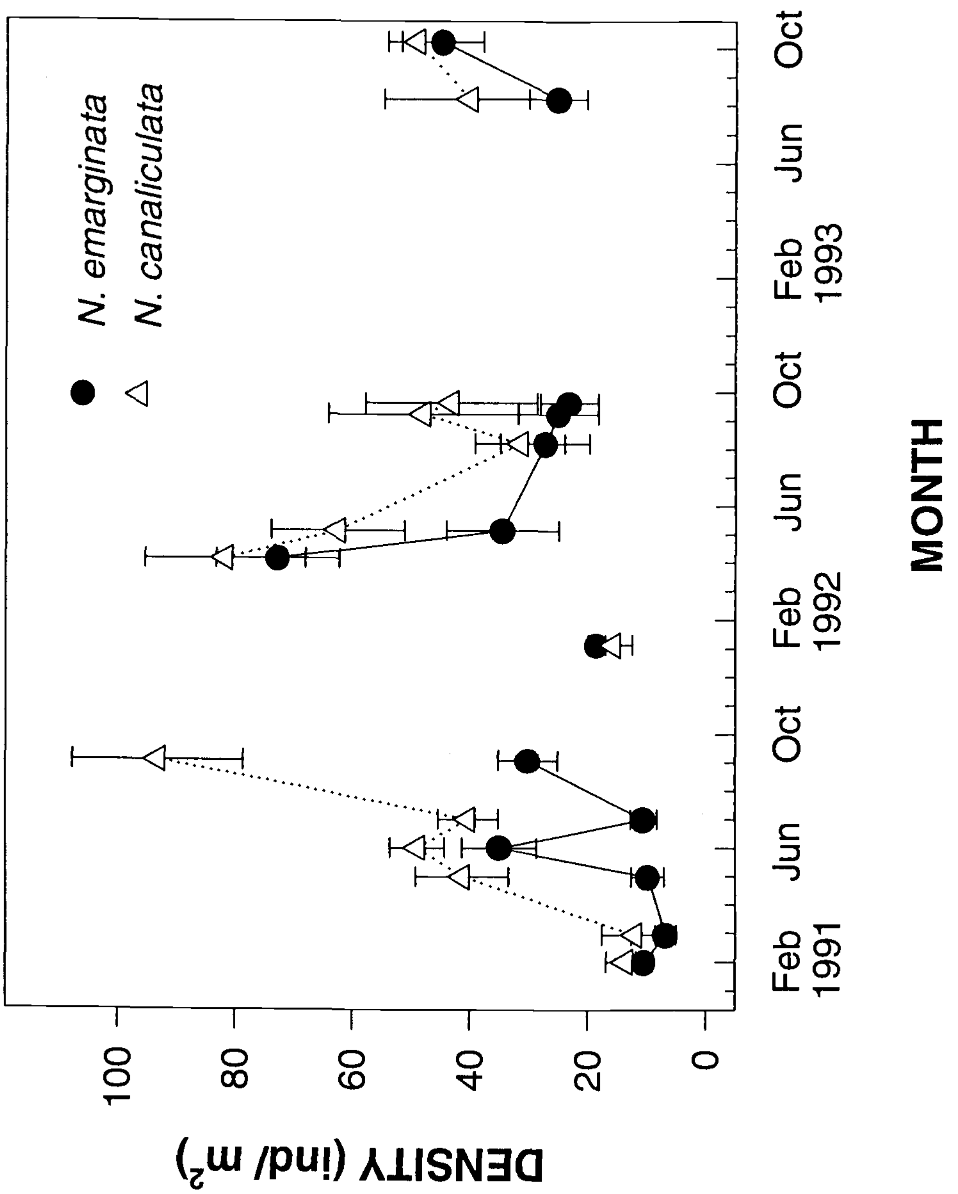
3) Predation regime has no effect on species richness or species diversity. Tested by rank ANOVA on species richness and by RM-ANOVA on species diversity (see section on Predator Exclusion above). Two more specific hypotheses derived from the intermediate disturbance hypothesis (Connell 1978, and see Hixon 1986 for review) are of interest here: a) That intermediate levels of intensity increase species diversity, and b) that variable predation increases species diversity.

Results

Abundance and Distribution of Whelks

Densities of whelks in the study site fluctuated over an order of magnitude between February 1991 and October 1993 (Fig. 1). In general, densities were higher in spring and summer months than in late fall or winter, but the time at which the highest densities were observed varied among years.

Figure V.1. Density of *Nucella canaliculata* and *N. emarginata* in the study site at Fogarty Creek, Oregon. Each point is the mean (± SE) of 60-80 0.25 m^2 quadrats regularly positioned along 6 transects in the mid zone of two flat rocky benches. A discontinued line means that sampling could not be done for two consecutive months.

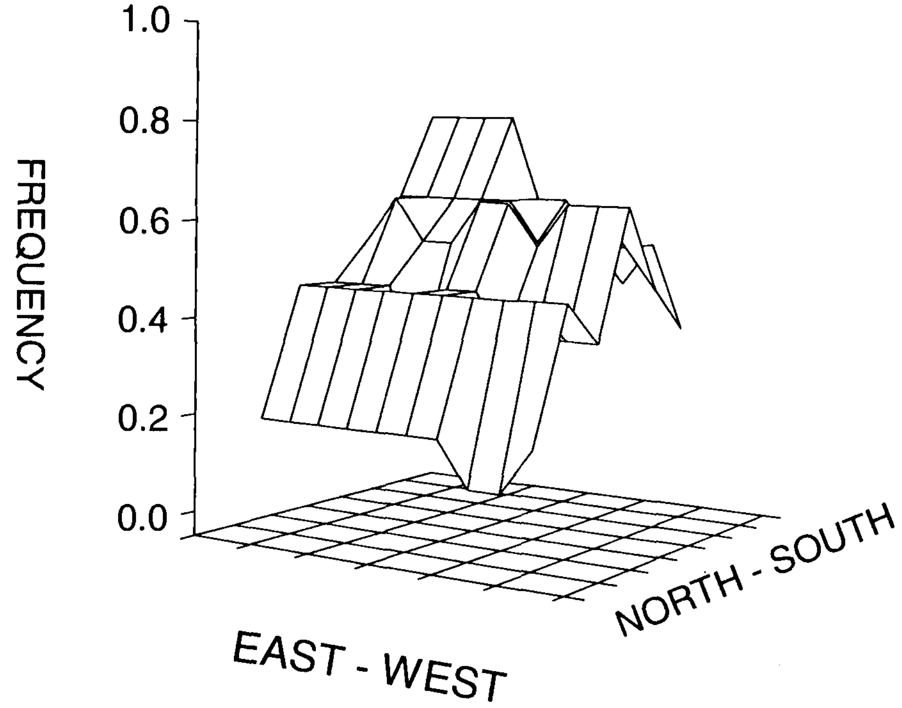


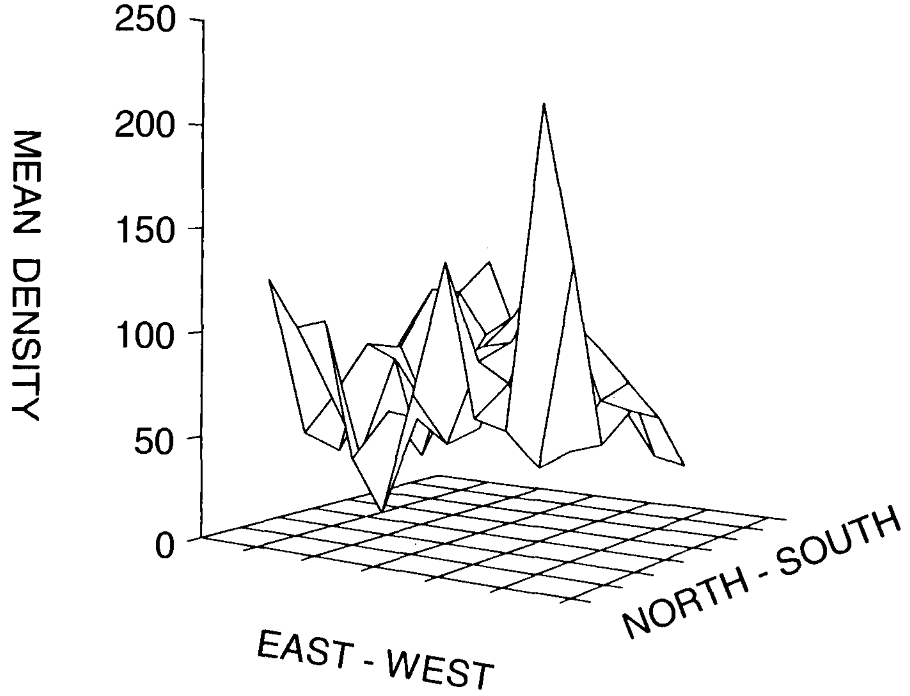
Density values peaked late in summer 1991, while the next year the highest densities were observed in late spring. Mean densities of *Nucella canaliculata* and *N. emarginata* were highly correlated over time (Pearson's r = 0.79, P= 0.0037, N= 11, Fig. 1), but negatively correlated over space when using the mean density over time observed in 50 x 50 cm quadrats (Spearman Rank r = -0.30, P= 0.0186, N= 60). Density of neither species was correlated to the cover of mussel (*M. californianus*) at the study site (P > 0.05).

The frequency with which whelks (both species pooled) were observed in different fixed-position quadrats varied widely over small spatial scales in the study site. One area of the study site tended to have whelks present most of the time, while in other areas whelks were only occasionally observed (Fig. 2 a). The pattern was similar when separated by species of *Nucella*, but the position of the high frequency area (peak in figure 2a) was slightly different. The spatial distribution of frequencies shown in figure 2a was not correlated to the mean density of whelks observed in those places (Fig. 2b, Spearman Rank r= -0.005, P> 0.05, N= 60), but it was, however, significantly and positively correlated to the maximum density of whelks recorded during the study (Spearman Rank r= 0.528, P= 0.0001, N= 60).

Figure V.2. Spatial distribution of the frequency at which whelks were observed in fixed position quadrats (50 x 50 cm) within the study site out of 13 observations in a period of 34 months (top panel) and the mean whelk density (Ind./m^2) in the same quadrats during that time (bottom panel). Both figures have the same orientation, showing the East-West orientation of 6 transects 2 m apart and the North-South orientation of 10 quadrats 1 m apart. A point with the same coordinates in both panels represent the same quadrat with a fixed position within the study site.

Figure V.2.


1.0
0.8
0.6
0.4
0.2
0.0
FREQUENCY
EAST - WEST
NORTH - SOUTH


250
200
150
100
50
0
MEAN DENSITY
EAST - WEST
NORTH - SOUTH

Both the size (grain) and the intensity or degree of aggregations of whelks in the study site varied with season of the year and to a lesser extent with the species on *Nucella* (Fig. 3). In figure 3 a relatively flat curve or one with peaks and troughs but not a single clearly defined peak represent a relatively random distribution of whelks over space. A peaked curve represent an aggregated distribution in which the position of the peak indicates the average size of the aggregation and the 'peakness' the intensity of the aggregation (Ludwig and Reynolds 1988). In fall and winter months whelks tended to be more uniformly distributed in the study site or, in the case of *N. canaliculata,* formed small aggregations of low intensity (low variance) and of about 3-4 m in diameter. Toward the summer aggregations of both species increased in diameter (grain) to about 6-7 m, but the most significant change was the increase in the degree of aggregation, particularly in *N. canaliculata*. This means that while the overall mean whelk density in the study site increased toward the summer, the magnitude of the increase with respect to winter months varied over space.

Predation by Whelks: Exclusion Experiments

Changes in the abundance (cover) of a number of sessile species were observed as a response to the exclusion of predators from exclusion cages for a period of 30 months. The bay mussel *Mytilus trossulus* was significantly more abundant in the absence of predators than in the presence of predators, both in the control or cage-control (roof) plots (Fig. 4, Table 2, significant between subjects contrast 'Control vs Exclusion'). Heavy recruitment of *M. trossulus* (when they become visible in the substratum) to all plots occurred early in the spring of 1991 (S. Navarrete, personal observations). The effect of predators was apparent within few months (Fig. 4) and did not change over time (Table 2, $P > 0.05$ for all within subject factors). The cover of mussels did not increase over time and fluctuated between 15-35% throughout the experiment (non-significant Time effect in Table 2). Mean shell length of mussels in exclusion plots increased from 0.56 ± 0.04 cm (mean ± SE of 25 mussels measured from pictures) in August 1991 to 2.84 ± 0.12 cm (N= 22) in May 1993.

The cover of the California mussel, *M. californianus* also increased in the absence of predators (Table 3, significant between subjects contrast 'Control vs. Exclusion'), but the effect was observed only after 2 years of exclusion (Fig. 4, Table 3, significant within subjects effects of 'Time x Treatment' and contrast 'Time-Control vs. Exclusion'). *M. californianus* was not observed in the plots in 1991 (statistical analysis did not include data before May 1992) and in 1992 the effect of predator exclusion had not yet been detected (Fig. 5). The effect of predator exclusion on the California mussel, although statistically significant might appear unimportant given the low cover values (Fig. 5). However, *M. californianus* is the competitively dominant species in the mid intertidal zone of the wave exposed coast of Oregon, Washington and other places (Paine 1966, 1974, Dayton 1971, Menge et al. 1994), and once it establishes on the substratum it can grow and smother other species (S. Navarrete, personal observations). In June 1994 the two remaining exclusion cages had a mean cover of California mussels of 45% (Table 4) and mean shell length had increased from 3.98 ± 0.24 (N= 18, measured from pictures) in May 1993 to 6.11 ± 0.98 (N=20, measured in the field). Mussel cover in the 8 control plots and the one roof remaining had not changed since May 1993 (Table 4).

The gooseneck barnacle *Pollicipes polymerus* responded to the removal of predators in much the same way as did *M. californianus* (Fig. 4). *P. polymerus* were almost totally absent from the plots in 1991 and 1992 and only in 1993 the positive effect of predator exclusion became apparent (Fig. 5, Table 5, significant within subjects contrast 'Time-Exclusion vs. Control'). Because data for individual dates was non-normal and heteroscedastic (Sokal and Rohlf 1981), the analysis was based on the yearly means of 1991 and 1992 (Table 5).

Table V.2. Repeated measures analysis of variance of the effects of constant exclusion of *Nucella* on the abundance of *Mytilus trossulus* (arcsin transformed cover data) from April 1991 through May 1993. Treatment refers to the simultaneous comparison of controls (uncaged plots), exclusions (cages) and roofs (cage controls). The planned contrast 'Control-Exclusion' tests for the effect of predators and the contrast 'Control-Roof' tests for cage effects and also predation by birds (see text). Data did not exhibit homogeneity of treatment differences variance (test for Sphericity $P < 0.001$). Huynh-Feldt corrected probabilities (P H-F) are given for the univariate within subjects analysis (H-F epsilon = 0.466). df: degrees of freedom; MS: mean squares. Bold face P values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	0.525	5.40	**0.0288**
Error	9	0.097		
Contrasts				
Control-Exclusion	1		6.29	**0.0334**
Control-Roof	1		1.96	0.1945

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F H-F	P H-F	num df	den df	Wilks' λ	P
Time	5	0.042	2.69	0.0840	5	5	0.565	0.6095
Time x Treatment	10	0.008	0.49	0.7668	10	10	0.265	0.5363
Error (Time)	45	0.016						

Table V.3. Repeated measures analysis of variance of the effects of constant exclusion of *Nucella* on the abundance of *Mytilus californianus* (arcsin transformed cover data) from May 1992 through May 1993. See table V.2 for explanation of labels and contrasts. Data showed homogeneity of treatment differences variance (test for Sphericity P= 0.09) and non-corrected probability values are given for the univariate within subjects analysis (P).

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	0.024	14.07	**0.0017**
Error	9	0.001		
Contrasts				
Control-Exclusion	1		26.56	**0.0006**
Control-Roof	1		0.01	0.9081

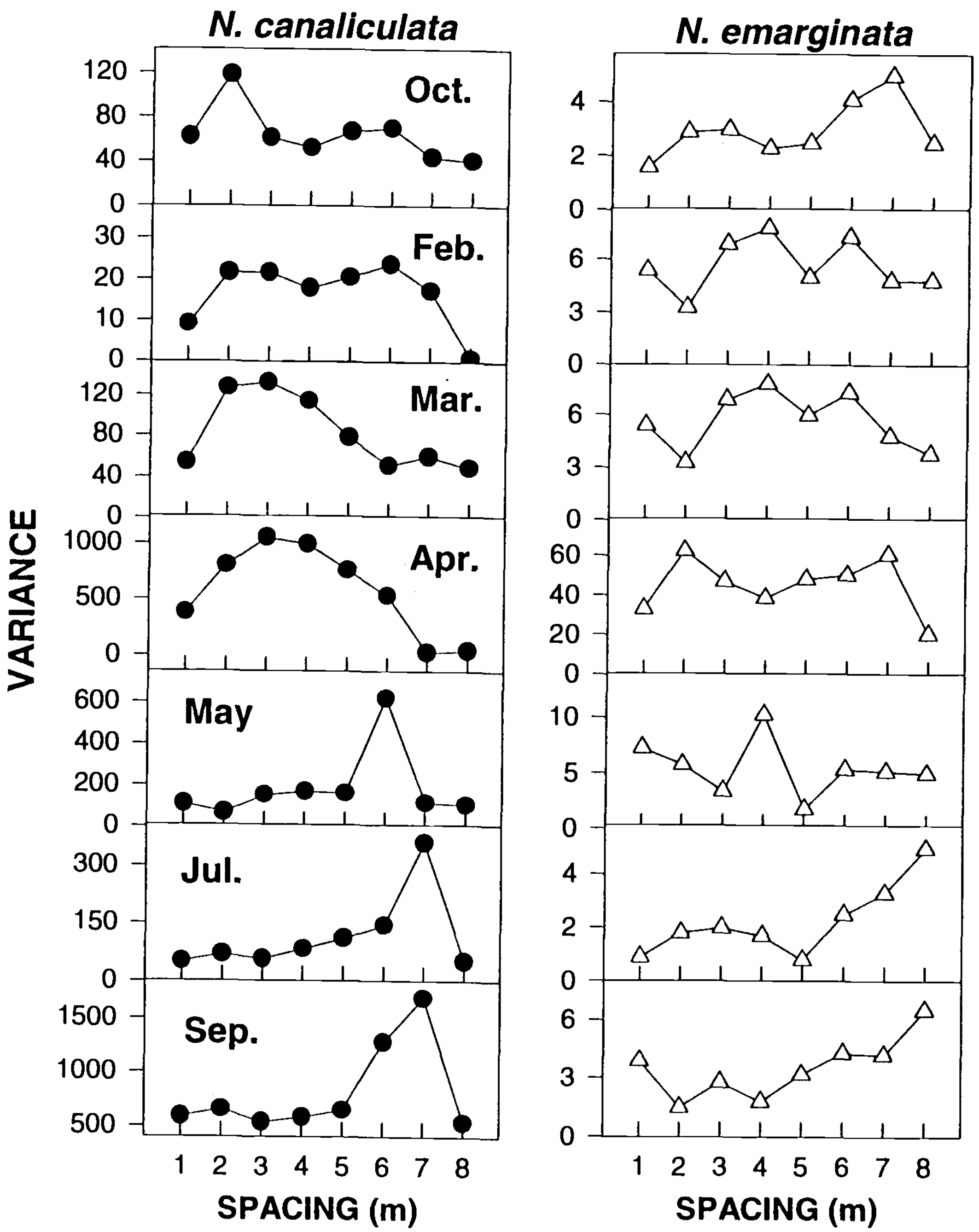
B. WITHIN SUBJECTS

Univariate Analysis

SOURCE	df	MS	F	P
Time	3	0.013	7.30	**0.0010**
Time x Treatment	6	0.009	5.15	**0.0012**
Error (Time)	27	0.002		
Contrasts				
Time x Control-Exclusion	3	0.018	10.3	**0.0001**
Time x Control-Roof	3	0.001	0.58	0.6339

Figure V.3. Variance in the density of *Nucella canaliculata* and *N. emarginata* at different quadrat spacings (distance between quadrats along 30 m long transects) using the paired-quadrats variance method. Note that the y-axis scale is different among panels because of large differences in variance within species (among months) and among months (between species). A relatively flat line, or one with ups and downs but not clear peaks represent a relatively random distribution of whelks within the site, while a peaked line represent an aggregated distribution (see text).

Figure V.3.


N. canaliculata
N. emarginata
VARIANCE
Oct.
Feb.
Mar.
Apr.
May
Jul.
Sep.
120
80
40
0
30
20
10
0
120
80
40
0
1000
500
0
600
400
200
0
300
150
0
1500
1000
500
4
2
0
6
3
0
6
3
0
60
40
20
0
10
5
0
4
2
0
6
3
0
1 2 3 4 5 6 7 8
SPACING (m)
1 2 3 4 5 6 7 8
SPACING (m)

The exclusion of predators had no effects on coralline algae and only a minor, temporary effect (October 1991) on fleshy algae (mostly *Pterosiphonia* spp., *Odonthalia* spp, *Polysiphonia* spp., Fig. 6). The shading of the cages had no effect on algal cover ($P > 0.05$ for all between and within subjects contrasts involving 'Control vs Roof'). The presence of an algal turf, although of short duration, might have facilitated the recruitment or survival of the bay mussel, which can then overgrow the algae (personal observations).

The cover of the sea anemone *Anthopleura xanthogrammica* was significantly higher in the absence of predators, although much variation was observed over time (Fig. 6, Table 6, significant 'Time x Treatment' effect and the contrast 'Time-Control vs Exclusion'). Anemones were both more abundant and larger in the exclusion cages, particularly among mussels *M. californianus* and large individuals of the acorn barnacle *Semibalanus cariosus*.

Recruitment of barnacles (estimated by the cover of barnacles smaller than 2 mm in diameter) was not affected by the treatment (either predator exclusion or cages, $P > 0.05$), although temporal variation in recruitment was significant in all three barnacle species, *Balanus glandula, Chthamalus dalli, Semibalanus cariosus* (within subjects effect of 'Time' $P = 0.0032, 0.0262, 0.0074$, respectively).

Figure V.4. Mean cover (± SE) of the mussels *Mytilus trossulus,* and *M californianus,* and the gooseneck barnacle *Pollicipes polymerus* in the predator exclusion experiment. The 'Exclusion' treatment consisted of 20 x 20 cm cages from which invertebrate predators were removed from April 1991 through May 1993. The 'Control' treatment refers to the cover of species in 20 x 20 cm plots that were left undisturbed for the duration of the experiment. The 'Roof' treatment consisted of 20 x 20 cm squares of mesh (same kind used for exclusion cages) that were held 5 cm off the rock surface with PVC tubes in the four corners. Roofs provided a control for the shading produced by the exclusion cages and served also as a barrier to predation by birds (see text). Note that the different panels have different y-axis scales.

Figure V.4.

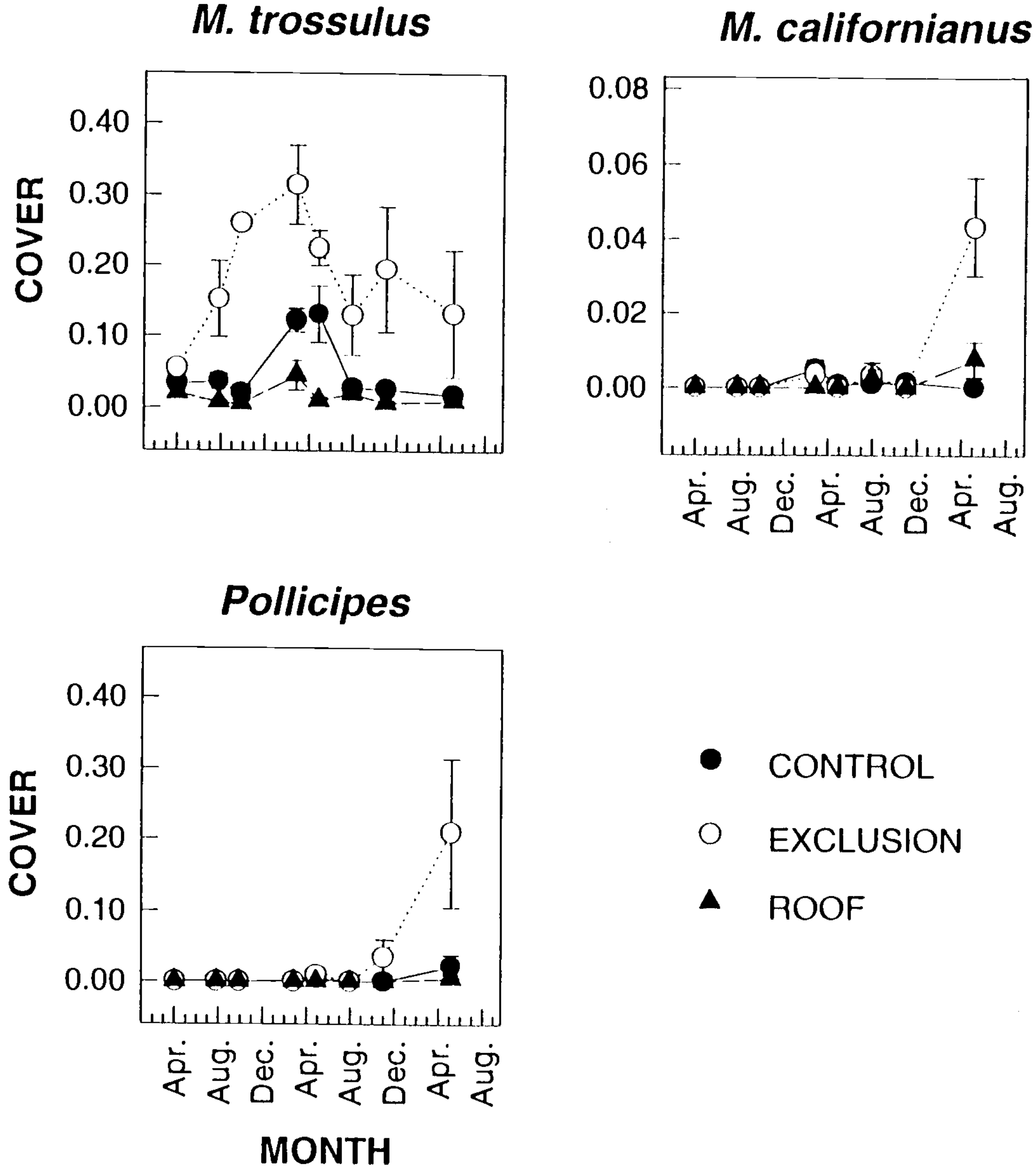

M. trossulus
M. californianus
Pollicipes
COVER
0.40
0.30
0.20
0.10
0.00
0.08
0.06
0.04
0.02
0.00
Apr.
Aug.
Dec.
Apr.
Aug.
Dec.
Apr.
Aug.
MONTH
● CONTROL
○ EXCLUSION
▲ ROOF

Figure V.5. Mean annual cover (± SE) of the mussels *Mytilus trossulus*, and *M californianus*, and the gooseneck barnacle *Pollicipes polymerus* in the predator exclusion experiment. Each bar (91, 92 , 93) is the average for the year 1991, 1992 and 1993. Solid bars are the covers in the 'Control' treatment and open bars the covers of the same species in the predator 'Exclusion' treatment. See figure 4 for further explanation.

Figure V.5.

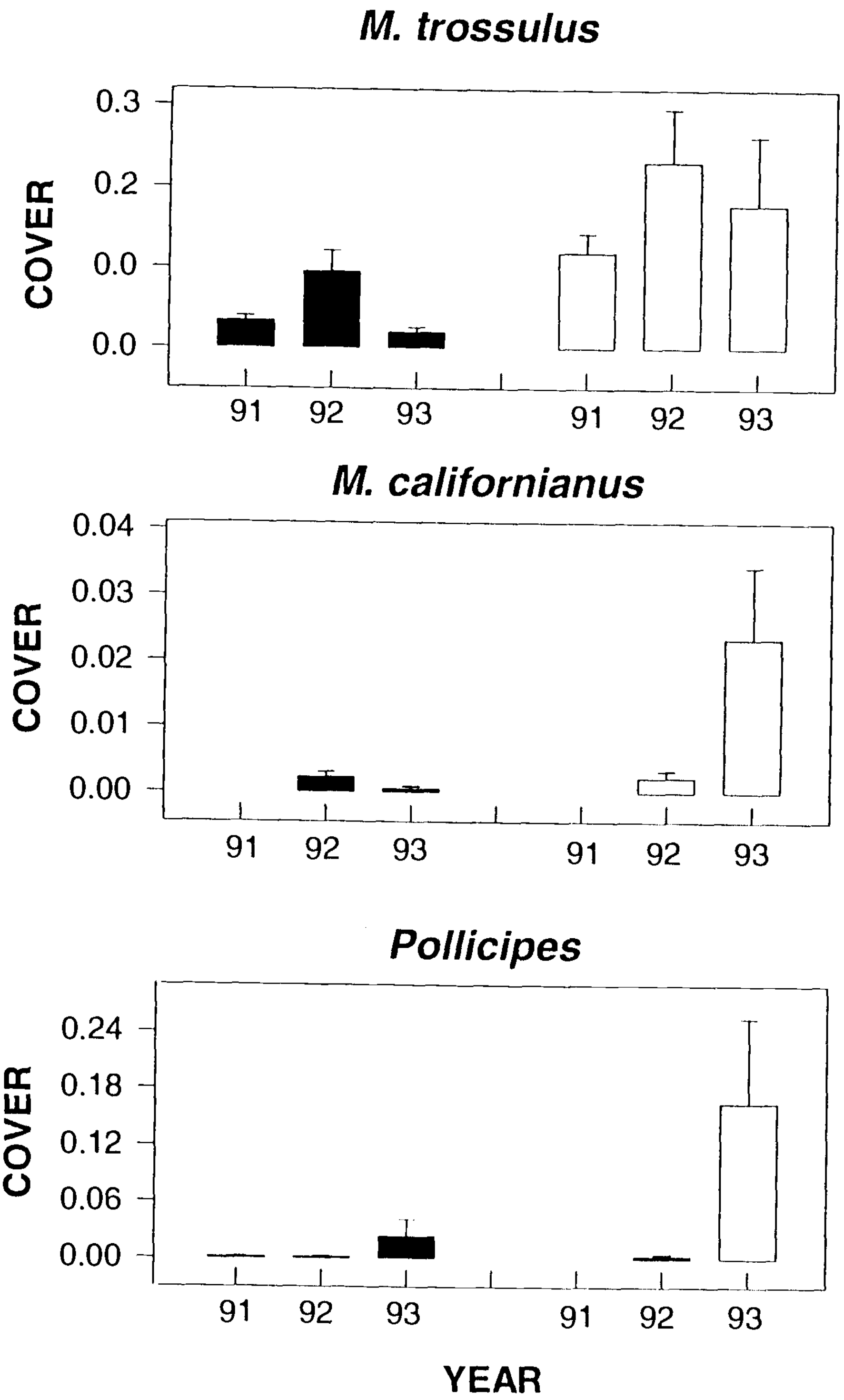
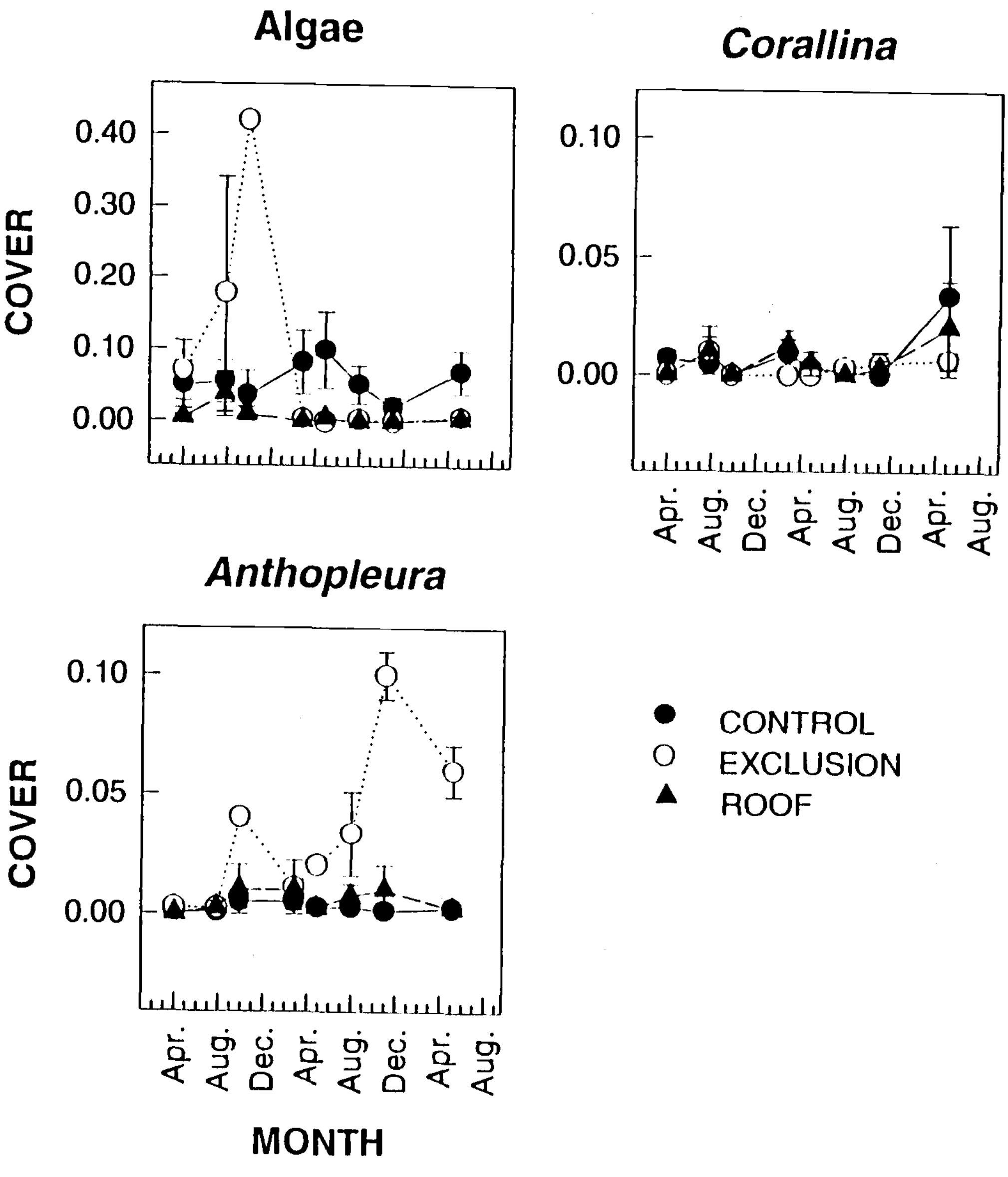

M. trossulus
COVER
0.3
0.2
0.0
0.0
91
92
93
91
92
93
M. californianus
COVER
0.04
0.03
0.02
0.01
0.00
91
92
93
91
92
93
Pollicipes
COVER
0.24
0.18
0.12
0.06
0.00
91
92
93
91
92
93
YEAR

Figure V.6. Mean cover (± SE) of all fleshy macroalgae (pooled), the calcareous red alga *Corallina* spp., and the sea anemone *Anthopleura xanthogrammica* in the predator exclusion experiment. See figure 4 for explanation. Note differences in the y-axis scales among panels.

Figure V.6.


Algae
Corallina
Anthopleura
COVER
COVER
0.40
0.30
0.20
0.10
0.00
0.10
0.05
0.00
0.10
0.05
0.00
Apr.
Aug.
Dec.
Apr.
Aug.
Dec.
Apr.
Aug.
MONTH
● CONTROL
○ EXCLUSION
▲ ROOF

Treatment effects on adult acorn barnacles (> 2 mm diameter) varied with species. The smallest barnacle, *Chthamalus*, increased in cover toward the end of the experiment (Fig. 7) in the controls and roof plots, but not in the predator exclusions (Table 7, significant between and within subjects contrasts comparing 'Control vs. Exclusion', but not the contrasts 'Control vs, Roof'). The cover of *Balanus*, initially the most abundant species in the study site, decreased rapidly after August 1991 and remained low (3-7 %) until the end of the experiment, regardless of the presence/absence of predators or cage (Fig. 7, the only significant effect was 'Time', P = 0.0001). In contrast, the large *Semibalanus* increased in abundance after October 1991 and then decreased again toward the end of the experiment in December 1992 (Fig. 7). Exclusion of invertebrate predators had no significant effect on this changes (Table 8, within subjects contrast "Time-Control vs. Exclusion' P> 0.05), but the roofs themselves significantly increased the abundance of *S. cariosus* with respect to the control areas toward the end of the experiment (Fig. 7, Table 8, significant within subjects contrast 'Time-Control vs Roof'). This was the only significant cage (or bird predation, see Discussion) effect observed in the experiment.

Results of the MANOVA and canonical analyses on the cover of *Semibalanus cariosus*, *Mytilus trossulus*, *Pollicipes polymerus*, *Chthamalus dalli*, *Anthopleura xanthogrammica*, and *M. californianus* (the six most abundant sessile species in the study), corroborated the species-based analyses described above (Tables 9 and 10). There was a significant effect of treatment, which resulted from the exclusion of predators and not from the cages themselves (Table 9, only the contrast 'Control vs. Exclusion' was significant). The cage effect on *S. cariosus* observed in the repeated measures analysis was not detectable in the multivariate analysis. The differences between predator exclusions and controls were produced mostly by the predator direct or indirect effects on *M. trossulus*, *Anthopleura* and *Chthamalus*, while the variation in the cover over time as a result of predator exclusions was due mostly to the effects on *M. californianus*, *Pollicipes*, and *Anthopleura* (Table 10).

The permanent exclusion of predators had no effects on the amount of bare rock available in the plots (Fig. 7) or on the total number of species present through time, although a slight, non significant tendency to higher richness in the predator exclusion plots was observed toward the end of the experiment (Fig. 8). No effects of the treatments were observed on the diversity of species as measured by Shannon's H' index (Fig. 9)

Table V.4. Cover (%) of the most abundant sessile species found in June 1994 in two exclusion cages, one roof and the mean cover (± SE) of 8 control plots.

SPECIES	Exclusion 1	Exclusion 2	Roof 1	Control
Mytilus californianus	24	64	< 2	1.2 ± 1.2
Mytilus trossulus	10	6	4	3.2 ± 1.4
Pollicipes polymerus	27	8	< 5	5.2 ± 1.0
Semibalanus cariosus	17	11	25	15.6 ± 3.8

Figure V.7. Mean cover (± SE) of all the barnacles *Semibalanus cariosus, Balanus glandula,* and *Chthamalus dalli,* and the total cover of bare rock not yet colonized by sessile organisms in the predator exclusion experiment. See figure 4 for explanation. Note differences in the y-axis scales among panels.

Figure V.7.

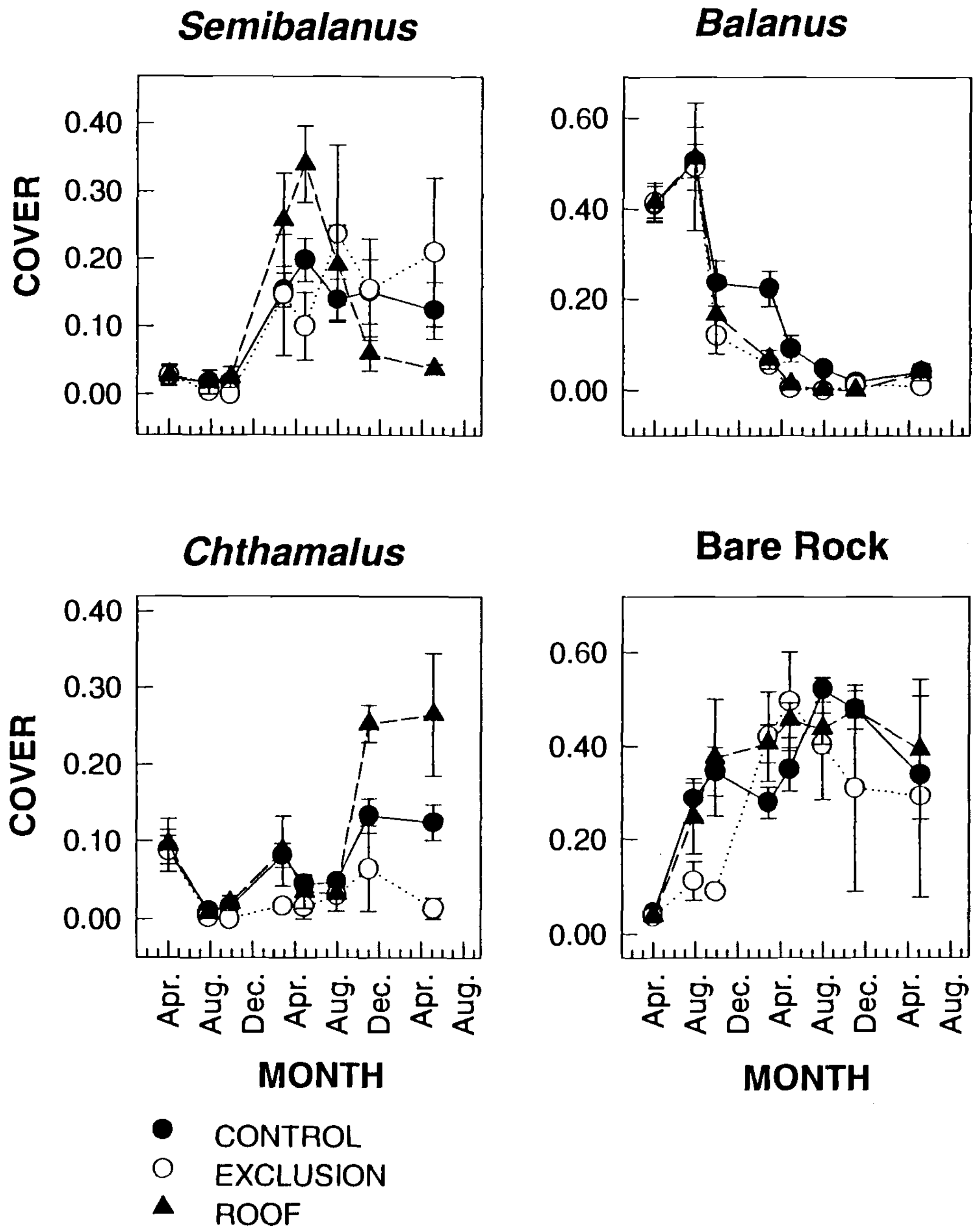

Semibalanus
Balanus
Chthamalus
Bare Rock
COVER
COVER
0.40
0.30
0.20
0.10
0.00
0.60
0.40
0.20
0.00
Apr.
Aug.
Dec.
Apr.
Aug.
Dec.
Apr.
Aug.
MONTH
MONTH
● CONTROL
○ EXCLUSION
▲ ROOF

Figure V.8. A) Total number of sessile species (richness) observed in the plots under the different treatments of the predator exclusion experiment. B) The number of species standardized by the total cover of species in the plots using a modification of Margalef's index of species richness (see text). See figure 4 for explanations.

Figure V.8.

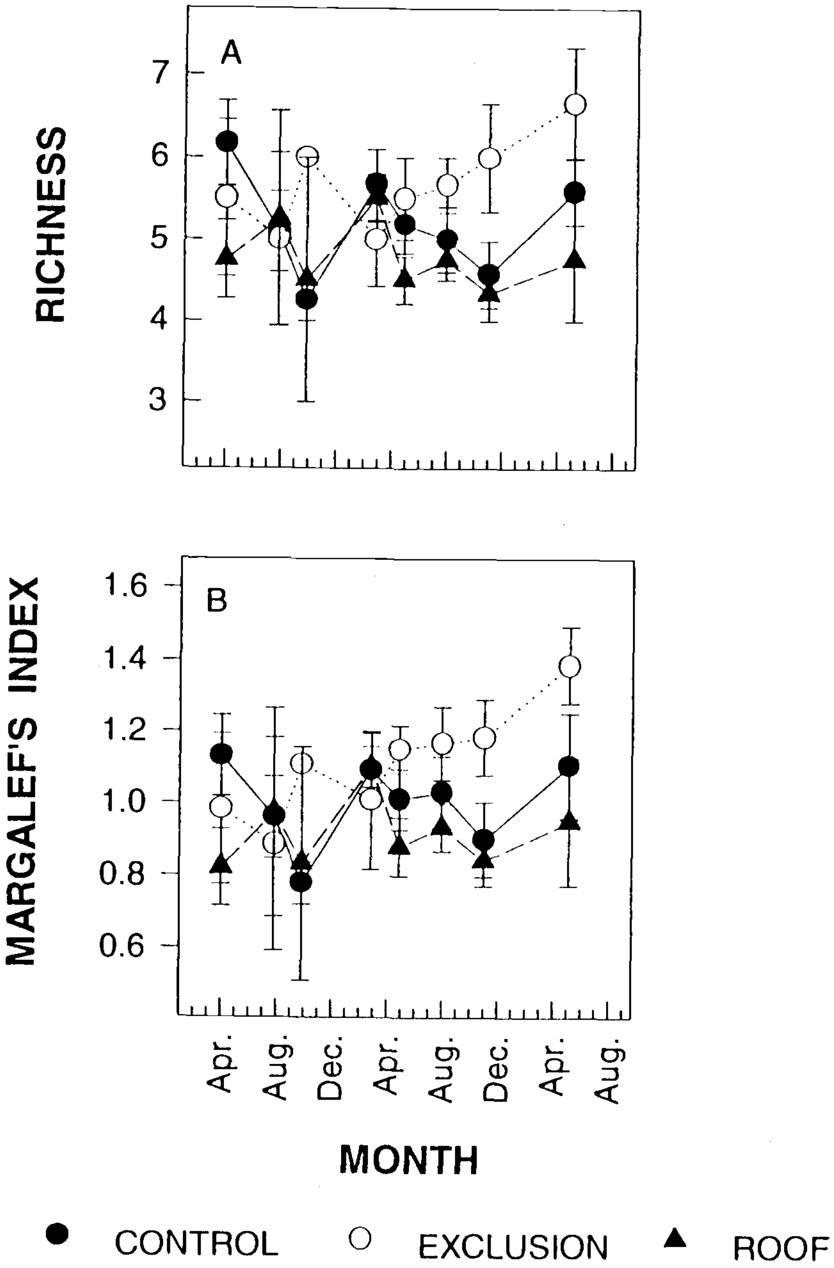

A
RICHNESS
7
6
5
4
3
B
MARGALEF'S INDEX
1.6
1.4
1.2
1.0
0.8
0.6
Apr.
Aug.
Dec.
Apr.
Aug.
Dec.
Apr.
Aug.
MONTH
● CONTROL
○ EXCLUSION
▲ ROOF

Figure V.9. Mean values (± SE) of the Shannon index of species diversity (H') in the different treatments of A) the predator exclusion experiment and B) the variable predation experiment. Error bars are one standard error obtained from 1000 bootstrapped samples by randomizing the original replicates.

Figure V.9.

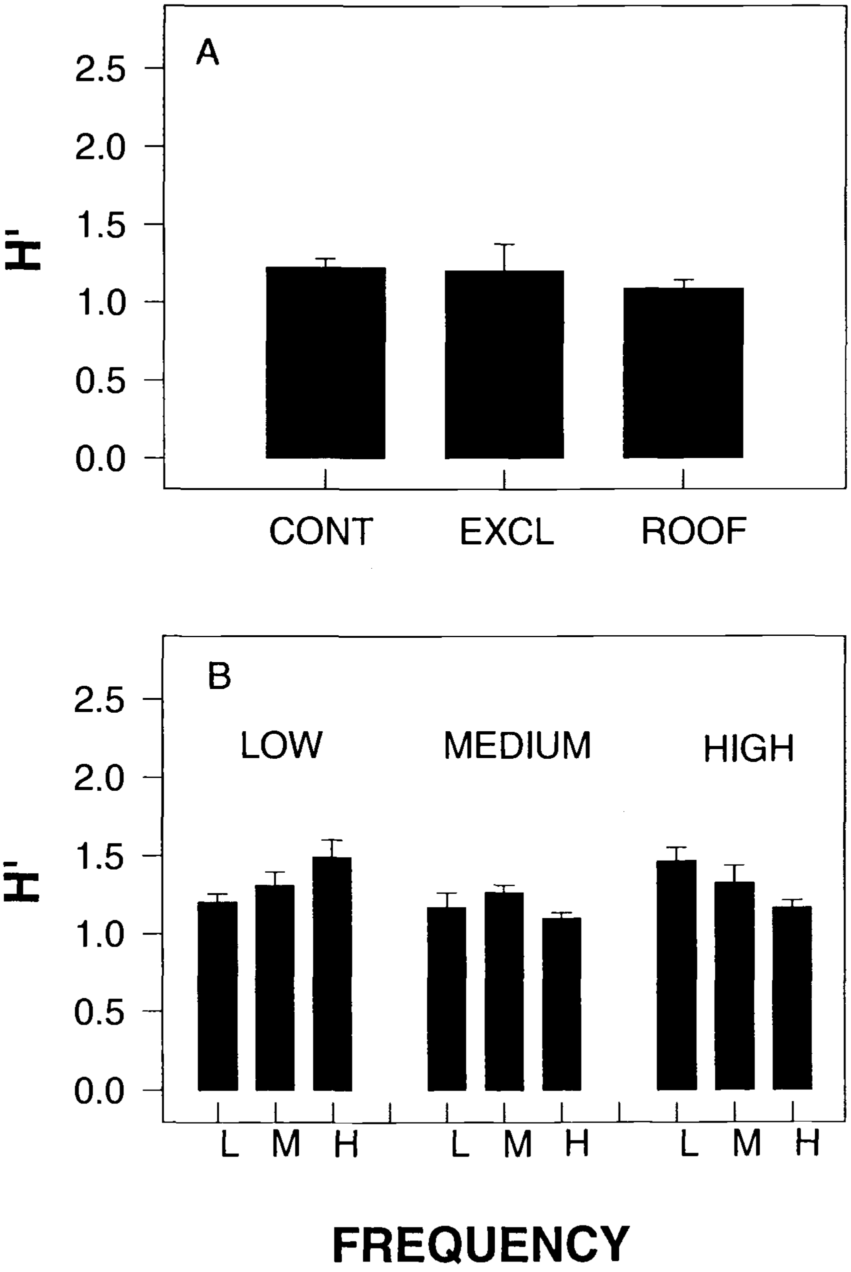

A
2.5
2.0
1.5
1.0
0.5
0.0
H'
CONT
EXCL
ROOF
B
LOW
MEDIUM
HIGH
2.5
2.0
1.5
1.0
0.5
0.0
H'
L
M
H
L
M
H
L
M
H
FREQUENCY

Table V.5. Repeated measures analysis of variance of the effects of constant exclusion of *Nucella* on the abundance of *Pollicipes polymerus* (arcsin transformed cover data) for the years 1992 and 1993 (averages for each year). See table 2 for explanation of labels and contrasts. Since only 2 levels of time were considered, data conformed to assumptions of univariate split-plot analysis of variance and only these results are presented.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	0.102	3.59	0.0515
Error	16	0.228		

B. WITHIN SUBJECTS

		Univariate Analysis		
SOURCE	df	MS	F	P
Time	1	0.129	11.65	**0.0036**
Time x Treatment	2	0.044	4.01	**0.0388**
Error (Time)	16	0.011		
Contrasts				
Time x Control-Exclusion	1	0.079	7.17	**0.0166**
Time x Control-Roof	1	0.001	0.09	0.7691

Table V.6. Repeated measures analysis of variance of the effects of constant exclusion of *Nucella* on the abundance of *Anthopleura xanthogrammica* (arcsin transformed cover data) from April 1991 through May 1993. See table 2 for explanation of labels and contrasts. Data did not show homogeneity of treatment differences variance (test for Sphericity P= 0.0107). Huynh-Feldt corrected probabilities (P H-F) are given for the univariate within subjects analysis (H-F epsilon = 0.944).

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	0.140	12.03	**0.0029**
Error	9	0.012		
Contrasts				
Control-Exclusion	1		23.87	**0.0009**
Control-Roof	1		0.73	0.4148

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	P H-F	num df	den df	Wilks λ	P
Time	5	0.017	8.39	**0.0008**	5	5	0.081	**0.0094**
Time x Treatment	10	0.011	5.33	**0.0017**	10	10	0.033	**0.0127**
Error (Time)	45	0.002						
Contrasts								
Time x Control-Exclusion	5	0.019	9.00	**0.0001**	5	5	0.103	**0.0165**
Time x Control-Roof	5	0.002	0.88	0.4965	5	5	0.307	0.1972

Table V.7. Repeated measures analysis of variance of the effects of constant exclusion of *Nucella* on the abundance of *Chthamalus dalli* (arcsin transformed cover data) from April 1991 through May 1993. See table 2 for explanation of labels and contrasts. Data did not show homogeneity of treatment differences variance (test for Sphericity P= 0.048). Huynh-Feldt corrected probabilities (P H-F) are given for the univariate within subjects analysis (H-F epsilon = 0.899).

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	0.100	4.62	**0.0417**
Error	9	0.022		
Contrasts				
Control-Exclusion	1		5.79	**0.0395**
Control-Roof	1		1.37	0.2716

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	P H-F	num df	de n df	Wilks ' λ	P
Time	5	0.099	11.87	**0.0001**	5	5	0.029	**0.0008**
Time x Treatment	10	0.015	1.84	0.0909	10	10	0.224	0.4346
Error (Time)	45	0.008						

Table V.8. Repeated measures analysis of variance of the effects of constant exclusion of *Nucella* on the abundance of *Semibalanus cariosus* (arcsin transformed cover data) from April 1991 through May 1993. See table 2 for explanation of labels and contrasts. Data did not show homogeneity of treatment differences variance (test for Sphericity P= 0.049). Huynh-Feldt corrected probabilities (P H-F) are given for the univariate within subjects analysis (H-F epsilon = 1.34).

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	0.025	0.33	0.7279
Error	9	0.076		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	P H-F	num df	den df	Wilks' λ	P
Time	5	0.129	9.46	**0.0001**	5	5	0.132	**0.0297**
Time x Treatment	10	0.027	1.97	0.0605	10	10	0.058	**0.0428**
Error (Time)	45	0.014						
Contrasts								
Time x Control-Exclusion	5	0.015	1.09	0.3807	5	5	0.339	0.2411
Time x Control-Roof	5	0.028	2.04	0.0914	5	5	0.095	**0.0138**

Table V.9. Multivariate analysis of variance (MANOVA) on the cover of the six most abundant sessile species in the predator exclusion experiment (see table V.10). See table V.2 and text for explanation of experimental design and labels.

SOURCE	Wilks's λ	num df	den df	P
Years	0.106	12	86	**0.0001**
Treatment	0.170	12	86	**0.0001**
Years x Treatment	0.239	24	151	**0.0001**
Contrasts on main effect of Treatment:				
Control vs Exclusion	0.224	6	43	**0.0001**
Control vs Roof	0.804	6	43	0.1327

Table V.10. Standardized canonical coefficients of the sessile species considered in the MANOVA analysis of the *Nucella* exclusion experiment (Table V.9). The magnitude of the coefficient is proportional to the contribution of a species to the significance of that factor in the MANOVA.

	Standardized Canonical Coefficient	
Species	Treatment (Main Effect)	Treatment x Years (Interaction Effect)
Semibalanus	-0.2356	-0.095
M. trossulus	0.9401	-0.1626
M. californianus	-0.0028	0.7873
Pollicipes	0.4319	0.5214
Chthamalus	-0.7511	-0.7078
Anthopleura	1.2598	1.1001

Table V.11. Repeated measures analysis of variance of the effects of intensity (density of predators) and frequency (temporal pattern of variability) of predation by *Nucella* on the abundance of *Mytilus trossulus* (arcsin transformed cover data) from April 1991 through May 1993. The experiment included three levels of intensity of predation, low (2 whelks per cage), medium (4 whelks per cage) and high (8 whelks per cage), and three levels of frequency, low (predation every 4 months), medium (predation every 2 months) and high (constant predation). See text for details. Data did not show homogeneity of treatment differences variance (test for Sphericity P = 0.0001). Huynh-Feldt corrected probabilities (P H-F) are given for the univariate within subjects analysis (H-F epsilon = 0.85). df: degrees of freedom; MS: mean squares. Bold face P values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Intensity	2	0.091	2.09	0.1637
Frequency	2	0.026	0.60	0.5640
Intensity x Frequency	4	0.277	4.54	**0.0163**
Error	13	0.044		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	P H-F	num df	den df	Wilks' λ	P
Time	5	0.013	2.00	0.1035	5	9	0.187	**0.0042**
Time x Intensity	10	0.009	1.32	0.2506	10	18	0.204	0.0716
Time x Frequency	10	0.012	1.77	0.0979	10	18	0.274	0.1745
Time x Inten. x Frequen.	20	0.012	1.72	0.0670	20	31	0.068	**0.0491**
Error (Time)	65	0.007						

Figure V.10. Mean cover (± SE) of the mussels *Mytilus trossulus* and *M. californianus* in the variable predation experiment. The different panels for each species represent a different level of predation intensity from 'Low' (2 whelks per 20 x 20 cm cage) to 'Medium' (4 whelks) and 'High' (8 whelks). The different lines within each panel represent the different levels of predation frequency, from 'Low' (every 4 months), to 'Medium' (every 2 months) and 'High' (constant predation). Note differences in the y-axis scale between species.

Figure V.10.

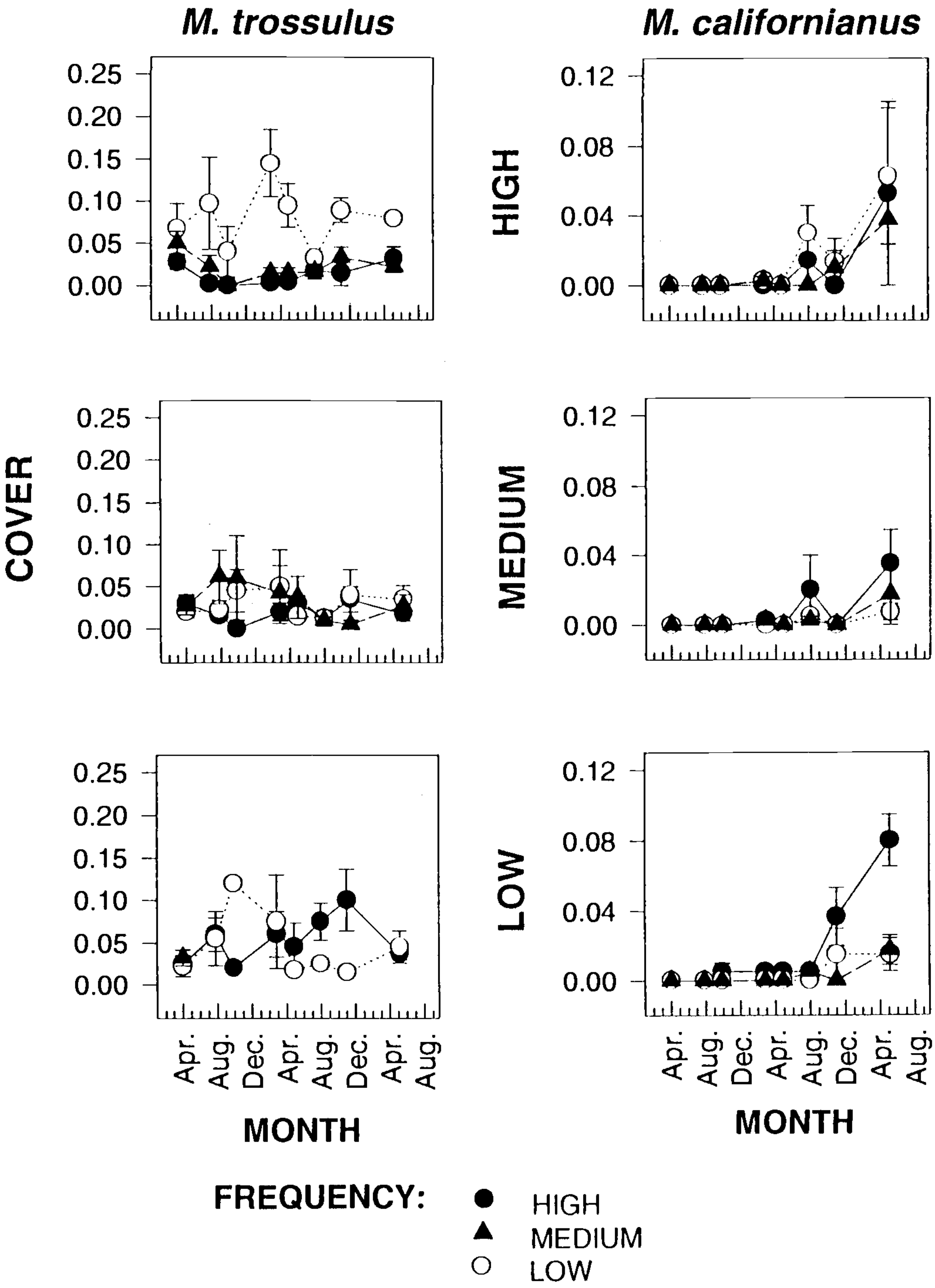
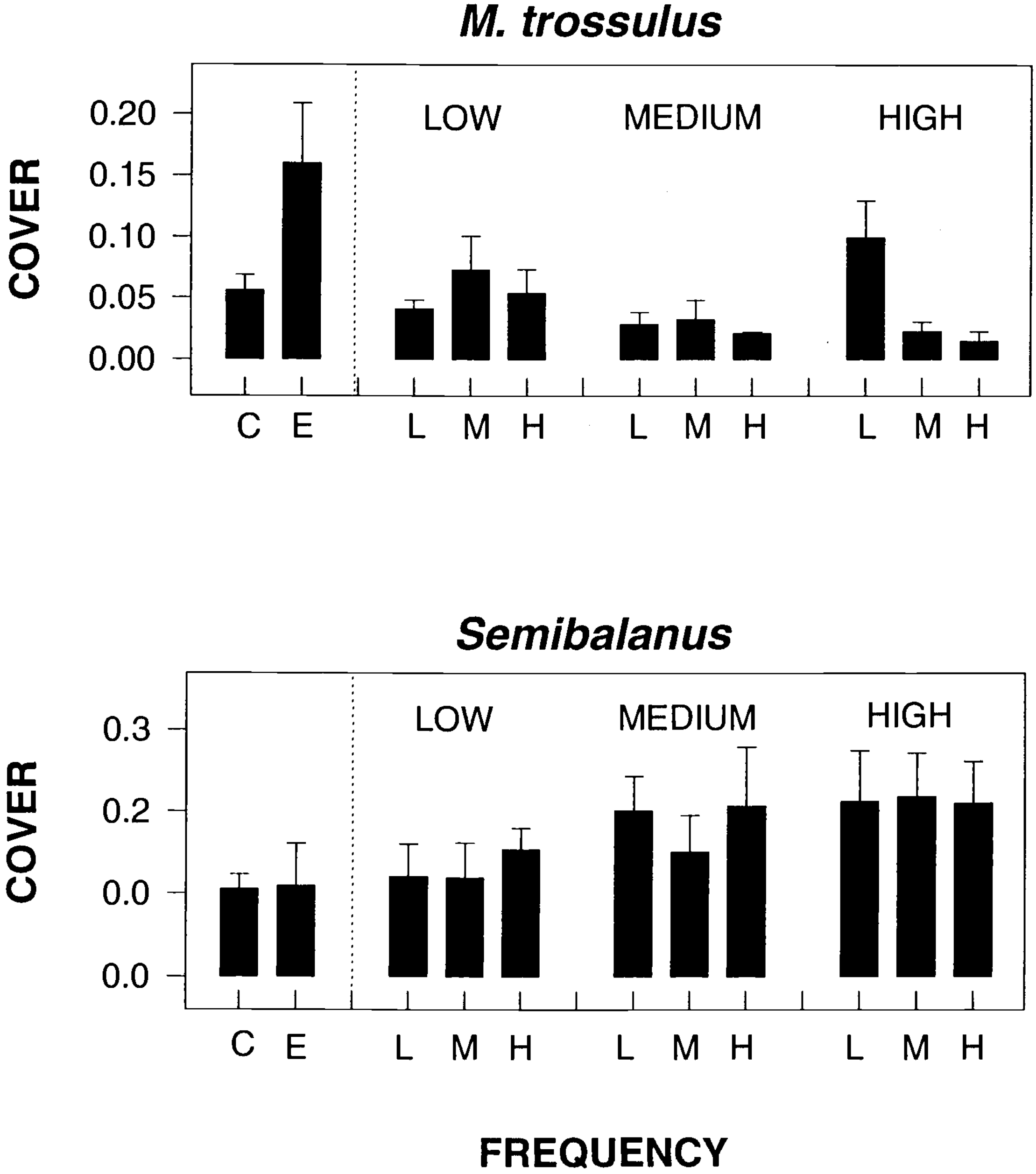

M. trossulus
M. californianus
COVER
HIGH
MEDIUM
LOW
0.25
0.20
0.15
0.10
0.05
0.00
0.12
0.08
0.04
0.00
Apr.
Aug.
Dec.
Apr.
Aug.
Dec.
Apr.
Aug.
MONTH
FREQUENCY:
● HIGH
▲ MEDIUM
○ LOW

Figure V.11. Mean cover (± SE) of the mussel *Mytilus trossulus* and the barnacle *Semibalanus cariosus* in the variable predation experiment averaged for the entire duration of the experiment (April 1991 through May 1993). The mean covers in the exclusion (E) and control (C) treatments of the cage exclusion experiment are also shown in the left side of the panels. Each group of three bars is a level predation intensity (Low, Medium, High). The letters L, M and H in the x-axis indicate the Low, Medium, and High predation frequency treatments. See figure 10 for explanation of treatments.

Figure V.11.


M. trossulus
COVER
0.20
0.15
0.10
0.05
0.00
LOW
MEDIUM
HIGH
C
E
L
M
H
L
M
H
L
M
H
Semibalanus
COVER
0.3
0.2
0.0
0.0
LOW
MEDIUM
HIGH
C
E
L
M
H
L
M
H
L
M
H
FREQUENCY

Variable Predation: Frequency and Intensity of Predation

Statistical analyses of this experiment were confined to inclusion cages, so the potential artifact introduced by cages or factors other than invertebrate predators (e.g. birds, see above) were kept constant across treatments. Changes in the abundance of a number of sessile species were observed as responses to the treatments. I succinctly describe here the changes in the most abundant or ecologically most important species only, to convey briefly the complex pattern of species response to the treatments. The other species, including those for which the individual species-based analysis showed no significant effects of treatment, were considered in the species richness, species diversity and the multivariate ordination analyses.

The mussel *Mytilus trossulus*, whose cover increased in the predator exclusions (see above), was negatively affected by the increasing density of whelks inside the cages under a medium frequency and constant predation regimes (Figs. 10 and 11. Note in figure 11 the progressively lower mean cover of mussels from predator exclusion to high intensity under the constant, H, and medium, M, frequency regimes). However, its cover was significantly higher under the highest predation intensity, but the lowest frequency regime (Fig. 10, Table 11, significant between and within subjects interactions between intensity and frequency). Thus, at medium to high (constant) frequencies of predation the effect of increasing intensity of predation on the cover of *M. trossulus* was linear, but at low frequencies its effect was significantly non-linear.

The large barnacle *S. cariosus*, was not affected by the temporal pattern of predation (Table 12, non-significant main effects of frequency and interaction), but it increased in abundance with an increase in the intensity of predation (Fig. 11, Table 12, significant within subjects effect of treatment). The repeated measures analysis for *S. cariosus* was performed on the yearly means for 1991, 1992 and 1993 because large variation of individual dates did not conform with assumptions of variance homogeneity or normality. Note that the permanent exclusion of predators had no effect on this species, but the presence of them at intermediate to high densities increased the barnacle cover above the values observed in the exclusions plots (from 11 to 23 %).

The responses of the California mussels, *M. californianus* and the gooseneck barnacle *P. polymerus* to the different predation regimes were more complex. Covers the mussels, and particularly *P. polymerus* were lower at intermediate levels of intensity (Fig. 11), and at low and high intensities the effects of predator density depended on if predation was variable or constant (Fig. 12, Tables 13 and 14, significant interactions between frequency and intensity). For easy of comparison the cover of all species in figure 11 were averaged over the entire duration of the study. This resulted in substantially lower cover values for *M. californianus* and *P. polymerus*, species that were not present the first two years of experiments, but it preserved the pattern of differences among treatments.

Results of MANOVA on the cover of the same species considered in the exclusion experiment (see above) confirmed the general pattern of species response to predation regimes determined by RM-ANOVA. The intensity of predation had significant main effects on the cover of sessile species and the effects were consistent over the 3 different years of the experiment (Table 15, non significant effects of interaction 'Years x Intensity'). On the other hand, the main effects of the temporal pattern of predation or its variation over time were not significant (Table 15). However, the contrast between the two variable predation regimes (low and medium frequency) against the constant predation treatment (high frequency) was marginally significant (P= 0.0587), while the other two combinations (low vs medium-high, and medium vs low-high) were highly non-significant (P= 0.5312 and 0.6120, respectively). The frequency of predation significantly affected species relative abundances, but its effect depended on the actual intensity or density of predators (Table 15, significant interaction "Intensity x Frequency'). The interaction between frequency and intensity of predation was due mostly to the effects on *M. trossulus, M. californianus* and *Pollicipes* (Table 16).

The treatments had no effect on the number of species present in the plots. Some of the predation regimes did change the diversity of species in the local community, however (Fig. 9b). Predation frequency by itself had no effect on diversity (Frequency main factor effect, P= 0.7958), while predation intensity had a small but significant and non-linear (Fig. 9) effect on diversity (Intensity main factor effect, F= 4.62, P= 0.0154, df= 2, 28). This effect of predation intensity on diversity was not as predicted by the intermediate disturbance hypothesis (i.e. higher diversity at intermediate levels of intensity, Connell 1978): diversity was slightly lower, not higher at intermediate predation intensity, regardless of the frequency of predation. The effects of predation frequency on species diversity depended on the level of intensity (Intensity x Frequency interaction factor, F= 3.79, P= 0.0139, df= 4,28). At low intensities of predation, an increase in predation frequency tended to increase species diversity, while at high intensity increasing predation frequency led to a decrease in species diversity (Fig. 9). At intermediate intensities the frequency of predation had no clear effects on species diversity.

Table V.12. Repeated measures analysis of variance of the effects of intensity (density of predators) and frequency (temporal pattern of variability) of predation by *Nucella* on the abundance *Semibalanus cariosus* (arcsin transformed cover data) for the years 1991, 1992, and 1993 (yearly means). See table 11 and text for further explanation of the experimental design and labels. Data did not show homogeneity of treatment differences variance (test for Sphericity P = 0.0155). Huynh-Feldt corrected probabilities (P H-F) are given for the univariate within subjects analysis (H-F epsilon = 1.07).

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Intensity	2	0.066	1.64	0.2134
Frequency	2	0.028	0.70	0.5065
Intensity x Frequency	4	0.016	0.41	0.7977
Error	27	0.040		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	P H-F	num df	den df	Wilks' λ	P
Time	2	1.793	87.67	**0.0001**	2	26	0.184	**0.0001**
Time x Intensity	4	0.054	2.65	**0.0429**	4	52	0.619	**0.0130**
Time x Frequency	4	0.003	0.19	0.9444	4	52	0.967	0.9277
Time x Inten. x Frequen.	8	0.003	0.14	0.9967	8	52	0.936	0.9859
Error (Time)	54	0.020						

Table V.13. Repeated measures analysis of variance of the effects of intensity (density of predators) and frequency (temporal pattern of variability) of predation by *Nucella* on the abundance of *Mytilus californianus* (arcsin transformed cover data) from May 1992 through May 1993. See table 11 and text for further explanation of the experimental design and labels. Data showed homogeneity of treatment differences variance (test for Sphericity P = 0.1490). Non-corrected probabilities (P) are given for the univariate within subjects analysis.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Intensity	2	0.017	1.42	0.2772
Frequency	2	0.006	0.52	0.6060
Intensity x Frequency	4	0.022	1.72	0.2053
Error	13	0.007		

B. WITHIN SUBJECTS

	Univariate Analysis			
SOURCE	df	MS	F	P H-F
Time	3	0.051	11.09	**0.0001**
Time x Intensity	6	0.006	1.23	0.3112
Time x Frequency	6	0.002	0.53	0.7839
Time x Inten. x Frequen.	12	0.010	2.26	**0.0272**
Error (Time)	39	0.005		

Table V.14. Repeated measures analysis of variance of the effects of intensity (density of predators) and frequency (temporal pattern of variability) of predation by *Nucella* on the abundance of *Pollicipes polymerus* (arcsin transformed cover data) from April 1991 through May 1993. See table 11 and text for further explanation of the experimental design and labels. Data did not show homogeneity of treatment differences variance (test for Sphericity P < 0.0001). Huynh-Feldt corrected probabilities (P H-F) are given for the univariate within subjects analysis (H-F epsilon = 0.505).

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Intensity	2	0.047	0.55	0.5901
Frequency	2	0.020	0.24	0.7928
Intensity x Frequency	4	0.066	0.76	0.5669
Error	13	0.086		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	P H-F	num df	den df	Wilks' λ	P
Time	5	0.082	4.44	**0.0135**	5	9	0.226	**0.0095**
Time x Intensity	10	0.008	0.46	0.8013	10	18	0.143	**0.0219**
Time x Frequency	10	0.022	1.17	0.3453	10	18	0.165	**0.0356**
Time x Inten. x Frequen.	20	0.007	0.40	0.9370	20	31	0.060	**0.0344**
Error (Time)	65	0.019						

Figure V.12. Mean cover (± SE) of the mussel *Mytilus californianus* and the gooseneck barnacle *Pollicipes polymerus* in the variable predation experiment averaged for the entire duration of the experiment (April 1991 through May 1993). The mean covers in the exclusion (E) and control (C) treatments of the cage exclusion experiment are also shown in the left side of the panels. Each group of three bars is a level predation intensity (Low, Medium, High). The letters L, M and H in the x-axis indicate the Low, Medium, and High predation frequency treatments.

Figure V.12.

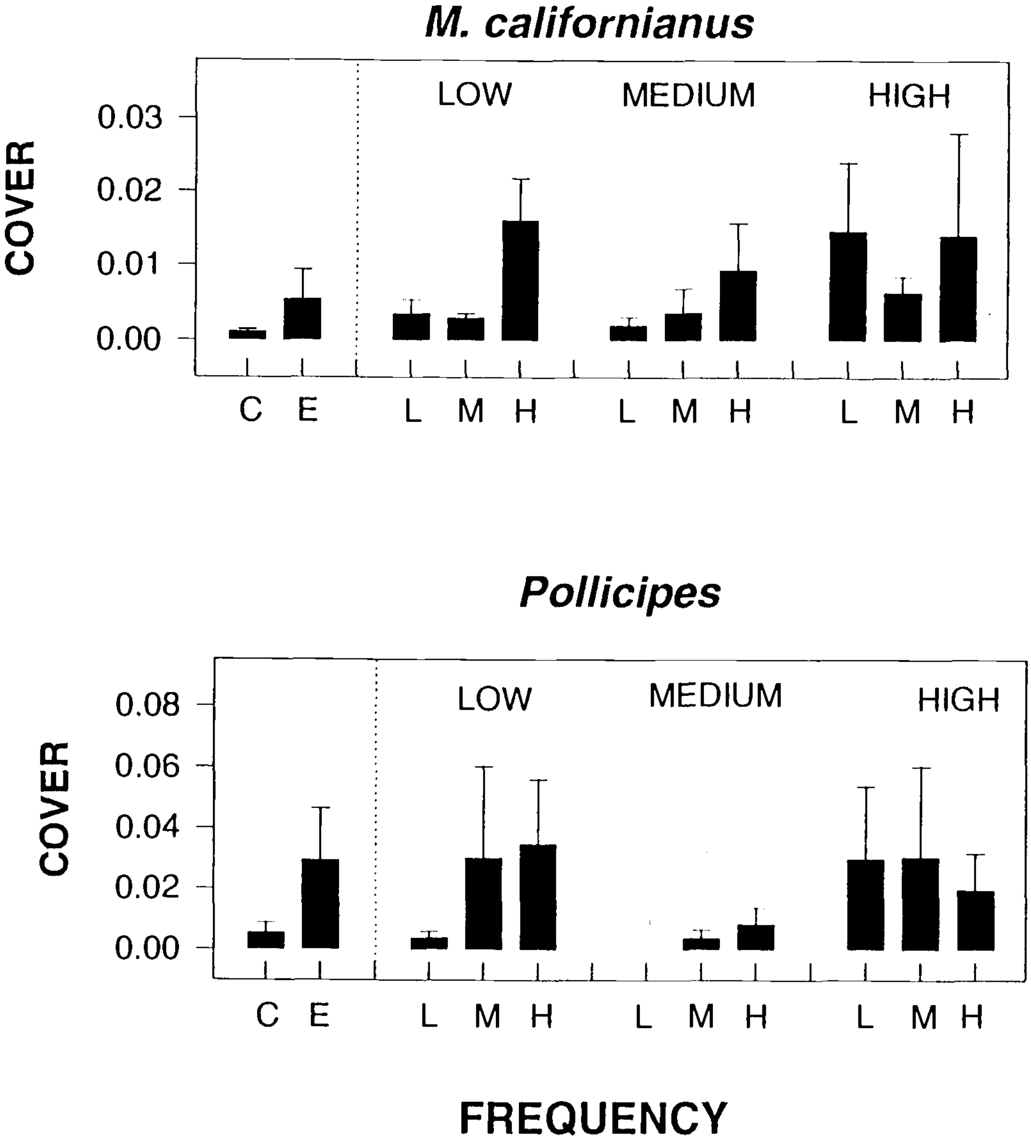

M. californianus
COVER
0.03
0.02
0.01
0.00
LOW
MEDIUM
HIGH
C E
L M H
L M H
L M H
Pollicipes
COVER
0.08
0.06
0.04
0.02
0.00
LOW
MEDIUM
HIGH
C E
L M H
L M H
L M H
FREQUENCY

Figure V.13. Graphical representation of the first two axes of the PCA ordination of the replicated plots in the exclusion and variable predation experiments. The control plots (C) and predator exclusion plots (E) were included in the analysis. The species composition in the exclusion plots (circled with a heavy solid line) was different to those in any of the other variable or constant predation treatments and different to that observed in the unmanipulated controls (encircled with a dashed line). In the top panel (A) the symbols are the different levels of predation frequency, from low (l) to medium (m) and high (h= constant predation). The constant predation treatment created a rather defined type of community composition (encircled with a fine solid line) that overlapped little with the controls. The composition in the low frequency treatment is encircled with fine dotted line. In the bottom panel (B) the symbols indicate the low (l) medium (m) and high (h) intensity treatments. The composition in the medium intensity treatment is encircled with a fine solid line.

Figure V.13.

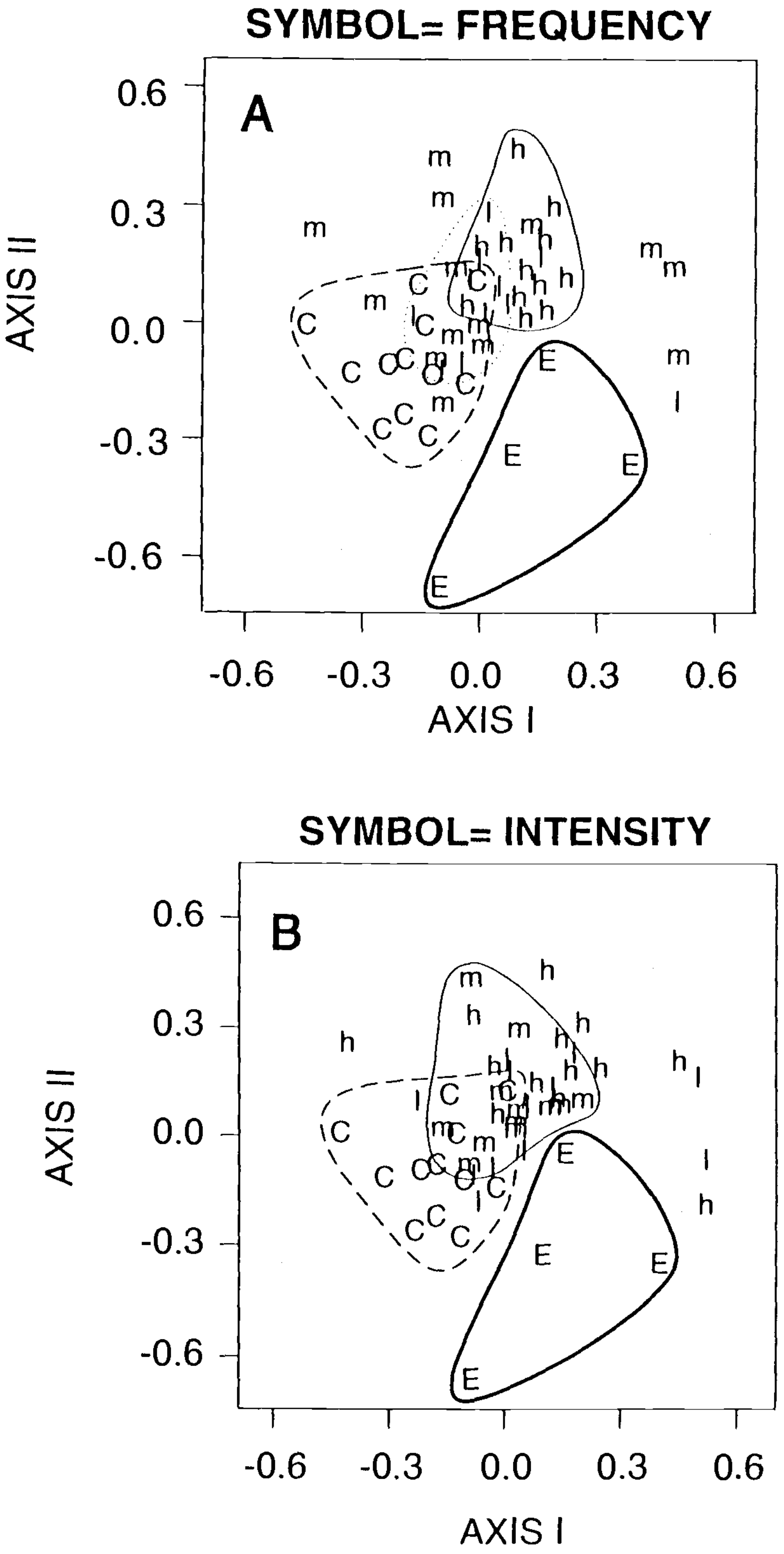
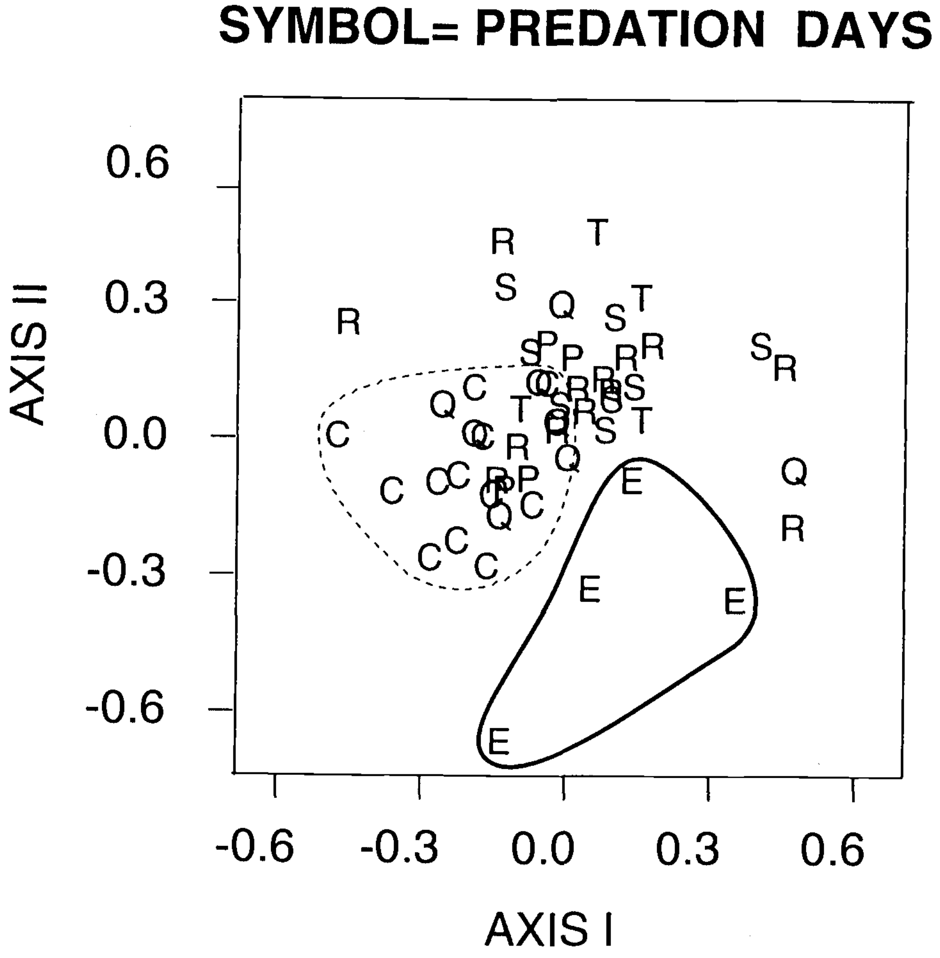

SYMBOL= FREQUENCY
A
AXIS II
0.6
0.3
0.0
-0.3
-0.6
-0.6
-0.3
0.0
0.3
0.6
AXIS I
SYMBOL= INTENSITY
B
AXIS II
0.6
0.3
0.0
-0.3
-0.6
-0.6
-0.3
0.0
0.3
0.6
AXIS I

Figure V.14. Graphical representation of the first two axes of the PCA ordination of the replicated plots in the exclusion and variable predation experiments. See figure 13 for details. The symbols represent the predator exclusions (E), unmanipulated controls (C), and the five different groups of 'predation days', P, Q, R, S, and T (see Table 1 and text).



The effects of the different predation regimes on the entire species assemblage , including the predator exclusions and the unmanipulated controls can be represented by the ordination of the plots in species space (Fig. 13). A total of 12 species were used in the PCA analysis; 6 species were not included because they were only occasionally observed and at abundances below 1% cover. The PCA ordination gave better results than Bray Curtis (polar) ordination or non-metric multidimensional scaling (NMDS) but it produced some clustering in the middle (Figs 13 and 14). One predator exclusion replicate also had a large effect in the ordination and could be considered an outlier, but due to the importance of this treatment it was left in the analysis. The community composition in the exclusion plots was clearly different from that in the controls and from that in any of the predation regimes used in the variable predation experiment. The most important species differentiating the groups in figure 13 were *M. trossulus, M. californianus, Pollicipes, Pterosiphonia, Cthamalus,* and *Anthopleura* (based on the correlations of species with the PCA axes) . The highest variation in community composition was observed under the medium frequency (m) treatments (across intensity levels), while constant predation (h= high frequency) produced a rather restricted pattern of community composition (Fig. 13 a). With the exception of one replicate (plot under a low frequency and high intensity of predation), low predation frequency (l) also produced a relatively confined pattern of community composition, in comparison to the intermediate level of predation frequency. Community composition in the unmanipulated control plots overlapped mostly with the composition observed under low and medium predation frequency, and least with that observed under constant predation (h). However, none of the predation regimes completely overlapped in community composition with the control plots. Community composition in the controls was also closer to that observed under low and medium predation intensities (Fig. 13 b). The combination of high predation intensity and medium frequencies produced the largest variation in community composition of all predation regimes (compare figures 13a and b). The differences in community composition among the plots can hardly be explained by differences in 'predation days', which are a measure of the total expected mortality of prey in a year. Treatments with similar number of predation days produced very different communities depending on the particular predation regime (Fig. 14). The combination of high frequency and high intensity (T), was the only 'predation day' level producing a relatively defined pattern of community composition, but this level also correspond to a unique predation regime.

Table V.15. Multivariate analysis of variance (MANOVA) on the cover of the six most abundant sessile species in the variable predation experiment (see table V.10). See table V.11 and text for explanation of experimental design and labels.

SOURCE	Wilks's λ	num df	den df	P
Years	0.134	12	152	**0.0001**
Intensity	0.662	12	152	**0.0012**
Intensity x Years	0.790	24	266.3	0.7686
Frequency	0.829	12	152	0.2577
Frequency x Years	0.889	24	266.3	0.9968
Intensity x Frequency	0.589	24	266.3	**0.0131**
Intensity x Frequency x Years	0.754	48	378	0.9992
Contrasts on main effect of Frequency:				
Low and Medium vs. High	0.701	6	76	0.0587
High and Low vs. Medium	0.946	6	76	0.5312
High and Medium vs. High		6	76	0.6120

Table V.16. Standardized canonical coefficients of the sessile species considered in the MANOVA analysis of the variable predation experiment (Table V.15). Coefficient are given only for the significant factors of MANOVA in table V.15. The magnitude of the coefficient is proportional to the contribution of a species to the significance of that factor in the MANOVA.

	Standardized Canonical Coefficients		
Species:	Intensity (Main Effect)	Intensity x Years (Interaction)	Intensity x Frequency (Interaction)
Semibalanus	-0.6539	1.4705	0.0961
M. trossulus	0.9690	0.2226	0.9328
M. californianus	-0.2311	0.1083	0.0552
Pollicipes	0.2059	-0.2067	0.1444
Chthamalus	0.2162	0.2053	-0.1760
Anthopleura	-0.3984	0.5077	0.7415

Table V.17. Pearson correlation coefficients (r) and significance (P, probability of $|r| > 0$) between the abundance of sessile species (arcsin transformed cover data) across treatments and dates. Bold face indicates significant association at $\alpha = 0.05$.

		Semibalanus cariosus	*Mytilus trossulus*	*Mytilus californianus*	*Anthopleura*
Semibalanus	r	1	-0.012	0.158	0.387
	P		0.3170	**0.0019**	**0.0001**
M. trossulus	r		1	0.106	0.004
	P			**0.0376**	0.9319
M. californianus	r			1	0.311
	P				**0.0001**
Anthopleura	r				1
	P				

Discussion

Spatial and Temporal Variation in Whelk Predation

Large within and between year variability in the abundance of whelks was observed in the study. Within year variation was mostly seasonal. Densities increased in the spring and summer months and declined in late fall and winter, a pattern that seems typical of *Nucella* species in the northeastern Pacific (Connell 1970, Spight and Emlen 1976, Spight 1982, Navarrete and Menge in prep.) . Densities of both species were highly correlated over time, suggesting that the two species are affected in similar ways by temporal variation in the same or similar factors. Both physical stress (e.g. freezes killing whelks during low tides, Connell 1970) and variation in food supply (recruitment of barnacles (Spight 1982, and S. Navarrete, personal observations) promote temporal correlation between species. Temporal variability the presence and the density of whelks not only occurred over large spatial scales (e.g. this study site), but it varied over small spatial scales within the study site. Some areas within the site had whelks most of the time, while in others whelks were only occasionally observed. Areas with high frequencies of whelks were not necessarily areas with higher densities (frequency and mean density were uncorrelated), so within the site, high frequency of predation could occur at either high or low mean intensities. The effect of this spatial variation in the frequency and density of whelks on the sessile community will depend among other things on the effectiveness of the predator and the recovery rates of the prey populations. Spatial variation in whelk density is reflected in variability in predation intensity (or mortality of prey) with community-level consequences in the lower zone of other wave exposed areas in Oregon (Navarrete and Menge in prep.) and the barnacle-dominated communities of San Juan Island (Berlow and Navarrete in prep.).

Careful determination of the pattern of temporal variation in predation at a given site is relatively easy in some systems and with some predators (Marsh 1984, Butler 1989). In the case of small intertidal organisms inhabiting wave exposed habitats, which spend part of the time under water, determination of predation frequency over small scales cannot be based on direct observations and inferential methods have to be used. Telemetry or continuous tracking of individual movements (e.g. Della Santina and Chelazzi 1991) might be an alternative for these organisms, if sufficient numbers of individuals could be followed.

The observed pattern of whelk aggregation and its variation with season is also likely to lead to spatial variability not only in predation intensity, but also in predation frequency. If within a habitat a predator is randomly distributed over the space, or similarly if it moves over space at a faster pace than that allowing prey populations to recover, an increase in its density will lead to proportional increases in the frequency at which areas of the habitat are visited. Thus, frequency and intensity of predation are expected to be highly correlated. If instead the predators are aggregated and the intensity and sizes of the aggregations vary over time, as observed in this study (see also Spight 1974, Menge et al. 1994), then the frequency of predation will be less or not correlated to its intensity. The importance of the interaction among predator behavior, prey population dynamics, and the grain or patchiness of the system has long been recognized e.g. (Huffaker 1958) but spatially-explicit theoretical models of predator-prey interactions have only recently been introduced (although now at very high pace). However, experimental studies in field conditions are rare (Levin 1992, Marquet et al. 1993).

Effects of Predator Exclusion on the Sessile Community

Exclusion of invertebrate predators had direct and indirect effects on the relative species abundance of the sessile community. Since no differences were observed between roofs (cage controls) and the unmanipulated control plots (except for a significant but small effect on the abundance of *Semibalanus cariosus*), and since invertebrate predators other than whelks were either naturally absent (e.g. *Pisaster*) or allowed in the exclusion cages (e.g. low densities of *Leptasterias*), I attribute these changes primarily to the direct and indirect effects of predation by *Nucella canaliculata* and *N. emarginata*. The most clear and fastest response to whelk exclusion was an increase in the cover of the bay mussel *Mytilus trossulus*. This was most likely the direct effect of release from predation. Whelks are effective predators of this mussel species, and in the low zone of sites from which the starfish *Pisaster ochraceus* is naturally absent or experimentally removed they can keep the mussels under check (Menge et al. 1994). The exclusions also had positive effects on the cover of the competitively dominant California mussel *M. californianus*, but only after more than 2 years of predator exclusions. Whelks also prey on this mussel species, but at much lower rates than on *M. trossulus* (Palmer 1984, and S. Navarrete, personal observations). The positive effect of predator exclusion on the California mussel is probably due to both the direct effect of release from predation and an indirect positive effect mediated by *M. trossulus*. The California mussel does not usually recruit on bare rock but it prefers filamentous (e.g. algal) substratum (Paine and Levin 1981, Suchanek 1981). *Mytilus trossulus* appears to facilitate the recruitment of its dominant and larger conspecific, which over a few years start to replace and dominate mussel clams originally formed by the bay mussel (Menge et al. 1994, Navarrete and Menge in prep., and E.L. Berlow, personal communication). This is reflected in the significant positive correlation between these two species observed across replicates (Table 17), despite the existence of interspecific competition for space.

The positive effect of predator exclusions on the sea anemone *Anthopleura xanthogrammica* must be an indirect effect of predation since whelks do not feed on the anemone. This indirect effect could have been mediated by the positive effect of the California mussels and big *Semibalanus* on the anemones as suggested by the significant positive correlation between these species (Table 17). Indeed, juvenile anemones usually recruit or migrate into the mussel bed of the California mussel, where they experience higher survival rates (Sebens 1981).

Results of whelk exclusion experiments at Fogarty Creek contrast sharply with those obtained by (Wootton 1994) in a similar community at Tatoosh Island, Washington (see also Wootton 1992). Wootton's manual removals of whelks from patches among the California mussel bed for a period of 2 years did not lead to any significant changes in the cover of any sessile species. The only detectable effect of his treatment was a positive, indirect effect on the density of *Pollicipes polymerus*, but because of density compensation in the barnacle, no changes in their cover were observed (Wootton 1994). On the other hand, Wootton demonstrated that in this system predation by birds can have important direct and indirect effects on the sessile community (and also on whelk density), altering the successional trajectory if not the final outcome of the succession (Wootton 1992, 1994). The 'roofs' used in my study, only 5 cm off the rock surface, were effective barriers against predation by any bird species, yet no differences (except for one positive effect of roofs on *Semibalanus* cover) were observed when compared to the controls. Why this large differences between these two seemingly similar communities (Fogarty Creek and Tatoosh Island)? Differences in experimental protocols and within site variation in community structure might explain part of the differences. Manual removals of whelks over long periods of time are difficult to maintain and only produce a reduction in whelk density as opposed to complete exclusion (Wootton 1994, pp. 159). Re-invading whelks into removal areas might have had some impact on the removal plots in Wootton's studies, a problem greatly minimized with the use of cages. On the other hand, cages might introduce other artifacts besides shading (e.g. the basal rim might have affected water circulation inside the plot), which were not controlled for in my experiments. Within site spatial variation in community organization might also help explain the differences in results. For instance, birds were common at Fogarty Creek Point (see also Farrell 1991), but they usually were observed on the north end of the site and rarely on the south benches this experiments were conducted.

In general, comparisons between sites are made difficult by the lack of information on the within site variability (Underwood and Petraitis 1993). The differences between these two communities can also have a biological/ecological basis, however. Two related factors are important to consider: First, neither birds at Tatoosh Island, nor whelks at Fogarty Creek have dramatic effects in these successional communities (see below), as for example occurs after the removal of *Pisaster* from the lower zone of Oregon or Washington (Paine 1966, 1976, Menge et al. 1994), lobsters from the upper zone of Catalina Island (Robles 1987), or the same whelk species from the mid zone of San Juan Island (Berlow and Navarrete in prep.). These rather weak interactions might lead to substantial dependency on the initial conditions of the experiment and to magnification or increase in the number of indirect effects over time (E.L. Berlow, personal communication). These effects would also lead to high within site variation in community organization. Second, in Fogarty Creek most of the changes in sessile species abundance following predator removals can be traced back to the initial direct effects on one single species, *Mytilus trossulus.* The subsequent changes in *M. californianus, Pollicipes* and other species are most likely correlated to the initial increase in the cover of the bay mussel (see above). The bay mussel is also the species mediating the community-wide effects of *Nucella* in the lower zone of Oregon (Navarrete & Menge in prep.). In Wootton's (1992, 1994) experiment, the bay mussel was absent from the experimental area.

Predator exclusions did not affect species richness or their evenness, nor did they affect the amount of bare rock available for recruitment. The successional community that inhabits the patches in the California mussel beds is a diverse assemblage of invertebrate and algae species, which can, in the course of succession can become dominated by any of a number of different species. Whelks can have important effects on the trajectory followed by the community and the rate of succession. For instance, by removing *M. trossulus* from the patches, whelks slow down the succession toward the California mussel (see Table 4 with results after more than 3 years of exclusions).

Variable Predation as a Source of Community Variation

Variable predation created invertebrate communities different from those produced by constant predation regimes. Despite the fact that *Nucella* is not a strong interactor in this mid intertidal community (see above), changes in the temporal pattern of predation affected the way species responded to the variation in predation intensity (density). In general the species response to variable predation regimes was not predictable from the results obtained in the exclusion experiment or from considering a correlate of the total mortality of prey expected in the different predation regimes (predation days). For instance, *M. trossulus*, which is directly and negatively affected by whelk predation, was positively affected by the highest intensity of predation used in the experiments, as long as that predation was low (variable) in frequency. It is hard to explain the mechanisms involved in the response of the different species to the different predation regimes. In the case of *M. trossulus* an hypothesis is that high predation intensity might negatively affect the mussel, but also its competitors. If the mussel grows faster than its competitors and escapes predation in size (or reduces it to insignificant levels), then the mussel might do best under a predation regimes that is intense enough to remove competitors yet infrequent enough to allow escapes in size of at lest some individuals.

If it becomes difficult to explain the mechanisms involved in the direct effects of predation under a variable predation regime, explaining the mechanisms involved in the indirect effects of variable predation would at the moment be only tentative. Indirect effects themselves could be magnified by a variable predation regime and become the dominant source of variability, obscuring the direct effects of predation (see e.g. Miller 1994) and making predictions from permanent predator exclusion and constant predation treatments much more difficult.

Variable predation in combination with the intensity of predation can create very different patterns of community structure. I suspect that many if not most ecosystems are affected by this kind of predation regimes, rather than by constant predation levels. In this study the community composition in the unmanipulated control plots resembled more closely the composition under variable (low to medium frequencies) than constant predation regimes as shown by multivariate ordination (compare also the single species responses to variable predation and control treatments). However, the unmanipulated community did not completely overlap with any of the predation regimes. This suggests that either the cages (cage rim) introduced an artifact not present in the controls, that the temporal pattern in natural conditions is different from any of the ones used in the experiments, or that an important predator (carnivore or herbivore) was left out in the variable predation experiment. The latter two possibilities seem more likely. The temporal pattern of variation most relevant to this community might be in the order of 4-7 months, when seasonal changes take place, rather the shorter time variation used in the experiment. Also, not having incorporated *N. canaliculata* in the experiment might have produced part of the difference with the control areas. *Nucella canaliculata* and *N. emarginata* are often considered equivalent, but small differences in the ranking of prey preferred by them might be magnified under a variable predation regime.

The relative importance of variable predation within and between ecosystems will vary with the aggregation behavior and mobility of the predator within homogeneous habitats and the ability of prey populations to recover from predation events or to escape in size. For instance, predation by the starfish *Pisaster ochraceus* has much more dramatic effects on the lower intertidal than those described here for *Nucella*, but although the starfish distribution is aggregated (Menge et al. 1994), short term (< year) variability in predation regime is probably irrelevant for the community because of the large mobility of the starfish and its ability to eat all but the largest prey. Over larger temporal and spatial scales (tens of kilometers), however, the pattern of temporal variability in predation by this and other keystone species might have important effects on the entire community. An indication of this is the study on the effects the removal and subsequent reintroduction of 3 starfish to areas in the lower zone of Washington, New Zealand, and Chile (Paine et al. 1985). After several years of *Pisaster* removals in Washington, the California mussels reached a size-refuge from predation and the community was largely unaffected by the re-introduction of the predator. (Paine et al. 1985) compare the variability in community recovery in Chile and New Zealand, and concluded that size escapes from predation can lead to important variability in marine communities.

An important message from this and Butler's (1989) studies of variable predation on bluegill fish in lakes is that variable predation regimes can be an important source of variability in natural communities and the traditional protocols to study predation in the field might obscure this effect. Recent field experimental studies directly address the problem of spatial variability in predation intensity and its consequences for prey populations and communities (e.g. Duggins 1983, Hixon and Brostoff 1983, Marsh 1986, Dethier and Duggins 1988, Fairweather 1988b, Menge et al. 1994), yet studies addressing the effects of predation frequency or duration are rare. The current knowledge on the mean predator effects in many ecosystems is substantial, yet the information about the variation in space and time is limited and future experiments should address the effects of different components of predation.

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CHAPTER VI

CONCLUSIONS

The consequences body size (usually expressed as weight) on the physiology of animal species has been the subject of intensive research for many decades. Information about the physiological correlates of body size of invertebrates and vertebrates fill the pages of many books and reviews. By comparison, research into the consequences of this organismal attribute (body size) on large-scale ecological and evolutionary processes within natural communities is only starting to flourish. Most of the research has focused on the identification of patterns relating body size to population density, home ranges, or the number of species within communities or entire continents. One of the most general, although not universal patterns identified so far is the negative relationship between the body size of the organisms and their population density (number of organisms of a given species in a given area). However, differences among methods of measurement of population density and its definition (e.g. ecological, regional, or continental density), the inevitable sampling biases introduced when compiling the data (e.g. under-sampling of small and rare species), and the taxonomic bias introduced by researches when working with taxonomically-restricted "communities" (bird, insect "communities") have left the field in some disarray. Recent reviews of the topic have helped clarify some of the issues, but failed to identify many other problems that remain unresolved. For instance, few have recognized the limitations of ecological explanations (e.g. effects of interspecific competition, predation, etc.) when applied to taxonomic assemblages of species inhabiting large areas (e.g. continents) over which species might never interact. Despite all this confusion, it is clear that many patterns of body size distributions and its correlation with population density are recurrent in a wide variety of species assemblages (e.g. bacteria, plants, invertebrates, reptiles mammals, birds). Little do we know, however, about the causes, significance, or consequences of such patterns for the stability, dynamics or evolution of natural assemblages.

Body size patterns vary in a yet unpredictable way among different animal assemblages and ecosystems and only an understanding of the underlying causes of these patterns will help us predict when and under what conditions they occur. The results presented in Chapter II shed light into the question of statistical versus biological control of the expression of the body size-population density pattern. We (Navarrete and Menge) showed that tropical intertidal communities exhibit log-normal distributions of body sizes (number of species of different body sizes) and of their densities (number of organisms per unit area) but unlike their temperate counterparts, there is no correlation between population density and body size. Previous theoretical work had shown that the body size-population density relations can be spuriously generated by the combination of these two other general distributions, for which independent explanations have been proposed. The results in Panama showed that these patterns are not necessarily statistically correlated; the expression of a body size-population density relation is independent of other community-wide patterns. The characteristic inverse relationship between body size and population density in Panama did appear when a diverse guild of subtidal fish predators (carnivorous, herbivorous, and omnivorous) was experimentally excluded using large cages at different tidal heights. The cages allowed slow moving, invertebrate predators (carnivorous and herbivorous snails, chitons, limpets, crabs) while preventing access to the highly mobile fishes. These results suggested that in intertidal communities the expression of the body size-population density scaling can be under the control of ecological forces. Unlike intertidal predators in temperate systems, which do not have an effects on the population density scaling, the diverse array of subtidal fish in Panama are probably energetically independent from the intertidal zone. All these fish also feed in nearby subtidal areas where they spend most of the time and likely obtain most of their energy. This energetic independence might be 'necessary' for predators to restrict the abundance of all other species in the community to levels below those allowing the expression of a body size-population density scaling. Although the study in Panama does not answer the question of what processes give rise to similar patterns of association between these variables among different ecosystems (similitude of slopes of the log-log relationship), the results allow for specific predictions about the occurrence of the pattern in different regions. For instance, we predicted that in places where fish predation is low, a negative relationship between body size and density (like the one observed in temperate systems) should characterize tropical or subtropical communities formed by the same assemblage of species that occur in Panama. This proposition has not yet being tested.

Recent studies have shown that phylogenetic relatedness plays a role in the body size-population density relationship within assemblages of birds. The study showed that a different relationship between body size and population density was observed within tribes of phylogenetically related bird species as compared to the relationship observed when considering all birds occurring over Great Britain. Consistently, more negative slopes characterized the log-log relationship within these closely related groups than assemblages including more distantly related bird species. These results have been interpreted as reflecting the fact that phylogenetically related tribes of birds, and particularly those without close relatives in the continent conform entire 'ecological guilds', which would be subjected to the evolutionary processes molding the body size population density relationship. The general recommendation here is the intensification of studies of these relationships within taxonomic and phylogenetically related groups of animals.

While body size is probably subjected to direct evolutionary pressures and its evolution can usually be traced along lineages of related species, the density that local populations of that species achieve in natural communities is probably less directly affected by these evolutionary constraints and more closely determined by ecological factors. Some of this ecological factors are also correlate with body size and thus render the association between size and density statistically significant. Under this scenario, one would emphasize the study of the body size population density relation among groups of interacting species in natural communities, regardless of phylogenetic relatedness or taxonomic affiliation. In Chapter III I investigated the effect of phylogenetic relatedness in assemblages of intertidal gastropods of temperate and tropical regions. Data for this study was, for the most part compiled from the literature so as to be able to compare with studies on different groups of animals (e.g. birds) for which data have been gathered from previously published surveys. I also complemented this data set with my own field data and observations. The results showed that within local assemblages of intertidal gastropods, mean population density was not correlated with body size in two tropical regions and in the temperate zone of San Juan Island, but it was significantly and negatively correlated with body size in central Chile. The degree of taxonomic affiliation, a correlate of phylogenetic relatedness, did not have any effect on the body size-density relationship within the species of gastropods considered. The patterns observed in two of the four regions studied corresponded well with previous community-wide studies which included all intertidal organisms, regardless of taxonomic affiliation. These results suggest that among these intertidal organisms, the ecological unit(s) subjected to the evolutionary processes that determine the body size-population density relationship are independent of phylogenetic relatedness. It was also clear that in this organisms phylogenetically related organisms (as indicated by taxonomic affiliation) do not conform entire ecological guilds. Ecological guilds in this system are truly multiphyletic and can be studied only by transcending the [artificial] boundaries imposed by taxonomy.

In many ecosystems predation plays an important role in the maintenance and variation of the major patterns of community structure, including relative abundance of species, species diversity, species composition, body size distributions, productivity, etc. However, demonstration of predation effects has usually been limited to the removal of a single species or of all predator species together, making it difficult or sometimes impossible to determine the pattern of predation and to quantify the relative importance of different predator species. With these limitations, the experimental evidence gathered so far suggest that both 'keystone' (one or few strong and numerous weak interactions) and 'diffuse' (a number of equally weak interactions) kinds of predation pattern occur in natural systems (although this are not the only patterns of predation observed in natural communities). When the effects of several predator species have been investigated, the results have generally but not always shown important interactive effects between predators (indirect effects) on the rest of the community. Thus, the relative importance of predator species within a community, as well as the consequences of interactions between predators on lower trophic levels appear to vary among ecosystems and among habitats within a given system. Field experiments remain as a the only means to determine which predation pattern occurs and what is the relative importance of different species.

Quantification of the relative importance and interactive effects of predators in systems in which a keystone pattern of predation seems prevalent, has rarely been done (see exceptions below). When testing for the existence of a keystone, the effects of other predators in the system are usually assumed rather than experimentally demonstrated to have only minor effects, if any, on the rest of the community. This assumption is usually well justified by the lack of compensatory responses from other predators following the removal of the keystone, an extensive knowledge of natural history of the system under study, and by the logistic limitations of performing manipulations on all the potentially important species. However, failing to perform manipulations of other predators has prevented us from developing a more comprehensive understanding of the actual role of these species in the system and the nature of the interactions between them and the keystone. In Chapter IV we (Navarrete and Menge) tested the assumption that in the presence of a keystone, other predators in the system have no ecologically significant effects and quantify the interaction strengths of the keystone and the 'weak predators' under different environmental conditions. We selected a well studied system , the rocky intertidal zone of the Northwest coast of USA where the first keystone species ever identified, the seastar *Pisaster ochraceus* overlaps in distribution and diet with a number of other vertebrate and invertebrate predators. In this system we sought to answer the questions: Is the effect of a keystone affected by the presence of other predator species? Is the effect of other species dependent on the presence of a keystone? Is the effect of non-keystone species (weak interactors) more variable across environmental gradients than that of the keystone (strong interactor)? And is the *per capita* effect of a keystone species less variable across environmental gradients than that of a non-keystone?

Results showed that predation intensity by the keystone predator was strong under all site x wave exposure combinations and was unaffected by the presence of whelks. On the other hand, whelks had ecologically important effects on the survival of mussels in the absence, but not in the presence of the keystone. We suggest that this pattern of interactive effects between keystone and weak predators may be general to all keystone predator-dominated systems, but currently there are limited data to test this proposition. The total (population) interaction strength between seastars and mussels was stronger and less variable across sites and wave exposures than that of whelks and the *per capita* interaction strength of seastars was two orders of magnitude larger than that between whelks and mussels. However, *per capita* effects of seastars were much more variable between sites and wave exposures, probably because simple density values grossly underestimate the ability of keystone predators to localize prey. Negative effects of seastars on whelk density were observed within less than 4 months following *Pisaster* removals. Seastars also had a negative effect on whelk sizes, but the effect was evident only after more than 6 mo. of continuous *Pisaster* removal. Negative effects of seastars on whelks appeared to be stronger in places with higher densities of predators and can explain, in part, the reduced predation intensity of whelks observed in the presence of seastars.

These results support the idea that in keystone-dominated systems, species other than the keystone have only minor, if any effects on the rest of the community and may be an example of 'redundant species'. However, they also suggest that after the loss of the keystone species previously 'redundant' species can compensate for the reduced predation and adopt a major role in the altered system. Such responses are potentially and important force in stabilizing communities.

Much empirical information on the effects of predators has accumulated since the pioneering field studies of Paine and Connell in the early sixties, and the vast majority comes from an insightful albeit simple approach, the short- or long-term deletion of predators from a system and monitoring of prey responses to this perturbation for reviews. Nevertheless, predation as other disturbance agents is not invariable but it usually fluctuates widely over time. Both within year (seasonal) and between year fluctuations in predation regimes are apparent in many ecosystems and their effects are manifested in prey species composition, abundance or size structure. However, experimental manipulation of the pattern of temporal variation is rare. In many cases prey variability could easily be attributable to variation in the intensity of predation between seasons or years. Indeed, much experimental evidence obtained through repetition of exclusion experiments in different areas or times shows that the intensity of predation, as measured by prey mortality or by the total biomass removed by predators from a given habitat, vary significantly over space and time and can produce significant variation in prey community structure.

The extent of the effects of variable predation on community structure cannot be evaluated unless the correlated variation in predation intensity is experimentally isolated from the frequency at which predation events occur. Of course, it is possible that within natural communities temporally variable predation has no distinctive effects from those of a constant predation regime that produces the same total mortality of prey when a period of time longer than the interval of time between predation events is considered. At some simplified theoretical level the community-level consequences of predation (or disturbance) frequency are the same as those produced by varying predation intensities.

To my knowledge the only previous experimental approach to directly answer these questions in a natural system is Butler's (1989) elegant study of the effects of variable predation by the bluegill sunfish, *Lepomis macrochirus* on the invertebrate community of a small in Florida, USA. His results showed that a variable predation regime produced distinctive prey compositions, resembled closer the species composition and variability of natural (unmanipulated) mid-depth areas of the lake than a constant predation regime, and increased the mean body size and body size variance of some prey species over those observed under the constant predation regime or a constant exclusion treatment. Bluegill sunfish exhibited aggregating behavior and the degree of aggregation changed among habitats and between seasons. This produced a variable pattern of predation and spatial variation in the frequency at which patches of habitat were visited by the fish schools. Although Butler's experimental design did not allow him to separate the effects of frequency and intensity of predation (in the variable predation treatment both the frequency and the number of fish per cage were manipulated in an effort to emulate the natural regime in control areas; Butler 1990, pp. 325), his results highlight the importance of variable predation for this ecosystem.

Whelks are ubiquitous predators in mid and mid-low zones of rocky intertidal communities where they can have from very minor to very dramatic effects on their prey. On the wave exposed coast of Oregon, the whelks, *Nucella emarginata* and *N. canaliculata*, are found in dense aggregations in the mid-low zone below the mussel beds of the California mussel *Mytilus californianus*, or in the patches within the mussel bed at mid-zones. Both species are limited by the size of mussel or barnacle prey they can handle, yet in the lower zone they can have important negative effects on mussel mortality over small spatial scales if the keystone predator *Pisaster ochraceus* is removed. These characteristics and comparatively slow mobility and size of whelks make them a good model to study the effects of variable predation in rocky intertidal communities.

In Chapter V I studied the small-scale spatial distribution and persistence of whelks at a mid-zone habitat on the Oregon coast and experimentally evaluated the effects of 1) long-term (3 years) predator exclusions and 2) variable predation by whelk on the successional sessile prey community that occupy patches within the California mussel beds. The experimental design allowed me to distinguish between the effects of frequency and intensity of predation and test the hypotheses that 1) temporally persistent exclusion of whelks lead to changes in prey abundance and prey composition, 2) variable predation creates prey communities different from those resulting from a constant predation regime, 3) variable predation contributes to the temporal and spatial variability in prey populations, 4) variable predation increases local species richness and diversity, 5) variable predation creates communities that resemble more closely the natural predation regimes than the constant predation treatments.

Results of these experiments and observations showed how the direct and indirect effects of the exclusion of invertebrate predators led to several changes in the abundance of sessile species, notably a rapid increase in the cover of the bay mussel *Mytilus trossulus* and a slow and small increase in the cover of gooseneck barnacles and the California mussel *Mytilus californianus*. With one exception, cage shading and bird predation had no effect on the sessile species assemblage. Variable predation produced community composition different from those observed under a constant predation regime or predator exclusions. In general, the individual species responses to the different predation regimes could not be predicted from the results of the exclusion experiment. Non-linearities and indirect effects could be magnified by a variable predation regime. Community composition in the unmanipulated control plots resembled closer the composition observed under the low and medium frequency treatment (variable predation) and least that one observed under a constant predation regime, regardless of the intensity. However, none of the predation regimes used in the experiment completely matched the community observed in the controls.

Temporal variability in predation by whelks can increase spatial variability in the sessile community and create distinctive community compositions, even though the overall effects of whelks in this successional communities are rather mild. Variability in predation in probably an important, yet poorly understood cause of spatial heterogeneity in most ecosystems.

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Appendix

APPENDIX

Sources of data on body size and population density of gastropods by region and site of collection within each region (see details in Chapter III). References for body size include both the original shell length data and the wet weight-shell length regression used to convert lengths to body weight.

REGION	**HABITATS**	**SITES**	**REFERENCES**	
			Density	**Body Size**
Panama	Rocky benches moderately exposed to exposed	Taboguilla Is. (reef1-reef6)	1-4	4
		Urava Is.	3	4
		Uva Is.	3	4
Costa Rica	Rocky benches moderately exposed to exposed,	Playa del Coco	5,6	5-7
		Punta Mala	8	6,7
San Juan Island	Rocky benches, protected, cobbles	Turn Point Is.	5,9,10	7
		Eagle Point	9	7

(Appendix 1. Continued)

REGION	HABITATS	SITES	REFERENCES	
			Density	Body Size
Chile	Rocky benches, moderately exposed and exposed, cobbles	Las Cruces	11	11
		Montemar	11	11
		Punta de	7	7,11
		Tralca	7	7,11
		Salinas		

1: (Menge et al. 1985); 2: (Menge et al. 1986); 3: (Menge and Lubchenco 1981); 4: (Navarrete and Menge in prep.); 5: (Spight 1976); 6: (Keen 1971); 7: SAN unpublished data; 8: (Ortega 1986); 9: (Dayton 1971); 10: (Berlow and Navarrete in prep.); 11: (Marquet et al. 1990)