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As ecologists are being called upon to predict the consequences of human perturbations to natural communities, an important goal is to understand what factors drive variability or consistency in nature.

In the rocky intertidal of San Juan Island, Washington, a comparative experimental approach was used to investigate spatial and temporal variation in community organization. The effect of predation on B. glandula varied dramatically over small spatial scales between microhabitats but was remarkably consistent over time withing a given microhabitat. The effects of predation on S. cariosus varied over time within the same microhabitat. By repeating previous landmark experiments at our study site, and replicating these experiments across microhabitats, the domain of applicability of previous experimental information was greatly expanded.

In an early successional assemblage on the Oregon coast, I tested the hypothesis that, when the direct effect of one species on another increases in relative strength, its total effect (direct + indirect) is less variable or conditional than if the link between those species is weak. The effect of strong predation by whelks was less sensitive to the

presence of additional species and more consistently dampened natural variation between experimental starting dates and between individual replicates within a given experiment. In contrast, the outcome of weak predation was more spatially and temporally variable in sign, and whether it magnified or dampened differences between individual replicates varied between experiments. Consequently the mean total effect of weak predation generally did not differ significantly from zero. However, in some cases, the range of variation (both within and between experiments) in the effect of weak predation exceeded the magnitude of the strongest total effect observed.

Longer term results of the experiments on the Oregon coast examined the role of historic factors in influencing the degree to which successional paths are canalized and repeatable or contingent and variable. Succession in mid-intertidal patches in the mussel bed displayed complex patterns of historic effects that varied between species and between different stages of succession. Despite its potential complexity, this system exhibited some consistent and repeatable patterns of succession. Some important canalizing, or noise-dampening forces in this system included: 1) physiological and life-history constraints, 2) compensatory responses of functionally redundant species, and 3) strong interactions between species.

Patterns and Dynamics of Context-Dependency in the Marine Rocky Intertidal

by

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Eric L. Berlow

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CHAPTER I

GENERAL INTRODUCTION:

Most natural communities have the dialectical property of being both tremendously variable and complex yet, at the same time, compellingly regular and predictable. As ecologists are increasingly being called upon to understand and predict the consequences of human perturbations to natural communities, an important goal is to understand what factors drive variation or consistency in nature.

Large spatial and temporal variability in population abundances and/or species composition have always fascinated field ecologists (e.g., Watt 1947, Andrewartha and Birch 1954, Hutchinson 1959), and often frustrated the non-ecologist. While this variation can sometimes be explained simply by variation in environmental conditions, interactions between species can also be an important determinant of community structure (e.g., Connell 1961a, b, Paine 1966). One important obstacle to predictability is the fact that the outcomes of species interactions often depend on the spatial, temporal, or historical context in which they occur (e.g., Dayton 1971, Menge 1976, Fairweather et al. 1984, Thompson 1988, Cushman & Whitham 1989, Drake 1990, Cushman 1991, Carpenter and Kitchell 1993, Wedin and Tilman 1993, Menge et al. 1994, Berlow Ch. II and III). In addition, the effect of one species on another often depends on the presence of other species (i.e. indirect effects) (Wootton 1994a, Menge 1995). When all possible indirect interactions between species are considered, any community with more than just a few species can be theoretically intractable: the consequences of a species deletion (e.g., extinction) on the abundance of another species of interest can be indeterminate in both sign and magnitude (Abrams 1987, Yodzis 1988). Indeed, complex and contingent interactions between species are often the source of 'unanticipated' consequences of field experiments and other human-induced changes to natural communities (e.g., Sih et al. 1985, Brown et al. 1986, Carpenter and Kitchell 1993). Consequently, some might argue that the most general and consistent 'law' of ecology is: "It depends".

However, in the face of this theoretical complexity, many empirical ecologists have documented remarkably regular and repeatable patterns that can be predicted based on an *a priori* knowledge of causal mechanisms (e.g., Paine 1966, 1974, Menge 1976, Lubchenco 1978, Lubchenco and Menge 1978, Menge et al. 1986, Carpenter et al. 1985, Schmitt 1987, Karban 1989, Power 1990, Tilman 1990, Hixon and Brostoff 1993). For example, on wave-exposed rocky shores of the Pacific Northwest, the mussel, *Mytilus californianus*, often occupies a distinct horizontal band in the mid-intertidal zone. Its sharp lower limit is predictably established by the foraging activities of a low intertidal 'keystone' predator, *Pisaster ochraceus* (Paine 1966). In the absence of predation in the mid-intertidal, *M. californianus* is capable of forming extensive monocultures, and the patterns of disturbance and recovery in the mussel bed are "monotonously regular" (Paine 1984, p. 1341). In this case, the interactions between species are strong and consistent, and variation in the interactions (e.g., variation in the effect of *Pisaster* between the mid- and low-intertidal) is predictable with a knowledge of causal processes.

Field experiments have proven to be the most powerful tool used by ecologists to elucidate the causal processes of community organization (Paine 1977, Hairston 1989, Lubchenco and Real 1991). However, field experiments are also necessarily limited in their spatial and temporal extent. Their site-specific nature has been instrumental in demonstrating the contingent nature of many organizing processes, but, for the same reason, this has raised many questions about the generality of experimental results (Bender et al. 1984, Diamond 1986, Underwood and Petraitis 1993).

Thus, a critical challenge for the successful development of predictive models and natural resource management strategies is to determine not *if* natural communities can be complex and variable, but *when*. Why *aren't* all natural systems always completely chaotic? When can we expect species interactions to dampen, rather than magnify, natural variation in environmental conditions? Many theories in physics are successful because they neglect complicating, non-linear effects (e.g., who ever worries about friction in high school physics?). Some of the questions which have guided the research for this thesis include: 1) How can we increase our ability to generalize from the results of small scale field experiments? 2) When can we expect the outcome of an experimental manipulation (or management strategy) to be intractably contingent, and when can we expect it to be dependably robust? 3) Are there any rules in ecology that determine when we can safely ignore a large number potentially complex, site-specific, and species-specific details without compromising our predictive capacity? I explored these questions in a marine rocky-intertidal system, which is ideal for experimental manipulation because the species are relatively small, sessile or slow-moving, and have relatively rapid growth rates and short generation times.

In Chapter II, a 'comparative experimental' approach (Lubchenco and Real 1991, Menge 1991a) was used to understand the causes of variation and consistency in community structure in the rocky intertidal zone of San Juan Island, Washington. We (Berlow and Navarrete) took advantage of experiments conducted by Dayton (1971) at the same site 23 years earlier and repeated those experiments both in the same microhabitat as the original study and in a different microhabitat, occurring just meters away but with the same species assemblage. By repeating small scale field experiments both over time and across microhabitats, the domain of applicability of previous experimental information was greatly expanded.

In Chapter III, I took advantage of the power of temporal replication of field experiments to understand some of the causes of variation in the outcome of species interactions. In particular, I tested the hypothesis that, when the direct effect of one species on another increases in relative strength, its total effect (direct + indirect) is less variable or conditional than if the link between those species is relatively weak. On the central Oregon coast, in an early successional, rocky intertidal interaction web, consisting primarily of one predator (whelks) and two early colonizing sessile prey that compete for space (acorn barnacles and mussels), the presence/absence of the two prey species was manipulated under each of three predator densities in a replicated factorial design. Three identical experiments were repeated over three successive years. This design allowed me to address the following questions: 1) Does the strength of indirect effects increase with an increase in the relative strength of predation (direct effect) by snails? 2) As the strength of the direct effect of predation increases, is the total effect (direct + indirect) less sensitive to variation between experimental starting dates or between different replicates within an experiment?

The direct effects of whelks on this successional, mid-intertidal community are transitory since the species which eventually dominate the substratum reach an effective size refuge from predation by whelks. In Chapter IV, I used the longer term results of this set of experiments to investigate some of the causes of variation and consistency in the patterns successional change in this community. With the three succession experiments of Chapter III running concurrently in the same place, but with starting dates staggered by one year, I was able to explore the role of historic factors in influencing the degree to which successional paths are canalized and repeatable or contingent and variable. In particular, I addressed the following questions: 1) What are the separate and interactive effects of successional age, yearly variation, and initial conditions on the temporal changes observed after disturbance? 2) When do interactions between early species dampen or magnify natural variation between years or starting dates?

In Chapter V, I discuss the combined results of the above-mentioned field experiments and their implications for ascribing levels of certainty to our predictions about perturbations to natural communities.

CHAPTER II

GENERALIZING FROM FIELD EXPERIMENTS: SPATIAL AND TEMPORAL VARIATION IN COMMUNITY ORGANIZATION

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Abstract

A critical challenge to increasing the predictive capacity of ecology is to understand how results of small-scale field experiments can serve as a predictive framework for other systems or conditions. We used information from previous experiments (Dayton 1971) and present observations of a marine rocky intertidal community to predict community organization a) in the same microhabitat and the same experimental site as the original work, but 23 years later, and b) under slightly different conditions occurring just meters away with the same species assemblage.

In the mid-intertidal zone of the western rocky shores of San Juan Island, Washington, USA, patchy beds of loosely aggregated adult (>10 mm) barnacles, Semibalanus cariosus ("S.c."), which have reached a size refuge from whelk predation (Nucella spp.), create two distinct microhabitat types (±S.c.). Smaller barnacles (primarily Balanus glandula, and juvenile S. cariosus) are present in mid-zone -S.c. areas, but are absent from available space in +S.c. areas, where consumer densities (whelks and limpets) are higher. Earlier work at this site demonstrated the importance of predation and biotic disturbance (e.g., 'bulldozing') in small areas cleared of S.c. (-S.c. microhabitats). Based on this foundation of experimental and observational information, we predicted that adult Semibalanus indirectly enhance predation on new barnacles in +S.c. microhabitats by providing a refuge from potential environmental stresses.

Experiments demonstrated that whelks and some limpet species actively preferred +S.c. areas. Measurements of physical conditions suggested that +S.c. areas provided a refuge from intense summer thermal-related stresses. From these results we inferred that the relative paucity of small barnacles in +S.c. areas was due to more intense predation. Factorial manipulations of whelks, limpets, and adult Semibalanus directly tested for differences in predation intensity in +S.c. and - S.c. areas.

Our results confirmed that predation by whelks and limpets is important in determining the abundance of B. glandula in -S.c. areas. However, contrary to our predictions, exclusion of predators in +S.c. areas had virtually no effect on the cover of B. glandula. Large Semibalanus preempted any effect of predators by having an unexpectedly strong, negative effect on the abundance of recruits (B. glandula and S. cariosus < 3mm). Also, contrary to previous results, predators had no effect on the colonization of new Semibalanus in either microhabitat, probably because our experiment was conducted during a year of low Semibalanus recruitment.

Repeating small scale experiments over time and across different microhabitats provided two benefits: 1) The consistency between current results and previous experiments permitted the conclusion that the spatial differences in community organization were not confounded by temporal differences; and 2) the variation in results, both between spatially distinct microhabitats (±S.c.) and within one microhabitat through time (-S.c.), offers insights into how spatial variation in community organization might differ with yearly variation in recruitment.

Introduction

A major goal of community ecology is to determine the causes of spatial and temporal variation in natural communities. This knowledge can help to identify general rules of community regulation and, thus, contribute to the development of predictive models about the responses of a community to specific perturbations. Predictive models are essential if ecology is to play a significant role in addressing environmental problems (Lubchenco et al. 1991, 1993, Keddy 1992, Navarrete et al. 1993). However, predicting community responses to perturbations has been an elusive goal (Yodzis 1988, Peters 1991). Ecological systems exhibit great temporal and spatial variation in both patterns and processes (Levin 1989, 1992, Wiens 1989, Fairweather and Underwood 1991, Lively et al. 1993) and complex pattern-process relations seem to characterize most natural systems (Hastings 1987, Cale et al. 1989, Brown and Heske 1990).

Many ecologists have argued that models of community organization that reliably predict the outcome of perturbations must be based on an understanding of causal processes (Dayton 1973, Paine 1980, Tilman 1990, Lubchenco and Real 1991, Menge 1991a, Keddy 1992, Werner 1992). The critical challenge under this view is to understand when the knowledge about the pattern-process relation, obtained from a specific system and environmental condition, can serve as a predictive framework for another system or other conditions. Field experiments have proven to be the most powerful tool used by ecologists to elucidate the causal processes of community organization (Paine 1977, Hairston 1989, Lubchenco and Real 1991). However, field experiments are also necessarily limited in their spatial and temporal scale. Their site-specific nature has been instrumental in demonstrating the contingent nature of many organizing processes, but, for the same reason, they have raised many questions about the generality of experimental results (Bender et al. 1984, Diamond 1986, Underwood and Petraitis 1993). Can we increase our ability to use results from small scale experiments to predict the response of a community to a similar perturbation, but under different environmental conditions?

The "comparative experimental" approach has facilitated the extrapolation of small scale experiments into a larger conceptual context (Lubchenco and Real 1991, Menge 1991a, Underwood and Petraitis 1993). It involves performing identical replicated experiments at different sites across a range of conditions (e.g., Dayton 1971, 1975, Menge 1976, Lubchenco and Menge 1978, Underwood 1980, Louda 1982, Lubchenco 1986, Brown et al. 1986, Inouye and Tilman 1988, Butler 1989, Power 1992, Menge et al. 1994). While this approach does not specifically address the question of how community organization varies with the spatial scale of observation (Wiens 1989, Levin 1992), it has proven to be a useful tool for expanding the range of conditions in which community organization is understood and for exploring the consistency of processes across environmental conditions. While there are many examples of spatial replication of experiments across gradients of physical conditions, repeating studies over time is much less common (Connell 1974, Elner and Vadas 1990).

We used the comparative experimental approach in the rocky intertidal of the San Juan Island to expand the predictive framework of previous experiments. The rocky intertidal zone of the island has a long history of experimental determination of community organization (e.g., Connell 1970, Menge 1972, Spight 1972, Menge and Menge 1974). Our particular study site served as one of the sites for the landmark studies of Dayton (1971), who, through a series of experiments conducted between 1967 and 1970, determined the main processes responsible for the distribution and abundance of the dominant sessile species on a local (few meters) spatial scale. Using this experimental foundation, we predicted community organization a) in the same microhabitat and at the same experimental site studied by Dayton (1971), identical in general appearance 23 years later, and b) under different microhabitat conditions occurring just meters away with the same species assemblage. Our results suggest that general organizing processes were consistent over time in the same microhabitat as the original studies. However, some predictions, based in part on earlier work, were incorrect, evidently due to small-scale (meters) qualitative variation in species interactions and prey recruitment.

The System

This study was conducted at Eagle Point, on the west coast of San Juan Island, WA (48°27’N, 123°2’W) from August 1990 to March 1993 . Rocky intertidal communities of the moderately wave-exposed west shores of the San Juan Island have been described in detail by Connell (1970, 1971), Dayton (1971), Menge (1972), Spight (1972), Schubart (1992), and Kozloff (1973). Briefly, the mid intertidal zone at our site was characterized by patchy beds of the large balanoid barnacle, *Semibalanus cariosus* (Connell 1971, Dayton 1971, Sebens and Lewis 1985) which covered areas from a few to tens of meters. Individuals of this species can reach sizes of about 3 cm in basal diameter and 4 cm in height. The beds consisted almost exclusively of adult individuals (1-3 cm in diameter, see also Sebens and Lewis 1985) spaced millimeters to 5 cm apart. The rock surface among the adult *Semibalanus* was relatively smooth and markedly devoid of juveniles of the same species or individuals of the smaller barnacle, *Balanus glandula*. On a larger spatial scale, these small barnacles were notably more abundant in patches free of large, adult *Semibalanus* than in the spaces available within the beds of large barnacles (author's personal observations, see Results). In contrast, large limpets (*Lottia pelta* and *Tectura scutum*) and predatory whelks (*Nucella emarginata* and *N. canaliculata*) were generally more abundant among 'crevices' provided by large *Semibalanus* than in patches free of large barnacles. Hereafter, the beds of adult *Semibalanus* and the areas at the same tidal height that are free of adult *Semibalanus* will be referred to as '+S.c.' and '-S.c.' areas, respectively.

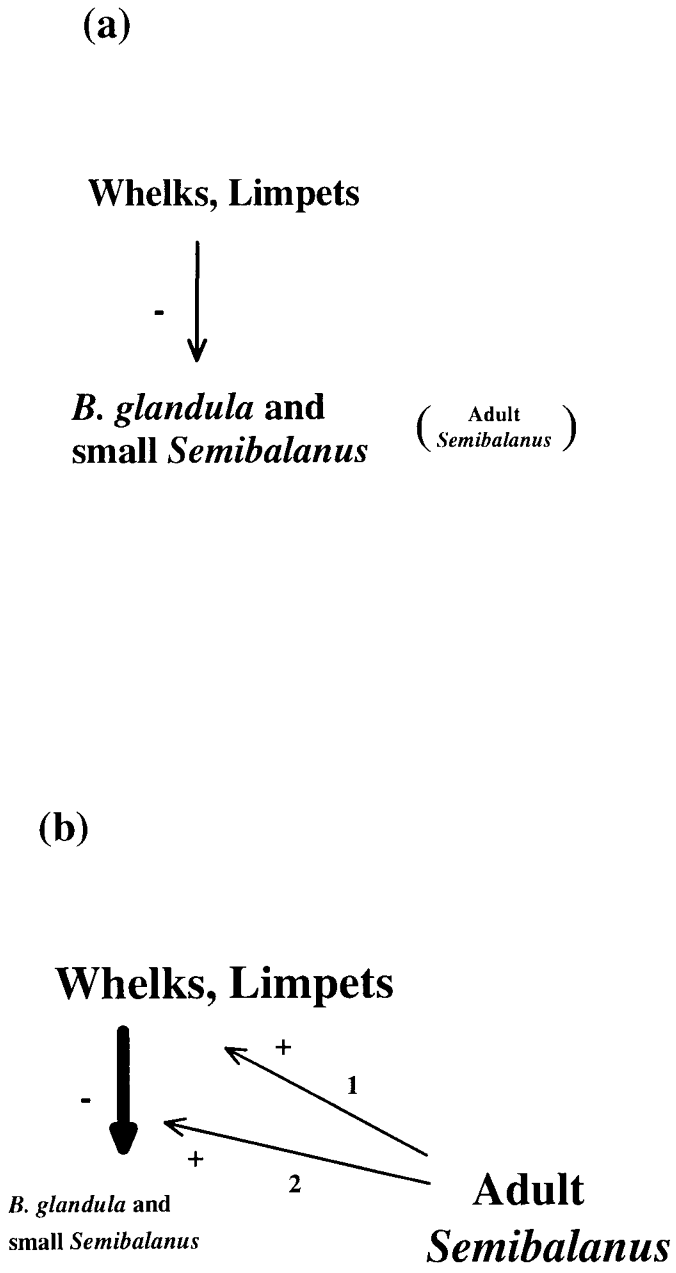
Predation is known to be an important organizing process in this community (Connell 1970, Dayton 1971). Small *Semibalanus* and *B. glandula* have many potential predators, including whelks (*Nucella emarginata*, *N. canaliculata*, *N. lamellosa*, *Searlisia dira*, *Ceratostoma foliatum*), nemerteans (*Emplectonema gracile*), starfish (*Pisaster ochraceus*, *Leptasterias hexactis*), nudibranchs (*Onchidoris bilamellata*) and flatworms.

Many of these occur primarily lower on the shore, however, at our site N. emarginata and N. canaliculata were the most conspicuously abundant predators in this zone (Connell 1971, Dayton 1971). Limpets can also have negative effects on both B. glandula and Semibalanus by either 'bulldozing' recruits off the rock or eating recruits inadvertently while grazing algae (Dayton 1971, Paine 1982, see also Hawkins 1983, Miller and Carefoot 1989). Experimental exclusions of whelks alone (primarily N. emarginata and N. canaliculata) from small areas cleared of sessile species (i.e. -S.c.) within the mid-intertidal demonstrated that, together, whelks and limpets can kill all the new Semibalanus and B. glandula that settle in a given year (Connell 1970, Dayton 1971). Large (>10 mm basal diameter) Semibalanus were relatively immune to 'predation' (including bulldozing) by whelks and limpets because of their large size and strong shells (Connell 1970, Dayton 1971, Palmer 1984). The third species of barnacle at our site, Chthamalus dalli, was relatively immune to predation due to its small size and flat morphology (Dayton 1971, Paine 1981). It was facilitated by whelk and limpet predation on the competitively superior B. glandula and Semibalanus (Dayton 1971, Paine 1981, Chapter III). In view of this weak direct link between C. dalli and its predators, this study focused primarily on factors determining the abundance of B. glandula and small Semibalanus.

Thus, based on 1) the previously demonstrated importance of predation in -S.c. areas and 2) the observation that predators are more abundant and appropriate prey (B. glandula and small Semibalanus (< 5mm)) are more scarce in +S.c. areas, we hypothesized that large Semibalanus barnacles indirectly inhibit local establishment of new barnacles by enhancing predation (Fig 1). Some mechanisms by which adult Semibalanus could increase predation include: 1) increasing the local density of whelks and limpets (an 'interaction chain', sensu Wootton 1993a) by providing favorable habitat, 2) increasing per capita foraging rates, for instance, by ameliorating physical stress (an

Figure II.1.Model of species interactions and the relative importance of predation in areas with and without adult Semibalanus. (a) In -S.c. areas, prior experiments by Dayton (1971) demonstrated the importance of predation by whelks an limpets. (b) In +S.c.areas our observations led us to hypthesize that large Semibalanus indirectly strengthen the effect of predators on B. glandula and small Semibalanus by (1) increasing the local density of predators and/or (2) increasing the per capita effect of predators. In each case, the relative thickness of the arrow represents the relative strength of the interaction, and the font sizes relative abundances of the species.

Figure II.1.


(a)
Whelks, Limpets
-
B. glandula and small *Semibalanus*
(Adult *Semibalanus*)
(b)
Whelks, Limpets
-
+
1
+
2
B. glandula and small *Semibalanus*
Adult *Semibalanus*

'interaction modification' or 'higher-order interaction', Werner 1992, Wootton 1993a), or 3) both mechanisms acting concurrently (Fig. 1).

Our experiments were designed primarily to test 1) if predation was still a key organizing process in -S.c. areas, 2) if beds of adult Semibalanus affected the distribution (local density) of predators, and 3) if the effect of whelks and limpets on new Semibalanus and B. glandula was indeed stronger in +S.c. areas (Fig. 1). We also conducted additional experiments and measurements to gain insight into some of the mechanisms involved in these processes.

Methods

I. Patterns of community structure

The relative cover and abundance of sessile and mobile organisms in the mid intertidal zone were quantified in July 1991 and July 1993 using a method described in detail in Lubchenco et al. (1984). July 1991 data were collected by B. Menge as part of another study. Briefly, a 10 meter horizontal transect was positioned within the mid-zone, and ten 50 x 50cm quadrats were positioned at 1 meter intervals along the transect. Percent cover of sessile species was estimated with 50 x 50cm vinyl quadrats with 100 randomly positioned dots. Whelks, limpets, and other large mobile species, and large barnacles (S. cariosus) were counted in 50 x 50cm quadrats. Smaller barnacles (<5mm) were counted in a 10 x 10cm quadrat in the lower left corner of the larger quadrats. In July 1993, 40 meter belts of contiguous 50 x 50cm and 10 x 10 cm quadrats were used. When small barnacles were too dense to be accurately counted in a 10 x 10cm quadrat, they were subsampled in five 1 x 1cm quadrats along its diagonal.

To quantify the relationship between the vertical (i.e. perpendicular to the shoreline) distribution of Semibalanus beds and that of whelks and limpets, two vertical transects spanning the vertical range of adult Semibalanus (from ≅ 0 m to ≅ 1.25 m above Mean Low Water Line (MLWL)) were positioned at random along a two meter horizontal transect. This was repeated at three different vertical walls within a 100m stretch of shore. Along the vertical transects, all mobile organisms >5mm in size were counted in 25cm x 25cm contiguous quadrats.

II. Effect of Semibalanus on the distribution of whelks and limpets

To test the effect of beds of adult Semibalanus on the spatial distribution of mobile predators, we conducted two complementary experiments:

1) Experiment I: Semibalanus additions:

To separate the effect of the distribution of food (small barnacles) and the presence of Semibalanus beds on the persistence of whelks in mid intertidal areas during low tides, we used 'artificial' barnacles in a short term field experiment in August, 1990. Six 25 x 25 cm plots of flat rock covered by ~50% Balanus glandula (primarily) and Chthamalus dalli were chosen in the mid intertidal zone. In three of these plots we glued shells of adult Semibalanus with marine epoxy putty (Z-spar™) to simulate a natural bed of barnacles. Shells were filled with modeling clay to simulate the heat capacity of live barnacles and to prevent snails from crawling inside shells. By transplanting shells to areas with B. glandula and C. dalli, we could keep constant the spacing of shells in +S.c. plots and the abundance of food (small barnacles) between +S.c. and -S.c. plots. In the center of each plot, 10 marked Nucella emarginata were released at the beginning of low tide and the number remaining inside the plots was recorded for the duration of the low tide (about 5 hours) and again during the low tide the next day. The effects of handling and releasing Nucella were assumed to be constant across treatments. Disturbing Nucella may have caused them to move more than usual, thus, the experiment probably tested for differences in the rates of dispersal of Nucella from each microhabitat. The experiment was repeated twice during the low tide series. Long-term monitoring of the Semibalanus additions was not possible because most of the shells were dislodged within a few weeks (probably by floating logs; Connell 1970, Dayton 1971).

As an index of preferences of whelks for different microhabitats, in this experiment we also measured the local distribution of marked whelks after three days of releasing 20 snails to each of the 6 plots. We recorded the microhabitat where each snail was recaptured and the distance to the point of release for each individual. Microhabitat availability was estimated with 8 120cm long transects radiating out, in 45 degree increments, from the center of each release point. At every 5 cm along each transect we measured the type of microhabitat available according to the following categories: horizontal surface with adult Semibalanus (Sh), sloping surface with adult Semibalanus (Sv), crevice with adult Semibalanus (Scr), horizontal rock surface without adult Semibalanus (Rh), sloping rock surface without adult Semibalanus (Rv), crevice without Semibalanus (Rc).

2) Experiment II: Semibalanus removals:

The effect of Semibalanus on whelks and limpets on a larger spatial and longer temporal scale than described in Experiment I was evaluated by removing adult Semibalanus and monitoring the densities of whelks and limpets in these and in undisturbed beds. Three areas of homogeneous vertical rock, approximately 3 m wide and 1.5 m tall, each with a distinct bed of Semibalanus, were chosen. In May, 1991 one half of each was randomly selected, and all the large, adult Semibalanus were removed along the entire extent of their vertical distribution. The other half served as an unmanipulated control. The densities of whelks (N. emarginata, N. canaliculata, N. lamellosa, Searlesia dira, and Ceratostoma foliatum) and limpets (Lottia pelta, L. digitalis, and Tectura scutum) within the vertical extent of the Semibalanus zone were estimated with contiguous 25 x 25 cm quadrats along two randomly positioned, permanently marked vertical transects in both the +S.c. and -S.c. areas. Densities were estimated just prior to the manipulation and then every 2-3 months for two years. Since Semibalanus has no basal plate, some barnacle meat remained attached to the rock where Semibalanus was removed. However, by the first post-manipulation census (1.5 months) there were no visible signs of barnacle flesh on the rock surface (authors' personal observations). While some whelks and limpets were inevitably disturbed by during the process of removing adult Semibalanus, the experiment was presumably long enough to allow new individuals to migrate into the area.

III. Measurement of physical conditions inside/outside Semibalanus beds

To gain insight into the potential mechanisms involved in the apparent preference of whelks for +S.c. areas (see Results), we measured hydrodynamic forces and thermal conditions in + S.c. areas and -S.c. areas. Measurements were taken during summer months, when whelks are most active (Connell 1970, Dayton 1971, Spight 1981) and, thus, when the potential effects of large Semibalanus on whelk foraging was most relevant to this study . While these measurements did not provide a complete picture of the complex physical regimes affecting Nucella throughout the year (e.g., desiccation stress, various thermal fluxes which comprise an individual's overall heat balance, acceleration forces), they did provide a measure of whether adult Semibalanus potentially modify the physical environment experienced by whelks when the effect of whelk predation was potentially greatest.

Maximum shear forces experienced by N. emarginata during two separate summer high tides were estimated by using a modification of the shear force dynamometer described by Denny (1983). Dynamometers consisted of a fiberglass tube 8 cm in diameter and 3 cm high. A shell of N. emarginata 22 mm long was fixed to the center of a movable top plate. The top plate was attached to the walls of the cylinder with three rubber bands and was attached to a pencil, which recorded the displacement of the top plate by tracing on a fixed bottom plate of acrylic. The maximum displacement of the top plate recorded on the bottom acrylic plate is proportional to the local maximum shear forces for the time period during which the measurements were recorded (Denny 1983). The dynamometers were placed into holes chiseled into the bedrock so that the top plate was roughly flush with the surrounding rock surface and were attached to the rock with three stainless steel screws. Two dynamometers were set in two +S.c. areas and two in nearby -S.c. areas. The dynamometers were left in the field for ca. 24 hours on two days in August, 1990, a time of year when shear forces are typically low, but when whelks are most active.

On San Juan Island, periods of calm waters and dry/sunny weather often occur during mid-day low tides. This means that thermal stresses (including desiccation) can be potentially intense during summer months at our site (Connell 1970, Dayton 1971, Spight 1982a and b). The effects of Semibalanus beds on the thermal conditions experienced by N. emarginata during mid-day low tides were evaluated in August, 1990 and July, 1992. In August 1990, local air temperatures, rock temperatures, and whelk body temperatures were measured in three replicated areas where adult Semibalanus were naturally absent (-S.c.) and three nearby areas where adult Semibalanus were naturally present (+S.c.). Rock temperatures were measured by placing a thermocouple into a piece of modeling clay that had equilibrated with the rock temperature. The clay was covered with aluminum foil to avoid the effect of direct solar radiation. To record body temperatures, fine thermocouples were inserted through a hole drilled in the shell of snails and fixed to the shells with marine epoxy putty (Z-spar™). Snails with thermocouples were maintained in the lab 24 hours before taking them to the field. Snails were placed in the field 1.5 hours before starting to record data to allow time for equilibration. Temperatures were recorded at five intervals from 11:30 to 13:55 during the low tide.

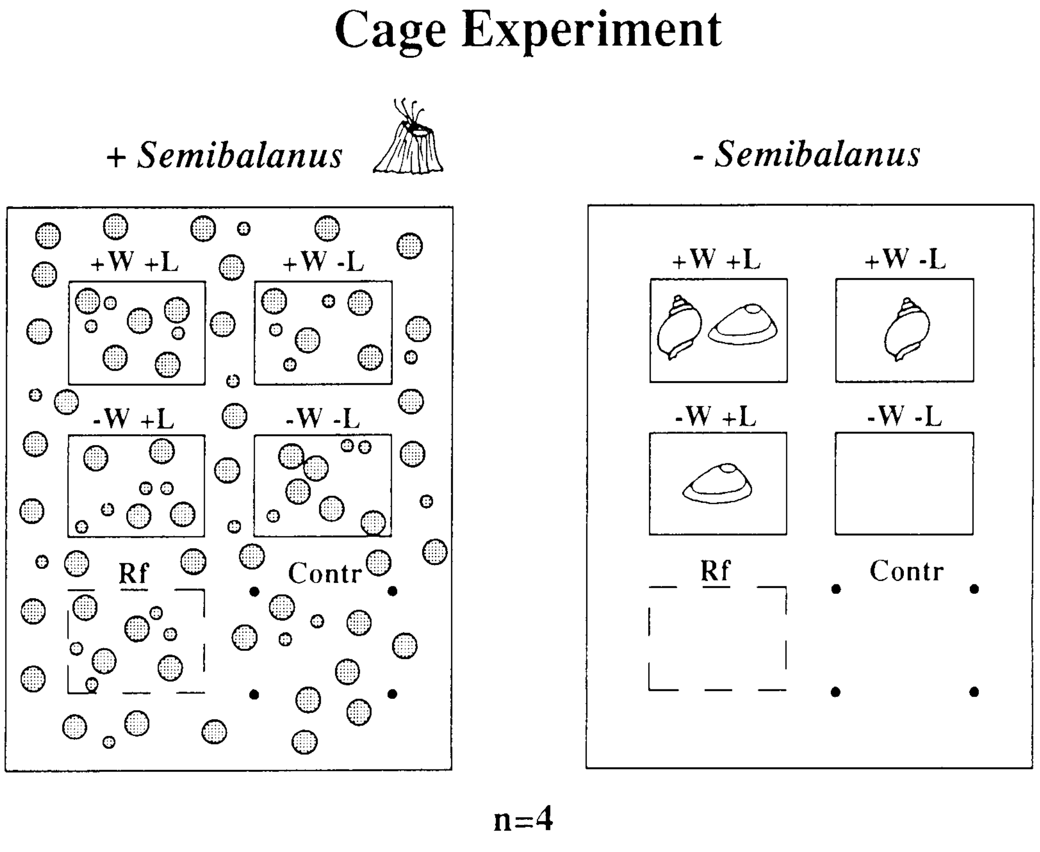
In July 1992, during a mid-day low tide, temperatures were measured in three replicate areas (ca. 1.5 x 1.5 m) from which all adult Semibalanus were manually removed (-S.c.) and three nearby areas with adult Semibalanus (+S.c.). These were the same areas used as the treatment and controls in the Semibalanus removal experiment (Experiment 2) described above. Three snails were placed in each microhabitat and allowed to equilibrate with the local temperature. Snail body temperatures were measured by removing each snail and quickly placing a fine thermocouple in the space between the foot and the shell. Two snails were not measured because they did not attach to the rock, thus the total number of snails measured was 16 .

IV. Predator manipulations: Effects of Semibalanus on whelk and limpet foraging.

To evaluate directly whether or not beds of adult Semibalanus beds locally enhance the predatory effect of whelks and limpets on small Semibalanus (< 5mm) and B. glandula, we manipulated the presence and absence of these two predators in an orthogonal (factorial) design within larger replicated areas where adult Semibalanus were either present or removed (+S.c. and -S.c.), thus using a split-plot design (Mead 1988). Eight areas (roughly 1 m^2 each) of gently sloping, homogeneous rock with beds of adult Semibalanus were chosen. Four of these were selected at random and cleared of large, adult Semibalanus (-S.c.) while the other four were left intact (+S.c.). Within each of the 8 areas, all combinations of the presence/absence of whelks and limpets were included or excluded using 10 x 10 x 5 cm stainless steel cages (Fig. 2). Cages were tall enough to easily include large, adult Semibalanus individuals. In addition, each area contained an unmanipulated plot marked with stainless steel screws ('control') and a roof which served as a control for the effects of the cages. The roofs had incomplete walls in contact with the rock surface in two of their sides. This allowed limpets to crawl on top of the roofs, as we saw them doing on the complete cages. Note that the -S.c. treatment of this experiment is analogous to previous experiments by Dayton (1971) at the same site,

Figure II.2. Diagrammatic representation of the Semibalanus and predator manipulations, illustrating the 'split-plot' experimental design. The large circles represent adult Semibalanus. 'W'= Whelks (N. emarginata). 'L'= Limpets (L. pelta). 'Rf'= roof. 'Contr'= unmanipulated plot. 4 of 8 areas (~1m2 each) were randomly selected to be cleared of adult Semibalanus (>9mm). Within the areas 10 x 10 cm cages received treatments of either 2 whelks, 2 limpets, 2 of each, or neither. In addition, each area contained an unmanipulated plot and a roof which served as a cage control.

Figure II.2.


Cage Experiment
+ *Semibalanus*
- *Semibalanus*
+W +L
+W -L
-W +L
-W -L
Rf
Contr
+W +L
+W -L
-W +L
-W -L
Rf
Contr
n=4

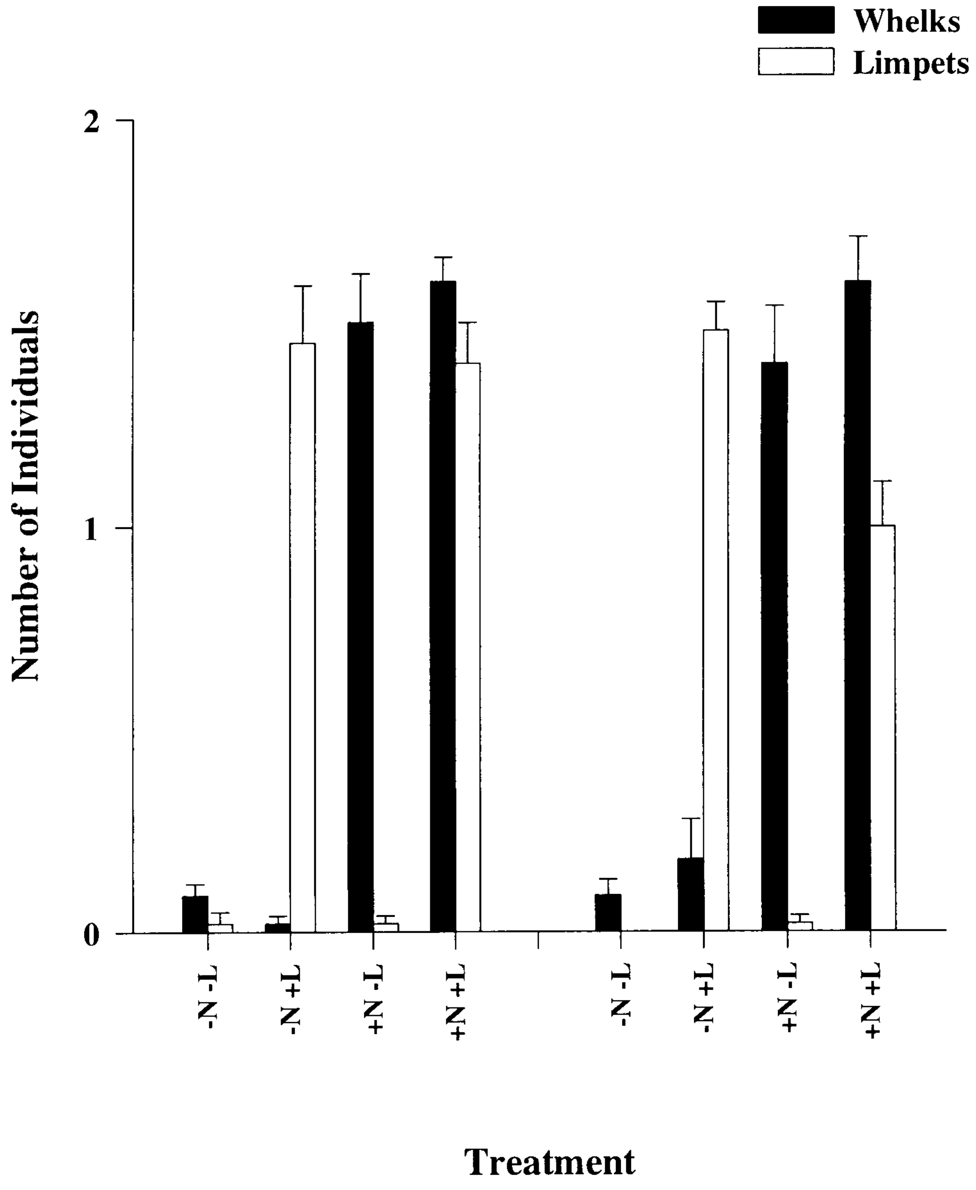
allowing an evaluation of the consistency of our results with those of Dayton, while expanding the design to include the effects of adult Semibalanus.

Treatments with whelks ('+ whelk') received 2 N. emarginata (~ 20 mm in length from apex to siphonal canal) per cage, and '+ limpet' treatments received 2 Lottia pelta. These densities are at the upper end of those naturally observed in the area. The experiment was initiated in August 1991 and cages were monitored and treatments maintained roughly every 2-3 months. While some whelks or limpets occasionally escaped or entered cages or died during this interval, the treatments were generally effective at maintaining different densities of whelks and limpets (Fig. 3). Changes in the sessile community in the cages were monitored photographically through the spring of 1993. Percent cover of sessile species was estimated from the photographs using vinyl quadrats with 100 regularly spaced dots. Barnacle 'recruits' at each sampling date were defined as individuals < 3 mm. The sampling interval was long enough that 'recruits' generally represented new individuals that had settled after the previous sampling and survived to the subsequent sampling date. In this size class, any mortality of new individuals in the sampling interval was probably not due to predation by Nucella in the cages (Connell 1970, Palmer 1983). Densities of barnacle recruits were estimated by counting recruits visible on the rock surface in the photos. While we were able to distinguish Chthamalus recruits in the photos, it was difficult to consistently or reliably separate Semibalanus from B. glandula recruits in the photos, thus, hereafter, we use 'recruits' refers to those of the latter two species (see also Connell 1970). 'New Semibalanus' and 'new B. glandula' were defined as individuals that recruited after the initial manipulation of Semibalanus and survived to be > 3 mm. In +S.c. cages, covers of sessile species and densities of recruits were adjusted by the amount of 'bare' (= free of pre-existing adult Semibalanus) space available.

To evaluate the effects of these manipulations on the local thermal conditions, we measured air temperatures, rock temperatures, and body temperatures of two snails in: a)

Figure II.3. Mean (±SE, n = 4) number of whelks (adult N. emarginata) and limpets (large L. pelta) present in cages at a given census date. Data were averaged over all census dates. At each date, individuals were added or removed to maintain the appropriate treatment: '-N' = all Nucella removed, '+N'= 2 Nucella enclosed, '-L' = all large limpets removed, '+L' = 2 large L. pelta enclosed; '-adult Semibalanus' = adult Semibalanus removed at the start of the experiment, '+adult Semibalanus' = adult Semibalanus present.

Figure II.3.


Whelks
Limpets
Number of Individuals
2
1
0
-N -L
-N +L
+N -L
+N +L
-N -L
-N +L
+N -L
+N +L
Treatment

cageless ‘control’ plots, and b) inside the exclosure cages in three of the four replicate areas for each Semibalanus treatment . These temperature measurements were taken on the same day as those described under 'Thermal Conditions' above for July 1992. Since those Semibalanus removal areas were approximately twice as large as those for these predator manipulations, we did not pool the two sets of temperature measurements.

In some +S.c. cages with predators, the availability of small Semibalanus and B. glandula was so low that we observed whelks eating large Semibalanus and, on occasion, the limpets enclosed with them. The predator manipulation was terminated in the spring of 1993 because the deaths of adult Semibalanus in some +S.c. cages suggested that this treatment would soon be ineffective.

Data Analysis

Data analysis was done using the SAS (v. 6.04; SAS Institute Inc. 1988) statistical package for IBM-compatible PC's. Assumptions of normality and variance heterogeneity were checked by visual inspection of residual plots. In all cases, arcsin-squareroot transformed cover and log transformed density data exhibited better distribution and homogeneity than the raw data. Temperature data were shown to have variance homogeneity by an F-max test (Sokal and Rohlf 1981).

Effects of transplanted Semibalanus shells on the distribution of whelks. Numbers of whelks remaining in the plots through the low tide were compared using a repeated measures analysis of variance (RM-ANOVA) to take into account the temporal serial correlation of the data (see details of RM-ANOVA below under 'Predator Manipulations'). The two separate days of release were considered as independent treatments in a 2x2 factorial design.

Habitat preferences. A chi-squared test was used to compare the observed numbers of whelks recaptured in different microhabitats against expected numbers based on the percent cover of those microhabitats in the field. Data from the two releases were pooled for this analysis.

Effects of Semibalanus removals on the distribution of whelks and limpets. Densities of mobile species in treatment and control areas before the Semibalanus removals were compared to determine if there were differences in densities prior to the manipulation. Data were analyzed with a one-way ANOVA with the three spatially segregated replicates considered as blocks (Randomized Block Design, Mead 1988). The mean of all quadrats within the Semibalanus zone of each replicated area was considered as an estimate of density for that replicate. After the removal of Semibalanus, densities were compared using RM-ANOVA. (See details of RM-ANOVA below under 'Predator Manipulations'.)

Hydrodynamic forces. Measures of wave forces in areas ±S.c., expressed as Newtons/m^2, were compared using a Student t-test. Measurements taken on two different days were considered as replicates.

Thermal conditions. Temperature data from August 1990, were compared using a Student t-test. Comparisons were based on the average temperature over time for each of three replicates in the two microhabitats. Temperature data from the large-scale Semibalanus removals in July 1991, were analyzed using a one-way ANOVA with the three spatially segregated areas considered as blocks (the same randomized block design as the Semibalanus removals described above). Because the individuals within each area were widely spaced, individual snails were considered as independent estimates (replicates) of the mean body temperature under the two conditions (±S.c.).

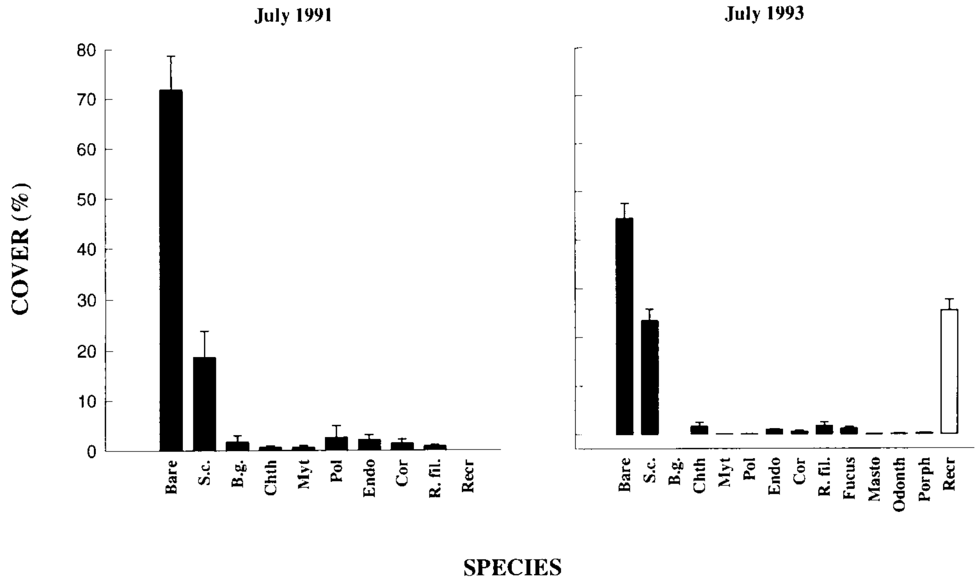
Predator Manipulations: Effects of Semibalanus on whelk and limpet foraging. The experimental design used in this experiment was a split-plot design (Miliken and Johnson 1984, Mead 1988), in which the experimental units for the Semibalanus treatment (removal areas) were larger than those for both the whelk and limpet treatments (cages). The latter two were arranged in a 2x2 factorial design 'inside' the Semibalanus treatment. A split-plot repeated measures ANOVA was used to take into consideration time correlations (von Ende 1993). Appropriate error terms to test hypotheses are indicated in the tables with results. The repeated measures data were evaluated for conformity with split-plot assumptions (compound symmetry, see Miliken and Johnson 1984, von Ende 1993) by the Mauchly's sphericity test criterion (Crowder and Hand 1990) applied to the orthonormalized matrix (von Ende 1993). In some cases, a RM-ANOVA was precluded because the cover of new B. glandula in +S.c. areas was often zero in all replicates (thus the variance was zero); therefore, we assigned a value of 0.01% cover for B. glandula in all cases where the cover of recruits in that plot was greater than zero and then did the analysis. Finally, estimates of body temperatures of snails in the predator manipulation experiment were also analyzed in a split-plot ANOVA (design did not include time). In this case, because the cages were much smaller than the Semibalanus removal areas (described above) the mean of the two snails in each cage under each condition was used for the analysis.

Results

I. Patterns of community structure

Although Semibalanus was the most abundant sessile organism occupying primary space in the mid intertidal zone at Eagle Point, this zone is also characterized by much ‘bare’ space (includes bare rock, diatoms, and some fleshy algal crusts) (Fig. 4). This pattern of community structure remained virtually unchanged from early 1990 through the early spring of 1993 (pers. obs.), and it is considered the 'typical' or 'normal' seascape for these shores (Dayton 1971, Kozloff 1973, B.A. Menge and J. Lubchenco pers. comm.). However, the spring-summer of 1993 was characterized by unusually high recruitment of new Semibalanus and B. glandula to the ‘bare’ space previously available

Figure II.4. Average cover of sessile species in the mid-intertidal zone at Eagle Point in July, 1991, and July, 1993. Error bars represent one standard error from the mean (n = 10 and 40 quadrats for 1991 and 1993, respectively). Codes for abscissa: BARE, bare rock, benthic diatoms, fleshy crusts; S.c., Semibalanus cariosus; B.g. Balanus glandula; Chth, Chthamalus dalli; Myt, Mytilus trossulus, Mytilus californianus; Pol, Pollicipes polymerus; Endo, Endocladia muricata; Cor, coralline algae; R. fil., filamentous red algae; Fucus, Fucus gardneri; Masto, Mastocarpus papillatus; Odonth, Odonthalia floccosa; Porph, Porphyra spp.; Recr, barnacle recruits (includes B. glandula and *S.* cariosus ≤ 3mm).



(Fig. 4, open bar); density of new 'recruits' (individuals < 3 mm) was an order of magnitude higher than previous years for which data on recruitment (similarly defined) are available (Navarrete & Berlow unpublished data). Thus, in general, the seascape is dominated by patchy beds of adult Semibalanus (~20-25 percent cover) and large amounts of 'bare' space (includes fleshy algal crusts) either between the widely spaced individuals within a bed or in larger patches free of adult Semibalanus. Generally, the total cover of B. glandula and new 'recruits' was below 5 percent throughout the experiment. However, in the summer of 1993, after the experiment was terminated, approximately 25 percent of the previously 'bare' space was covered by recruits of *S.* cariosus and B. glandula.

On all dates sampled, densities of the most abundant whelks (N. emarginata and N. canaliculata) and the most abundant large limpets (L. pelta and T. scutum) were highest within the vertical range of adult Semibalanus, despite seasonal changes in overall population densities over time (Fig. 5). Starfish (*Leptasterias hexactis*) were occasionally observed, but generally were not abundant in this zone. Within the Semibalanus zone, the tendency of whelks and limpets to reside in patches where adult Semibalanus are present is described below.

II. Effect of Semibalanus on the distribution of whelks and limpets

1) Effect of Semibalanus additions on the dispersal of whelks.

The short term dispersal of marked whelks was faster in the control plots (-S.c.) than in plots with added Semibalanus shells (+S.c.) (Fig. 6; RM-ANOVA, Semibalanus effect, F=68.43, p=0.0001, df=1, 9). There was no significant difference between the 2 days in which the experiment was conducted (RM-ANOVA, ‘day’ effect, F=3.20, p=0.11, df=1, 9). For both days together, the effect of Semibalanus was significant by the first hour after release (ANOVA, F=50.12, p=0.0001, df=1, 9), and the differences persisted

Figure II.5. Vertical distribution of whelks (N. emarginata and N. canaliculata) and limpets (L. pelta and Tectura scutum) at Eagle Point in the unmanipulated areas of the 'Semibalanus Removal Experiment' over the time course of the experiment. Data are mean densities ± 1 std. err.. Densities were estimated with two vertical transects of contiguous 20 x 20 cm quadrats at three different areas. The arrows indicate the upper limit of the Semibalanus zone.

Figure II.5.

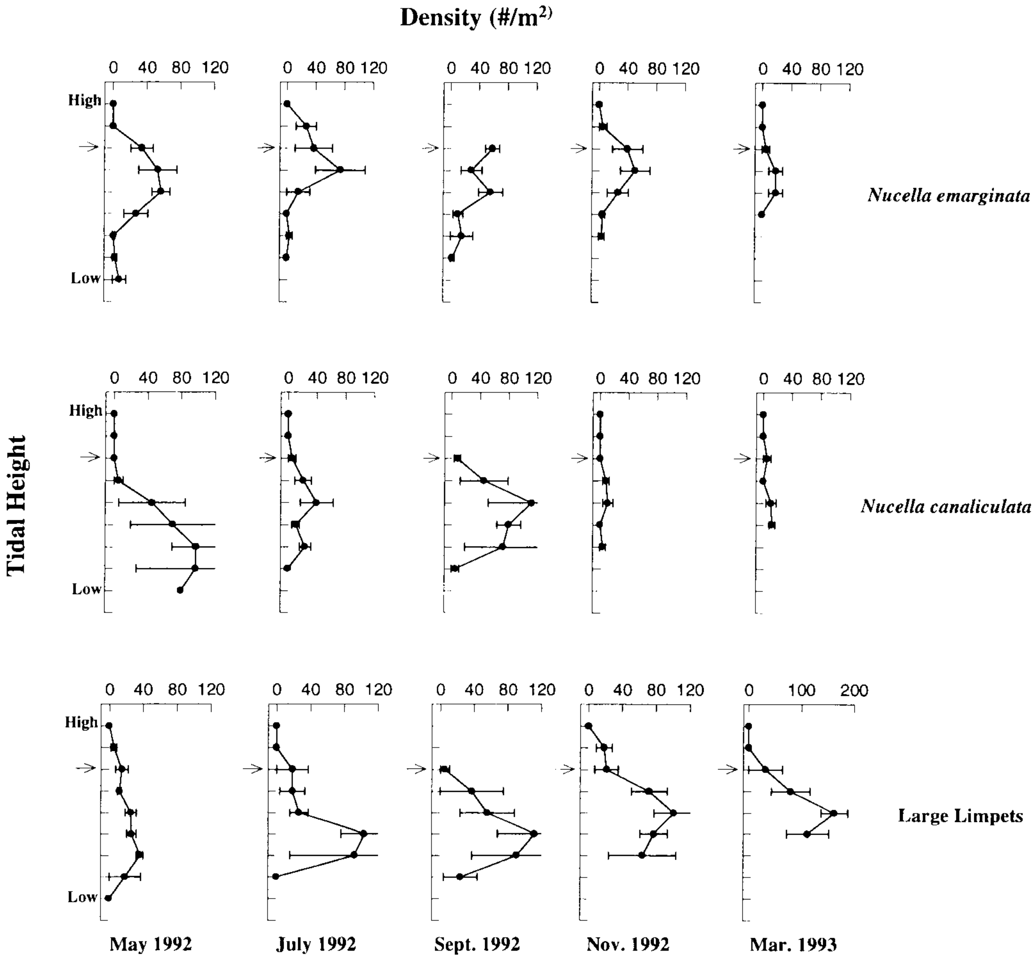
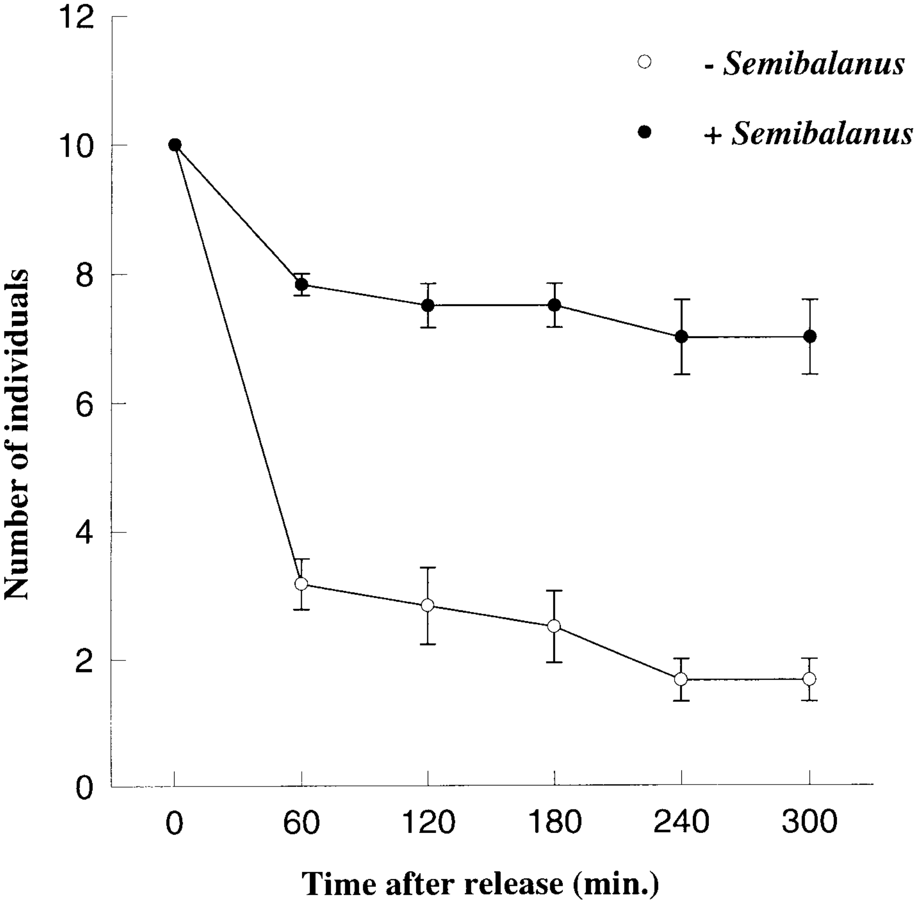

Density (#/m2)
Tidal Height
0 40 80 120
0 100 200
High
Low
Nucella emarginata
Nucella canaliculata
Large Limpets
May 1992
July 1992
Sept. 1992
Nov. 1992
Mar. 1993

Figure II.6. Dispersal over the course of the low tide of N. emarginata released in areas with and without glued Semibalanus shells. Data are mean number of individuals ± 1 std. err.. Since there were no significant differences between the results of 2 separate runs on consecutive days, the data were pooled. Snails were released at time 0.



until the end of the low tide (RM-ANOVA, Time*Semibalanus interaction not significant, Wilk's $\lambda=0.78$, $p=0.38$, df=2, 8). After 24 hours all of the whelks had dispersed from the areas in which they were released. The microhabitats to which they dispersed are discussed below.

2) Habitat preference:

Three days after the releases, 66% of the snails released at the 6 experimental plots were recaptured within 2 meters of their point of release. Although rock surfaces free of adult Semibalanus (-S.c.) were the most abundant microhabitats available to the released N. emarginata, most of the snails were found among adult Semibalanus (+S.c.), despite the fact that prey items (generally B. glandula) were more abundant in the former microhabitat (Fig. 7, inset) (X^2 test on pooled categories: $p<0.001$, df=1). N. emarginata appear to prefer sloping surfaces to horizontal surfaces. Despite the relative equal availability of +S.c. and -S.c. areas on sloping surfaces, a disproportionate number of snails were found among Semibalanus (Fig. 7) (X^2 test on all categories: $p<0.001$, df=9). The apparent preference for adult Semibalanus should be considered a conservative estimate because, if anything, snails in the 'crevices' created by large barnacles were harder to find than snails in -S.c. areas, however this was generally not a problem.

3) Effects of Semibalanus removals on the distribution of whelks and limpets:

N. emarginata and N. canaliculata were the most abundant whelks observed, and because they exhibited similar trends over time in their response to the manipulation of Semibalanus, their densities were pooled in the analysis. Prior to the removal of large Semibalanus, whelks were more abundant in the areas where Semibalanus were to be removed (-S.c.); however, these differences were not significant (Fig. 8a: $p=0.07$, df=1, 2). Immediately following the removals, the densities of whelks declined dramatically in the removal areas (-S.c.) relative to the adjacent control areas (+S.c.) (Fig. 8a). Some of the initial decline may have been due to the fact that some whelks were inadvertently removed during the process of scraping off adult Semibalanus. However, the first post-

Figure II.7. Proportion of the released N. emarginata which were recaptured in different microhabitats relative to what was expected if there were no preferences for any microhabitat. The inset figure pools all the microhabitats into + and - adult Semibalanus (+S.c. and -S.c., respectively). Codes for abscissa: Sh, horizontal surface with adult Semibalanus; Sv, sloping surface with adult Semibalanus; Scr, crevice with adult Semibalanus; Rh, horizontal surface without adult Semibalanus; Rv, sloping rock surface without adult Semibalanus; Rc, crevice without Semibalanus. Solid bars indicate the proportion of snails recaptured. Open bars represent the proportion expected if snails selected microhabitats solely on the basis of their relative availability. Data are means ± S.E. (n = 3 replicate areas each).

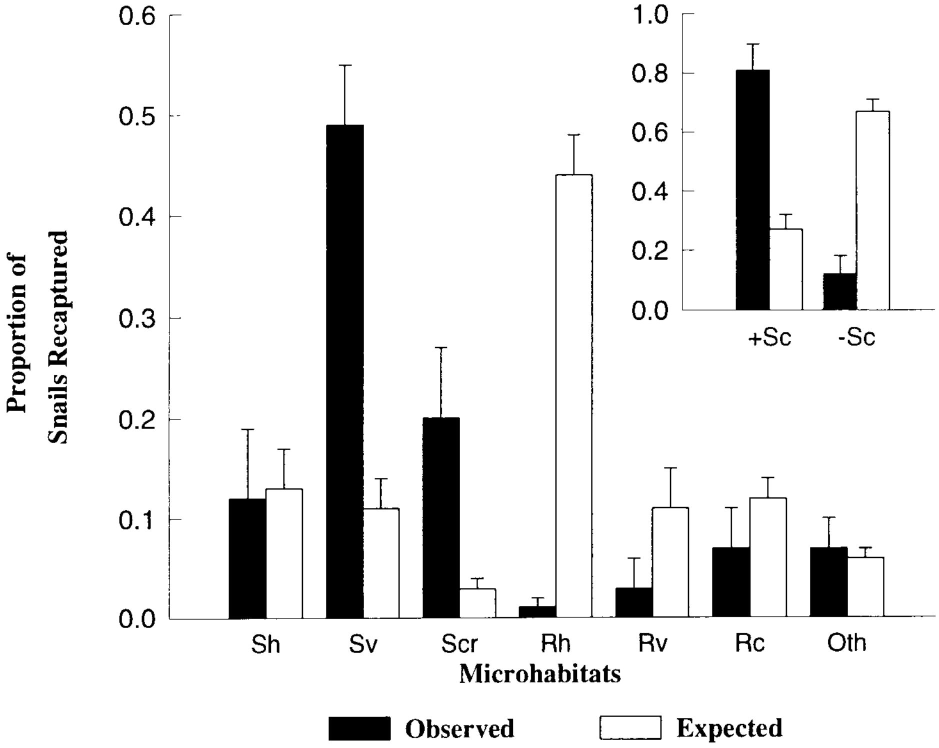
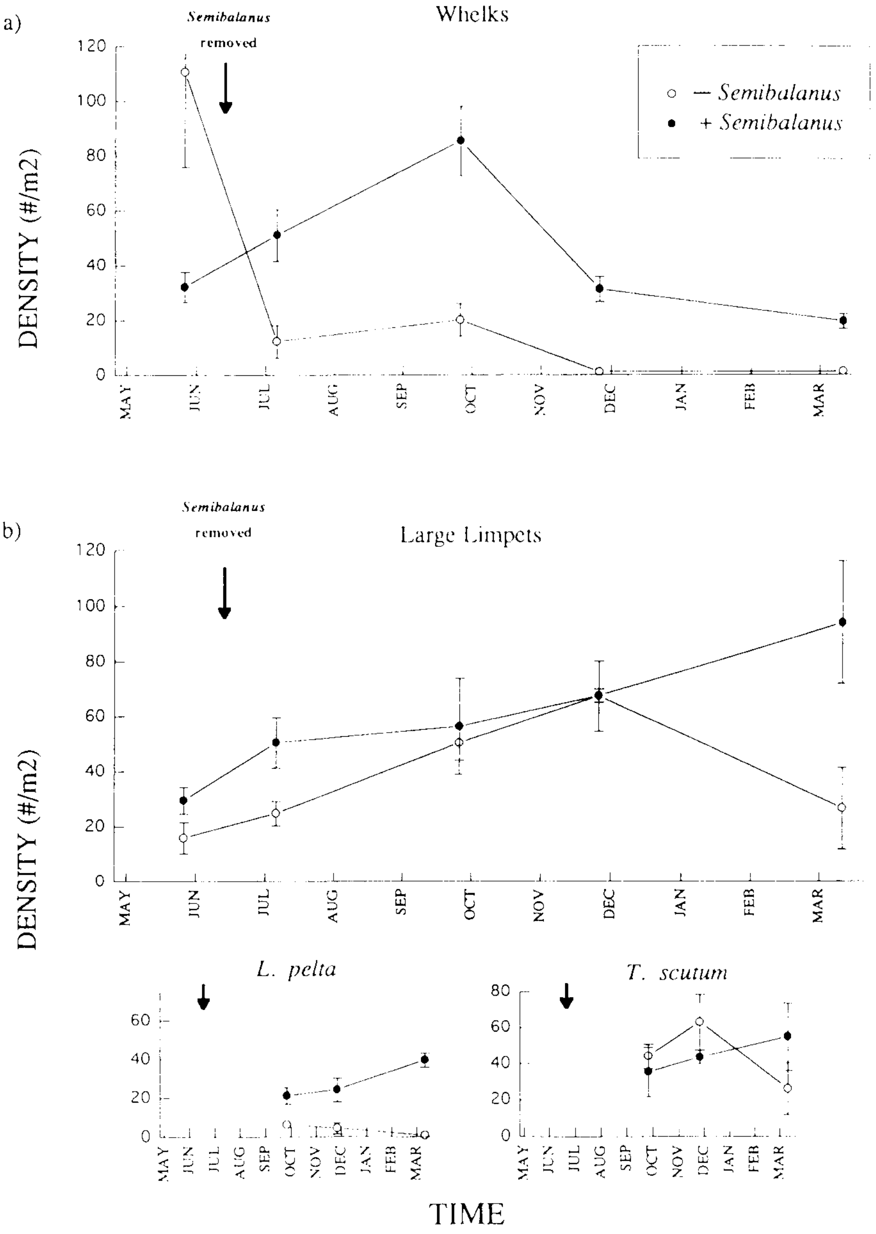


Figure II.8. Changes in mean densities (±S.E.) of a) whelk (N. emarginata and N. canaliculata) and b) large limpet (L. pelta and T. scutum: separate in lower panels) following the removal of adult Semibalanus (arrows). Densities are averaged over the quadrats which fell within the Semibalanus zone in each experimental area, and the standard errors were calculated based on three replicate areas for each treatment. L. pelta and T. scutum were differentiated starting September 1992 because it became clear that they were responding differently to the removal of Semibalanus.

Figure II.8.


a)
Semibalanus removed
Whelks
○ — Semibalanus
● + Semibalanus
DENSITY (#/m2)
0
20
40
60
80
100
120
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
b)
Semibalanus removed
Large Limpets
DENSITY (#/m2)
0
20
40
60
80
100
120
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
L. pelta
0
20
40
60
T. scutum
0
20
40
60
80
TIME

treatment census was not until 1.5 months after the removal Semibalanus, presumably long enough for new individuals to migrage in from adjacent areas. In addition, the differences in whelk densities between treatments persisted over time, although overall densities declined in the winter months (Fig. 8a; Table 1: Semibalanus effect was significant; Time*Semibalanus interaction was not significant).

The response of limpets to the removal of large Semibalanus was more complicated in that it varied with species and over time (Fig. 8b; Table 1). Prior to the manipulations, both Lottia pelta and Tectura scutum had relatively low densities in all experimental areas, and there were no significant differences between + and - S.c. areas (univariate ANOVA for effects of Semibalanus on limpets, June 1991: F=2.15, p=0.28, df=1, 2). In September, 1992, we began distinguishing between L. pelta and T. scutum because it was clear that they were responding differently to the treatment. L. pelta was significantly less abundant in the Semibalanus removal areas by September, 1992 , and the difference increases through the winter (Table 1; effects on L. pelta: Semibalanus and Time*Semibalanus interaction are both significant). This coincided with a seasonal increase in L. pelta densities in the control areas. On the other hand, T. scutum showed no consistent response to the treatment over time. In September and November of 1992 , this species was slightly more abundant in the Semibalanus removal areas, and by the spring of 1993 it was less abundant than in the control areas. None of these differences were significant (Table 1; effects on T. scutum: Semibalanus effect was not significant). Lack of a consistent treatment effect on T. scutum was reflected in high spatial variability in its density (Table 1; effects on T. scutum: Block effect was significant).

III. Measurement of physical conditions inside/outside Semibalanus beds

1) Hydrodynamic forces:

In August, 1990, the presence/absence of Semibalanus beds had no significant effect on the mean maximum shear forces (averaged over two replicates and two days) experienced by N. emarginata for the days they were measured (one-tailed t-test: p=0.54, df=3). The range of maximum shear forces (mean ± S.E.) experienced by N. emarginata were 2.45 - 4.29 and 2.30 - 3.40 N/cm^2 in +S.c. and -S.c. areas, respectively. While these data are limited to a small temporal window of observation, the days that the measurements were made were typical of the relatively calm summer conditions on San Juan Island (Connell 1970, Dayton 1971, authors' personal observations).

2) Thermal conditions:

In August, 1990, throughout a mid-day low tide when the mean air temperature was 20.0°C, snail body temperatures and rock temperatures were significantly warmer in areas where adult Semibalanus were naturally absent (-S.c.) than in adjacent +S.c. areas (Fig. 9; one-tailed t-test: t=6.11, p=0.002 and t=4.56, p=0.005, respectively, df=2). On a mid-day low tide in July, 1992, when the mean air temperature was 23.3°C, snail body temperatures were significantly warmer in the areas where large Semibalanus were removed (-S.c.) than in adjacent control areas with Semibalanus (+S.c.) (Fig. 9; one-way ANOVA, Semibalanus effect, F=15.3, p=0.0021, df=1, 12). Some individuals in the -S.c. (removal) areas reached body temperatures of 33°C while individuals in +S.c. (control) areas never reached more than 23°C. At least part of the differences in snail body temperatures can be explained by the warmer rock temperatures in the -S.c. areas (Fig. 9).

In the smaller scale removals of Semibalanus in the predator manipulations, there was no significant effect of adult Semibalanus on snail body temperature (Fig. 10; split-plot ANOVA: F=0.02, p=0.90, df=1, 4). Shade provided by the cages, however, did

Figure II.9. Effects of Semibalanus beds on thermal conditions at low tide in August, 1990 and July, 1992. For the 1990 data, areas with and without Semibalanus were areas where adult Semibalanus were naturally present and absent, respectively. For the 1992 data, the microhabitats were the same as those used in the Semibalanus removals (see text for details). Data are means ± 1 standard error. The air temperatures for the respective dates averaged over the sampling time during low tide were 19.96 and 23.3°C. Codes for abscissa: T_{body}, snail body temperature; T_{rock}, rock temperature. 1990 body temperatures were averaged over three replicate areas of each microhabitat (with one snail in each) and over 5 measurements made during the course of a single low tide. Standard errors for 1990 are those of the time-averaged data. 1992 body temperatures were averaged over three snails (N. emarginata) for each treatment in each of the three replicated areas. Temperatures were measured only once during the low tide. Standard errors for 1992 were based on three replicates per treatment.

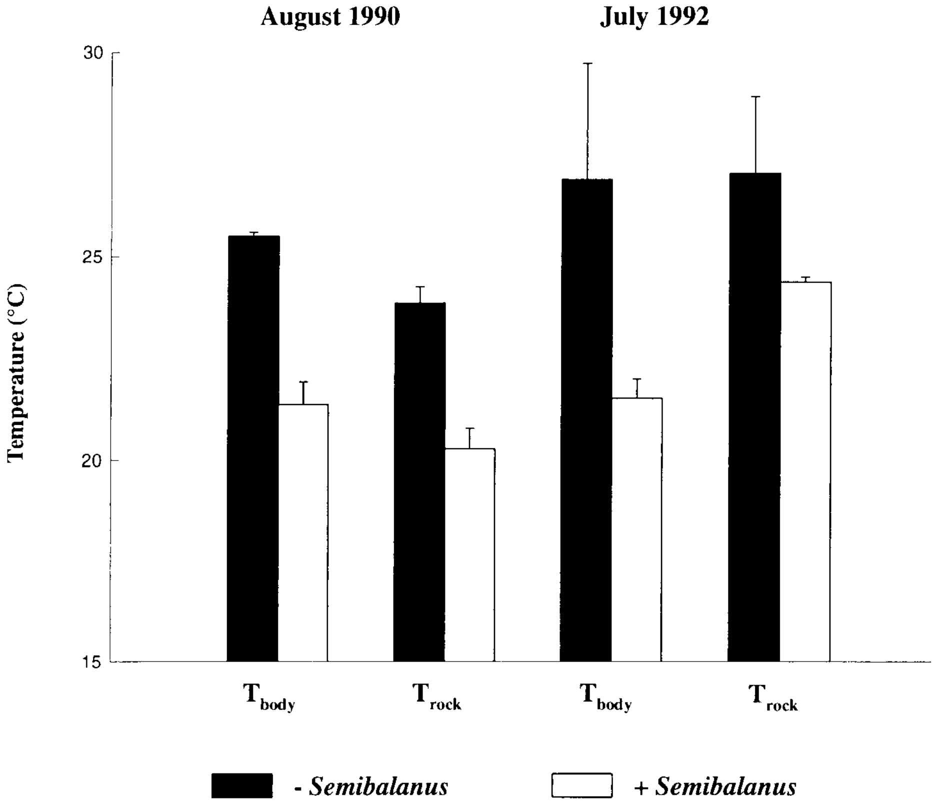
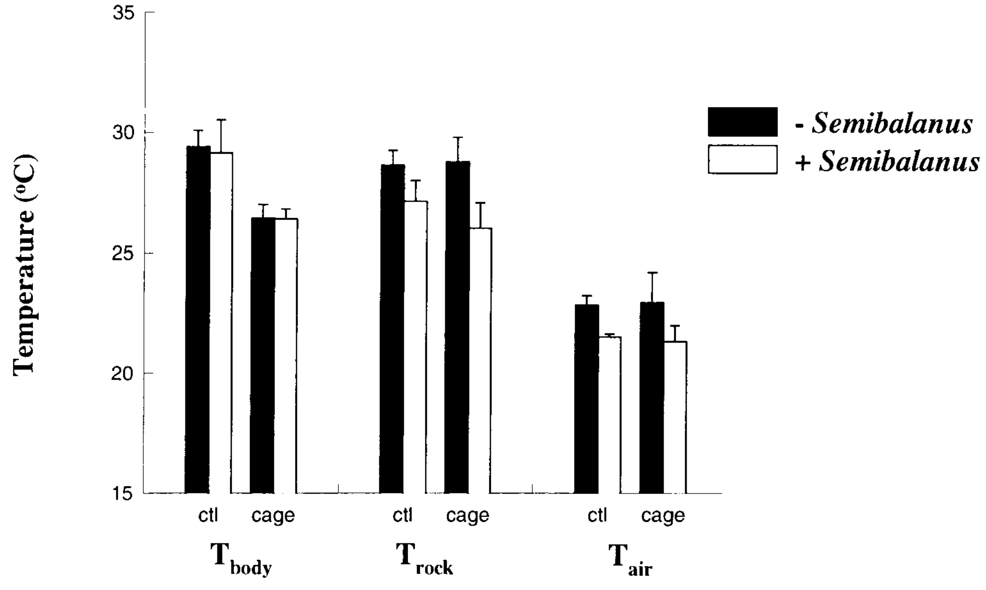


Figure II.10. Effects of cages on thermal conditions in the Semibalanus and predator manipulations in July, 1992. Data are means ± standard errors. Codes for abscissa: T_{body} = snail body temperature; T_{rock} = rock temperature; T_{air} = air temperature; 'ctl' = no cage; 'cage' = inside cage. Body temperatures were averaged over two snails (N. emarginata) for each plot in each treatment in three randomly selected replicate areas of the experiment. Temperatures were measured only once during the low tide. Standard errors were based on three replicates (plots) per treatment.



result in significantly lower body temperatures inside the cages relative to the uncaged 'control' plots (split-plot ANOVA: F=35.67, p=0.004, df=1, 4). Rock temperatures were, on average, slightly warmer in the areas without adult Semibalanus (-S.c.), although the differences were not significant (split-plot ANOVA: F=5.20, p=0.08, df=1, 4), and rock temperatures were not significantly affected by the presence of cages (split-plot ANOVA: F=0.32, p=0.60, df=1, 4). Some of the differences between these results and those described above could be due to differences in slope between the areas where the two sets of measurements were taken (the predator manipulation experiment was on a more horizontal area of the shore, while the larger Semibalanus removals described above were on vertical walls), or it could be due to differences in the areas of removals of Semibalanus (≈1m^2 versus ≈2.25m^2).

IV. Predator manipulations: Effects of Semibalanus on whelk and limpet foraging.

N. emarginata had a significant negative effect on the cover of new B. glandula, but, contrary to our expectations, their effect occurred only in the areas where Semibalanus were removed (-S.c.) (Fig.11, Table 2). The effect of L. pelta on B. glandula varied over time and with the presence of Semibalanus (Table 2: Time*SEM*LIM is significant). By the spring of 1993, there was a trend toward fewer B. glandula in cages with L. pelta (independent of Nucella), but, again, only in -S.c. areas (Table 2: , Fig. 11). However, when averaged over time the effects of L. pelta on B. glandula were not significant (Table 2: 'Between Subjects' effects). The separate effects of whelks and limpets on small barnacles appear to be additive (Tables 2 and 3, no NUC*LIM interactions were significant). Overall, the presence of adult Semibalanus (+S.c.) had a significant negative effect on the cover of B. glandula when whelks and limpets were absent (Fig. 11, Table 2).

Figure II.11. Mean cover of new B. glandula (>3mm) over the time course of the Semibalanus and predator manipulations. Data are means ± 1 standard error (n = 4 replicates each). The covers have been standardized for the amount of bare space available at the start of the experiment (i.e. space not already occupied by adult Semibalanus). The two left panels are areas where adult Semibalanus were not removed (+S.c.). The two right panels are areas where adult Semibalanus were removed (-S.c.).

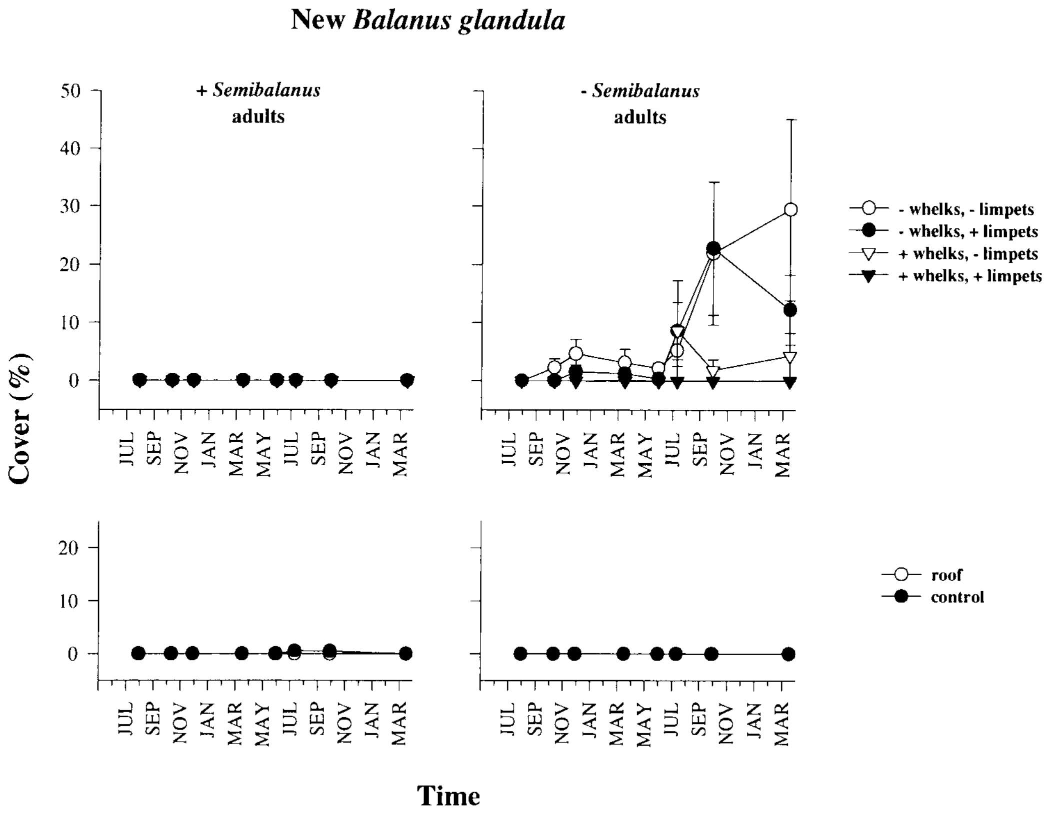
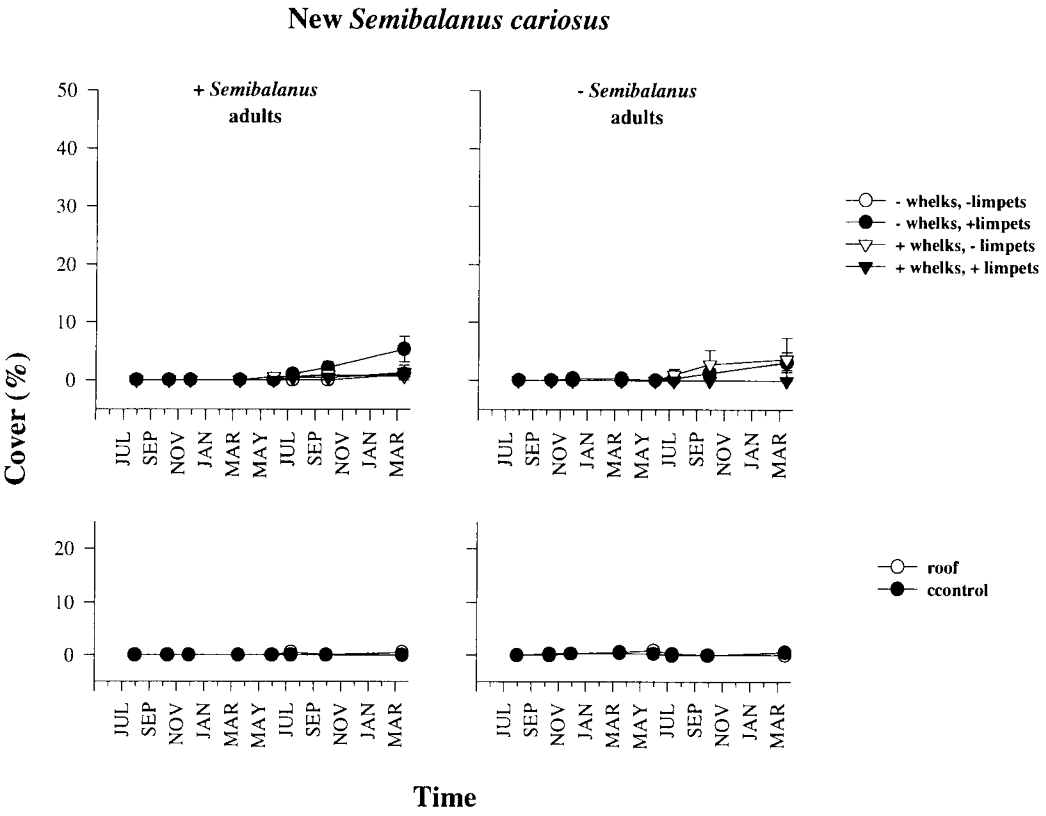


Figure II.12. Mean cover of new Semibalanus (>3mm) over the time course of the manupulations of adult Semibalanus and predators. Data are means ± 1 standard error (n = 4 replicates each). The covers have been standardized for the amount of bare space available at the start of the experiment (i.e. space not already occupied by adult Semibalanus). The two left panels are areas where adult Semibalanus were not removed (+S.c.). The two right panels are areas where adult Semibalanus were removed (-S.c.).



In general, very few new Semibalanus colonized the plots regardless of the presence of adult Semibalanus during the years that this experiment was conducted (Fig 12). Thus, neither whelks, limpets, nor the presence of adult Semibalanus had an effect on the cover of new Semibalanus (Table 3: 'Between Subjects' effects). There was a tendency for limpets to have a positive effect in +S.c. areas by the end of the experiment (Table 3: Time*SEM*LIM is significant). However, the absolute difference in cover of new Semibalanus was less than 5% (Fig. 12), and it consisted of only a few individuals.

Although we were not able to distinguish between Semibalanus and B. glandula 'recruits' in the photos, the extremely low abundance of new Semibalanus (> 3 mm) in all treatments suggests that most of the 'recruits' (< 3 mm) observed during the study were B. glandula. The low cover of new B. glandula in cages with adult Semibalanus (+S.c.) can be explained by the significantly lower densities of 'recruits' (mostly B. glandula) in those areas during May and July, 1992, when recruits were the most abundant (Fig.13, Table 4). In -S.c. areas, recruitment was patchy in space, and the effects of limpets on the density of recruits were not significant for any one date during the spring pulse of recruitment. However, there was a non-significant trend toward fewer recruits in -S.c. cages with limpets (Fig. 13), and the significant Time*LIM effect on small barnacle cover (Fig. 11, Table 2) suggests that the cumulative effect of limpets on barnacle recruits was enough to be manifested eventually as a decrease in the cover of small barnacles (Gaines and Bertness 1993). There was a trend toward more recruits in -S.c. cages with whelks, and this effect was significant in July 1992 (Table 4, SEM*NUC interaction was significant). Again, contrary to our expectations, any effects of whelks or limpets on barnacle recruits occurred only in areas without Semibalanus (-S.c.).

Because the cover of individual algal species was very patchy in time and space and the total cover of algae was generally less than 20 percent, all algal species were pooled in the analysis (species, in order of abundance, included Fucus gardneri, ulvoids (including Ulva spp. and Enteromorpha spp.), Endocladia muricata, Odonthalia floccosa,

Figure II.13. Mean densities of barnacle recruits (B. glandula and *S.* cariosus <3mm) over the time course of the Semibalanus and predator manipulations. Data are means ± 1 standard error (n = 4 replicates each). The densities have been standardized for the amount of bare space available at the start of the experiment (i.e. space not already occupied by adult Semibalanus). The two left panels represent areas where adult Semibalanus were not removed (+S.c.). The two right panels represent areas where adult Semibalanus were removed (-S.c.).

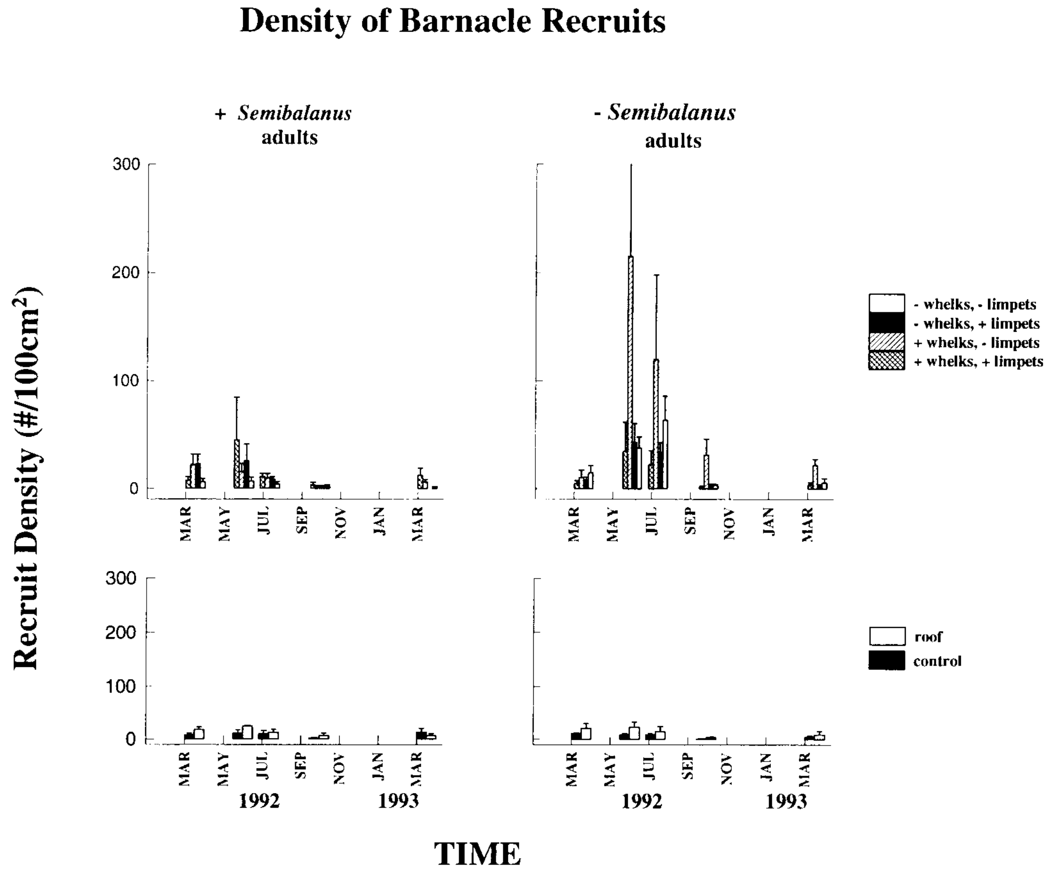
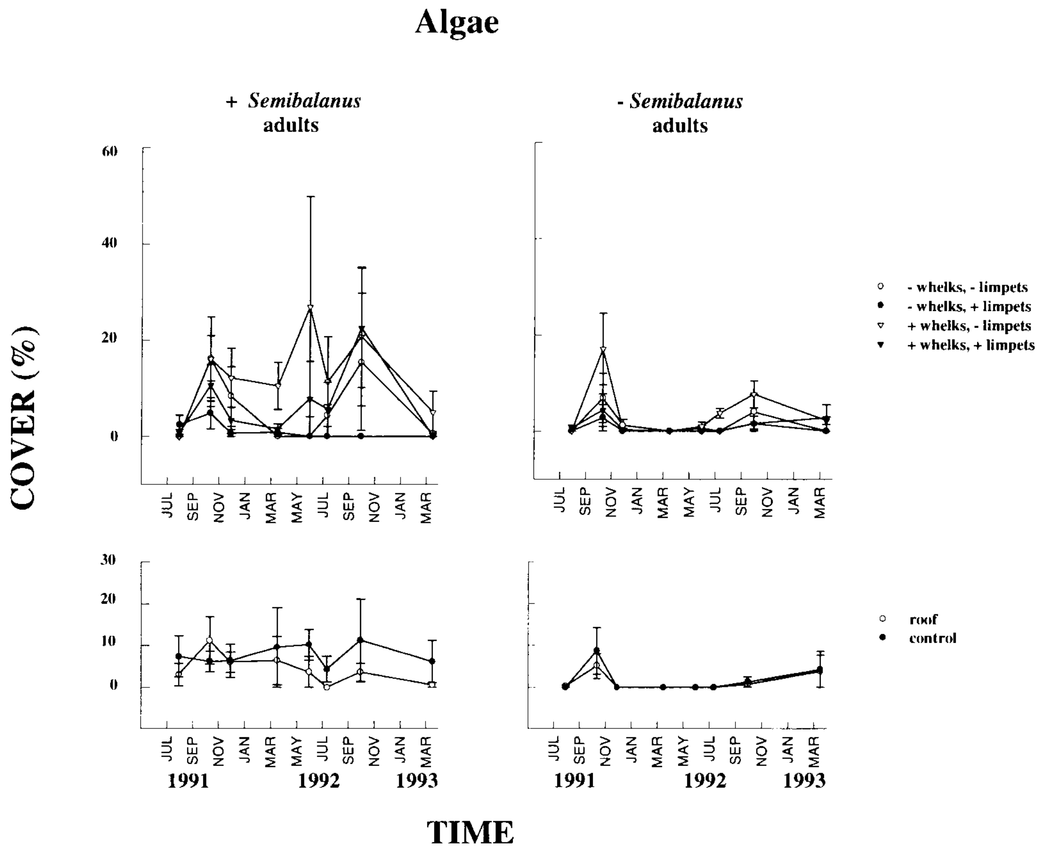


Figure II.14. Mean cover of macro-algae occupying primary space (pooled for all species) over the time course of the Semibalanus and predator manipulations. Data are means ± 1 standard error (n = 4 replicates each). The covers have been standardized for the amount of bare space available at the start of the experiment (i.e. space not already occupied by adult Semibalanus). The two left panels represent areas where adult Semibalanus were not removed (+S.c.). The two right panels represent areas where adult Semibalanus were removed (-S.c.).



and Pterosiphonia bipinnata; although the relative abundances varied greatly with time). Averaged over time, adult Semibalanus had a significant positive effect on the cover of algae (Fig. 14, Table 5: 'Between Subjects' effect of SEM). Limpets had a significant negative effect on the cover of algae, when averaged over time. Cages in which whelks were present had significantly more algae than cages without whelks (Fig. 14, Table 5). Because the cover of algae varied significantly over time (peaks in algal cover were produced by settlement of ephemeral species such as Porphyra spp.), the combined effects of Semibalanus, whelks, and limpets varied significantly over time as well (Table 5).

There were no significant differences between the roofs and control plots in the covers of new Semibalanus, new B. glandula, or algae (Figs. 11, 12 and 14; RM-ANOVA, 'Between Subjects' effects of roofs: F=1.3, p=0.30, df=1, 5; F=0.71, p=0.44, df=1, 5; F=1.44, p=0.28, df=1,5, respectively), suggesting that the cages did not introduce important artifacts. Similarly, none of the univariate tests for the effects of roofs on recruit density were significant for any date (Fig. 13; ANOVA, p>0.05, df=1, 6, for all dates).

In sum, whelks and limpets had a significant negative effect on B. glandula, but only in areas where adult Semibalanus were removed (-S.c.). Neither whelks nor limpets had an effect on the cover of new Semibalanus in either microhabitat, apparently because very few new Semibalanus colonized any of the plots during the time the experiment was conducted. In +S.c. areas, whelks and limpets had no effect on B. glandula probably due to the strong negative effect that adult Semibalanus had on the abundance of recruits. Similarly, any negative effect of limpets on recruits in +S.c. areas was swamped by the negative effect of adult Semibalanus. In -S.c. areas, although the negative effect of limpets on recruits at any one date was not significant, there was a trend toward fewer new B. glandula in cages with limpets (independent of whelks) toward the end of the experiment.

Discussion

In -S.c. areas, our results confirmed that predation is important in determining the abundance of B. glandula. Limpets reduced the cumulative abundance of newly settled B. glandula. Whelks killed almost all the new B. glandula that colonized during the experiment. Furthermore, the presence of adult Semibalanus did increase the local density of predators. Whelks actively sought +S.c. areas or avoided -S.c. areas, probably to ameliorate thermal-related stresses during summer low tides. However, unexpectedly, in +S.c. areas, predation on B. glandula was less, rather than more, important. Furthermore, predators had no effect on the colonization of new Semibalanus in either microhabitat.

I. Spatial and temporal variation in community organization:

The combination of the positive interaction between large Semibalanus and consumers, the short-term tendency of snails to remain longer in artificial +S.c. areas, and the active preference of snails for +S.c. microhabitats, together demonstrated that adult Semibalanus enhanced the local density of these predators. The short term (one low tide) persistence of snails released to artificial +S.c. areas suggests that Semibalanus may simply slow the movement of snails due to increased habitat heterogeneity. However, the other experiments suggest the effect is also due to an active preference by whelks and L. pelta for +S.c. microhabitats. These results are consistent with Connell's observations (1970) that large Semibalanus appeared to provide a refuge for whelks.

Preliminary measurements of physical conditions experienced by whelks in each microhabitat (±S.c.) suggest a possible mechanistic explanation for these microhabitat preferences. Although our data are restricted, it appears that beds of Semibalanus do not greatly modify the hydrodynamic forces experienced by whelks during the summer days when the weather is typically calm, small barnacles are most abundant, and whelks most active (Connell 1970, Spight 1981, 1982a and b). In contrast, whelk body temperatures were almost 5°C higher in the large areas ($\cong 2.25m^2$) where adult Semibalanus were removed, some snails reaching 32-33°C. While these differences did not have direct lethal consequences for the snails, they are potentially physiologically important sublethal differences that could affect snail behavior (e.g., movement, feeding performance) (Cossins and Bowler 1987, Lefcort and Bayne 1993, E. Dahlhoff, pers. comm.). In addition to the direct effects of temperature on snail physiology, the indirect effect of temperature on desiccation stress is likely to be even more ecologically important (Dayton 1971, Menge 1978a, b, 1983, Spight 1982a, b). Since summer low tides on San Juan Island occur in the middle of the day, and since the effect of whelk predation on small barnacles is most pronounced during the summer (Connell 1970, Dayton 1971, authors' personal observations), cooler temperatures among large Semibalanus could increase whelk predation rates on barnacles by allowing them to forage longer, or more often, at low tide (Spight 1981, 1982 b).

In contrast to our results, Gosselin and Bourget (1989) did not find differences in body temperatures of N. lapillus between homogeneous and heterogeneous rocky substrata under stressful sunny conditions. The discrepancy between their and our results may reflect interspecific differences between species of Nucella, and/or it may be because fields of large barnacles, by retaining water longer, provide a better refuge against high temperatures than simple substratum heterogeneity.

Our results suggest that, in the intertidal zone of San Juan Island, large barnacles might buffer whelks and other benthic predators from thermal-related stresses (especially desiccation). Indeed, Dayton (1971, p.373) argued that adult Semibalanus stabilized populations of Anthopleura elegantissima living among them by providing a refuge from desiccation stress. This is in agreement with the idea that facilitation mechanisms may be common in physically stressful environments (Bertness 1989, Stephens and Bertness 1991, Bertness and Shumway 1993, Bertness and Callaway 1994).

The preference of whelks and some limpets for physically benign spaces between adult Semibalanus is consistent with the prediction that large Semibalanus (+S.c.) indirectly enhance predation on B. glandula and small Semibalanus by increasing predator densities and/or per capita foraging rates. Together with Dayton's (1971) experiments in -S.c. areas, these results provided the basis for our prediction that the relative paucity of small barnacles in nearby +S.c. microhabitats was due to increased predation intensity in these areas. However, contrary to predictions, removing whelks and/or limpets in +S.c. areas had virtually no effect on the cover of either new Semibalanus or B. glandula. The primary reasons for this were apparently 1) the strong negative effect of adult Semibalanus on the abundance of recruits (individuals < 3 mm) and 2) marked differences between our experiment and Dayton's (1971) experiments in the abundance of newly colonizing Semibalanus. In both cases, since available settlement space was not limiting in either +S.c. or -S.c. areas, this suggests that low recruitment (and not competition for space with adult Semibalanus) preempted any important effects of whelks or limpets.

Extreme temporal variation in the recruitment of Semibalanus has been observed by others on San Juan Island (Connell 1970, 1971, Dayton 1971, Spight 1981, Strathmann et al. 1981, Sebens and Lewis 1985). In addition, our own field observations and subsequent studies (Navarrete and Berlow, unpublished data) demonstrated that the present study took place during a year of relatively low Semibalanus recruitment. In contrast, the recruitment of B. glandula on San Juan Island has been reported to be more temporally consistent (Connell 1970), and the density of B. glandula recruits in -S.c. areas in our experiments appeared to be fairly typical of recruit densities on San Juan Island reported by others over the past 60 years (Navarrete and Berlow, unpublished data). In this study, we did not explicitly test for the mechanisms producing spatial variation in barancle recruitment (primarily B. glandula) between +S.c. and -S.c. microhabitats. While the available data on larval settlement behavior is very species- and site-specific, some potential mechanisms consistent with the patterns we observed include: 1) Larval preferences for shells of adult barnacles: Our observation of low recruitment on the available rock surface in areas and cages with adult Semibalanus (+S.c.) could be an artifact of barnacle larvae choosing to settle on the available shells of adults instead of on the bare rock (see Wethey 1984, Bros 1987, Raimondi 1988, Qian and Liu 1990, Schubart 1992 for examples of similar mechanisms). 2) Larval avoidance of predator-dense areas: The higher densities of whelks in areas with adult Semibalanus could result in behavioral avoidance by potential recruits (e.g., Johnson and Strathmann 1989, but see Raimondi 1988). 3) Effect of algal canopy: The slightly greater macro-algal cover in cages with adult Semibalanus could have inhibited the recruitment of barnacles (e. g. Menge 1976, Johnson and Strathmann 1989; but see Strathmann et al. 1981). 4) Larval avoidance of potential competitors: The presence of superior competitors (adult Semibalanus: Dayton 1971) could result in behavioral avoidance by potential recruits (e.g., Grosberg 1981). 5) Predation/Filtration of barnacle larvae by adult Semibalanus: Filtration of larvae may be enough to prevent the local establishment of recruits in their vicinity (e.g., Mileikovsky 1974, Young and Gotelli 1988). 6) Modification of flow regimes by Semibalanus beds: The presence of large barnacles as physical structures may modify the local flow regime in a way that passively diverts the supply of planktonic recruits (e.g., Wethey 1986, Eckman 1990).

Considering each of these alternatives in turn, if larvae prefered adult shells (Alternative 1), predator exclusion cages should show 1) more new, small barnacles growing on shells of live adult Semibalanus than on bare rock in +S.c. areas, and 2) more new, small barnacles overall in +S.c. cages than -S.c. cages, due to more surface area available for settlement in +S.c. cages. However, we observed very few new barnacles, either on the rock or on the shells of other barnacles, in any of the +S.c. predator exclusion cages (Table 6). This pattern suggests that estimates of low recruitment to the rock surface in +S.c. cages were not an artifact of preferential settlement to the shells of adult barnacles. Similarly, new Semibalanus and B. glandula did not recruit more intensely to cages without whelks (Alternative 2), as would be expected if they actively avoided predator trails (e.g., Johnson and Strathmann 1989). If anything, there was a trend in the opposite direction (Fig. 13, Table 4; see Raimondi 1988 for similar effect).

It is unlikely that algae inhibited the recruitment barnacles in our experiments (Alternative 3). First, although there was more algae (primarily Fucus, Enteromorpha, and Ulva) in +S.c. areas (Table 5, Fig. 14), its cover rarely exceeded 20 percent (after adjusting for space occupied by adult Semibalanus). Second, within the +S.c. treatments, more of the few recruits that did settle tended to occur in the cages with the most algae (Figs. 13 and 14). This is consistent with Strathmann et al.'s (1981) observation that both B. glandula and Semibalanus prefer to settle on plates with greater algal cover.

The results of our study and other available data cannot address the other three hypothesized mechanisms (larval avoidance of superior competitors, filtration of recruits, and modified water flow). However, both preliminary results from subsequent experiments (Navarrete and Berlow in prep.) and differences in the spatial distribution of recruits between years of low and high recruitment (discussed below) are consistent with the filtration hypothesis (Alternative 5).

By repeating landmark experiments at our study site, as advocated by Elner and Vadas (1990) and Connell (1974), the inferential power of our manipulations was greatly increased. If we had only manipulated predators in +S.c. areas and had not also repeated Dayton's (1971) manipulations in -S.c. areas, it would have been difficult to infer whether differences between +S.c. (our study) and -S.c. (Dayton 1971) microhabitats represented actual spatial (and not temporal) differences in community organization. Similarly, if our -S.c. manipulations had not been conducted at the same site as Dayton's, we may have attributed differences between our study and Dayton's to subtle spatial differences between sites rather then to variation between years the experiments were conducted. Together, the experiments demonstrate 1) that the effects of predation on B. glandula, while consistent over time in the same microhabitat, varied dramatically over small spatial scales between +S.c. and - S.c. areas and 2) that the effects of predation on S. cariosus varied over time in the same microhabitat.

The transitional dynamics between these community patterns may be determined by the processes regulating the formation of patches within large beds of adult Semibalanus (e.g., disturbance by logs creating large patches of bare rock: Dayton 1971), by interannual variation in predation intensity (e. g. mass mortality of whelks: Connell 1971, Sebens and Lewis 1985), and/or by variation in barnacle recruitment intensity (Connell 1971, Spight 1981, 1982a, Navarrete and Berlow in prep.).

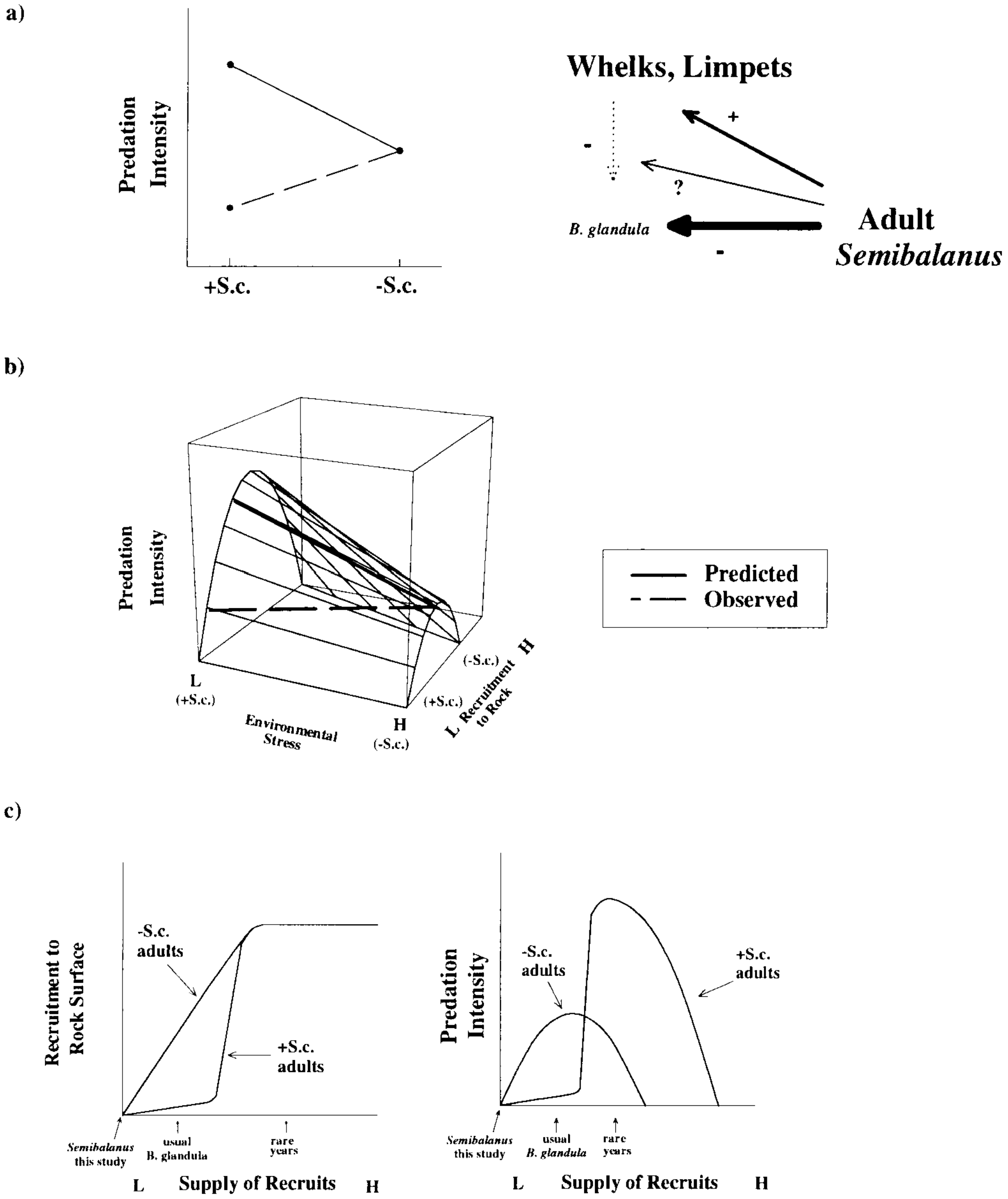
II. Conceptual model of community organization at Eagle Cove:

The 'comparative experimental' (Menge 1991a, Underwood and Petraitis 1993) approach employed in this study allows us to expand our conceptual model of this community and potentially increase the range of conditions over which we have predictive power.

Originally, we assumed that, when barnacles recruit, their abundance does not vary spatially with the presence or absence of adult Semibalanus (Figs. 1 and 15a). Thus, we predicted that large Semibalanus would indirectly enhance predation by whelks and limpets on B. glandula by increasing the local density and/or feeding performance of predators (Figs. 1 and 15a). Instead, large Semibalanus indirectly weakened predation on B. glandula by pre-preempting the effects of predators, despite a strong positive effect on local whelk and limpet densities (Fig. 15a). When these results are viewed under Menge & Sutherland's (1987) general model of community regulation to incorporate variation in the number of recruits settling to each microhabitat, the discrepancies between our predictions and our observations are more clearly resolved (Fig. 15b).

Figure II.15. Conceptual models of community organization based on previous experiments by Dayton (1971) and the results of this study: a) Previous model based on Dayton's work, showing the predicted and observed relative importance of predation (i.e. the measured difference in small barnacle cover between predator exclusions and inclusions) in areas with and without beds of adult Semibalanus (± S.c.). The solid line indicates predicted values; the dotted line indicates values observed in this study. The interaction web detected in this study illustrates the unanticipated strong negative effect that adult Semibalanus had on the barnacle recruits, which weakened the measured effect of predators despite a clear positive effect of Semibalanus on predator densities. We were unable to measure the effect of Semibalanus on per capita foraging rates because the effect of predators was pre-empted by low recruitment. b) Revised conceptual model based on Dayton's results, the results of this study, and the Menge-Sutherland (1987) model of community regulation, showing the relative importance of predation on small barnacles in relation to variation in environmental stress and the density of recruits on the rock surface. The previous model assumed that Semibalanus beds influenced only the level of environmental stress, but the results of this study suggest they also influence the position along the recruitment axis. c) Model of effects of variation in the supply of recruits on spatial patterns of recruitment to the rock surface and predation intensity. 'Supply of recruits' is the pool of larvae in the water column that are available to settle. 'Recruitment to the Rock Surface' is the density of recruits (individuals < 3mm) on the rock. '+S.c. adults' and '-S.c. adults' indicate areas with and without Semibalanus beds, respectively. This hypothesis assumes that, at high densities, either preferred settlement sites are saturated or recruits are able to swamp the filtration effect of Semibalanus adults and settle equally in each microhabitat. Eventually, the number of recruits on the rock is independent of supply because there is no space left to settle. Note that this hypothesis predicts that the effect of Semibalanus beds on predation intensity changes in sign depending on the supply of recruits in the water column. This study, observations of recruitment after this study, and previous data on recruitment on the San Juan Islands suggests that relatively low larval availability is the usual condition and that pulses of intense recruitment are relatively rare. See text for further explanation.

Figure II.15.


a)
Predation Intensity
+S.c.
-S.c.
Whelks, Limpets
+
-
?
B. glandula
-
Adult
Semibalanus
b)
Predation Intensity
Predicted
Observed
L
(+S.c.)
Environmental Stress
H
(-S.c.)
(+S.c.)
(-S.c.)
L Recruitment to Rock H
c)
Recruitment to Rock Surface
-S.c. adults
+S.c. adults
Semibalanus this study
usual B. glandula
rare years
L Supply of Recruits H
Predation Intensity
-S.c. adults
+S.c. adults
Semibalanus this study
usual B. glandula
rare years
L Supply of Recruits H

In this model, the relative strength of predation (as measured by the difference in prey cover between predator exclusions and inclusions) is unimodally related to the density of recruits that settle (Fig. 15b). At very low levels of recruitment, removing predators (no matter how voracious they are) will have little measurable effect on prey abundance. At very high levels of recruitment (relative to the capacity of predators to consume prey), predators will get 'swamped' by prey and have very little effect on prey abundance. In areas where environmental stress for the predators is low, the curve will have a higher peak and be broader (i. e. predators will be more dense in benign areas and/or have greater per capita effects and, thus, will consume more prey for a given level of recruitment and get swamped less easily than in a harsher environment). Our original hypothesis (Figs. 1 and 15a, that predators caused the absence of small barnacles in +S.c. areas) assumed that the presence of Semibalanus beds, by modifying the local thermal regime, would only influence the community's position along the 'Environmental Stress' axis; however, they also simultaneously influenced the position along the 'Recruitment' axis. Thus, these two axes could not be considered independent, and the original model was a 2-dimensional subset of the expanded, 3-dimensional framework (Fig. 15 a and b).

The extremely low abundance of new Semibalanus in all plots regardless of predators during our study suggests that the spatial differences we observed between +S.c. and -S.c. areas might vary over time. In the summer of 1993, when the abundance of recruits (both B. glandula and Semibalanus) was unusually high (Fig. 4: July, 1993), we observed a much more spatially homogeneous distribution of recruits between +S.c. and -S.c. microhabitats than during the present study. This pattenr suggests that the negative effect of Semibalanus on recruitment disappears in places or years when the supply of recruits is either extremely low (new Semibalanus in this study) or unusually high (summer 1993) (Fig. 4, 15c). This pattern of recruitment is consistent with both the 'larval avoidance hypothesis' (saturation of preferred settlement sites, Bertness et al. 1992) and the 'filtration hypothesis' (saturation of Semibalanus filtration) discussed above.

Consequently, in years when the supply of recruits is relatively low (but not zero: 'usual condition' for B. glandula on San Juan Island), predation should be less intense in +S.c. microhabitats (as observed in this study), while in years of unusually high supply of recruits, predation should be more intense in these areas (Fig 15c). Thus, experimental information about how community organization varies spatially between microhabitats (± S.c.) and temporally within one microhabitat (-S.c.), suggests how spatial variation in community organization might vary temporally between years of low and high recruitment.

While we did not explicitly measure the abundance of larvae in the water column or the patterns of larval settlement to the rock surface, our study is consistent with others that suggest the supply of recruits can set the boundaries on the potential importance of other community processes (Underwood et al. 1983, Gaines and Roughgarden 1985, Menge and Sutherland 1987, Raimondi 1990, Menge 1991b, Minchinton and Scheibling 1991, Lively et al. 1993). In addition, while the integration of empirical results and theoretical models enhances our ability to anticipate some indirect interactions between species (Dayton 1973, Carpenter et al. 1992, Hawkins et al. 1993, Ritchie and Tilman 1993, Wootton 1993a, 1994a, b, c, Menge 1995), our predictive capacity critically depends on our ability to correctly characterize how the relative importance of key organizing processes vary over space and time (Kitching 1987, Hunter and Price 1992, Cohen et al. 1993, Mills et al. 1993, Menge et al. 1994). In our case, we correctly anticipated the potential for an indirect negative effect of Semibalanus on B. glandula and new Semibalanus through an increase in local predator densities. However, we did not anticipate the comparatively strong negative effect of Semibalanus on the abundance of recruits, which weakened the relative strength of predation by whelks and limpets on B. glandula in +S.c. microhabitats (Fig 15a).

Thus, because the results of field experiments are sensitive to spatial and temporal variation in community organization, our ability to generalize from individual experiments is severely limited. However, for the same reason, field experiments, when replicated in time and over space, can help characterize the patterns of variation that are reasonable to expect and, thus, can potentially increase the predictive capacity of theoretical models.

Table II.1. Repeated-measures split-plot analysis of variance on the effect of Semibalanus on the log-transformed densities of whelks (N. emarginata and N. canaliculata) and limpets (L. pelta and T. scutum) within the vertical extent of Semibalanus beds. The analysis of whelk densities did not include the initial sampling date (pre-manipulation). The analysis of limpets (spp. pooled) included all dates because there were no clear initial differences in temporal trends. The analysis of separate limpet species included only the last three sampling dates because the species were not differentiated in the monitoring procedure until September 1992. Data are type III mean squares, standard F-values, and associated p-values. The test for sphericity to evaluate whether the univariate tests for within-subjects effects satisfied the Huynh-Feldt condition (i.e. that they have Type H covariance matrices) was not performed due to insufficient error degrees of freedom (SAS Institute, 1988). Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

Source of Variation	df	MS	F	p
Whelks (N. emarginata + N. canaliculata):				
Between Subjects (Treatment effects)				
BLOCK	2	0.16	0.44	0.69
Semibalananus	1	26.47	73.59	**0.01**
ERROR	2	0.36		
Within Subjects (Time effects)				
TIME	3	4.97	22.29	**0.001**
TIME*BLOCK	6	0.38	1.72	0.26
TIME*Semibalanus	3	0.64	2.88	0.12
ERROR(TIME)	6	0.22		

Table II.1. (continued)

Source of Variation	df	MS	F	p
Limpets (L. pelta + T. scutum):				
Between Subjects (Treatment effects)				
BLOCK	2	0.53	2.13	0.32
Semibalanus	1	2.47	9.65	0.09
ERROR	2	0.25		
Within Subjects (Time effects)				
TIME	4	1.11	4.10	**0.04**
TIME*BLOCK	8	0.16	0.61	0.75
TIME*Semibalanus	4	0.56	2.08	0.18
ERROR(TIME)	8	0.27		
Lottia pelta:				
Between Subjects (Treatment effects)				
BLOCK	2	0.24	2.62	0.28
Semibalanus	1	19.92	217.13	**0.0046**
ERROR	2	0.09		
Within Subjects (Time effects)				
TIME	2	0.38	1.05	0.43
TIME*BLOCK	4	0.53	1.46	0.36
TIME*Semibalanus	2	1.98	5.46	0.07
ERROR(TIME)	4	0.36		

Table II.1. (continued)

Source of Variation	df	MS	F	p
Tectura scutum:				
Between Subjects (Treatment effects)				
BLOCK	2	0.97	42.69	**0.02**
Semibalanus	1	0.01	0.42	0.58
ERROR	2	0.02		
Within Subjects (Time effects)				
TIME	2	0.44	0.77	0.52
TIME*BLOCK	4	0.42	0.75	0.61
TIME*Semibalanus	2	0.79	1.39	0.35
ERROR(TIME)	4	0.57		

Table II.2. Repeated-measures split-plot analysis of variance on the effect of Semibalanus (SEM), Nucella (NUC), and Limpets (LIM) on the cover of new B. glandula (>3mm) on the last 5 sample dates of the experiment. Because cages were nested within Semibalanus plots, Semibalanus effects were tested using rep(SEM) as the error term. Nucella effects and Nucella*Semibalanus effects were tested using rep*NUC(SEM) as the error term. Limpet effects and Limpet*Semibalanus effects were tested using rep*LIM(SEM) as the error term. Temporally correlated data did not satisfy the Huynh-Feldt condition (Type H covariance matrices; Test for Sphericity; p=0.0028 with 9 df), thus the multivariate results for within subjects effects are presented (SAS Institute, 1988). df: degrees of freedom; MS: type III mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

Between Subjects (Treatment effects)

Source of Variation	df	MS	F	p
SEM	1	0.809	11.97	**0.013**
rep(SEM)	6	0.068	1.61	0.290
NUC	1	0.416	33.22	**0.001**
SEM*NUC	1	0.439	35.03	**0.001**
rep*NUC(SEM)	6	0.012	0.30	0.917
LIM	1	0.040	0.70	0.435
SEM*LIM	1	0.040	0.71	0.431
rep*LIM(SEM)	6	0.058	1.37	0.356
NUC*LIM	1	0.001	0.03	0.859
SEM*NUC*LIM	1	0.001	0.02	0.889
ERROR	6	0.042		

Table II.2 (continued)

Within Subjects (Time effects)

Source of Variation	Num df	Den df	Wilk's λ	p
TIME	4	3	0.039	**0.019**
TIME*SEM	4	3	0.241	0.253
TIME*rep(SEM)	24	12	0.0002	**0.003**
TIME*NUC	4	3	0.014	**0.004**
TIME*SEM*NUC	4	3	0.018	**0.005**
TIME*rep*NUC(SEM)	24	12	0.001	**0.036**
TIME*LIM	4	3	0.011	**0.003**
TIME*SEM*LIM	4	3	0.017	**0.005**
TIME*rep*LIM(SEM)	24	12	0.002	0.068
TIME*NUC*LIM	4	3	0.087	0.061
TIME*SEM*NUC*LIM	4	3	0.110	0.085

Table II.3. Repeated-measures split-plot analysis of variance on the effect of adult Semibalanus (SEM), Nucella (NUC), and Limpets (LIM) on the cover of new *S. cariousus* (>3mm) on the last 5 sample dates of the experiment. Because cages were nested within Semibalanus plots, Semibalanus effects were tested using rep(SEM) as the error term. Nucella effects and Nucella*Semibalanus effects were tested using rep*NUC(SEM) as the error term. Limpet effects and Limpet*Semibalanus effects were tested using rep*LIM(SEM) as the error term. Temporally correlated data satisfied the Huynh-Feldt condition (Type H covariance matrices; Test for Sphericity; $p=0.063$ with 9 df) (SAS Institute, 1988). df: degrees of freedom; MS: type III mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

Between Subjects (Treatment effects)

Source of Variation	df	MS	F	p
SEM	1	0.0004	0.03	0.862
rep(SEM)	6	0.013	0.65	0.691
NUC	1	0.024	2.30	0.180
SEM*NUC	1	0.001	0.14	0.721
rep*NUC(SEM)	6	0.010	0.52	0.800
LIM	1	0.001	0.13	0.735
SEM*LIM	1	0.029	3.03	0.132
rep*LIM(SEM)	6	0.010	0.48	0.800
NUC*LIM	1	0.050	2.46	0.168
SEM*NUC*LIM	1	0.001	0.06	0.822
ERROR	6	0.020		

Table II.3. (continued)

Within Subjects (Time effects)

Source of Variation	Num df	Den df	Wilk's λ	p
TIME	4	3	0.090	0.064
TIME*SEM	4	3	0.210	0.210
TIME*rep(SEM)	24	12	0.025	0.594
TIME*NUC	4	3	0.431	0.524
TIME*SEM*NUC	4	3	0.942	0.993
TIME*rep*NUC(SEM)	24	12	0.026	0.604
TIME*LIM	4	3	0.607	0.751
TIME*SEM*LIM	4	3	0.039	**0.019**
TIME*rep*LIM(SEM)	24	12	0.056	0.839
TIME*NUC*LIM	4	3	0.522	0.648
TIME*SEM*NUC*LIM	4	3	0.598	0.741

Table II.4. Effects of adult *Semibalanus* (SEM), *Nucella* (NUC), and Limpets (LIM) on the density of barnacle recruits (*B. glandula* and *S. cariosus* <3mm) by sample date (univariate ANOVA's). Densities have been standardized for the amount of space occupied by adult *Semibalanus*. The data are log-transformed densities. Because cages were nested within *Semibalanus* plots, *Semibalanus* effects were tested using rep(SEM) as the error term. *Nucella* effects and *Nucella***Semibalanus* effects were tested using rep*NUC(SEM) as the error term. Limpet effects and Limpet**Semibalanus* effects were tested using rep*LIM(SEM) as the error term. Data are type III mean squares, F-values, and p-values. Because recruitment of new individuals at each date is independent, significance levels are not adjusted for time correlations. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

Year:			1992	1992	1992	1992	1993
Month:			Mar	May	Jul	Sep	Mar
Source	df	Statistic					
SEM	1	MS	0.22	3.00	3.06	0.20	0.67
		F	0.44	8.08	11.27	0.47	4.31
		p	0.53	**0.03**	**0.02**	0.52	0.08
rep(SEM)	6	MS	0.50	0.37	0.27	0.43	0.16
		F	5.21	1.52	2.38	3.82	1.57
		p	**0.03**	0.31	0.16	0.08	0.30
NUC	1	MS	0.07	0.27	0.02	0.78	2.16
		F	1.65	1.17	0.59	4.13	10.54
		p	0.25	0.32	0.47	0.09	**0.02**
SEM*NUC	1	MS	0.14	<0.01	0.29	<0.01	0.28
		F	3.25	0.00	7.60	0.00	1.37
		p	0.12	0.99	0.03	0.97	0.29
rep*NUC(SEM)	6	MS	0.04	0.23	0.04	0.19	0.20
		F	0.45	0.94	0.33	1.66	2.07
		p	0.82	0.53	0.90	0.30	0.20

Table II.4. (continued)

Year:			1992	1992	1992	1992	1993
Month:			Mar	May	Jul	Sep	Mar
Source	df	Statistic					
LIM	1	MS	0.09	0.07	0.01	1.35	0.54
		F	0.67	0.29	0.02	10.81	3.05
		p	0.44	0.61	0.90	0.17	0.13
SEM*LIM	1	MS	0.27	1.17	0.74	0.15	0.34
		F	1.89	4.79	1.38	1.19	1.96
		p	0.22	0.07	0.28	0.32	0.21
rep*LIM(SEM)	6	MS	0.14	0.24	0.54	0.12	0.18
		F	1.50	1.00	4.27	1.10	1.77
		p	0.32	0.50	**0.04**	0.50	0.25
NUC*LIM	1	MS	0.67	0.95	0.26	0.69	0.07
		F	7.01	3.88	2.24	6.09	0.67
		p	**0.04**	0.10	0.18	0.06	0.44
SEM*NUC*LIM	1	MS	0.64	0.13	<0.01	0.13	0.37
		F	6.67	0.54	0.00	1.11	3.73
		p	**0.04**	0.49	0.95	0.34	0.10
MODEL	5	MS	0.25	0.42	0.38	0.28	0.31
		F	2.60	1.74	3.32	2.49	3.09
		p	0.12	0.25	0.07	0.16	0.08
ERROR	3	MS	0.095	0.244	0.114	0.114	0.099
R^2			0.92	0.88	0.93	0.93	0.93

Table II.5. Repeated-measures split-plot analysis of variance on the effect of Semibalanus (SEM), Nucella (NUC), and Limpets (LIM) on the cover of algae occupying primary space on the last 5 sample dates of the experiment. Data are arcsin(squareroot)-transformed covers. Because cages were nested within Semibalanus plots, Semibalanus effects were tested using rep(SEM) as the error term. Nucella effects and Nucella*Semibalanus effects were tested using rep*NUC(SEM) as the error term. Limpet effects and Limpet*Semibalanus effects were tested using rep*LIM(SEM) as the error term. Data are type III mean squares, standard F-values, and associated p-values. Temporally correlated data satisfied the Huynh-Feldt condition (Type H covariance matrices; Test for Sphericity; p=0.08 with 9 df), thus the univariate (split-plot) results are presented with untransformed F- and p-values (SAS Institute, 1988). Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

Response variable: cover Algae (1^o space)

Between Subjects (Treatment effects)

Source of Variation	df	MS	F	p
SEM	1	0.22	15.87	**0.007**
rep(SEM)	6	0.014	0.29	0.92
NUC	1	0.41	7.43	**0.034**
SEM*NUC	1	0.085	1.54	0.26
rep*NUC(SEM)	6	0.055	1.16	0.45
LIM	1	0.21	7.78	**0.032**
SEM*LIM	1	0.01	0.55	0.49
rep*LIM(SEM)	6	0.027	0.56	0.75
NUC*LIM	1	0.02	0.39	0.56
SEM*NUC*LIM	1	0.006	0.13	0.73
ERROR	5	0.048		

Table II.5. (continued)

Within Subjects (Time effects)

Source of Variation	df	MS	F	p
TIME	4	0.083	3.79	**0.019**
TIME*SEM	4	0.013	0.35	0.84
TIME*rep(SEM)	24	0.04	1.65	0.13
TIME*NUC	4	0.02	0.69	0.60
TIME*SEM*NUC	4	0.04	1.58	0.21
TIME*rep*NUC(SEM)	24	0.02	1.12	0.40
TIME*LIM	4	0.007	0.27	0.89
TIME*SEM*LIM	4	0.02	0.59	0.67
TIME*rep*LIM(SEM)	24	0.03	1.20	0.34
TIME*NUC*LIM	4	0.04	1.60	0.21
TIME*SEM*NUC*LIM	4	0.07	3.21	**0.035**
ERROR(TIME)	20	0.02		

Table II.6. Number of small barnacles (*B. glandula* and *S. cariosus* <5mm) growing on the tests of other barnacles (either adult *Semibalanus* or other small barnacles) and on the rock surface in March, 1993, in predator exclusion cages.

		On Tests of Other Barnacles	**On Rock**
Treatment	**n**	**Mean (Std. Err.)**	**Mean (Std. Err)**
- *Semibalanus* adults	4	15.0 (5.91)	35.25 (15.56)
+ *Semibalanus* adults	4	2.5 (1.60)	1.50 (0.75)

CHAPTER III

LINKAGE STRENGTH AND CONTEXT-DEPENDENCY: VARIATION IN THE EFFECTS OF WHELKS ON A ROCKY INTERTIDAL ASSEMBLAGE

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Abstract

In any community with more than two species, indirect interactions between species can complicate predictability by making the effect of one species on another depend on the dynamics of additional species in the community. However, while indirect effects are often the source of 'unanticipated' results in field studies, experimental community ecologists have demonstrated that some communities exhibit remarkably regular patterns of organization that can be easily predicted based on an a priori knowledge of causal mechanisms. When can we expect the outcomes of species interactions to be extremely contingent? When can we safely neglect a large number of possible indirect effects without compromising our ability to predict the consequences of a species loss?

Direct interactions between species are often not equally important; thus, the range of what is probable is a small subset of what is possible. In this study, I tested the hypothesis that, when the direct effect of one species on another increases in relative strength, its total effect (direct + indirect) is less variable or conditional than if the web is characterized by a more uniform distribution of interaction strengths. In an early successional, rocky intertidal interaction web, consisting primarily of one group of predators (whelks: Nucella emarginata and N. canaliculata) and two groups of early colonizing sessile prey that compete for space (acorn barnacles: Balanus glandula and Chthamalus dalli, and mussels: Mytilus trossulus), I manipulated the presence/absence of

the two groups of prey species under each of three predator densities in a replicated factorial design. The direct effects of predation by whelks increased monotonically in strength with the density of whelks manipulated. Three identical experiments were repeated over three successive years to address the following questions: 1) Does the strength of indirect effects increase with an increase in the relative strength of predation (direct effect) by snails? 2) As the strength of the direct effect of predation increases, is the total effect (direct + indirect) less sensitive to variation between experimental starting dates or between different replicates within an experiment?

The indirect effects of Nucella on both B. glandula and M. trossulus varied between experiments and with the density of Nucella. The absolute change in cover attributable to indirect effects was smallest in treatments where the direct effect of predation was strongest. Thus, when the direct effect of Nucella on a given prey species was relatively strong, its total effect (direct + indirect) was less sensitive to variation in the abundance of the other prey species than when predation was weak.

Similarly, when the direct effect of predation by Nucella was potentially strongest, the sign of the total effect was relatively consistent within and between experiments, despite the potential complexity of indirect effects in the web examined, and despite natural variation in the recruitment of prey, disturbance events, and other environmental conditions. Strong predation treatments consistently dampened natural variation between individual replicates within a given experiment. In contrast, the outcome of 'weak' predation was more spatially and temporally variable in sign, and whether it magnified or dampened differences between individual replicates varied between experiments. Consequently, the mean total effect of 'weak' predation across replicates was generally not significantly different from zero. However, in some cases, the range of variation (both within and between experiments) in the total effect of 'weak' predation exceeded the magnitude of the strongest total effect observed.

These results suggest that a knowledge of the relative strengths of direct interactions in a community may provide information about the level of certainty we can ascribe to our predictions about the consequences of a species loss. When relatively few interactions are disproportionately strong and are all located along one main interaction chain (e.g., keystone effects and trophic cascades), we may be able to safely neglect the details of a large number of possible indirect effects without compromising our predictive capacity. In contrast, if the interaction strengths are more evenly distributed, predictions about the total effect of a species loss (or removal) may be so context-dependent that considerable 'baseline' information is necessary to make even the simplest predictions.

Introduction

A major challenge for community ecologists is predicting the outcome of perturbations to natural communities given the potential complexity of species interactions that can produce unanticipated effects. This is particularly important as ecology develops from a historically explanatory science to a predictive one that plays an active role in addressing environmental problems (Drake et al. 1989, Lubchenco et al. 1991, Peters 1991, Keddy 1992, Kareiva et al. 1993). One important obstacle to predictability is the fact that the outcomes of species interactions are often context-dependent (Carpenter and Kitchell 1993). Indirect interactions between species occur when the effect of one species on another depends on the presence of a third species. Consequently, such interactions can impede our ability to predict the dynamics of multispecies assemblages (Levine 1976, Holt, 1977, 1984, Vandermeer 1980, Puccia and Levins 1985, Abrams 1987, Wilbur and Fauth 1990, Wootton 1994c). Indirect effects have long been recognized (e.g., Darwin 1859, Forbes 1887, Hairston et al. 1960) and experimental examples abound (e.g., Connell 1961a, b, Paine 1966, Dayton 1971, Menge 1976, Lubchenco 1978, Sih et al. 1985, Carpenter et al. 1987, Schmitt 1987, Spiller & Schoener 1994, Menge 1995). Currently, a critical challenge for the successful application of basic ecological theory is to determine not if indirect effects can be important, but when (Abrams 1983, Strauss 1991, Adler and Morris 1994, Wootton 1994a, b, Menge 1995). Many theories in physics are successful because they neglect 'higher order terms' (Kareiva 1994). Are there any rules in ecology that determine when we can safely neglect indirect effects without compromising our predictive capacity?

One type of indirect effect, an 'interaction chain' (sensu Wooton 1993a), results from a series of direct interactions between species pairs (Wootton1994a, Billick and Case 1994). In contrast, 'interaction modifications' (sensu Wooton 1993a), or 'higher order interactions', occur when one species affects the nature of the direct interaction between two other species (Miller and Kerfoot 1987, Abrams 1991, Werner 1992, Billick and Case 1994, Wootton 1994c). While interaction chains can theoretically be predicted from a simple knowledge of pairwise interactions in the community, interaction modifications cannot, and , thus, have been considered particularly problematic (Holt 1977, 1984, 1987, Abrams 1987, 1991, 1992, Werner 1992, Ritchie & Tilman 1993, Wootton 1993a, 1994c). Consequently, much recent attention has focused on the problem of empirically distinguishing interaction modifications from interaction chains (e.g., Adler and Morris 1994, Billick and Case 1994, Karieva 1994, Wootton 1994c).

Despite the fact that interaction chains are theoretically simpler than interaction modifications, the interaction chains can be an important source of variation in the outcome of species interactions (Menge 1995). For example, when different possible interaction chains are of opposite sign (e.g., Brown et al. 1986, Dethier and Duggins 1984, Dungan 1986, Spiller and Schoener 1990), predicting just the sign of the outcome the interaction between two species can be extremely difficult. In addition to a general knowledge of all possible pairwise species interactions, it requires a knowledge of the relative abundances of those species, of the relative strengths of all possible interaction pathways , and of how all of these change over space and time (e.g., Vandermeer 1980, Dethier and Duggins 1984, Dungan 1986). Thus, both types of indirect effects are important in making the outcome of species interactions conditional on the context in which they occur (Price et al. 1980, Fairweather et al. 1984, Thompson 1988, Cushman & Whitham 1989, Cushman 1991, Steneck et al. 1991). The fact that an interaction is more context-dependent does not necessarily mean that it is less predictable, however, it does mean that more 'baseline' information is necessary to make even the simplest predictions (MacArthur 1972a, Colwell 1984, Carpenter and Kitchell 1993).

When all possible indirect interactions are considered, any assemblage consisting of more than just a few species can be theoretically intractable. In models of multi-species assemblages that incorporate interaction chains and/or interaction modifications, the total effect of one species on another (i.e. the sum of direct and indirect effects) can be indeterminate in both sign and magnitude (Abrams 1987, Yodzis 1988). In the most extreme case of context-dependency, the outcomes of species interactions depend so critically on initial conditions that the species exhibit chaotic dynamics (Gilpin 1979, Hain & Logan 1991, Hastings & Powell 1991, Tilman & Wedin 1991, Wilson 1992, Hastings 1993, Abrams & Roth 1994, McCann & Yodzis 1994). In this case, indirect interactions between species (both interaction chains and modifications) may act to magnify even the smallest stochastic variation in environmental conditions, recruitment, disturbances, etc. (Drake 1990, 1991, Wilson 1992, Ellner and Turchin 1995).

In empirical studies, indirect effects are often the source of 'unanticipated' results (e.g., Sih et al. 1985, Brown et al. 1986, Carpenter et al. 1987, Carpenter and Kitchell 1993); however, experimental community ecologists have demonstrated that some communities exhibit remarkably regular patterns of organization that can be predicted based on an a priori knowledge of causal mechanisms (e.g., Paine 1966, 1974, Menge 1976, Lubchenco 1978, Lubchenco and Menge 1978, Menge et al. 1986, Carpenter et al. 1985, Schmitt 1987, Karban 1989, Power 1990a, Tilman 1990, Hixon and Brostoff 1993, Ritchie and Tilman 1993, Chapter II). Some of these consistent patterns are the result of strong indirect effects (e.g., the 'keystone' effect: Paine 1966, 1974). When do indirect effects make the outcomes of species interactions intractably contingent, and when do they make them dependably robust? When can we expect species interactions to dampen, rather than magnify, natural variation in environmental conditions?

In this light, an important contribution of experimental ecology has been a rigorous demonstration of the way interaction strengths vary within and between communities (Dayton 1971, Menge 1976, Lubchenco and Menge 1978, Durham 1980, Hairston 1980, Underwood et al. 1983, Palumbi 1985, Menge et al. 1986, 1994, Barkai and McQuaid 1988, Dethier & Duggins 1988, Karban 1989, Power 1992, D'Antonio 1993, Chapter II). Direct interactions between species are often not equally important; thus, the range of what is probable is often a small subset of what is possible (Paine 1980, Jordano 1987, Tilman 1990, Menge 1995). Many theoretical analyses of multispecies food webs have explored the topology of species interactions (Pimm 1982, Pimm et al. 1991, Cohen et al. 1990, Law & Blackford 1992). However, few have explicitly explored the consequences of the way in which interaction strengths are distributed within the web (Vandermeer 1980, Yodzis 1981, Mills et al. 1993).

In this study, I tested the hypothesis that, in a web of interacting species, when the direct effect of one species on another increases in relative strength, its total effect (direct + indirect) is less variable or conditional than if the web is characterized by a more uniform distribution of interaction strengths. Using an early successional, marine rocky intertidal, interaction web consisting primarily of one group of predators (whelks: Nucella emarginata and N. canaliculata) and two groups of early colonizing sessile prey that compete for space (acorn barnacles: Balanus glandula and Chthamalus dalli, and mussels: Mytilus trossulus), I manipulated the presence/absence of the two groups of prey species under each of three predator densities in a replicated factorial design. Three identical experiments were repeated over three successive years to address the following questions:

1) Does the strength of indirect effects increase with an increase in the relative strength of predation (direct effect) by snails?

2) As the strength of the direct effect of predation increases, is the total effect (direct + indirect) on a given prey species less sensitive to differences between experimental starting dates or between different replicates within an experiment?

Definitions and Hypotheses

I. Definitions:

Traditionally, theoreticians have defined interaction strength by the coefficient which describes the per capita effect of one species on the per capita population growth rate of another (e.g., MacArthur 1972b). Empirical studies traditionally measure the magnitude of difference in abundances between treatments after an elapsed time (Wootton 1994c). Empiricists have also used 'interaction strength' to refer both to the direct effect that one species has on another or to the total effect that it has on the community if removed (i.e. the direct plus indirect effects) (MacArthur 1972b, Dayton 1975, Paine 1980, 1993).

In this study, I use 'interaction strength' to mean the magnitude of the direct effect (also referred to as 'linkage strength': e.g., Menge 1995, and 'effect strength': sensu Wootton 1994a) of one species (A) on a target species (B). Because of the logistical problems in estimating effects on per capita growth rates in field experiments (see Wootton 1994c), I measured interaction strength as:

$$\mathbf{IS_{A\rightarrow B} = DE_{A\rightarrow B} = (T\text{-}C) \,/\, (T+C)} \qquad (1)$$

where 'IS' is the interaction strength, or direct effect ('DE') of species A on species B. 'T' is the abundance of species B in the 'treatment' where species A and B are together, and 'C' is the abundance of B in the 'control' where B is alone. Thus, IS is the relative difference between the treatment and the control. This is similar to the method used by Paine (1993) and Grace (1995: 'Relative Competion Index'), in that it measures the proportional effect of A on B. 'IS' is different from Paine's Index in two respects:

1) IS here is the population effect of A on B (rather than the per capita effect) because, in the current study, A was either 1) a mobile, aggregating species for which density estimates are very scale-dependent (Spight 1982a, Navarrete 1994) or 2) a sessile species whose abundance was measured in percent cover. In addition, the experiment was designed to compare the effects of different densities of A.

2) The denominator is the sum of T and C rather than just C. This has the advantage of bounding the index between -1 and 1, so that negative and positive effects are symmetrical and comparable. Paine's Index varies from -1 (maximum negative effect) to infinity (maximum positive effect), making it difficult to compare the relative strengths of postitive and negative effects. Paine's index is useful when B is abundant in the controls (C) and most of the effects of A are expected to be negative (i.e. B alone forms a monoculture). However, if B is facilitated by A and is not abundant in the absence of A, then Paine's Index results in very large positive effects for relatively small proportional changes in B. For example, if the cover of B is 2% when alone (C) and 10% in the presence of A (T), then Paine's Index results in a positive effect of +4. A similar negative effect (i.e. from 10% to 2%) would result in a negative effect of -0.8. If positive effects are more likely to occur when B is low in the absence of A (i.e. in controls), Paine's Index will have a tendency to over-inflate positive effects. In the same example, the index used in the present study would result in a positive effect of +0.67 and a negative effect of -0.67, respectively. Note that, this index results in consistently smaller absolute values than Paine's Index. In the present study, B rarely formed a monoculture when alone, and facilitation was common.

Ideally, for IS to be a measure of the direct effect of A on B, no other species (C_i) which potentially alter the effect of A on B should be present. If C_i is present, then equation (1) represents the 'Total Effect' (TE) of A on B, which includes both direct and indirect effects.

With this measure of IS, the relative strength of any direct link between A and B (e.g., the direct effect of whelks on barnacles) will depend on 1) the abundance A (whelks), 2) the abundance B (barnacles), and 3) the per capita effect of A on B. Thus, in any given interaction web, the relative strengths of the direct links between species will vary as the component species vary in abundance over space and time (Fairweather 1988).

The relative strength of the Total Effect (TE) of A on B will additionally depend on 1) the presence/abundance of 'modifier' species (C_i : e.g., mussels), 2) the degree to which C_i alters the nature of the direct interaction between A and B (i.e. 'Interaction Modification', or 'Higher Order Interaction'; sensu Wootton 1993a, 1994c), and 3) the relative strength of the chain of direct links (i.e. 'Interaction Chain'; sensu Wootton 1993a, 1994c) through which A indirectly effects B through C_i (e.g., Spiller and Schoener 1990). 'Indirect Effects' here include both Interaction Chains and Interaction Modifications, or any way in which the effect of A on B is altered by the presence of C_i.

Some limitations of this proportional measure of interaction strength (either IS or TE) include:

1) If the abundance of B is very low in both T and C, very small changes in B due to the presence of A will be measured as large proportional changes. Depending on the system and the question of interest, these effects may be ecologically trivial. For this reason, I also present data on 'Absolute Changes' (AC) in B, where

$$\mathbf{AC = T - C} \qquad (2) \quad .$$

2) The strongest negative effect allowed by the index is -1. Thus, if A completely eliminates B at given density of A, one cannot estimate the potential effect of increasing the abundance of A. Any increase in the abundance of A would be measured as a <u>decrease</u> in the per capita effect of A. If B in the absence of A forms a monoculture of 100% cover, then a value of -1 indicates that A, at that density, was able to eliminate the

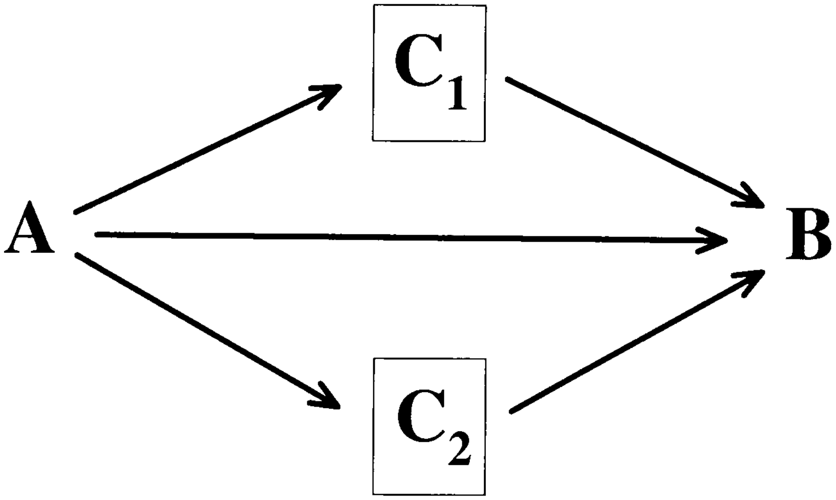
maximum abundance of B possible. However, if B alone only reaches 10% cover in a year of low recruitment, low densities of A may be able to eliminate B (i.e. IS = -1) in that year, but not in a year of high B recruitment. In contrast, high densities of A may be able to eliminate B (i.e. IS = -1) regardless of the abundance of B. Intuitively, high densities of A would have a stronger effect on B because they have the potential to eliminate B even during years of high B recruitment. Unfortunately, this information on the potential effect of high A densities is lost because IS cannot go below -1. Therefore, in this study, when predators (A) eliminated their prey (B) at both low and high densities of A, I used the per capita effects of A at low densities to estimate the 'Potential IS' of A at high densities of A. While this predicts unrealistic negative values of B (Wootton 1994c), it provides ecologically important information on the capacity of A to 'absorb' changes in the ambient abundance of B.

II. Hypotheses:

In any assemblage consisting of more than 2 species that interact, A can affect B by more than one possible path of interactions through chains of intermediary species (C_1, C_2, C_3, etc.. Fig. 1). The level of certainty with which we can predict the outcome of a change in A should depend on:

1) The signs of the different potential interaction pathways. In this simple case, if the different potential interaction pathways are of opposite sign, the total effect of A on B should depend critically on the balance of relative interaction strengths for all the direct and indirect pathways (e.g., Vandermeer 1980, Abrams 1987, Kerfoot 1987, Spiller and Schoener 1990). Even without interaction modifications, simple interaction chains which are opposite in sign mandate a thorough understanding of the relative interaction strengths to make the simplest qualitative predictions possible. If different interaction

Figure III.1. A simple interaction web illustrating the multiple interaction pathways by which 'A' (the Affector species) can affect 'B' (the Target species). 'C_1' and 'C_2' represent groups of intermediary species which may mediate the indirect effects of 'A' on 'B'.



pathways are all of the same sign, then at least the sign of the total effect can be easily predicted.

2) The relative strengths of direct interactions. If all the links from A to B are equally strong, then the total effect of A on B should be more sensitive to a) natural variation in the relative abundances of all the species along each possible path, and b) anything that influences the per capita effects of any of those species. Thus, all else being equal, as the direct effect of A on B increases in relative strength, the total effect should be less conditional, or less variable over space and time.

3) The mean strength of all the interactions. If all the links from A to B are equally important but all very weak, then the total effect of A on B may be highly conditional, but the consequences might be ecologically insignificant, depending on what one is interested in predicting and what is the magnitude of permissible error.

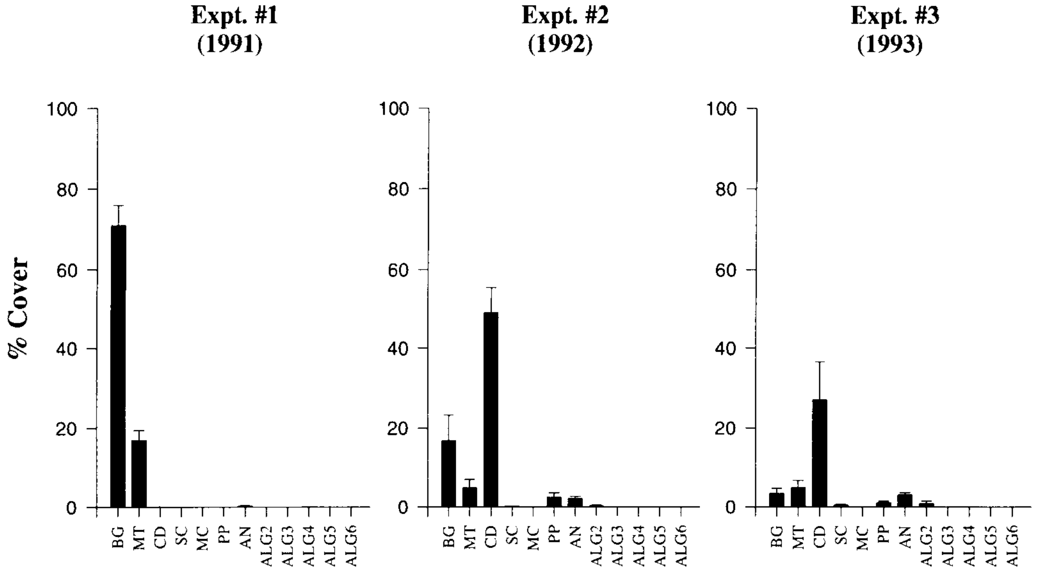
4) The location of strong interactions within the web. If all the strong links along the interaction pathways from A to B occur along the same path, then the total effect of A on B should be less conditional than if the strong links are distributed in a way which makes the different possible interaction chains more equal in mean strength. For example, the consistency of a 'keystone' effect (Paine 1966) or a 'trophic cascade' (Carpenter et al. 1987) may depend on the links along one interaction chain being disproportionately strong.

5) The range of natural variability of the component species. The interaction strength between any two species depends on their relative abundances (see Equation (1)). Thus, if some or all of the component species vary greatly over space and time, then the relative strengths of different interaction chains will vary as well (e.g., Gaines and Roughgarden 1985, Fairweather 1988, Menge, 1991). Consequently, the total effect of A on B may vary with changes in the relative strengths of different interaction pathways (Abrams 1987) .

The System

The study was conducted in the rocky intertidal zone at Fogarty Creek Point (44° 51'N, 124°03'W), about km north of Boiler Bay State Park, in the central coast of Oregon, USA. The zonation of intertidal organisms at this site is similar to that described for Boiler Bay by Menge et al. (1994). A more detailed description of the Fogarty Creek site is provided by Farrell (1991), Navarrete (1994), Brosnan (1994), and Blanchette (1994). Experiments for this study were carried out in a mid-intertidal zone consisting of a smooth, basaltic, horizontal, moderately wave-exposed bench . This area is characterized by an extensive bed of large California mussels, Mytilus californianus. Patches of bare rock of varying sizes are continually created by waves dislodging the mussels (Paine and Levin 1981, E. L. Berlow personal observation) or by a combination of freezing events and wave stress (D. Brosnan, 1994 and personal communication). On the wave-exposed coast of Washington, the patches are eventually reoccupied by M. californianus, but this process may take more than 10 yrs for patches greater than 3 m^2 (Paine and Levin 1981). In the interim, the substrate is colonized by sessile invertebrates and algae (Paine and Levin 1981, Wootton 1993b, 1994b). At this study site, the barnacles, Balanus glandula and Chthamalus dalli, and the mussel, Mytilus trossulus, are often the numerically dominant primary space occupiers in the first year after patch formation (Navarrete 1994, E. L. Berlow personal observation). In older patches, the barnacles Semibalanus cariosus and Pollicipes polymerus are common. Several algae, mostly 'filamentous algae' (sensu Steneck and Dethier 1995: e.g., Pterysiphonia spp., Plocamium spp., Microcladia spp., Polysiphonia spp.), 'corticated macrophytes' (e.g., Mastocarpus spp., Iridea spp. Endocladia muricata, Cryptosiphonia spp., and Odonthalia spp.), and 'articulated calcareous algae' (e.g., Corralina vancouveriensis, Bossiella plumosa), are common but, overall, not very abundant during the first year of succession (Fig. 2), although some small patches can be covered with an algal turf for a couple months. The predatory

Figure III.2. The cover of sessile species averaged across levels of Nucella in plots where neither barnacles nor mussels were removed. Data are means (± S. E., n = 12) over the first year of each experiment. Codes for x-axis: BG = Balanus glandula, MT = Mytilus trossulus, CD = Chthamalus dalli, SC = Semibalanus cariosus, MC = Mytilus californianus, PP = Pollicipes polymerus, AN = Anthopleura spp, ALG2-6 = Algal Functional Groups 2-6 described by Steneck and Dethier (1994). ALG2 = 'filamentous algae' (includes Pterysiphonia spp., Plocamium spp., Microcladia spp., Polysiphonia spp.); ALG3 = 'foliose algae' (includes Ulva spp, Enteromorpha spp, Porphyra spp); ALG4 = 'corticated macrophytes' (includes. Mastocarpus spp., Iridea spp. Endocladia muricata, Cryptosiphonia spp., Odonthalia spp.); ALG5 = 'leathery macrophytes' (includes Hedophyllum sessile, Fucus gardneri, Laminaria spp); ALG6 = 'articulated calcareous algae' (includes Corralina vancouveriensis, Bossiella plumosa). Algal functional groups 1 and 7 ('microalgae' and 'crustose algae', respectively) were included in the category of 'Bare Space' (not shown).

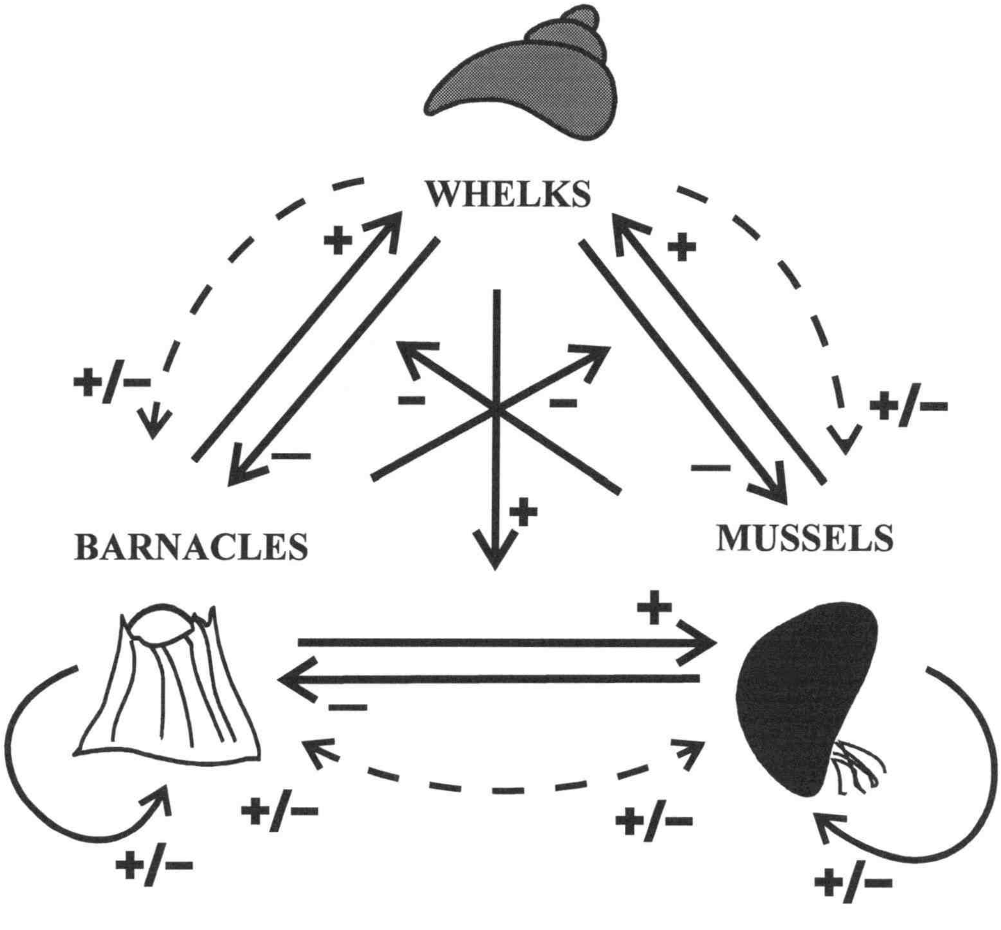


starfish, Pisaster ochraceus, is scarce in this area, occurring primarily below the lower limit of the mussel bed. In areas where Pisaster is absent, whelks (Nucella emarginata and Nucella canaliculata) have been shown to be important predators in on small mussels and barnacles (Connell 1970, Dayton 1971, Suchanek 1978, Navarrete 1994, Chapter II). Other potentially important predators of sessile invertebrates in the mid-zone patches include birds (mostly black oystercatchers, Hematopus bachmani, and gulls, Larus spp.) (Wootton 1992, 1993a, b, 1994b, Marsh 1984, 1986), the brooding starfish, Leptasterias hexactis, and recruits and juveniles (<3 cm total diameter) of P. ochraceus, although the latter two are generally restricted to the edges of patches among the M. californianus.

By using cages to exclude birds and enclose Nucella emarginata, and by initiating the experiments in large (>6m^2) areas recently cleared of sessile organisms, the early sucessional interaction web consisted primarily of one predator (Nucella) and three sessile prey that compete for space (C. dalli, B. glandula, and M. trossulus). In this study, I focused on the interactions between Nucella, B. glandula, and M. trossulus because Chthamalus is not a preferred prey of Nucella and is outcompeted by B glandula (Dayton 1971, West 1986, Farrell 1991).

Figure 3 summarizes some important direct and indirect interactions between Nucella, B. glandula, and M. trossulus that have been experimentally demonstrated for these species (Connell 1970, Dayton 1971, Suchanek 1978, 1985, Palmer 1984, 1990, West 1986, Spight 1981, 1982). Nucella feeds on both M. trossulus and B. glandula by drilling a hole through their shell or at the junction of shell plates. Neither M. trossulus nor B. glandula grow large enough to completely escape predation by whelks (Palmer 1990, E. L. Berlow personal observations). While Nucella do show dietary preferences, these preferences appear to vary markedly between individuals and in the same individual over time (Murdoch 1969, Palmer 1984, West 1985). Preliminary data from the Oregon coast suggest that Nucella have a stronger negative effect on M. trossulus than on B. glandula (E. Wieters, unpublished data). M. trossulus outcompete B. glandula for space

Figure III.3. An interaction web summarizing some of potentially important direct and indirect interactions between Nucella, M. trossulus, and B. glandula. Arrows in the center that point to other arrows are meant to indicate interaction modifications (sensu Wootton 1993a). Dotted arrows indicate indirect effects resulting from either interaction chains or interaction modifications. See text for details.



by growing on top of them and smothering them (Suchanek 1985, Dayton 1971, E. L. Berlow personal observation). Both M. trossulus and B. glandula produce planktonic larvae which eventually settle and metamorphose in the intertidal zone. Acorn barnacles can facilitate the recruitment of M. trossulus by providing an irregular surface which offers protection from predation and/or desiccation (Dayton 1971, Suchanek 1978, 1985). Intraspecific competition between B. glandula can be intense: if they settle densely, they develop a tall, thin, fluted morphology which is very susceptible to being dislodged by waves (e.g., Dayton 1971, Wethey 1984a, E. Berlow personal observation; see Barnes and Powell 1950 for examples of other species of Balanus). Similarly, dense, layered aggregations of M. trossulus are susceptible to dislodgment because many of the individuals are not able to reach the substrate and firmly attach (E. L. Berlow, personal observation). Thus, some level of predation by Nucella which thins densely settled barnacles or mussels could have a direct positive effect by reducing the effects of intraspecific competition and physical disturbance (Connell 1970, E. L. Berlow personal observation).

Some of the potentially important indirect interactions in this web include:

1) Interaction chains: Nucella should have a positive indirect effect on B. glandula by eating M. trossulus. Nucella should have a negative indirect effect on M. trossulus by eating B. glandula, their preferred settlement site. M. trossulus and B. glandula could have negative indirect effects on each other if they each have a positive effect on predator densities (i.e. 'apparent competition', sensu Holt 1977).

2) Interaction modifications: If Nucella's foraging on one prey species is reduced by the presence of an another prey species, each prey species should have a positive indirect effect on the other by serving as an alternative prey item (e.g., Fairweather 1985, Holt 1984, 1987, Abrams 1987, Menge 1995). If Nucella thin barnacles and make them a more stable settlement surface, they could have an indirect positive effect on mussels.

Therefore, while this early successional web, at first glance, may appear relatively simple, observations and previous experiments suggest that both interaction chains and interaction modifications pose a serious challenge to our ability to predict even the sign of the total effect of one species on another. Since the species are readily amenable to experimental manipulation, this system is ideal for exploring the relationship between interaction strengths, indirect effects, and the contingency of species interactions.

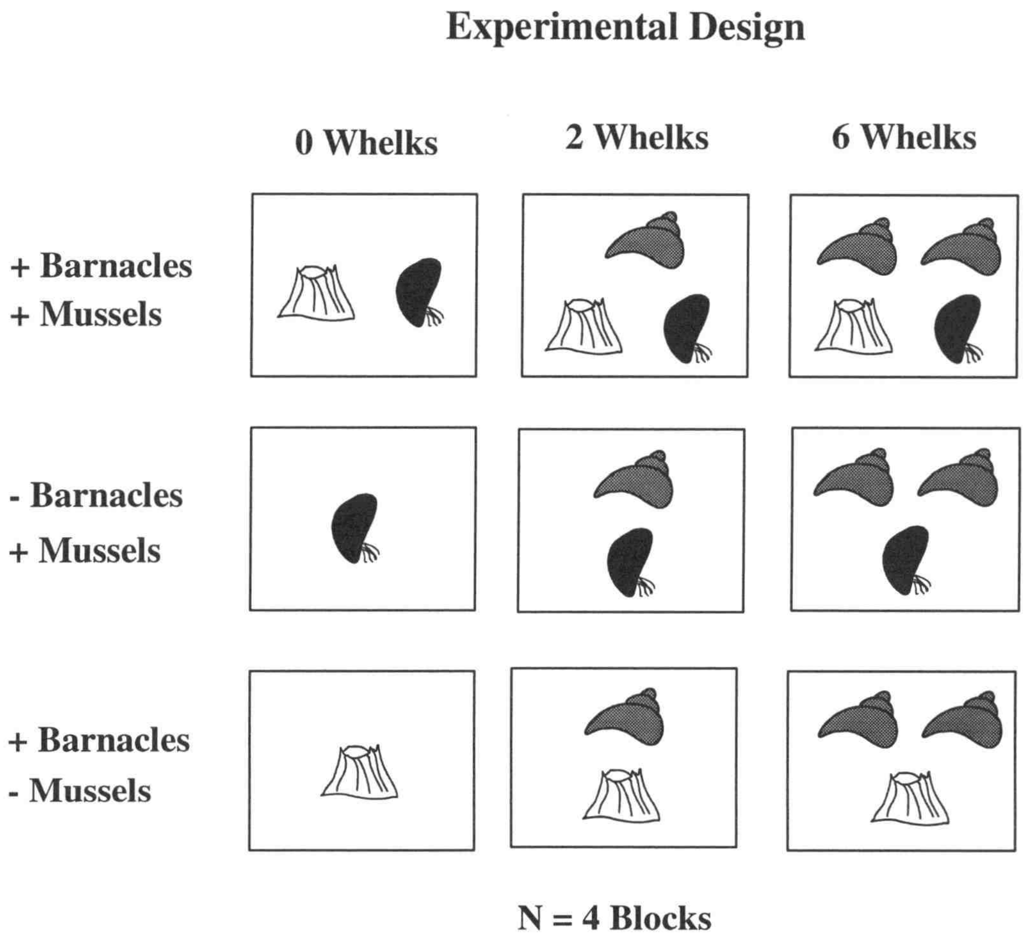
The three experiments in this study were initiated in three separate years which varied naturally in climatic and oceanographic conditions and in the relative abundances of prey species. Thus, for a given strength of predation, one would expect the relative strengths of indirect effects on either prey species to vary between years. The hypothesis proposed above predicts that the total effect of 'weak' predation on a given prey species should be more sensitive to: 1) the presence/absence of the other prey species (i.e. indirect effects), and 2) variation between experiments (and between replicates within and experiment) in the abundance of prey and/or environmental conditions, than the total effect of 'strong' predation.

Methods

To quantify direct and indirect effects in this early successional community and to evaluate how the importance of indirect effects varied with the strength of predation by whelks, I manipulated N. emarginata, acorn barnacles (primarily B. glandula and C. dalli), and M. trossulus in a replicated, randomized block, factorial design (Fig. 4). Three identical experiments were repeated over three successive years to evaluate the relationship between the strength of the direct effect of predators and variation in the outcome of their total effect on each prey species.

There were three levels of whelk densities (none, low, and high), and two levels of both barnacles and mussels (present/absent). The design for each experiment was not completely orthogonal because it did not include treatments where both barnacles and

Figure III.4. The experimental design used in this study. Each box indicates a separate stainless steel mesh cage which contained one of nine combinations of Nucella emarginata, Balanus glandula, and Mytilus trossulus. The nine cages constituted one of four total blocks of the experiment. Treatments were assigned at random within a block. See text for details.



mussels were removed (Fig. 4). All plots were initially scraped of macroscopic invertebrates and algae with a paint scraper and wire brush. Scraping, like natural disturbances in the mussel bed, left areas with algal crusts and byssal threads of M. californianus. The presence or absence of B. glandula and/or M. trossulus were subsequently manipulated by either allowing them settle naturally or removing the new individuals on a monthly basis with forceps or a blunt probe. Because it was practically impossible to selectively avoid removing the recruits of other acorn barnacles (C. dalli, and S. cariosus) and of M. californianus, these treatments were actually '± acorn barnacles' and '± mussels'. However, during the first year of succession, the abundance of S. cariosus and M. californianus were extremely low (Fig. 2).

Stainless steel mesh cages 20 x 20 x 5 cm in size (mesh size = 18 ga. (0.047"), 0.126" space, 51.6% open) were used to manipulate density of whelks. Cages either excluded whelks or enclosed two or six whelks (15-22 mm in length from apex to siphonal canal), corresponding to densities of 0, 50, and 150 whelks/m^2, respectively. These densities are well within the natural range of Nucella densities reported in the literature (Dayton 1971, Spight 1982, Sousa 1984a) and observed at this site (Navarrete 1994, E. L. Berlow unpublished data). While the predator treatments were maintained at a constant density throughout the experiment, the '+barnacle' and '+mussel' treatments varied naturally with recruitment and mortality (independent of predation and interspecific competition).

Recognizing that predator density is just one component of predation intensity (Menge 1978a, b, 1983), I measured the strength of predation on mussels (or barnacles) for each predator density using Equation 1, where 'T' was the treatment where Nucella was present (either at low or high density) and barnacles (or mussels) were excluded, and 'C' was the treatment where Nucella and barnacles (or mussels) were excluded. When all of the prey were eliminated at both low and high densities of Nucella, I used the per capita effect of Nucella in the low density treatment to estimate the 'potential' strength of predation in the high density treatment for that experiment. This assumes that the effects of individual Nucella on their prey are additive (e.g., if two Nucella can consume 10 barnacles, six Nucella can consume 30). Previous experiments suggest that the per capita rates of predation by Nucella on either B. glandula or M. trossulus are not affected by predator density (Murdoch 1969, Connell 1971, see Results).

Quantifying the direct interaction between two species ideally requires that one be able to isolate the pair from the rest of the community. One reason for focusing on the first year of succession in this study was that the species assemblage at this stage was dominated by barnacles and mussels (Fig. 2). In the first experiment, B. glandula and M. trossulus were by far the most abundant species colonizing the experimental plots. Thus, in treatments where either barnacles or mussels were removed, any effects of adding Nucella were interpreted as direct effects on the remaining prey species. In the second and third experiments, additional species, especially C. dalli, were more abundant (Fig. 2), thus any effects of Nucella on B. glandula or M. trossulus in the '-mussel' or '-barnacle' treatments could have included indirect effects mediated through other species that were not manipulated. Since C. dalli and S. cariosus were removed in the '- barnacle' treatments, the effects of Nucella on M. trossulus could have included indirect effects of algae, Anthopleura, Pollicipes, and M. californianus. However, the mean cover of these additional species in '-barnacle' treatments was generally less than 1% (Table 1). Thus, I considered the effects of Nucella on M. trossulus in '-barnacle' treatments to be primarily direct effects.

In the '-mussel' treatments, the effects of Nucella on B. glandula could have included indirect effects of C. dalli, S. cariosus, Anthopleura, Pollicipes, and algae. Of these species, the mean cover of S. cariosus and algae in '-mussel' treatments was generally less than 0.5%, and the cover of Anthopleura and Pollicipes did not exceed 3% and 2%, respectively (Table 1). C. dalli, however, reached almost 50% in experiment #2. Since 1) B. glandula outcompetes C. dalli, and C. dalli has no reciprocal negative effect on B. glandula (Farrell 1991, Dayton 1971), and 2) Nucella has a stronger negative direct effect on B. glandula than on C. dalli (Connell 1970, Dayton 1971, see Results), it is unlikely that the effects of Nucella on B. glandula were influenced by an interaction chain through C. dalli. Thus, any indirect effects due to C. dalli were more likely to be due to interaction modifications. This situation precluded the use of Path Analysis to estimate the relative strength of indirect effects of Nucella on B. glandula mediated through C. dalli (Dixon 1993, Wootton 1994b). Since Nucella appear to show a strong preference for B. glandula over C. dalli (Palmer 1983, 1984, West 1986), it is unlikely that the presence of C. dalli significantly altered the foraging behavior of Nucella eating B. glandula (Murdoch 1969). Thus, I considered the effects of Nucella on B. glandula in '-mussel' treatments to be primarily direct effects.

Cages had 5 cm wide outward-facing flaps along the bottom rim which were used to attach the cages to the rock with stainless steel screws. A strip of silicon tubing was attached to the bottom edge to provide a better fit to irregular rock. Small limpets and other small herbivores (e.g., small chitons, gammarus amphipods, and isopods) easily entered through the mesh, and only individuals that had grown larger than the mesh size were removed. To evaluate some of the 'cage effects', or artifacts introduced by the cages themselves, I used 'roofs' made of the same mesh as the cages and compared results in these to results in unmanipulated plots marked with four screws. Each block contained one roof and one unmanipulated, 'control' plot. Roofs were 20 x 20 cm and were held 5 cm above the rock surface with four PVC posts. Roofs provided shading similar to the full cages while allowing the free movement of whelks and other invertebrates under them. However, the roofs were also effective barriers against predation by birds (Marsh 1984, Wootton 1992, and personal observations). Thus the comparisons of roofs against marked, unmanipulated, 'control' plots, showed the magnitude of the effects of cage shading and bird predation, but these two factors could not be separated. In addition to the shading introduced by the mesh, the edges of cages attached to the rock potentially introduced another artifact. Nereis polychaetes were evidently attracted to the area under the flaps, as were small individuals (< 1.5 cm total diameter) of the brooding starfish, Leptasterias hexactis.

Each treatment was replicated four times in four separate blocks spaced approximately 50 meters apart. Each block was positioned in the bed of M. californianus in a patch recently created by physical disturbance. Additional M. californianus were manually removed to ensure that each patch was at least 6 m^2, or large enough to contain all the cages for each experiment. When the second and third experiments were initiated, some of the patches were further expanded to include the additional cages. Within each block for a given experiment, treatments were randomly assigned to cages. Successive experiments were installed in the same blocks, adjacent to the previous years' experiment(s).

Experiment #1 was initiated in April, 1991 and maintained through March 1994. Experiment #2 was initiated in April, 1992 and maintained through September 1994. Experiment #3 was initiated in April, 1993 and maintained through October 1994. Thus, the three experiments ran concurrently, with their starting dates staggered by one year. For the purposes of this study, I focused on the short-term, one year results of each experiment because: 1) During the first year of succession, B. glandula, M. trossulus, and C. dalli were the most abundant species (Fig. 2). After the first year, the abundance of B. glandula and M. trossulus declined in all treatments as additional species, which potentially reach a size refuge from predation by Nucella (e.g., large S. cariosus, P. polymerus, and M. californianus), increased in abundance (see Chapter IV). 2) Experiment #3 could only be maintained for approximately one year before a number of cages were damaged during severe storms. Thus this study focuses on species interactions during the early stages of patch succession, when the most abundant species are vulnerable to predation by Nucella. The longer term effects of these short-term, ephemeral interactions are addressed in a subsequent study (Chapter IV).

Plots were monitored every month for all three experiments and photographed (2 pictures of 20 x 10 cm per plot) approximately every month for Experiment #1 and once every 2-3 months for Experiments #2 and 3 after it became clear that monthly photos were too frequent to detect important changes. During the regular monitoring, any re-invading whelks or other predators (juvenile Nucella spp <5 mm, small Pisaster (<1.5 cm total diameter), Leptasterias hexactis, or nudibranchs (Onchydoris spp.)) were counted and removed. Cages were periodically scraped or brushed to remove algae (especially during the summer months) and barnacles that settled on the mesh (although some shading by these organisms was inevitable). Percent cover of sessile species was estimated from the pictures with the intersection-point method by projecting the image on a grid with 50 regularly spaced points (two pictures per cage x 50 points/picture = 100 points per cage). Using the same method in a related study, Navarrete (1994) found that picture estimates did not differ appreciably from field estimates (see also Foster et al. 1991). It was difficult, however, to identify algae and barnacle recruits at the species level from pictures. Field notes listing species present in each plot helped with this part of the analysis.

With this design, an indirect effect of whelks on mussels, for example, is detected as a significant interaction term in an Analysis of Variance which indicates that the effect of whelks on mussels differed depending of the presence of barnacles. This type of analysis does not, however, determine the actual mechanism by which that is occurring (e.g., interaction chain or interaction modification). It does indicate that the effects of whelks on mussels was conditional. For the purposes of this study, I was interested in evaluating how the relative strength of the direct interaction between two species influences the degree to which the total effect is context-dependent.

Because whelk densities were held constant throughout the experiment, the response variables analyzed were the covers of B. glandula and M. trossulus colonizing the plots. Therefore, this design allowed me to detect the direct and indirect effects of whelks on barnacles and mussels, but I could not measure an effect of barnacles or mussels on whelk densities. Any indirect effects of barnacles or mussels mediated through whelks were restricted to changes in whelk behavior rather than population-level responses.

Because barnacle and mussel densities varied naturally throughout the experiment in treatments where they were present, replicates in different, spatially separate blocks were likely to differ from one another due to stochastic variation in recruitment intensity and disturbance. In addition, '+barnacle' and +mussel' treatments varied naturally between experiments due to differences between years in colonization rates and environmental conditions (the second and third years of the experiment were El Niño years) (see Results). Thus, for a given predator density, one would expect the relative strengths of direct and indirect links to vary between blocks and/or between experiments which had different abundances of prey. This aspect of the design allowed me to test the prediction that the total outcome of 'weak' predation is more sensitive than 'strong' predation to natural variation between blocks and/or between years. On the other hand, this variation decreased the power of statistical tests to detect treatment effects.

Data Analysis

A randomized block, two-way factorial, analysis of variance (ANOVA) was used to analyze the combined effects of Nucella and barnacles/mussels on the cover of M. trossulus/B. glandula for each experiment. Separate analyses were conducted for M. trossulus and B. glandula. This procedure is not always desirable since correlations among species might affect the Type I error rate (Tabachnick and Fidell 1989, Scheiner 1993). However, since both mussels and barnacles were simultaneously manipulated factors and response variables, a separate ANOVA for each species allowed me to use only those treatments in which the response variable was not manipulated (i.e. '+mussel' or '+barnacle'). Assumptions of normality and variance heterogeneity were checked by visual inspection of residual plots. In all cases, arcsin-squareroot transformed cover data exhibited more normal distributions and homogeneity of variances than the raw data. To facilitate interpretation of significant non-additivity, the untransformed data are represented in the figures.

To avoid dependence between census dates, I analyzed the mean abundance of species averaged over the first year for each experiment (see Wootton 1994b). This facilitated comparisons between experiments, because the sampling dates were not always synchronous across experiments and because the frequency of sampling was not the same for each experiment. All plots were initially devoid of barnacles and mussels at the start of each experiment in April, and, with the exception of Experiment #1 (where B. glandula settled densely within one month of the starting date), M. trossulus and B. glandula were not appreciably abundant until the late summer/fall of the first year. Thus the time period over which data were pooled began in the first fall (September-November) and ended at the sampling date closest to spring of the following year (late March-June). All the factors (whelks, barnacles, and mussels) were considered fixed because they were chosen to represent discrete values of density (0, low, high) or cover (absent vs. present).

Interactions strengths (IS), total effects (TE), and absolute changes (AC) estimated with equations 1 and 2 were based on mean covers of mussels or barnacles in each treatment because the lack of significant block effects did not justify pairing T and C treatments within each block. To estimate variation in IS and TE, the complete data set was bootstrapped 1000 times and 95% confidence limits from the bootstrap distribution were used to compare treatments (Paine 1992, Dixon 1993).

Results

Comparisons of the roofs and controls generally provided no evidence for significant cage artifacts on the cover of B. glandula or M. trossulus during the first year of succession (the duration of this study). In all but one case (B. glandula in Experiment #3), the mean cover of B. glandula and M. trossulus did not differ between roofs and control plots (randomized block ANOVA for each experiment, p > .10 in all cases). In the third experiment, the cover of B. glandula was significantly lower in the roofs (randomized block ANOVA: F = 120.7, p = .002, df = 1, 3), suggesting that shading by roofs may have attracted more whelks (E. L. Berlow unpublished data).

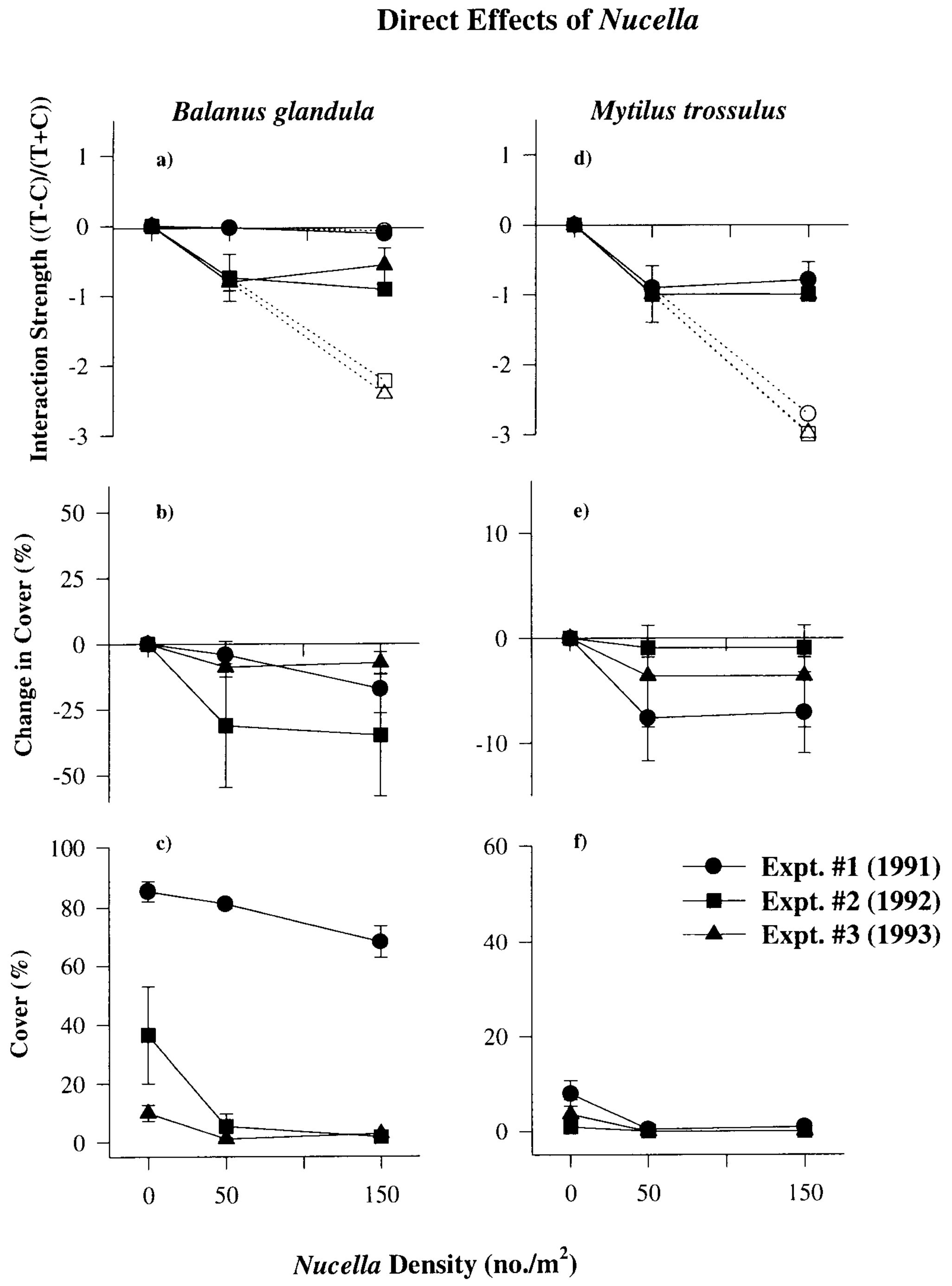
I. Direct effects of Nucella: Effects of whelk density on the strength of predation.

Nucella had significant effects on both M. trossulus and B. glandula in all three experiments (Tables 2a and 3a, respectively). Within each experiment, the strength of predation by Nucella increased monotonically with the density of Nucella manipulated (Fig. 5a and b). In Experiment #1 (circles), B. glandula was abundant and approximately 75% survived even in the high density treatment (Fig. 5e). In this case, the strength of predation increased linearly with an increase in the density of Nucella (Fig. 5a and c: circles). In Experiment #'s 2 (squares) and 3 (triangles), the mean abundance of B. glandula and M. trossulus when alone was less than 40 and 15%, respectively, and the low density Nucella treatments essentially prevented the establishment of either prey species (Fig. 5e and f: squares and triangles). The 'potential' strength of predation at high densities of Nucella, assuming additive effects of increasing Nucella density, are represented by the hollow symbols and dotted lines in Figure 5a and b.

The strength of predation on B. glandula, was relatively weak in the first experiment and strong in the second and third experiments (Fig. 5a). In Experiment #1, Nucella had a significant negative direct effect on B. glandula only in the high density Nucella treatment (Table 3b). Although the absolute magnitude of change in B. glandula cover in Experiment #1 was equal to or greater than the change observed in Experiment #3 (Fig. 5c), B. glandula was more abundant in Experiment #1 (Fig. 5e). Therefore, the

Figure III.5. a-b) The mean strength of the direct effect of Nucella on B. glandula and M. trossulus for each density of Nucella manipulated and for each experiment. 'T' = the mean cover of B. glandula (or M. trossulus) in treatments where Nucella were present. 'C' = the mean cover of B. glandula (or M. trossulus) when Nucella was excluded. Data are from '-mussel' treatments for B. glandula and '-barnacle' treatments for M. trossulus. Thus, they indicate the effect of Nucella on one prey species in the absence of the other prey species. Error bars represent 95% confidence intervals obtained from 1000 bootstrapped samples (see text). The dotted lines and hollow symbols represent the 'potential' strength of predation in high density treatments linearly extrapolated from the per capita interaction strengths in the zero and low density Nucella treatments (see text). c-d) Mean change in cover (T-C) of Balanus glandula and Mytilus trossulus relative to the density of predators (Nucella emarginata) enclosed for each experiment. Error bars represent 95% confidence intervals obtained from 1000 bootstrapped samples (see text). e-f) The absolute cover (raw mean ± SE) of B. glandula and M. trossulus relative to the density of Nucella for each experiment. Data are from '-mussel' treatments for B. glandula and '-barnacle' treatments for M. trossulus.

Figure III.5.


Direct Effects of *Nucella*
Balanus glandula
Mytilus trossulus
Interaction Strength ((T-C)/(T+C))
Change in Cover (%)
Cover (%)
a)
b)
c)
d)
e)
f)
1
0
-1
-2
-3
50
25
0
-25
-50
10
0
-10
100
80
60
40
20
0
60
40
20
0
0
50
150
Expt. #1 (1991)
Expt. #2 (1992)
Expt. #3 (1993)
Nucella Density (no./m²)

proportional change in cover due to predation in Experiment #1 was small (Fig. 5a, solid circles).

The effect of predation on M. trossulus was consistently strong in all three experiments (Fig. 5b). However, the cover of M. trossulus was very low in the absence of Nucella in Experiment #'s 2 and 3 (Fig. 5f, squares and triangles). Thus, while Nucella effectively eliminated M. trossulus in all three experiments (Fig. 5b and f), the absolute change in cover due to predation was only significant in Experiment #1 (Fig. 5d, circles; Table 2b: 'Direct Effects').

Almost no C. dalli colonized any of the cages in Experiment #1, regardless of the presence of whelks or mussels (Fig. 6a). However, in Experiments #2 and 3, Nucella had a significant positive effect on C. dalli, independent of the presence of mussels (Fig. 6b and c, Table 4: NUC effect is significant for Expt. #'s 2 and 3, MUS and NUC*MUS not significant). Since 1) C. dalli cover was greater when predators were present and 2) no C. dalli colonized Experiment #1, when the cover of B. glandula was high in all treatments (Fig. 5e, circles), the effects of Nucella on C. dalli were most likely not direct effects of predation. This supports the idea that the effects of Nucella on B. glandula described above were primarily direct effects of Nucella rather than indirect effects mediated through C. dalli.

II. Direct interactions between B. glandula and M. trossulus.

Unlike the whelks, which were held at a constant density throughout the experiment, the cover of B. glandula and M. trossulus varied naturally in treatments where they were 'present'. Therefore, the mean cover B. glandula and M. trossulus in the absence of predators (cumulative recruitment and mortality due to competition) differed significantly between experiments (Fig. 7a and b, ANOVA: $F = 33.63$, $p < .0001$, df = 2,6; $F = 5.44$, $p = .04$, df = 2,6 for B. glandula and M. trossulus, respectively). The mean

Figure III.6. a-c) The mean cover (± SE) of C. dalli relative to the density of Nucella enclosed for each experiment. Open circles represent treatments where mussels were removed monthly. Codes for legend: 'N' = Nucella, 'M' = Mytilus, 'B.g.' = Balanus glandula, 'C.d.' = Chthamalus dalli.

Figure III.6.

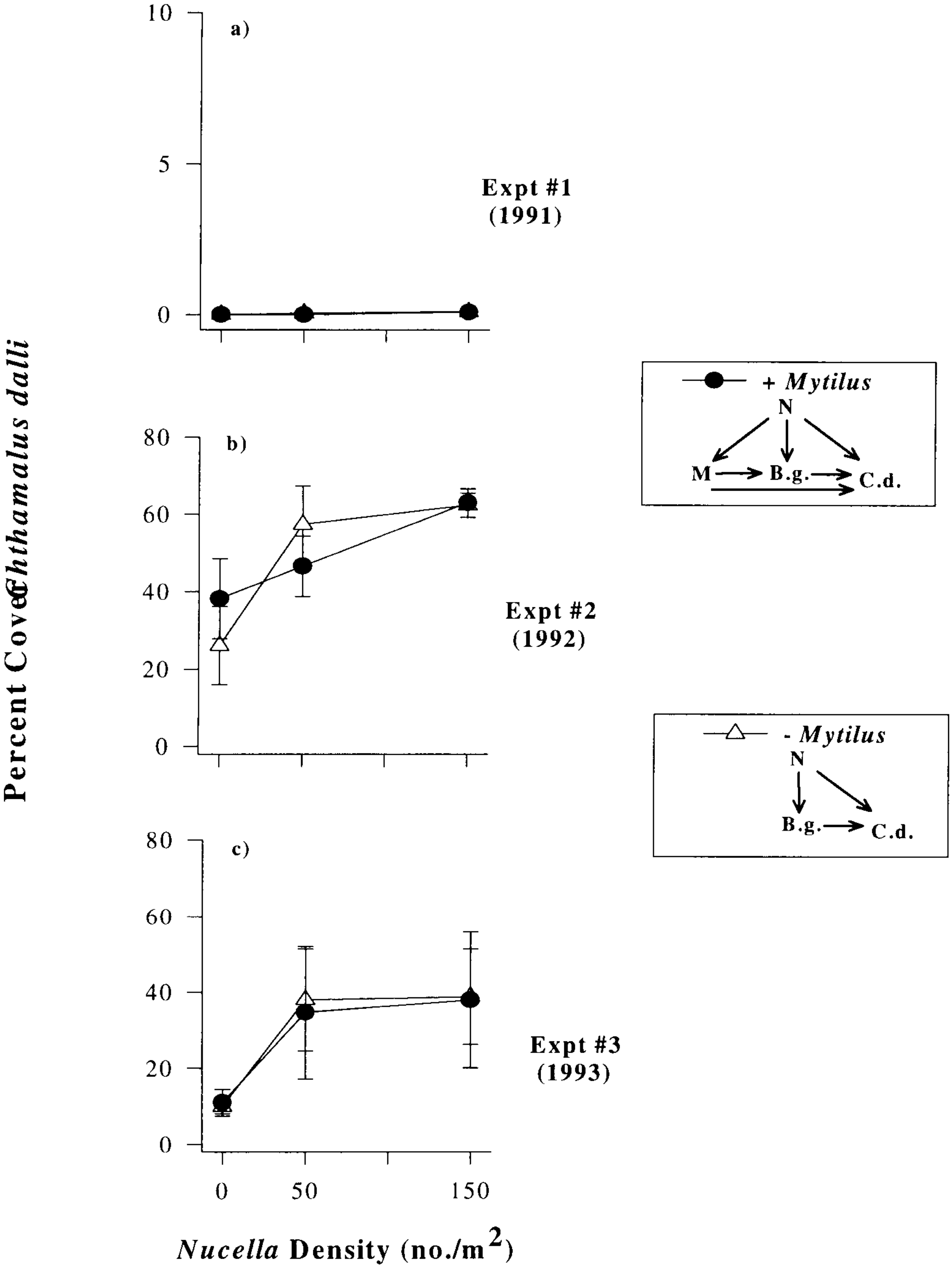
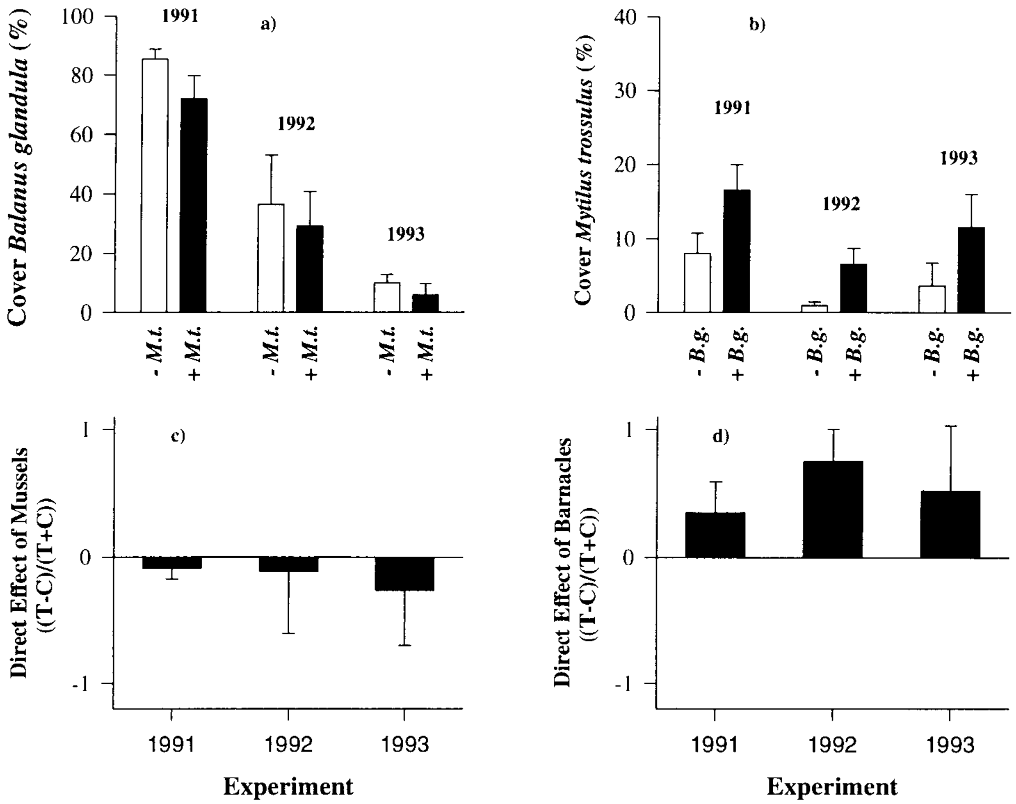

a)
10
5
0
Expt #1
(1991)
b)
80
60
40
20
0
Expt #2
(1992)
c)
80
60
40
20
0
Expt #3
(1993)
0
50
150
Nucella Density (no./m^2)
Percent Cover *Chthamalus dalli*
+ *Mytilus*
N
M
B.g.
C.d.
- *Mytilus*
N
B.g.
C.d.

Figure III.7. a-b) Mean cover of B. glandula and M. trossulus (± SE) in treatments where predators were excluded for each experiment. '-M.t.' and '-B.g.' indicate treatments where mussels or barnacles, respectively, were removed monthly. '+M.t.' and '+B.g.' indicate treatments where both mussels and barnacles were allowed to settled naturally. c-d) Mean strength of the direct effect of M. trossulus on B. glandula (left panel) and B. glandula on M. trossulus (right panel). 'T' = treatments where both species were present. 'C' = either M. trossulus (left panel) or B. glandula (right panel) was removed. Data are from treatments where Nucella were excluded. Error bars are 95% confidence intervals obtained from 1000 bootstrapped samples.



cover of B. glandula decreased in each subsequent experiment (Fig. 7 a). With the exception of Experiment #3, the cover of M. trossulus in the absence of predators was generally lower than the cover of B. glandula (Fig. 7a and b: note differences in y-axis scale).

Despite variation in the abundances of B. glandula and M. trossulus between experiments, the direct interactions between them remained consistent in sign, though variable in magnitude (Fig. 7c and d). B. glandula had a strong, significant positive effect on M. trossulus in all three experiments (Fig. 7d, Table 2b: 'Competition/Facilitation'). The direct effect of M. trossulus on B. glandula, though consistently negative, was comparatively weak and significant only in Experiment #1 (Fig. 7c, Table 3a NUC*MUS significant for Experiment #1, and Table 3b: 'Competition'). Thus, any indirect effect of Nucella on B. glandula which consists of an interaction chain through M. trossulus is likely to have been relatively weak.

III. Indirect effects of Nucella on B. glandula and M. trossulus.

Indirect effects of Nucella on B. glandula or M. trossulus were measured as significant interaction terms in an Analysis of Variance on the arcsin-squareroot transformed cover of each prey species. Thus, they are a measure of the degree to which the effect of Nucella on one prey species varies depending on the presence of the other prey species, assuming that the predator effects and the prey species effects on each other are additive. In Figure 8, the indirect effects are represented by the difference in slopes between the two lines in each panel. In Figure 9, this is represented by the dotted line, or the difference between the total effect and direct effect.

Nucella had significant indirect effects on both M. trossulus and B. glandula only during Experiment #1 (Tables 2a and 3a: NUC*MUS and NUC*BAR significant for Experiment #1; Figs. 8a and b, 9 a and b). In Experiment #1, the presence of mussels

Figure III.8. a-f) Mean cover (± SE) of B. glandula and M. trossulus relative to the density of Nucella enclosed for each experiment. '-M' and '-B' = treatments where mussels or barnacles, respectively, were removed monthly. '+M' and '+B' = treatments where mussels or barnacles were allowed to settle naturally.

Figure III.8.

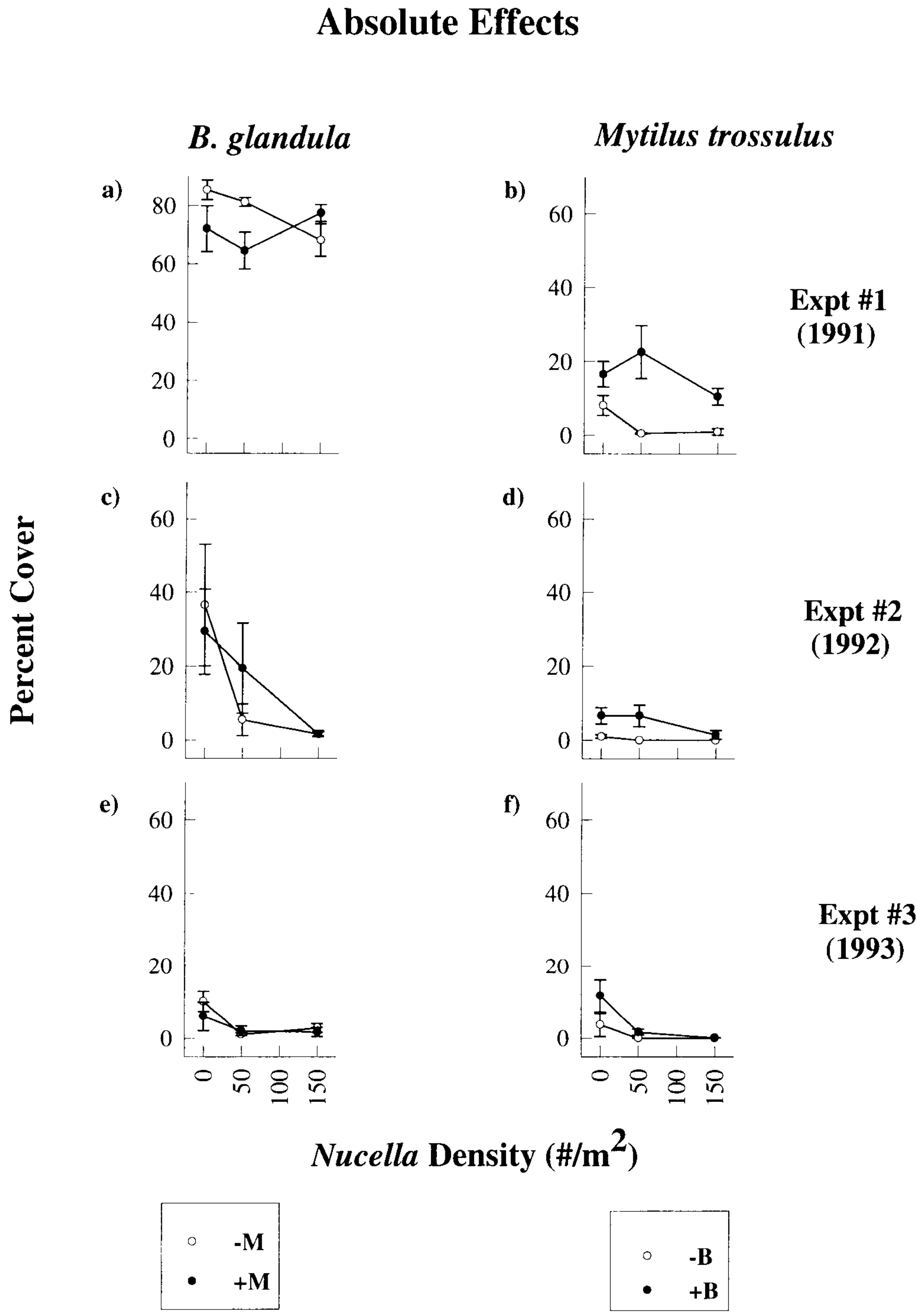
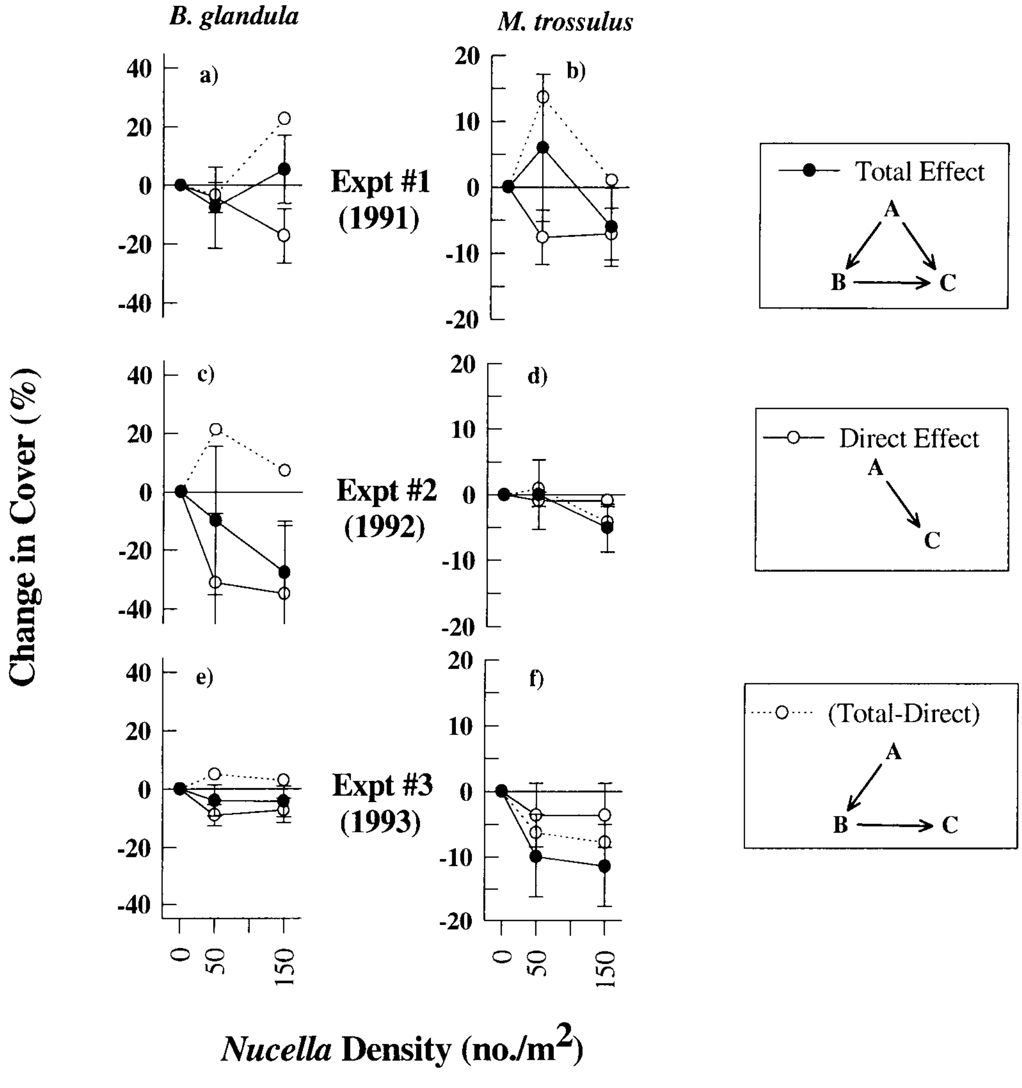

Absolute Effects
B. glandula
Mytilus trossulus
a)
b)
c)
d)
e)
f)
Expt #1 (1991)
Expt #2 (1992)
Expt #3 (1993)
Percent Cover
0
20
40
60
80
0
50
100
150
Nucella Density (#/m2)
○ -M
● +M
○ -B
● +B

Figure III.9. a-f) Mean change in cover (T-C) of B. glandula and M. trossulus for the three densities of Nucella manipulated and each experiment. 'T' = the mean cover of B. glandula (or M. trossulus) in treatments where Nucella were present. 'C' = the mean cover of B. glandula (or M. trossulus) when Nucella was excluded. The solid lines and open circles represent treatments where either mussels or barnacles were removed, respectively. The solid lines and solid circles represent treatments were both B. glandula and M. trossulus were present. The dotted lines represent the difference between the two solid lines, or the degree to which the treatment effects were non-additive. Error bars represent 95% confidence intervals obtained from 1000 bootstrapped samples (see text).

Figure III.9.

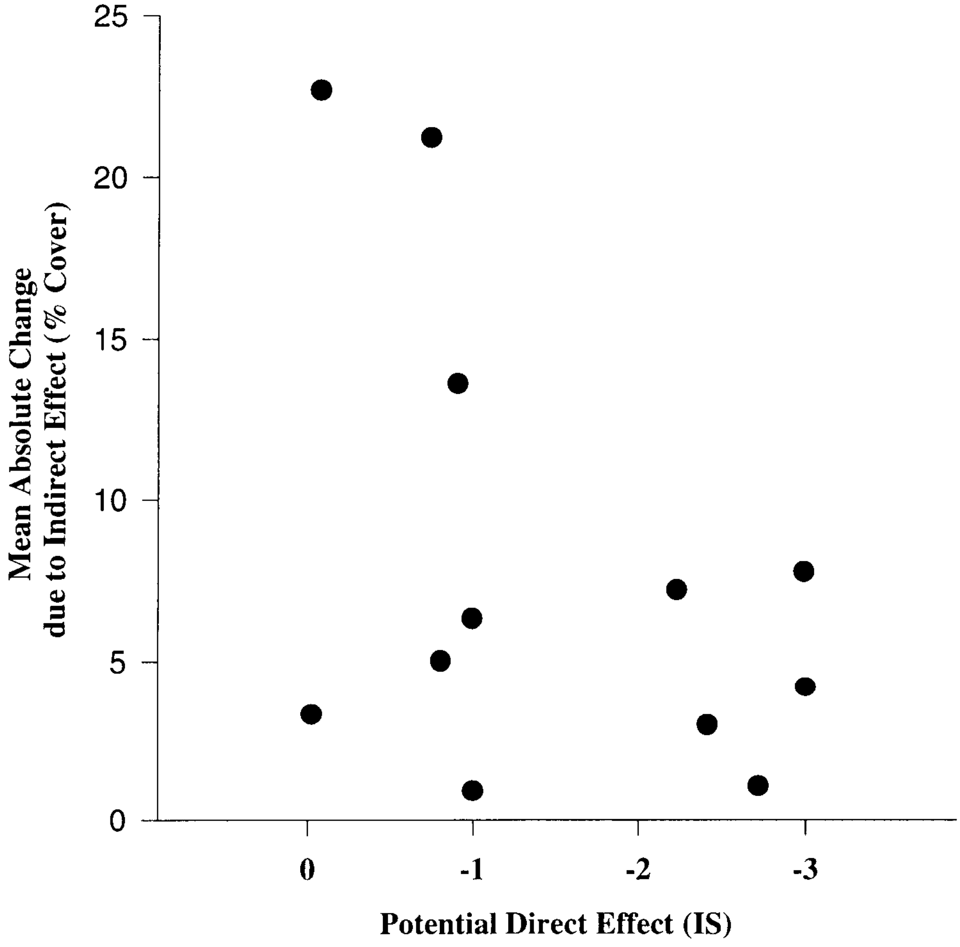

B. glandula
M. trossulus
a)
b)
c)
d)
e)
f)
40
20
0
-20
-40
10
-10
Expt #1
(1991)
Expt #2
(1992)
Expt #3
(1993)
Change in Cover (%)
0
50
150
Nucella Density (no./m2)
Total Effect
Direct Effect
(Total-Direct)
A
B
C

caused a positive indirect effect on B. glandula, but only at high whelk densities (Fig. 9a, dotted line). The positive indirect effect was slightly stronger than the direct negative effect (Fig. 9a). Thus, the total effect of high densities of Nucella on B. glandula was weakly positive, though not significant (Fig. 9a: solid circles; Table 3b: 'Total Effects: 0 vs. High' not significant for Experiment #1). In Experiment #2, there was a non-significant indirect positive effect on B. glandula of the same absolute magnitude as that observed in Experiment #1, but it occurred only in the low density whelk treatment (Fig. 9a and c: dotted line; Table 3a: NUC*MUS not significant for Expt. #2). In this case, the direct negative effect of low densities of whelks in Experiment #2 (Fig. 9c: open circles, solid line) was stronger than the positive indirect effect; thus the total effect on B. glandula remained weakly negative, but not significant (Fig. 9c: solid circles; Table 3b: 'Total Effects: 0 vs. Low' not significant for Experiment #2).

In Experiment #1, the presence of barnacles caused a positive indirect effect on M. trossulus, but only in the low density treatment of whelks (Figs. 8b and 9b: dotted line). In this case, the positive indirect effect was stronger than the direct negative effect of Nucella on M. trossulus (Fig. 9b: open circles). Consequently, M. trossulus was 37% more abundant, on average, in cages with low Nucella densities than in the absence of predators (Fig. 9b: solid circles; though not significant: Table 2b 'Total Effects: 0 vs. Low') despite the fact that the negative direct effect of predation (open circles, solid line) was strong enough to essentially eliminate M. trossulus (Fig. 5b: strength of direct effect for low Nucella densities $\cong -1$). In contrast, during Experiments #2 and 3, the indirect effect of Nucella on M. trossulus was weakly negative, but not significant (Fig. 9d and f: dotted lines; Table 2a: NUC*BAR not significant for Experiment #'s 2 and 3).

Thus, the absolute change due to indirect effects varied considerably in magnitude between experiments and with different densities of Nucella (Fig. 9: dotted lines, Fig. 10). The strongest indirect effects were not associated with the strongest direct effects of whelks. In fact, where the 'potential' strength of predation was strongest (i.e. most

Figure III.10. The mean absolute change in cover of M. trossulus and B. glandula due to the indirect effect of Nucella relative to the 'potential' strength of the direct effect of Nucella (see Fig. 5 caption and text for further explaination of 'potential' srength). The indirect effect was measured as the difference between the effect of Nucella on one prey species (M. trossulus or B. glandula) when the other prey species was absent (i.e. direct effect) and the effect when the other prey species was present (i.e. total effect). See Figure III.9, dotted lines and caption.



negative, Fig. 5a and c), the absolute change in cover attributable to indirect effects was relatively small (Fig. 10). While the indirect effects on B. glandula were generally positive, the indirect effects on M. trossulus varied in sign between experiments (Fig. 9: dotted lines).

IV. Variation in total effects within and/or between experiments

a) Effects of Nucella on M. trossulus .

The direct effects of Nucella on M. trossulus were consistently negative in all three experiments for both densities of Nucella enclosed (Fig. 11b, d, and f: open circles). At high densities of Nucella, when the 'potential' effect of predation was strongest (Fig. 5d: open symbols), the total effect was consistently negative for all three experiments (Fig. 11b, d, and f: solid circles). In contrast, the mean total effect of low densities of Nucella varied from weakly positive to zero to strongly negative (Fig. 11b, d, and f: solid circles). The range of variation between experiments in the total effect 'weak' predation by Nucella was greater than the magnitude of the total effect when predation was potentially three times as strong (Fig. 11b, d, and f: solid circles, and Fig. 12: solid circles). Similarly, when the 'potential' strength of predation on M. trossulus was weaker (closer to zero), the total effect was more likely to vary in sign within a given experiment than when the direct effect of predation was stronger (more negative) (Fig. 12: 95% confidence limits for the solid circles). While this meant that the total effect of 'weak' predation on M. trossulus often did not differ significantly from zero (Figs. 11 b, d, and f, and 12: 95% confidence limits for solid circles), the range of variation within an experiment sometimes equaled or exceeded the mean total effect of 'strong' predation. In Experiment #2, this meant that sometimes low density Nucella reduced the cover of M. trossulus by 50% and sometimes it increased the cover of M. trossulus by almost 100% relative to the controls without Nucella (a 100% increase = IS of +0.33).

Figure III.11. a-f) The mean strength of the direct and total effects of Nucella on B. glandula and M. trossulus for each density of Nucella manipulated and for each experiment. 'T' = the mean cover of B. glandula (or M. trossulus) in treatments where Nucella were present. 'C' = the mean cover of B. glandula (or M. trossulus) when Nucella was excluded. The solid lines and open circles represent treatments where either mussels or barnacles were removed, respectively. The solid lines and solid circles represent treatments were both B. glandula and M. trossulus were present. Error bars represent 95% confidence intervals obtained from 1000 bootstrapped samples (see text).

Figure III.11.

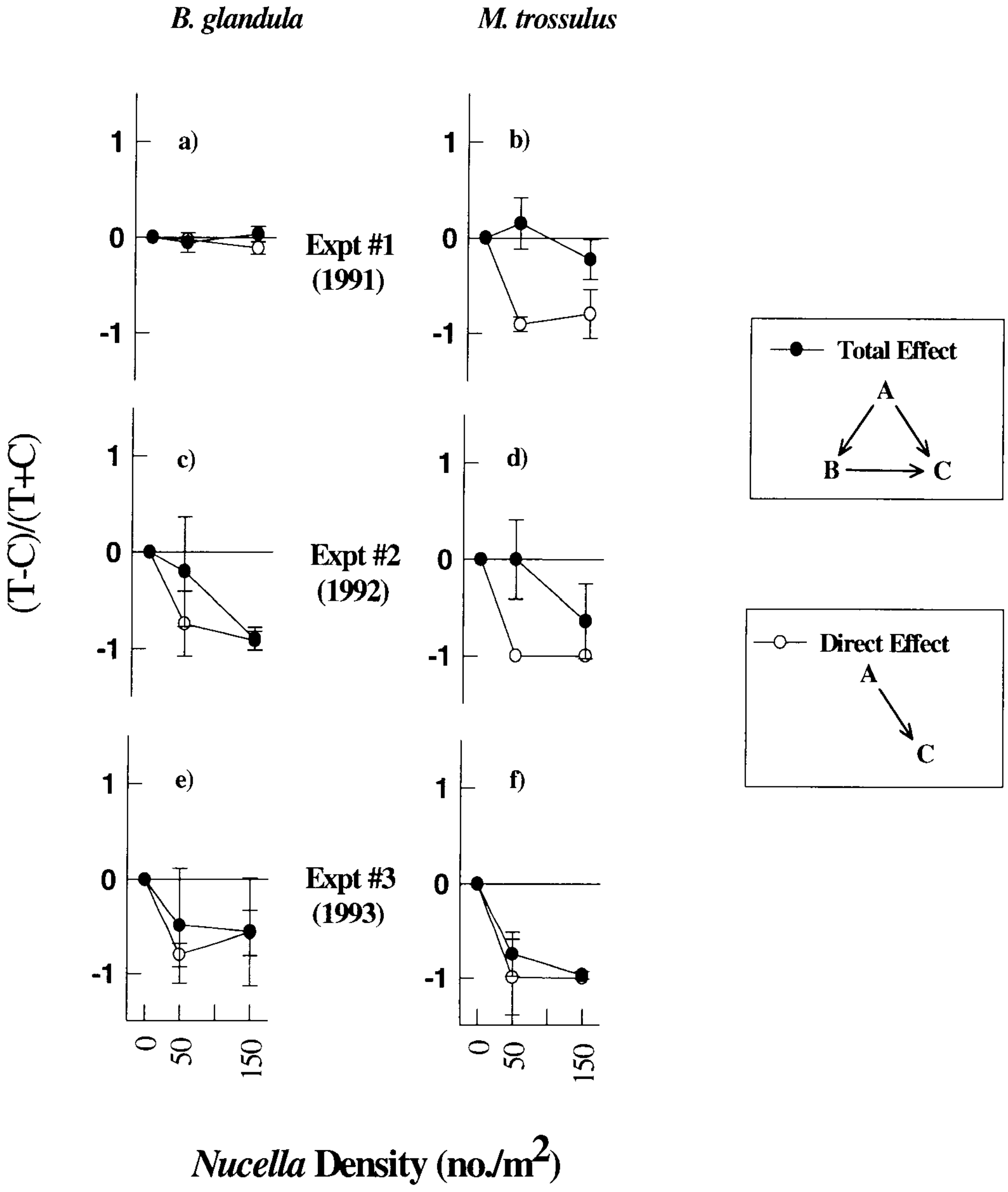
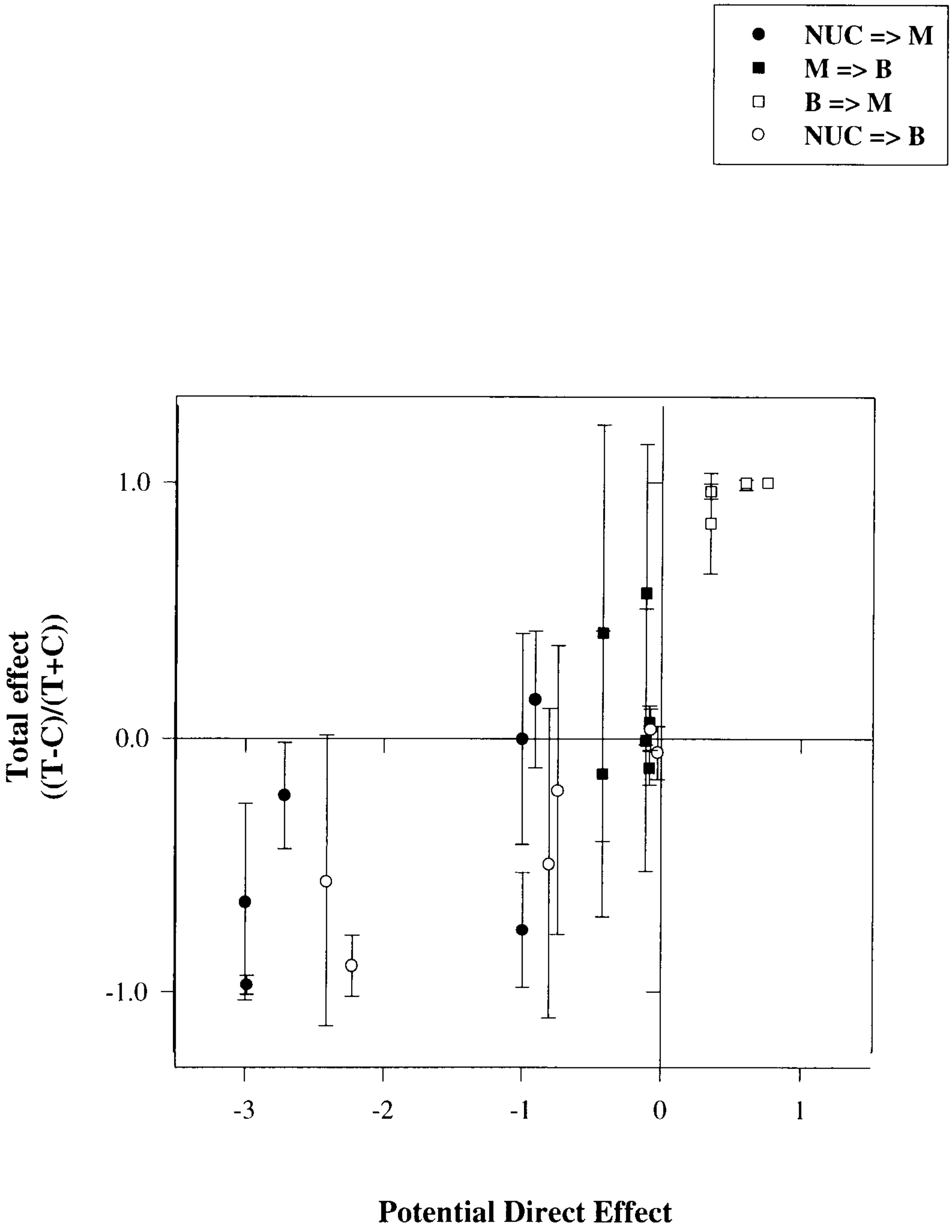


Figure III.12. The mean strength of the total effect ((T-C)/(T+C) see text) relative to the 'potential' strength of the direct effect (see Fig. 5 caption and text). 'NUC→B' and 'NUC→M' are the effects of Nucella on B. glandula and M. trossulus, respectively; 'M→B' and 'B→M' are the effects of M. trossulus on B. glandula and vice versa. Error bars represent 95% confidence intervals obtained from 1000 bootstrapped samples.

Figure III.12.



b) Effects of Nucella on B. glandula.

For a given density of Nucella, the direct effects on B. glandula varied more between experiments than they did for M. trossulus (Fig. 5a and d). In Experiment #1, the direct and total effects of both low and high Nucella densities on B. glandula were relatively weak (Fig. 11a). In this case, the mean total effect varied in sign with the density of Nucella, but the magnitude of variation was small (Fig. 11a: solid circles). In contrast, during Experiments #2 and 3, the direct effects of Nucella on B. glandula were comparatively strong (Figs. 5a: squares and triangles, 11c and e: open circles). While the mean total effect of Nucella was consistently negative in these experiments (Fig. 11c and e: solid circles), the effect of high Nucella densities was evidently less sensitive to the presence/absence of mussels than low Nucella densities (Fig. 11c and e: open circles vs. closed circles). Similarly, in Experiment #'s 2 and 3, the total effect of low Nucella densities on B. glandula was more likely to vary in sign within an experiment than the total effect of high Nucella densities (Fig. 11c and e: 95% confidence limits for solid circles).

The magnitude of the total effect of Nucella was directly related to 'potential' strength of the direct effect (Fig. 12: open circles). When the 'potential' direct effect was weakest (closest to zero), the mean total effect varied in sign, but the effects were so weak that the magnitude of variation was small (Fig. 12: open circles). When the direct effect was potentially strongest (most negative), the total effect was less likely to vary in sign within a given experiment (Fig. 12: 95% confidence intervals for open circles).

c) Interactions between B. glandula and M. trossulus.

Although the direct effect of M. trossulus on B. glandula was consistently negative (Fig. 7c), when Nucella were present, the mean total effect of M. trossulus on B. glandula varied in sign from strongly positive to weakly negative (Fig 12: solid squares). In all cases, the total effect of M. trossulus varied in sign within a given experiment (Fig.

12: 95% confidence limits for solid squares). The range of variation in the total effect of M. trossulus on B. glandula was greater than the magnitude of strongest effect on B. glandula observed (Fig. 12: solid squares).

B. glandula had a comparatively strong direct positive effect on M. trossulus (Fig. 7d). The total effect of B. glandula on M. trossulus was also consistently strong and positive (Fig. 12: open squares). In the absence of barnacles, Nucella essentially eliminated M. trossulus in all three experiments (Fig. 8b, d, and f) that survived in the presence of Nucella were in cages with barnacles

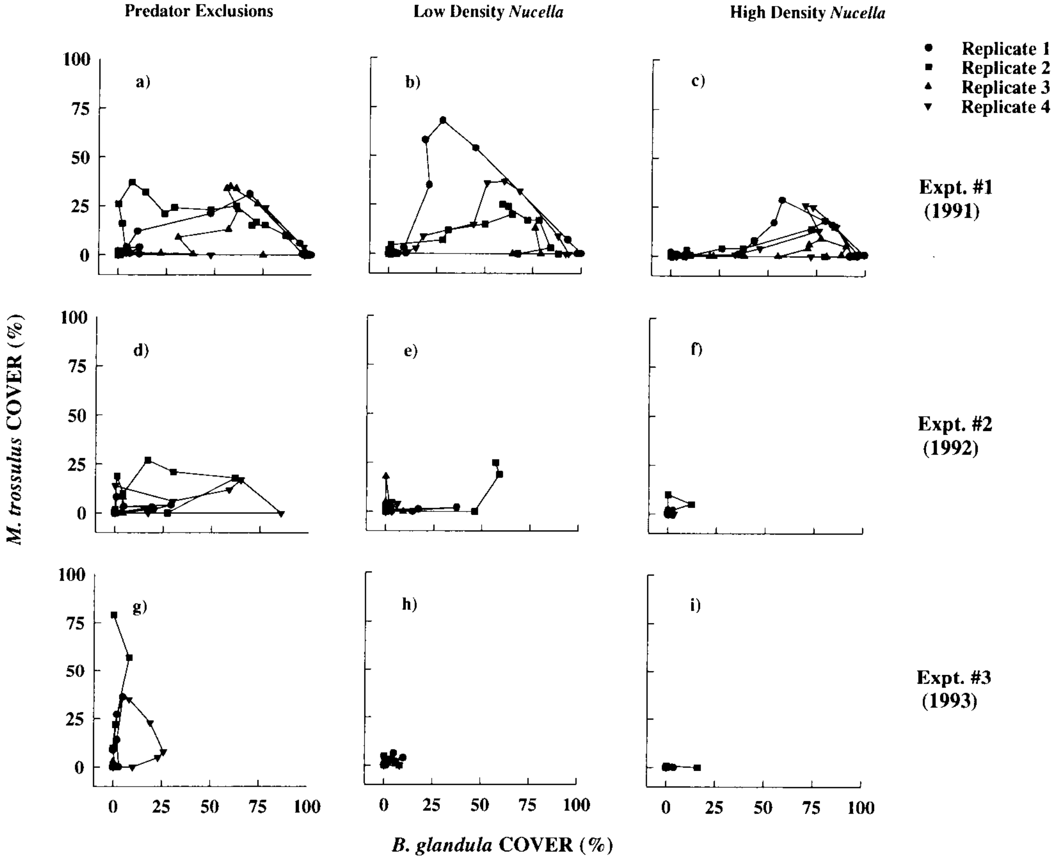
d) Spatial variation between replicates.

While all plots started with zero cover of barnacles and mussels, each replicate was subject to slightly different rates of colonization and environmental conditions. A prediction of the hypothesis proposed above is that the net outcome of 'weak' predation should be more sensitive than 'strong' predation to spatial variation between replicates in the abundance of prey or environmental conditions.

Figure 13 shows the trajectories of individual replicate plots in terms of the abundances of M. trossulus and B. glandula over the time course of each experiment for different predator densities. Only treatments where neither mussels nor barnacles were removed are represented. Thus, the patterns of trajectories indicate spatial variation in the total effect of different whelk densities on the relative cover of M. trossulus and B. glandula. Note that all experiments started at the origin and that Experiments #1, 2, and 3 ran for approximately 3, 2.5, and 1.5 years, respectively.

In Experiment #1, relative to the predator exclusions, the trajectories of the low density predator replicates tended to diverge more in mussel-barnacle space, while the high density predator replicates tracked each other more tightly (Fig. 13a-c). The 'dampening' effect of high density predator treatments was consistent across all three experiments, and it was stronger in Experiments #2 and 3 (Fig. 13 d-f and g-h), when the abundances of M. trossulus and B. glandula in the absence of predators were lower (Fig.

Figure III.13. a-i) The trajectories of individual replicate plots through the time course of each experiment for the different densities of Nucella manipulated. Each point represents the relative cover of M. trossulus and B. glandula for that replicate at that sampling date. Each line represents the trajectory that the plot takes through time in mussel-barnacle space. Only treatments in which both mussel and barnacle recruits were allowed to settle naturally are shown. Note that some treatments eventually lost a replicate due to winter storms. Experiment #1 lasted approximately three years and was the longest running experiment. All plots were initially scraped bare of barnacles and mussels, and, thus, started at the origin.



7a and b). In contrast, the effect of low density predators varied between experiments. While they appeared to magnify initial differences between replicates in Experiment #1(Fig. 13a and b), they had a dampening effect in Experiments #2 and 3 (Fig. 13d-e and g-h), when the direct effects on B. glandula were comparatively stronger (Fig. 5a). In Experiment #2, high density predator treatments had a stronger dampening effect than low density treatments (Fig. 13 d and f vs. d and e), where replicates varied from total elimination of both prey species to approximately 60% B. glandula and 25% M. trossulus.

It is important to note that in the longest running experiment (#1), the cover of B. glandula and M. trossulus declined nearly to zero in all treatments by the third year (Fig. 13). Thus, the effects of Nucella on B. glandula and M. trossulus were transient. The longer term consequences of these transient effects are reported elsewhere (Chapter IV).

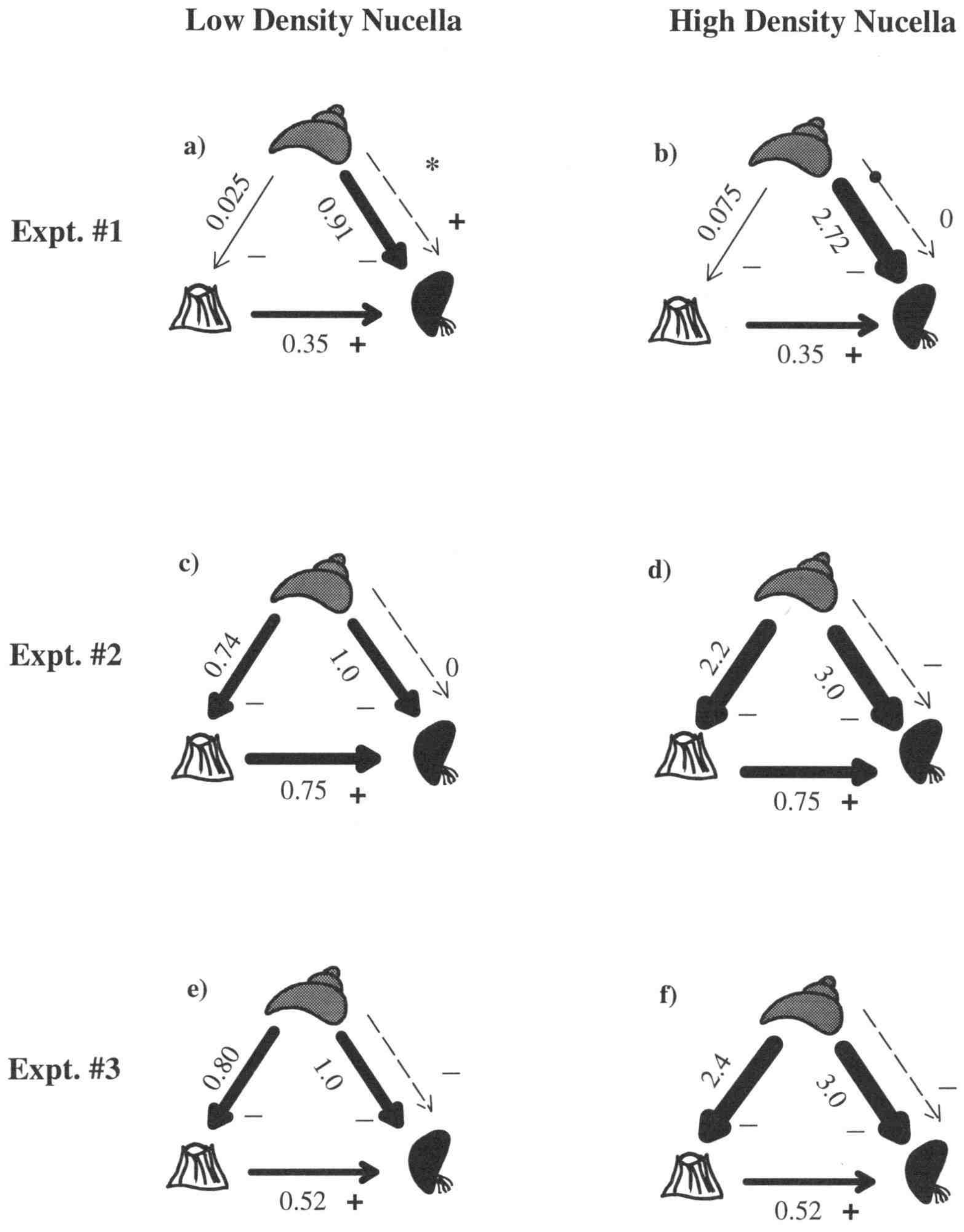
V. Interaction chains or interaction modifications?

This study was not designed to explicitly test for the mechanisms by which a non-additive effect of Nucella was occurring. The results provide information about the pairwise interactions and, thus, possible interaction chains. Interaction modifications can only be inferred when the measured pairwise interactions predict an indirect effect of the wrong sign than was observed (Billick and Case 1994).

Nucella had a significant positive indirect effect on M. trossulus in Experiment #1 (Figs. 9b and 14a, Table 2a: NUC*BAR significant). The interaction chain predicts a negative indirect effect because Nucella had a negative direct effect on B. glandula by eating them (Fig. 9a, solid line/open circles; Table 3a: NUC effect is significant), and B. glandula had a strong positive direct effect on M. trossulus by facilitating recruitment (Fig. 7d, Table 2b). Likely interaction modifications which are consistent with a positive indirect effect include: 1) Nucella eat B. glandula, stabilize the barnacle bed by thinning them, and ,thus, make them less susceptible to dislodgment when M. trossulus settles on

Figure III.14. a-f) Interaction pathways for the effects of Nucella on M. trossulus which illustrates the mean strengths ((T-C)/(C+T); see text) of the direct effects and the observed indirect effect for low and high densities of Nucella for each experiment. When most of the barnacles or mussels were eliminated in the low density Nucella treatment, the magnitude of the direct effect of high density Nucella is the 'potential' strength based on the per capita effects at low density (see text). Solid arrows indicate direct effects, and the thickness of the solid arrow represents the absolute magnitude of the direct effect where: thin line = 0-0.3, intermediate thickness = 0.3-0.6, thick line = 0.6-1, and thickest line > 1(for 'potential' strength). Dotted arrows represent the observed indirect effect (+, 0, -), and a '*' indicates that the Nucella * Barnacle interaction was significant at $p<0.05$ (see Table III.2).

Figure III.14.



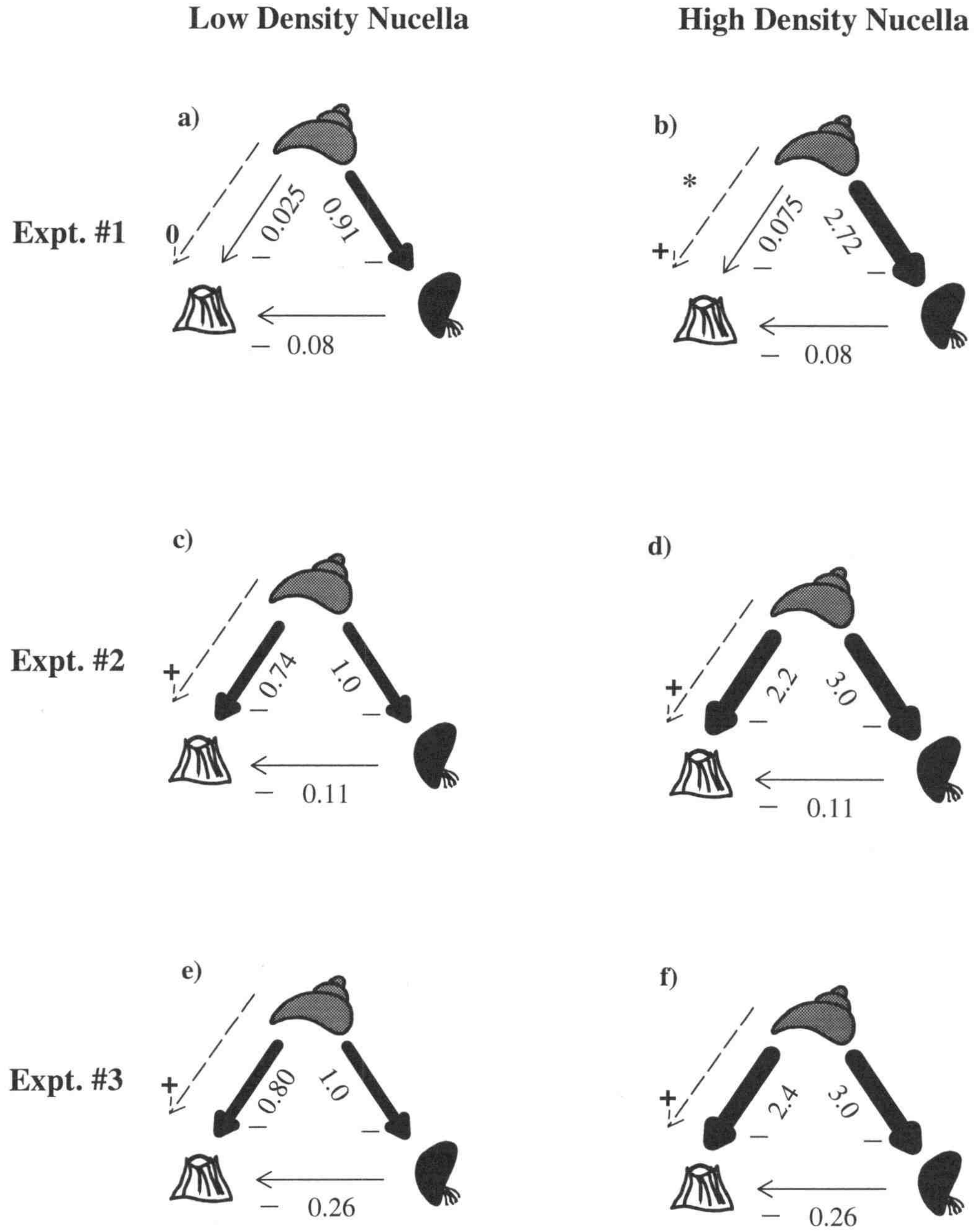
them. 2) Nucella eat fewer M. trossulus when there are also B. glandula present (Murdoch 1969).

Because the interaction chain predicts an indirect effect of the wrong sign, it is likely that an interaction modification consistent with field observations and natural history information was the likely mechanism. However, it would be difficult to distinguish between the two proposed interaction modifications without further experiments. In Experiments #2 and 3, Nucella had a slight negative indirect effect on M. trossulus (Fig. 14 d, e, and f), suggesting that the interaction chain was stronger when the negative direct effect on B. glandula was strong (Figs. 5a: squares and triangles, 14d, e, and f).

Nucella consistently had a positive indirect effect on B. glandula, but it was significant only during Experiment #1 (Figs. 9a and 15b; Table 3a, NUC*MUS significant for Experiment #1). Two likely interaction chains by which this could have occurred include: 1) Nucella had a negative direct effect on M. trossulus by eating them (Figs. 9b and 11b, solid line/open circles; Table 2b: 'Direct Effects'). M. trossulus had a weak negative direct effect on B. glandula by growing over them (Fig. 7c; Table 3b: 'Competition'). 2) Nucella had a negative direct effect on M. trossulus. M. trossulus had a weak, negative direct effect on B. glandula by weakening the bed of barnacles and making them more susceptible to dislodgment by waves (personal observation). One likely interaction modification that could have produced the same result is that the presence of M. trossulus could have modified the foraging behavior of Nucella such that they spend less time feeding on barnacles.

In this case, the interaction modification and interaction chains both predict a positive indirect effect. Furthermore, they could all be operating simultaneously. Teasing them apart would be difficult without further experiments.

Figure III.15. a-f) Interaction pathways for the effects of Nucella on B. glandula (see Fig. 14 caption for further explaination).



Discussion

The results of this study are consistent with the hypothesis that, all else being equal, when the direct effect of one species on another is relatively strong, the total effect (direct + indirect) is less variable or conditional than if the direct effect is weak. When the direct effect of predation by Nucella was potentially strongest, the sign of the total effect was relatively consistent within and between experiments, despite the potential complexity of indirect effects in the web examined, and despite natural variation in the recruitment of prey, disturbance events, and other environmental conditions (Figs. 12 and 13). In contrast, the outcome of 'weak' predation was more spatially and temporally variable in sign, and whether it magnified or dampened natural differences between individual replicates varied between experiments (Figs 12 and 13).

Similarly, when the direct effect of Nucella on a given prey species was relatively strong, its total effect was less sensitive to the presence/absence of the other prey species than when predation was weak (Fig. 10). Consequently, the absolute change in cover attributable to indirect effects was greatest (and most variable) in treatments where the direct effect of predation was relatively weak (Fig. 10).

The 'potential' strength of predation by Nucella on M. trossulus was similar across all three experiments for a given density of Nucella (Figs. 5b and 14). While the direct facilitation of M. trossulus by B. glandula was consistently strong (Figs. 7d and 14), the interaction chain through B. glandula appeared to vary in strength with variation between experiments in the strength of the direct link between Nucella and B. glandula (Figs. 5a and 14) . Thus, variation in the total effect on M. trossulus may have been due to variation between experiments in the sign and magnitude of indirect effects (Fig. 9 b, d, and f: dotted lines). When the 'potential' predation strength was strongest, the total effect appeared less sensitive to variation between experiments in the indirect effects (Fig. 12: solid circles)

In contrast, the 'potential' strength of predation on B. glandula varied between experiments for a given predator density (Figs. 5a and 15). The positive interaction chain through M. trossulus was generally weak, despite a consistently strong direct link between Nucella and M. trossulus (Figs. 5b and 15), because the direct negative effect of M. trossulus on B. glandula was consistently weak (Figs. 7c and 15). Thus, much of the variation in the mean total effect of Nucella on B. glandula appeared to be explained by variation in the potential strength of the direct effect alone (Figs. 12: open circles). Only when predation on B. glandula was very weak (closest to zero) (Experiment #1: Fig. 5a) did the sign of the mean total effect vary with predator density (although the magnitude of the total effect was also very weak) (Figs. 11a: solid circles, and 12: open circles).

Therefore, when the direct effect of Nucella on B. glandula or M. trossulus was potentially strong enough to 'swamp' other indirect effects, the total outcome of predation appeared to be less variable. When the direct effects were weak, the total effect was more likely to vary in sign both within and between experiments. Consequently, in these cases, the mean total effect observed was generally not significantly different from zero (Fig. 12). If the direct effect was weak enough (e.g., the effect of Nucella on B. glandula in Experiment #1), the variation in magnitude of the total effect was small and probably ecologically insignificant (Fig. 12: open circles). However, in many cases, when the direct effect was weak, the range of variation in the total effect (both within and between experiments) exceeded the magnitude of the direct effect at that density and exceeded the magnitude of the strongest total effect observed (Fig. 12). For example, in Experiment #2, the total effect of low density Nucella on M. trossulus ranged from reducing its cover by 50% to increasing it by almost 100% relative to controls without Nucella (Fig. 11d).

Experimental ecologists have historically recognized that an intuitive knowledge of the relative strengths of interaction can greatly simplify their work: Most use a basic knowledge of natural history to select, a priori, the few species that they expect to be important. Some theoretical work has suggested that the effects of ignored species in field experiments are negligible if the ignored species are weakly linked to the focal species (Bender et al. 1984). Many have also argued that conservation efforts could be made more efficient by identifying the species which play disproportionately important roles in structuring a community (Soulé and Simberloff 1986, Terborgh 1986, Cox et al. 1991, Rohlf 1991, Walker 1991, Bond 1993). Recent debate about the ecological importance of diversity hinges on the question of whether or not all species are equally important (Lawton 1992, Lawton and Brown 1993).

In addition to corroborating previous work which has suggested the importance of identifying the subsets of species in a community which are most strongly linked (e.g., Paine 1980, Mills et al. 1993, Menge 1995), the results of this study suggest that it may be equally important to identify the disproportionately weak links (Hall et al. 1990). For example, since the effects of M. trossulus on B. glandula observed here were consistently weak, the variation in the mean total effect of Nucella on B. glandula could largely be explained by variation in the magnitude of the direct effect alone (Fig. 12). Although Nucella had a consistently strong effect on M. trossulus (Fig. 15), the interaction chain (Nucella → M. trossulus → B. glandula) could be ignored without much consequence for predicting the total effect of Nucella on B. glandula.

The results of this study suggest that a knowledge of the relative strengths of interactions in a community may also have important consequences for our ability to ascribe levels of certainty to our predictions about species interactions. When relatively few interactions are disproportionately strong and are all located along one main interaction chain (e.g., keystone effects and trophic cascades), we may be able to safely neglect the details of a large number of possible indirect effects without compromising our predictive capacity. In this case, identifying the species which have the strongest effects and the factors which influence variation in those effects will determine the level of uncertainty about the consequences of a species loss.

In contrast, if the interaction strengths are more uniformly distributed between species, we may be able to say, with confidence, that predictions about the total effect of a species loss (or removal) is so context-dependent that it would require very detailed knowledge about the mechanisms of indirect effects, the individual dynamics of all the species involved, and the spatial and temporal patterns of variability in environmental conditions (e.g., Colwell 1984). Since determining the mechanism causing an indirect effect (i.e. interaction chain vs. higher-order interaction) can be extremely labor intensive and theoretically problematic (Case and Bender 1981, Pomerantz 1981, Wilbur and Fauth 1990, Worthen and Moore 1991, Adler and Morris 1994, Billick and Case 1994, Wootton 1994c), it is important to know when those indirect effects are worth worrying about in the first place.

Is the pattern observed in this study general? Is the total effect of removing a species generally less variable if the direct effect is strong? Preliminary evidence from experiments in the rocky intertidal of the Pacific Northwest are consistent with this trend (Menge et al. 1994, Navarrete 1994). However, a more thorough review of variability in the outcome of weak versus strong interactions is beyond the scope of this paper and is the subject of further investigation (Navarrete et al. unpublished data).

Systems theory suggests that a highly skewed distribution of interaction strengths may be a general characteristic of most adaptable complex systems of interacting parts (Kaufmann 1993). Consistent with this, ecologists have observed that many complex natural food webs are characterized by many species which have weak effects and a small subset which have strong effects (e.g., Paine 1980, 1992, Jordano 1987, Karban 1989, Lawton 1992, Fagan and Hurd 1994, Menge 1995). However, many examples exist of situations in which interaction strengths appear to be more uniformly distributed between species (Sale 1977, Ehrlich and Ehrlich 1981, Underwood et al. 1983, Quammen 1984, Hubbell and Foster 1986, Ehrlich and Wilson 1991, Raffaelli and Hall 1992, Bock et al. 1992, McNaughton 1993, Miller 1994, Robles and Robb 1993, Tanner et al. 1994, Tilman and Downing 1994, see Menge et al. 1994 for examples of 'diffuse' vs. 'keystone' predators). It is notable that, in many of these examples, interaction strengths are uniformly distributed because all species play similarly small roles. It is unclear whether this is generally because the range of variation in effects measured was so large that mean effects were determined to be not significant, or whether the magnitude of the effects were consistently small (Hall et al. 1990).

In addition to variation between systems, the relative strengths of interactions have been shown to vary dramatically over space and time within a particular system. A system which appears to fit a 'keystone' model at one locality may not everywhere (e.g., Paine 1980, Barkai and McQuaid 1988, Dethier and Duggins 1988, Robles and Robb 1993, Menge et al. 1994, Chapter II). Due to this variation both between and within systems in the distribution of interaction strengths, a critical challenge for ecologists is to develop easy, reliable techniques by which we can characterize the relative strengths of interactions in a community at a given site. While the 'ideal' characterization would require prohibitively laborious, pairwise manipulations of all the species, some potentially promising 'quick and dirty' alternatives have been proposed (e.g., Hairston 1988, Paine 1992, Menge et al 1994, Tanner et al., 1994, Wootton 1994a, b, Pfister 1995). More than one technique used simultaneously can provide complementary information, lend robustness to the interpretation of results, and still be more efficient than an exhaustive manipulation of all possible species pairs. Unfortunately, there has historically been little consensus regarding the ecological implications of different definitions of 'interaction strength' used by theorists and empiricists (McArthur 1972, Paine 1980, Yodzis 1981, 1988, Pimm et al. 1991, Lawton 1992, Wootton 1994a, c, Navarrete 1994). In addition, we are currently lacking a general theory which addresses the costs and benefits of different techniques for measuring interaction strengths in the field, the consequences of different methods for interpreting results, and the implications of different measures for integrating experiments with theory (but see Wootton 1994a, c).

With efficient and reliable field estimates of interaction strengths that are meaningful to theoreticians, predictability in ecology may then benefit enormously from methods used by meteorologists to forecast weather patterns. Historically, weather forecasting models have been plagued by higher-order interactions that result in chaotic weather patterns (Lorenz 1968, Tibbia & Anthes 1987). In this case, an important step in assessing the reliability of long-term forcasts is successfully identifying when a given weather pattern is likely to be stable or chaotic (Monastersky 1990). As ecologists are increasingly being called upon to predict the outcomes of perturbations to natural communities, it is essential that we be able to assess the reliability of our predictions (Ludwig et al. 1993). One important step in that direction may involve successfully identifying situations where we can say, with confidence, that the possible outcomes are extremely context-dependent.

Table III.1. Mean (Std. Error) % cover (averaged over *Nucella* levels) of the most abundant additional species present in treatments used to evaluate direct effects of *Nucella* on *B. glandula* and *M. trossulus* for each experiment.

Mussels removed: Direct Effect on *B. glandula*

Experiment	*C. dalli*	*Pollicipes*	*Anthopleura*	*S. cariosus*	Total Algae
1	0.05 (0.02)	0 (0)	0.1 (0.04)	0.01 (0.01)	0.01 (0.01)
2	49 (7)	1 (0.7)	2 (0.5)	0.2 (0.2)	0.1 (0.05)
3	31 (10)	2 (1)	3 (0.9)	0.4 (0.2)	0.3 (0.1)

Barnacles removed: Direct Effect on *M. trossulus*

Experiment	*Pollicipes*	*Anthopleura*	*M. californianus*	Total Algae
1	0 (0)	0.1 (0.1)	0 (0)	0.03 (0.03)
2	0.3 (0.3)	1.1 (0.006)	0 (0)	0 (0)
3	0.06 (0.03)	2 (0.7)	0.03 (0.03)	1 (0.5)

Table III.2a. Effects of *Nucella* (NUC) and barnacles (BAR) on the cover of *Mytilus trossulus* for each experiment. Data in the analyses were arcsin(squareroot)-transformed covers. df: degrees of freedom; MS: type III mean squares; F: standard F-values. Bold face p-values indicate that the factor is significant at α=0.05.

Response variable: arcsin(squareroot)-transformed cover *M. trossulus*.

Source	df	Statistic	Expt. #1 (1991)	Expt. #2 (1992)	Expt. #3 (1993)
BLOCK	3	MS	0.02	0.010	0.02
		F	2.27	1.67	2.53
		p	0.12	0.22	0.10
NUC	2	MS	0.04	0.03	0.10
		F	4.72	5.14	11.42
		p	**0.02**	**0.02**	**0.001**
BAR	1	MS	0.46	0.16	0.07
		F	48.16	28.24	8.21
		p	**0.0001**	**0.0001**	**0.01**
NUC*BAR	2	MS	0.04	0.01	0.014
		F	4.15	2.29	1.60
		p	**0.04**	0.14	0.23
MODEL	8	MS	0.09	0.04	0.04
		F	9.09	6.02	5.23
		p	**0.0002**	**0.001**	**0.003**
ERROR	15		0.010	0.006	0.008
R^2			0.83	0.76	0.74

Table III.2b. F-protected Least Squares Means comparisons for the separate effects of different levels of *Nucella* density (0, LOW, and HIGH) on *M. trossulus* in the presence and absence of barnacles (±B) and for the direct effects of competition/facilitation between mussels and barnacles in the absence of predators. Data in thte analyses were arcsin(squareroot)-transformed covers. Results presented are p-values. Bold face indicates that the comparison is significant at α=0.05.

	Response Variable: *Mytilus trossulus*		
Comparison	Expt. #1 (1991)	Expt. #2 (1992)	Expt. #3 (1993)
DIRECT EFFECTS:			
0 vs. LOW (- B)	**0.007**	0.23	0.08
0 vs. HIGH (- B)	**0.008**	0.23	0.07
LOW vs. HIGH (- B)	0.93	1.0	0.95
TOTAL EFFECTS:			
0 vs. LOW (+ B)	0.36	0.83	**0.005**
0 vs. HIGH (+ B)	0.21	**0.006**	**0.0005**
LOW vs. HIGH (+ B)	**0.04**	**0.009**	0.25
COMPETITION/ FACILITATION:			
- B vs. + B (0 *Nucella*)	**0.05**	**0.004**	**0.01**

Table III.3a. Effects of *Nucella* (NUC) and mussels (MUS) on the cover of *Balanus glandula* for each experiment. Data in the analyses were arcsin(squareroot)-transformed covers. df: degrees of freedom; MS: type III mean squares; F: standard F-values. Bold face p-values indicate that the factor is significant at α=0.05.

Response variable: arcsin(squareroot)-transformed cover *B. glandula.*

Source	df	Statistic	Expt. #1 (1991)	Expt. #2 (1992)	Expt. #3 (1993)
BLOCK	3	MS	0.016	0.22	0.02
		F	1.39	6.55	1.78
		p	0.29	**0.005**	0.19
NUC	2	MS	0.16	0.42	0.06
		F	1.31	12.20	6.36
		p	0.30	**0.0007**	**0.01**
MUS	1	MS	0.04	0.01	0.01
		F	3.33	0.37	1.37
		p	0.09	0.55	0.26
NUC*MUS	2	MS	0.05	0.39	0.006
		F	4.36	1.15	0.61
		p	**0.03**	0.34	0.56
MODEL	8	MS	0.03	0.20	0.02
		F	2.35	5.84	2.58
		p	0.07	**0.002**	**0.05**
ERROR	15		0.12	0.03	0.010
R^2			0.56	0.76	0.58

Table III.3b. F-protected Least Squares Means comparisons for the separate effects of different levels of *Nucella* density (0, LOW, and HIGH) on *B. glandula* in the presence and absence of mussels (±M) and for the effects of competition between mussels and barnacles in the absence of predators. Data in the analyses were arcsin(squareroot)-transformed covers. Results presented are p-values. Bold face indicates that the comparison is significant at $\alpha=0.05$. '---' indicates that the comparison was not made because that factor was not significant in the univariate ANOVA for that year.

	Response Variable: *B. glandula*		
Comparison	Expt. #1 (1991)	Expt. #2 (1992)	Expt. #3 (1993)
DIRECT EFFECTS:			
0 vs. LOW (- M)	0.44	**0.006**	**0.007**
0 vs. HIGH (- M)	**0.02**	**0.002**	**0.05**
LOW vs. HIGH (- M)	0.07	0.66	0.35
TOTAL EFFECTS:			
0 vs. LOW (+ M)	0.27	0.27	0.13
0 vs. HIGH (+ M)	0.49	**0.005**	0.11
LOW vs. HIGH (+ M)	0.08	**0.05**	0.94
COMPETITION			
- M vs. + M (0 *Nucella*)	**0.05**	---	---

Table III.4. Effects of *Nucella* (NUC) and mussels (MUS) on the cover of *Chthamalus dalli* for each experiment. Data in the analyses were arcsin(squareroot)-transformed covers. df: degrees of freedom; MS: type III mean squares; F: standard F-values. Bold face p-values indicate that the factor is significant at α=0.05.

Response variable: arcsin(squareroot)-transformed cover *B. glandula*.

Source	df	Statistic	Expt. #1 (1991)	Expt. #2 (1992)	Expt. #3 (1993)
BLOCK	3	MS	0.0003	0.11	0.02
		F	0.81	7.68	1.78
		p	0.50	**0.002**	0.19
NUC	2	MS	0.007	0.22	0.06
		F	0.22	15.83	6.36
		p	0.15	**0.0002**	**0.01**
MUS	1	MS	0.0002	0.001	0.01
		F	0.68	0.05	1.37
		p	0.42	0.83	0.26
NUC*MUS	2	MS	0.0001	0.03	0.006
		F	0.17	2.26	0.61
		p	0.84	0.14	0.56
MODEL	8	MS	0.0003	0.10	0.02
		F	0.98	7.41	2.58
		p	0.49	**0.0005**	**0.05**
ERROR	15		0.0003	0.01	0.01
R^2			0.34	0.80	0.58

CHAPTER IV

FROM CANALIZATION TO CONTINGENCY: HISTORY LESSONS IN A SUCCESSIONAL ROCKY INTERTIDAL COMMUNITY

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Abstract

Many landscapes are characterized by a mosaic of patches, in various stages of succession. Changes in community structure during ecological succession can be both tremendously variable, or contingent, and compellingly regular, or canalized. A critical challenge for the successful development of predictive models and natural resource management strategies is to determine not _if_ succession can be complex and contingent, but _when_. When can we safely ignore a large number of potentially complex, historical and site-specific details without compromising our predictive capacity?

Historic effects during succession can influence the degree to which successional paths dampen, track, or magnify stochastic variation during the course of succession. I investigated the patterns and importance of historic effects in a successional marine rocky intertidal community on the central coast of Oregon, USA. Patches in the mid-intertidal mussel bed (_M. californianus_) were manually cleared in a way that mimicked natural disturbance. In four separate blocks (large patches ~6m^2), three sets of plots were initiated with their starting dates staggered by one year. Within each set of plots, I manipulated the presence/absence of two groups of early successional sessile species under each of three predator densities. This design allowed me to address the following general questions: 1) What are the separate and interactive effects of successional age, yearly variation, and initial conditions on the temporal changes observed after

disturbance? 2) When do interactions between early species dampen or magnify natural variation between years or starting dates?

Succession in mid-intertidal patches in the mussel bed displayed complex patterns of historic effects which varied between species and between different stages of succession. Despite its potential complexity, this system exhibited some consistent and repeatable patterns of succession. Some important canalizing, or 'noise-dampening' forces in this system included: 1) physiological and life-history constraints, 2) strong, consistent interactions between species, and 3) compensatory ('buffering') responses of functionally similar species. The results of this study also suggest that weak links between species are important to identify because: 1) their effects may be more contingent than strong links, and, thus, more likely to amplify stochastic variation during succession, and 2) they may be so weak that they allow us to safely ignore the details of many potentially variable or conditional effects without compromising our predictive capacity.

Introduction

Ecological succession consists of the sequence of change in community structure that occurs after a site has been disturbed (Connell and Slatyer 1977, Pickett et al. 1987, Farrell 1991, McCook 1994). Because succession is inherently a historical process, studies of succession have long been interested in the importance of past events in shaping current variation in community structure and organization (Clements 1916, 1928, Gleason 1926, Egler 1952, reviewed in MacMahon 1980). Historic effects which influence variation in successional patterns can include both physical events in history (e.g., disturbance events, environmental conditions, recruitment/dispersal events, etc.) and/or biological interactions which are not currently measurable, but which have lasting effects (e.g., facilitation/inhibition by early species, consumption of early species, competition between early species, etc.) (e.g., Connell 1980, Lubchenco 1982, 1983, Sousa 1984b, Farrell 1991, McCune and Allen 1985, Franklin 1989, Hixon and Brostoff 1995). In addition, the outcome of biological interactions at a given point in time can vary dramatically with the spatial, temporal, and/or historical context in which they occur (e.g., Dayton 1971, Menge 1976, Fairweather et al. 1984, Thompson 1988, Cushman & Whitham 1989, Drake 1990, Cushman 1991, Carpenter and Kitchell 1993, Wedin and Tilman 1993, Menge et al. 1994, Chapters II and III).

Thus, whether or not a community has a singular, stable endpoint, the patterns and processes by which communities change during succession can be tremendously variable, complex, and context-dependent (Connell and Slatyer 1977, Cattelino et al. 1979, Paine and Levin 1981, Turner 1983a b, reviewed in Sousa 1984b, Connell et al. 1987, Pickett et al. 1987, McCook 1994). On the other hand, many empirical ecologists have also documented or inferred remarkably regular and repeatable patterns of change through time (e.g., Clements 1928, Odum 1969, Paine and Levin 1981, Paine 1984, Farrell 1989, 1991, McCook 1994). A critical challenge for the successful application of basic ecological theory is to determine not <u>if</u> succession can be variable and contingent, but <u>when</u> (Walker and Chapin 1987). When can potentially complex, historical and site-specific details be ignored without compromising predictive capacity?

Understanding the way in which successional paths depend on historic events has important consequences for the types and amount of information necessary to develop predictive models and natural resource management strategies (Colwell 1974, Drake 1990, 1991, Franklin 1989, Pickett 1989, Facelli and Pickett 1990). For example, historical factors can canalize successional paths into consistent repeatable patterns, or they can complicate predictability by making successional pathways highly contingent. Below I outline three patterns of historic effects and their consequences to represent a continuum in the degree to which successional changes dampen, track, or magnify stochastic variation during the course of succession.

1) 'Canalized Succession': If early species have strong and consistent effects on later species, the community may follow deterministic, repeatable patterns of change over time (e.g., Clements 1928, Egler 1952: 'Relay Floristics', Odum 1969, Connell and Slatyer 1977: 'Facilitation' and 'Inhibition' models; Lubchenco 1983, Farrell 1991). In this case, consistent historic effects 'canalize' successional changes. Much of the current variation in community structure can be explained by the length of time since the last disturbance and models that incorporate specific mechanisms underlying strong direct and indirect interactions between species. (Botkin et al. 1972, Huston and Smith 1987, Noble and Slatyer 1980, Tilman 1990, McCook 1994).

2) 'Stochastic Succession': If random events in override the effects of deterministic species interactions, variation in successional pathways may be driven 'externally' by stochastic variation in environmental conditions, recruitment, propagule availability, disturbance, etc. (e.g., Gleason 1926, Egler 1952: 'Initial Floristic Composition', Connell and Slatyer 1977: 'Tolerance' model, Sousa 1984a, b, Gaines and Roughgarden 1985, Chesson and Case 1986, Hubbell and Foster 1986). Current variation in community structure may be better explained by a combination of current and historic site characteristics (e.g., initial conditions) and probablistic or Markovian models of succession than by a detailed knowledge of species interactions (Horn 1975, Usher 1979, Greene and Schoener 1982).

3) 'Contingent Succession': If the sign and magnitude of species interactions depend strongly on the context in which they occur, the interaction between stochastic and deterministic processes may result in highly contingent, rarely repeatable patterns of succession (e.g., Cattelino et al. 1979: 'Multiple Pathways', Drake 1990, 1991: 'Assembly Rules', Sutherland 1974: 'Alternative Stable States', Paine 1977: 'Priority Effects', Franklin 1989: 'Biological Legacies', Wilson and Agnew 1992: 'Positive-Feedback Switches'). Current variation in community structure can only be explained by a detailed knowledge of species interactions and the way they vary with the timing, sequence, and

intensity of stochastic events. In the most extreme case of context-dependency, the outcomes of species interactions may depend so critically on initial conditions that they exhibit chaotic dynamics by magnifying small stochastic variation in environmental conditions, recruitment events, disturbances, etc. (Drake 1990, 1991, Wilson 1992, Ellner and Turchin 1995).

Many studies of successional processes involve either the reconstruction of historical species abundances at a site or the use of spatial chronosequences (Pickett 1989, McCook 1994). The latter attempts to substitute space for time by interpreting sites of different ages as different points in time for a single site. Neither of these allows for a rigorous evaluation of the causal processes regulating succession, and chronosequences necessarily confound the effects of site age with historic or stochastic differences between sites (Pickett 1989). At the other extreme, controlled 'microcosm' experiments have been instrumental in rigorously documenting the potential importance of historic effects (e.g., Wilbur and Alford 1985, Robinson and Edgemon1988, Drake 1991). While these experiments are ideal for teasing apart potential causal mechanisms of succession, they are less suited to explaining naturally observed patterns of succession (i.e. 'potential' is the operational word) (e.g Walker and Chapin 1986, Grover and Lawton 1994).

Field experiments have proven to be one of the most powerful tools to elucidate the causal mechanisms of succession (Connell and Slatyer 1977, Paine 1977, Lubchenco and Menge 1978, Hils and Vankat 1982, Lubchenco 1983, Sousa 1984a, Connell et al. 1987, Farrell 1991, Lubchenco and Real 1991, McCook1994, Hixon and Brostoff 1995). Unfortunately, field experiments are often necessarily limited in their spatial and temporal scale, thus our ability to generalize from individual experiments is severely limited (Bender et al. 1984, Diamond 1986, Underwood and Petraitis 1993). However, by replicating experiments over space and time, the site-specific nature of field experiments can be a powerful tool for characterizing contingencies and patterns of variation in successional processes (Dayton 1971, Menge 1991, Menge et al. 1994, Chapter III).

I used this 'comparative experimental' approach (sensu Menge 1991) to explore the patterns and importance of historical effects in a successional marine rocky intertidal community. In experimentally cleared plots, I manipulated the presence/absence of two groups of early successional species under each of three predator densities. The experiment was replicated in four large patches (blocks), and within each large patch, three identical experiments with starting dates staggered by one year, ran concurrently. This design allowed me to explore the following questions:

1) Are differences between plots in a given year attributable to successional age, independent of the starting date? (i.e. Is succession 'canalized'?)

2) Are differences over time driven by yearly (stochastic) variation independent of successional age? (i.e. Is succession 'stochastic'?)

3) Do different starting dates lead to fundamentally different patterns of change over time? (i.e. Is succession 'contingent' on the starting date?)

4) Do interactions between early species magnify or dampen natural variation between years or starting dates?

Distinguishing Historic Effects

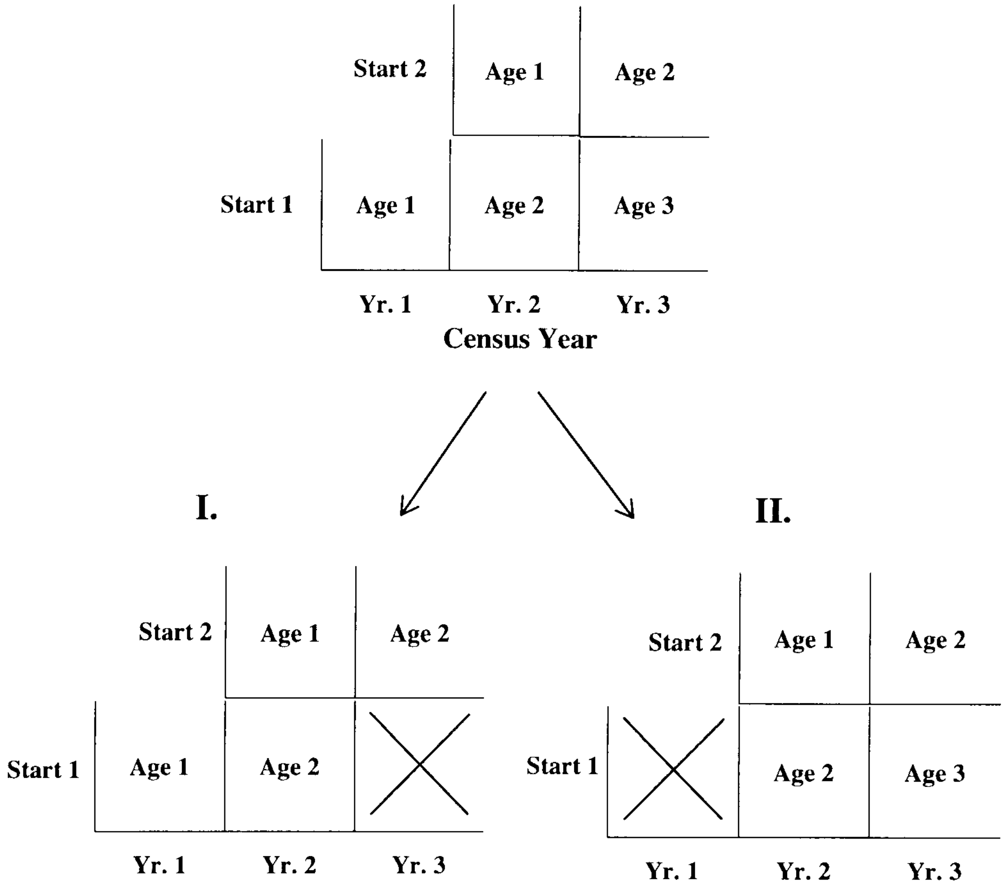
One primary objective of this study was to tease apart the separate and interactive effects 'successional age', 'starting date', and 'census year' (Fig. 1):

1) 'Successional age' (or 'Age') refers to the time elapsed since a plot was cleared, or 'initiated'.

2) 'Starting date' (or 'Start') refers to the actual year that a plot was cleared. In this study, there were three starting dates (see Methods). Hereafter, I use 'Experiment' to refer to a set of plots initiated at a given starting date. Thus, this study consisted of three replicate 'experiments' with different starting dates ('Experiment #'s 1, 2, and 3'). In actuality, the study was designed as one large experiment, with starting date as one of the factors with three levels. I also use 'initial conditions' to refer to conditions at a given

Figure IV.1. Experimental design for quantifying the separate and interactive effects of successional age ('AGE'), experimental starting date ('START'), and census year ('YEAR'). Because the full design was inherently not orthogonal, two separate factorial analyses of variance (ANOVA's I and II) were used to measure AGE*START and YEAR*START interactions. Information provided by both analyses can be combined to resolve some of these confounding factors present in each individual analysis. See text for details.

Figure IV.1.



I. ANOVA	II. ANOVA
Source of Variation	Source of Variation
AGE	YEAR
START	START
AGE * START	YEAR * START

starting date. Because all the plots were cleared in the same fashion and at the same time of year, differences between starting dates were assumed to be due to stochastic variation between years in recruitment, environmental conditions.

3) 'Census year' (or 'Year') refers to the actual date that a plot was observed. Thus, in the first year of succession, 'Year' is synonymous with 'Starting Date'. If two plots with different starting dates tracked each other from year to year, this was interpreted as an effect of yearly variation, independent of starting date.

The design of this study is inherently complicated by the fact that it is impossible to have different starting dates at the same time (Fig. 1). Thus one cannot design a completely orthogonal experiment to measure how the effect of successional age varies with starting date independent of stochastic variation between census years, or how the variation between census year varies with starting date independent of successional age. If two experiments are initiated one year apart, one can compare the first two years of each to explore the interaction between age and starting date; however, the effects of starting date per se are confounded with the effect of census year (Fig. 1: ANOVA I). For example, if the patterns of change with age differ between experiments (AGE*START), it could be because different initial conditions result in different successional trajectories, or because both experiments are similarly 'tracking' the same stochastic variation between years. Similarly, one can measure the interaction between starting date and census year by comparing census years two and three for both experiments (Fig. 1: ANOVA II). However, in this case, the effect of starting date is confounded with successional age. For example, if differences between census years varies between experiments (YEAR*START), it could be because different starting dates lead to different successional paths, or because both experiments are following the same, repeatable successional path which is staggered by one year.

Information provided by both analyses can be combined to resolve some of these confounding factors. For example, in figure 1, if the 'AGE*START' is significant in

ANOVA I and only the main effect of 'YEAR' is significant in ANOVA II, it is likely that both experiments are similarly 'tracking' the same stochastic variation between census years, regardless of successional age (i.e. 'Stochastic Succession'). If the 'YEAR*START' interaction is significant in ANOVA II and only the main effect of 'AGE' is significant in ANOVA I, it is likely that both experiments are following the same repeatable path of succession, regardless of starting date (i.e. 'Canalized Succession'). If both the 'AGE*START' and 'YEAR*START' interactions are significant, this suggests that experiments initiated in different years responded differently to the same stochastic variation between census years, resulting in different patterns of change with age (i.e. 'Contingent Succession').

Figure 2 provides a heuristic framework for interpreting the results of the experiment, by illustrating all possible combinations of temporal changes in a given trait (e.g., species abundance, diversity, ecosystem property, etc.) for the two starting dates ('experiments') in figure 1, assuming that in a given year that trait can be categorized as either 'high' ('^') or 'low' ('-'), and assuming that all '^' (and all '-') are of equal magnitude. For a given pair of temporal trends, the factors which would be significant in ANOVA's I and II (Fig. 1) are listed. In each case, the combined information provided by the two analyses is used to infer whether the successional paths were canalized ('Ca'), stochastic ('St'), or contingent ('Co'). In some cases, more information is required to distinguish between alternative patterns (either a longer time series, more starting dates, or information about specific causal mechanisms), and in other cases, more than one pattern could be occurring simultaneously (e.g., relatively canalized timing of colonization with some stochastic variation in the peak abundance).

The System

This study was conducted in the rocky intertidal zone at Fogarty Creek Point (44°51'N, 124°03'W), about 2 Km north of Boiler Bay State Park, in the central

Figure IV.2. A heuristic framework for interpreting the combined results of ANOVA's I and II in Figure IV.1. All possible combinations of temporal changes in a given trait (e.g., species abundance, diversity, ecosystem property, etc.) for the two starting dates ('Expt 1' and 'Expt 2') in Figure IV.1 are presented, assuming that in a given year that trait can be categorized as either 'high' ('^') or 'low' ('-') for each year of the experiment. The upper left corner illustrates the pair of trends over time, aligned the same as in Figure IV.1. For each pair, the factors that would be significant in ANOVA's I and II ('I' and 'II') of Figure IV.1 are listed. 'A' = AGE (successional age), 'S' = START (starting date), 'Y' = YEAR (census year), ns = no significant effects. In each case the combined results are interpreted with regard to whether they indicate that succession was 'canalized' ('Ca'), 'stochastic' ('St'), or 'contingent' ('Co'). Question marks indicate where there is not enough information to distinguish the patterns. See text for details.

Figure IV.2.

Expt #2

Expt #1	- -	- ^	^ -	^ ^
- - -	- - - - - **?** I: ns II: ns	- ^ - - - **Co** I: A, S, A*S II: Y, S, Y*S	^ - - - - **Co** I: A, S, A*S II: Y, S, Y*S	^^ - - - **Co/St?** I: S II: S
- - ^	- - - - ^ **Ca (?)** I: ns II: Y, S, Y*S	-^ - -^ **St (+Ca?)** I: A, S, A*S II: Y	^ - - - ^ **Co** I: A, S, A*S II: Y*S	^^ - -^ **Co** I: S II: Y, S, Y*S
- ^ -	- - -^ - **Co** I: A, S, A*S II: Y, S, Y*S	-^ -^- **Ca (+Co?)** I: A II: Y*S	^ - -^ - **St** I: A*S II: Y	^^ -^ - **Co** I: A, S, A*S II: Y, S, Y*S
- ^ ^	- - -^^ **Co** I: A, S, A*S II: S	-^ -^^ **Ca** I: A II: Y, S, Y*S	^ - -^^ **Co** I: A*S II: Y, S, Y*S	^^ -^^ **St** I: A, S, A*S II: ns
^ - -	- - ^ - - **St (+Ca?)** I: A, S, A*S II: ns	-^ ^ - - **Co** I: A*S II: Y, S, Y*S	^- ^ - - **Ca** I: A II: Y, S, Y*S	^^ ^ - - **Co** I: A, S, A*S II: S
^ - ^	- - ^ -^ **Co** I: A, S, A*S II: Y, S, Y*S	-^ ^ -^ **St** I: A*S II: Y	^ - ^ -^ **Ca (+Co?)** I: A II: Y*S	^^ ^ -^ **Co** I: A, S, A*S II: Y, S, Y*S
^ ^ -	- - ^^ - **Co** I: S II: Y, S, Y*S	-^ ^^- **Co** I: A, S, A*S II: Y*S	^ - ^^ - **St (+Ca?)** I: A, S, A*S II: Y	^^ ^^- **Ca /Co?** I: ns II: Y, S, Y*S
^ ^ ^	- - ^^^ **Co/St?** I: S II: S	-^ ^^^ **Co** I: A, S, A*S II: Y, S, Y*S	^- ^^^ **Co** I: A, S, A*S II: Y, S, Y*S	^^ ^^^ **?** I: ns II: ns

coast of Oregon, USA. The zonation of intertidal organisms at this site is similar to that described for Boiler Bay by Menge et al. (1994). A more detailed description of the Fogarty Creek site is provided by Farrell (1991), Navarrete (1994), Blanchette (1994), and Berlow (Chapter III). Characteristics relevant to the current study are described below.

Much of what we know about the details of succession in mid-intertidal mussel beds in the Pacific Northwest comes from the work of Paine and colleagues in Washington state (e.g., Levin and Paine 1974, Paine and Levin 1981, Paine 1984, Suchanek 1985, Wootton 1993b, 1994b). On wave-exposed shores of Washington, the mussel Mytilus californianus is the dominant competitor for primary space and has the potential to form extensive monocultures in the mid-intertidal zone in the absence of disturbance (Paine 1974, Paine and Levin 1981). The cycle of disturbance, succession, and re-establishment of M. californianus typically takes ~7 years for patches greater than 3 m^2 (Paine and Levin 1981). In the interim, the substrate is colonized by a suite of competitively subordinate sessile invertebrates and algae (Paine and Levin 1981, Wooton 1993, described below).

In this system, the endpoint of succession appears highly deterministic and repeatable, and some general trends in species replacement have been described (see Paine and Levin 1981, Paine 1984, Wootton 1993b). In addition, succession tends to proceed from small bodied to large bodies species (Wootton 1993b), and exhibits and early peak in diversity followed by a decline in species number (Paine and Levin 1981). Details of the early and mid-successional dynamics were complex and variable. The initial patterns of patch occupancy depended on patch size and the season of patch creation (Paine and Levin 1981. However, species composition was a poor predictor of patch age (Paine and Levin 1981).

Experiments for the present study were carried out in a mid-intertidal zone consisting of a smooth, basaltic, gently sloping, moderately wave-exposed bench. This area was characterized by an extensive bed of large California mussels, M. californianus. As in Washington (Paine and Levin 1981), patches of bare rock of varying sizes are continually created by waves dislodging the mussels (E.L. Berlow personal observation) or by a combination of freezing events and wave stress (D. Brosnan personal communication). Patches are eventually re-occupied by M. californianus.

Observations in Oregon suggest succession proceeds in a similar pattern to that in Washington. At Fogarty Creek, after an initial pulse of ephemeral diatoms and 'foliose algae' (sensu Steneck and Dethier 1995; e.g., Porphyra spp., Ulva spp., Enteromorpha spp.), acorn barnacles, Balanus glandula and Chthamalus dalli, and (subsequently) small mussels, Mytilus trossulus, are often the most conspicuous primary space occupiers in the first year or so after patch formation (Navarrete 1994, Chapter III). In older patches, larger acorn barnacles (Semibalanus cariosus), gooseneck barnacles (Pollicipes polymerus), and scattered clumps of M. californianus are common. Several algae, mostly 'filamentous algae' (sensu Steneck and Dethier 1995: e.g., Pterysiphonia spp., Plocamium spp., Microcladia spp., Polysiphonia spp.), 'corticated macrophytes' (e.g., Mastocarpus papillatus, Iridea spp. Endocladia muricata, Cryptosiphonia spp., and Odonthalia spp.), and 'articulated calcareous algae' (e.g., Corallina vancouveriensis, Bossiella plumosa), are common, but temporally variable in abundance, and generally not very abundant until after the first year of succession. As in Washington, patches that are the same age are often characterized by high between-patch variability in species composition (D. Brosnan, personal communication, E. L. Berlow personal observation).

Herbivores, primarily limpets (Lottia spp.) and littorine snails (Littorina scutulata), were seasonally abundant in mid-intertidal patches, while other grazers, such as chitons and urchins were scarce and restricted to lower intertidal areas (E. L. Berlow, personal observation). The most abundant predators in the mid-zone patches were whelks (Nucella emarginata and Nucella canaliculata) and birds (mostly black oystercatchers, Hematopus bachmani, and gulls, Larus spp.). The abundance of whelks varies seasonally, with peak abundances occurring during the summer months (Navarrete 1994, E. L. Berlow unpublished data). The predatory starfish, Pisaster ochraceus, is scarce in this area, occurring primarily below the lower limit of the mussel bed. The smaller, brooding starfish, Leptasterias hexactis, and recruits and juveniles (<3 cm total diameter) of Pisaster ochraceus, were seasonally common, although they were generally restricted to the edges of patches or to crevices and/or tufts of algae within the patches (E. L. Berlow, E. Sanford personal observation).

Early successional species and young individuals of some later species are susceptible to consumers. Limpets graze algae and can have important negative effects on recruits of B. glandula (Dayton 1971, Paine 1981, Farrell 1991, Chapter II). Nucella can be important predators on B. glandula and M. trossulus (Dayton 1971, Connell 1970, Palmer 1983, Wootton 1993b, Chapter II), however, the strength (and even the sign) of their effect at this site is variable and context-dependent (Navarrete 1994, Chapter III). Nucella can also consume small individuals of S. cariosus, Pollicipes, and M. californianus (Dayton 1971, Palmer 1983, Wootton 1994, Navarrete 1994). Birds can have important negative effects on M. trossulus, Pollicipes, and small M. californianus (Marsh 1984, 1986, Wooton 1992, 1993a, b, 1994b). Therefore, the direct effects of Nucella are restricted to the first few years of succession: the early successional species they consume (B. glandula and M. trossulus) eventually decline in abundance regardless of the presence of predators (Chapter III), and the later species they consume (S. cariosus, Pollicipes, and M. californianus) eventually achieve a size refuge from predation (Connell 1970, Dayton 1971, Palmer 1984).

Many interactions between early species and later sessile species have been documented and potentially affect the dynamics of succession in mid-zone patches. Some important interactions include: (1) B. glandula outcompete C. dalli for space, and (2) predation on B. glandula (including limpet 'bulldozing') can indirectly facilitate C. dalli (Farrell 1991, Dayton 1971, Paine 1981). (3) Several species of acorn barnacles, can facilitate the recruitment of mussels by providing an irregular surface which offers protection from predation and/or desiccation (Dayton 1971, Suchanek 1978, 1985, Chapter III). (4) B. glandula (but not C. dalli) also facilitate the recruitment of algae (Farrell 1991). (5) M. trossulus and S. cariosus can outcompete B. glandula for space by growing on top of them or undercutting them (Suchanek 1985, Dayton 1971, E. L. Berlow personal observation). However, at Fogarty Creek, the effects of M. trossulus can be weak and variable, depending on the relative abundance of M. trossulus that colonize (Chapter III). (6) Both M. trossulus and filamentous algae facilitate the recruitment of M. californianus (Sousa 1984a, Paine and Levin 1981, Suchanek 1985).

Many sessile invertebrates reproduce with planktonic larvae that eventually settle and metamorphose in the intertidal zone. While reproductive periodicity is common in many sessile intertidal species and settlement patterns can be influenced by larval preferences (e.g., Wethey 1986, Raimondi 1988, Johnson and Strathmann 1989), the timing and intensity of recruitment and colonization can be characterized by much variability over a wide range of spatial and temporal scales (Paine and Levin 1981, Sousa 1984b, Roughgarden et al. 1988, Lively et al. 1993). Variation in recruitment or colonization rates can influence the patterns and importance of interactions between the species inhabiting mid-intertidal patches (Paine and Levin 1981, Chapters II and III).

In sum, the early and mid-successional dynamics of this community are characterized by much variability embedded in a background of relatively consistent, repeatable trends. Many potentially complex and variable direct and indirect interactions between successional species have been documented, and stochastic variation in the timing and intensity of disturbance and recruitment can be important forces. Numerous questions remain unanswered, however in this study I ask: To what degree is stochastic variation magnified or dampened by the variety of interactions between successional species? How much detailed information about context dependent interactions is required to explain variation in patch composition?

Methods

To quantify patterns of historic effects in this successional community, I cleared three sets of plots with starting dates staggered by one year. The general design was similar to that illustrated in Figure 1 except that a third set of plots, which ran for ~1.5 years, were initiated in 'year 3'. Each set of plots (hereafter also called an 'experiment') were replicated over four blocks. Each block consisted of a patch in the bed of M. californianus that was partially created by a recent physical disturbance and partially expanded by manually removing additional M. californianus to ensure that each was at least 6 m^2 (or large enough to include all the plots). Successive experiments were installed in the same four blocks (patches). Within each block, each experiment consisted of 9 20 x 20 cm^2 plots which were cleared of macroscopic invertebrates and algae with a paint scraper and wire brush. Scraping, like natural disturbances in the mussel bed, left areas with algal crusts and byssal threads of M. californianus.

To evaluate whether interactions between early and mid-successional species influence the patterns of historic effects, in each plot I used cages to manipulated whelks (N. emarginata), acorn barnacles (primarily B. glandula, S. cariosus, and C. dalli), and mussels (M. trossulus and M. californianus) in a randomized block, factorial design. Details of the experimental design and monitoring protocols are described elsewhere (Chapter III). Information important for the present study is described below.

There were three levels of whelk densities ('none', 'low', and 'high'), and two levels of both barnacles and mussels (present/absent). The design for each experiment was not completely orthogonal because it did not include treatments where both barnacles and mussels were removed. Stainless steel mesh cages 20 x 20 x 5 cm in size (mesh size = 18 ga. (0.12 cm), 0.32 cm space, 51.6% open) were used to manipulate the density of whelks. Cages either excluded whelks or enclosed two or six whelks (15-22 mm in length from apex to siphonal canal), corresponding to densities of 0, 50, and 150 whelks/m^2, respectively. These densities are well within the natural range of Nucella densities reported in the literature (Dayton 1971, Spight 1982) and observed at this site (Navarrete 1994, E. L. Berlow unpublished data). Cages also excluded birds.

The presence or absence of acorn barnacles and mussels were manipulated by either allowing them settle naturally or removing the new individuals on a monthly basis with forceps or a blunt probe. It was practically impossible to selectively remove individual acorn barnacle or mussel species; however, during the first 2 years of succession, the abundances of S. cariosus and M. californianus were consistently extremely low (Chapter III, see Results). While the predator treatments were maintained at a constant density throughout the experiment, the '+barnacle' and '+mussel' treatments varied naturally with recruitment and mortality (independent of predation and interspecific competition). Hereafter, I use 'barnacle' to refer to acorn barnacles.

To compare treatments in the cages with successional patterns naturally occurring in the patches, each block contained three (one for each starting date) 20 x 20 cm unmanipulated plots ('controls') marked with four screws and three 'roofs' to evaluate artifacts introduced by the cages themselves. The comparisons of roofs against marked, unmanipulated, 'control' plots, showed the effects of cages per se and bird predation, but these two factors could not be separated. Unfortunately, by the second year of each experiment, most of the roofs were destroyed by severe wave action. On this short time scale, the roofs did not differ significantly from the controls (Chapter III), and these results are consistent with a concurrent study at this site by Navarrete (1994). However, during the second year of succession, when later successional invertebrates and algae increased in abundance, the few remaining roofs suggested that bird predation and/or the cages might have important effects at this stage (E. L. Berlow, unpublished data). In particular, algae were more abundant in the controls, while they almost never exceeded 10% cover (all species pooled) in any of the cages or roofs. In addition, anemones (primarily Anthopleura xanthogrammica) were common in the roofs and cages, and rarely observed in the controls. Together these patterns suggest that shading by the cages may have been important. Pollicipes were also markedly more abundant in cages and roofs than the controls, suggesting that predation by birds may have been important at this stage (e.g., Wootton 1993b). In addition to the shading introduced by the mesh, the cage rims attached to the rock potentially introduced another artifact. Nereis polychaetes and small starfish (Leptasterias hexactis and juvenile Pisaster < 1.5 cm total diameter) appeared to be attracted to the area under the flaps. Any individuals present were removed during monthly monitoring (see Chapter III).

Because of these possible artifacts, I restricted the analysis to the comparisons between treatments with cages and did not attempt to make comparisons between successional patterns in the cages and those in the control plots. Presumably, the effects of cages were the same across all treatments. Thus, the treatment effects in this study should be interpreted in the context of shading (and low algal cover) and exclusion of birds. Data from the control plots are presented to illustrate the natural patterns of succession at this site.

'Experiment #1' was initiated in April, 1991 and maintained through March 1994. 'Experiment #2' was initiated in April, 1992 and maintained through September 1994. 'Experiment #3' was initiated in April, 1993 and maintained through October 1994. All experiments were terminated because cages were damaged during severe storms, leaving less than three replicates for several treatments. In addition, by the beginning of the third year of succession, many of the species present which are consumed by Nucella had grown large enough to escape predation.

Data Analysis

I used a randomized block analysis of variance (ANOVA) to analyze the combined effects successional age (AGE), starting date (START), census year (YEAR), Nucella (NUC), barnacles (BAR), and mussels (MUS) on the cover of the seven most abundant sessile species. Separate factorial ANOVA's were conducted on 1) the first two years of the first two 'experiments' (Fig. 1: ANOVA I) and 2) census years 2 and 3 for the first two 'experiments' (Fig. 1: ANOVA II). While this procedure is soemwhat problematic because some of the data were used twice, it was the only way to explore both the interactions between age and starting date and between census year and starting date (see 'Distinguishing Historic Effects' above). Because Experiment #3 ran for only one year, it was not used in the analysis. However, information provided by these data was used to aid in interpreting the results of the ANOVA's on Experiment #'s 1 and 2.

Separate ANOVA's for each species is not always desirable since correlations among species might affect the Type I error rate (Tabachnick and Fidell 1989, Scheiner 1993). However, since mussels and barnacles were simultaneously both manipulated factors and response variables, separate univariate ANOVA's were preferable to a multivariate ANOVA, because 1) they allowed me to use only those treatments in which the response variable was not manipulated (i.e. '+ mussel' or '+ barnacle'). Thus, the design for each analysis was completely orthogonal. To facilitate interpretation of the univariate results and of correlations among species, I also present figures illustrating the patterns of change of all species together. Thus, I used only '+ barnacle' treatments to analyze effects on the three barnacle species (B. glandula, C. dalli, and S. cariosus) and '+ mussel' treatments to analyze the two mussel species (M. trossulus, and M. californianus). For the two other species (Pollicipes and Anthopleura), I first included all treatments in the ANOVA's, but since mussels had no significant effects on either species in any year or for either starting date ($p > 0.05$ in all cases), I pooled across mussel treatments. This had the advantage of making the resulting design completely orthogonal (because there were no '- barnacle, - mussel' treatments) and increasing the power to detect interactions among the remaining factors.

Assumptions of normality and variance heterogeneity were checked by normal probability plots, stem and leaf diagrams of residuals, and visual inspection of residual vs. predicted plots. In all cases, arcsin-squareroot transformed cover data exhibited more normal distributions and homogeneity of variances than the raw data. However, in many cases variances remained heterogeneous because some treatments exhibited extreme variance. This usually occurred when most or all of the replicates of a treatment group had zero values. One consequence of this was that, in an ANOVA, some treatments differed significantly (statistically) when the cover of a species was extremely low in one and absent in the other. Thus, the ecological difference may have been trivial. These cases are clear in the figures, and were taken into consideration when interpreting the results. One solution could have been to remove groups with extreme variance from the analysis or to perform separate t-tests on individual treatment pairs of interest (see Farrell 1992, Wootton 1993a, 1994b). However, a primary objective of the present study was to explore the interactions among manipulated factors, thus, the results of the factorial ANOVA's are presented. Data were also analyzed by performing ANOVA's on ranked data as recommended by Conover and Iman (1976) for complex designs which preclude the use of simple nonparametric tests. Rank transformations did not always reduce heteroscedasticity, and the results of the ANOVA's were generally similar to those for arcsin-squareroot-transformed data. Results from the latter analyses are presented.

To avoid dependence between census dates, I analyzed the mean abundance of species averaged over each separate year for each 'experiment' (starting date) (see Wootton 1994b). This facilitated comparisons between experiments within a given year, because the sampling dates were not always synchronous across experiments and because the frequency of sampling was not the same for each experiment. To facilitate interpretation of temporal trends, data from the separate sampling dates are also presented. In most cases, after plots were initiated in the spring, the cover of sessile species remained low until late summer/fall of the first year. Thus, data for the first year of each experiment were the means of all sampling dates from the first fall after plots were initiated (September-November) to the sampling date closest to spring of the following year (late March-June). Subsequent years (for Experiment #'s 1 and 2) were means from next sampling date to the sampling date closest to the following spring.

Results

I. General successional patterns in the cages.

Below I describe some qualitative trends of species replacement in the cages where all sessile species were allowed to settle naturally in order to 1) illustrate the general similarities and differences in successional patterns between starting dates and 2) facilitate interpretation of subsequent analyses of individual species.

a) Early species: B. glandula, M. trossulus, and C. dalli.

Plots cleared in the spring of 1991 (Experiment #1) (Fig. 3 top row) were rapidly colonized by B. glandula. Within the first couple months B. glandula reached ~80% cover in most cages. In the fall of the first year, M. trossulus colonized the tests of B. glandula and reached a peak in cover during the first winter. During the first year in '+ mussel +barnacle' cages, the effects of Nucella on B. glandula were weakly negative, and their effects on M. trossulus varied in sign depending on the density of Nucella manipulated (Chapter III). Both B. glandula and M. trossulus declined by the end of the second year in all cages, regardless of the presence of Nucella, although they reached their lowest cover sooner in the presence of Nucella. Space made available by the decline of B. glandula and M. trossulus was occupied by C. dalli during the second year, and the colonization by C. dalli was facilitated by the presence of Nucella (see below). The total cover of sessile species peaked early and then stabilized at ~45-60% during the second year regardless of the presence of Nucella, as C. dalli colonized newly available space.

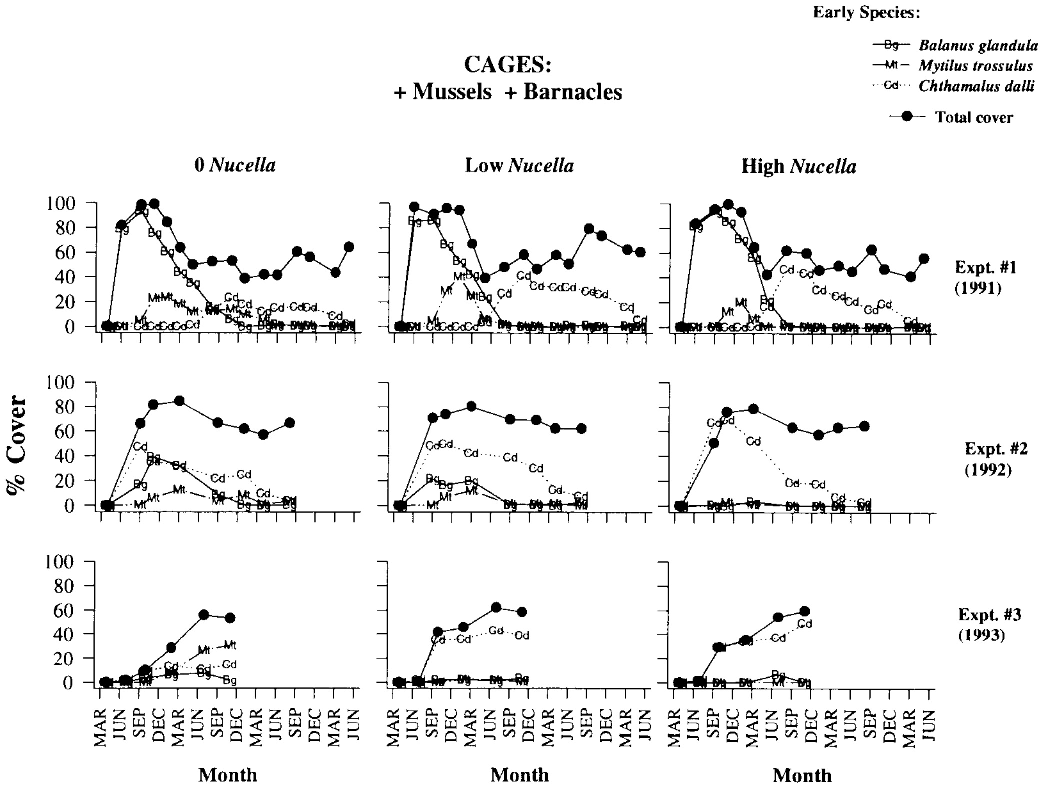
By the end of the third year, all three species (B. glandula, M. trossulus, and C. dalli) were scarce.

In plots cleared in the spring of 1992 (Experiment #2) (Fig. 3, middle row), the initial rapid pulse of B. glandula was notably absent. Instead, C. dalli colonized first, but more slowly than did B. glandula in Experiment #1. In this experiment, B. glandula gradually increased in cover in the absence of predators during the late summer and fall of the first year and peaked during the first winter. M. trossulus also reached peak abundance during the first winter, as it had in Experiment #1. Both B. glandula and M. trossulus were generally less abundant than in Experiment #1, and both were scarce or absent in cages with high densities of Nucella. C. dalli achieved higher cover for a longer amount of time when predators were present versus where they were excluded. Thus, as in Experiment #1, the total cover of sessile species stabilized at ~60-80% by the second year, regardless of the negative effects of Nucella on B. glandula and M. trossulus. Also, as in Experiment # 1, all three species declined after the second year of succession.

In plots cleared in the spring of 1993 (Experiment #3) (Fig. 3, bottom row), like those in Experiment #2, C. dalli was the first to colonize, and there was no initial rapid colonization of B. glandula. In cages with predators, B. glandula and M. trossulus were scarce or absent, and C. dalli was the dominant space occupier. In contrast to Experiment #1, in predator exclusion cages, B. glandula colonized more slowly and never exceeded 15%. M. trossulus also colonized more slowly than in the previous two experiments, but by the fall of the second year was the most abundant sessile species in predator exclusion cages. Like the previous two experiments, the early negative effects of Nucella on M. trossulus and B. glandula did not dramatically affect the total cover of sessile species, as C. dalli compensated by increasing in abundance.

In sum, Experiment #1 was characterized by an intense, early pulse of B. glandula, while in Experiments #2 and 3, C. dalli was the more abundant early colonizer. The effects of Nucella were most dramatic in Experiments #2 and 3, when B. glandula was

Figure IV.3. Mean cover of B. glandula, M. trossulus, C. dalli, and all macroscopic sessile species ('Total cover') in cages where both mussels and barnacles were allowed to settle naturally ('+ Mussels, + Barnacles'). All plots were initially cleared in April, but the starting dates were staggered by one year. 'Expt. #'s1, 2 and 3' represent sets of plots that were initiated at a given starting date (1991, 1992, and 1993, respectively). '0 Nucella' = predator exclusion; 'Low Nucella' = 2 Nucella enclosed; 'High Nucella' = 6 Nucella enclosed.



generally less abundant than in Experiment #1. M. trossulus generally peaked in cover during the first winter, except in the third experiment, where it did not increase markedly until the following fall. In both experiments which ran longer than 2 years, all three species eventually declined in cover regardless of the presence of Nucella. In all cases, the total cover generally remained above 50% regardless of the presence of Nucella.

b) Mid-successional species: S. cariosus, M. californianus, Pollicipes, and Anthopleura.

By the middle of the second year after plots were cleared, S. cariosus, M. californianus, Pollicipes, and Anthopleura gradually increased in abundance (Fig. 4). Three of these (S. cariosus, M. californianus, and Pollicipes) are capable of reaching a size refuge from predation by Nucella. The other (Anthopleura), is not eaten by Nucella. Experiment #3 was terminated after ~1.5 years, so the cover of all four species generally remained below 5% (Fig. 4, bottom row). In Experiment #1, all four species slowly increased in cover, but no single species clearly dominated this stage of succession (Fig. 4, top row). In contrast, Pollicipes was conspicuously more abundant Experiment #2, while S. cariosus and M. californianus were rare or absent (Fig. 4, middle row). After three years of succession in Experiment #1, the mean cover of M. californianus remained below 10%, regardless of the presence of Nucella (Fig. 4, top row).

II. General successional patterns in control plots.

The control plots exhibited some general trends and differences between starting dates that resembled those in the cages (Fig. 5). Experiment #1 was characterized by an immediate pulse of B. glandula, while in Experiment #'s 2 and 3 the recruitment of B. glandula to newly cleared plots was slower and less intense (Fig. 5a-c). As in the cages with Nucella, C. dalli was more abundant in Experiment #'s 2 and 3 than Experiment #1 (Figs 3 and 5a-c). In Experiment #3, C. dalli was the dominant space occupier for the

Figure IV.4. Mean cover of S. cariosus, M. californianus, Pollicipes, and Anthopleura in cages where both mussels and barnacles were allowed to settle naturally. See caption for Fig. 3.

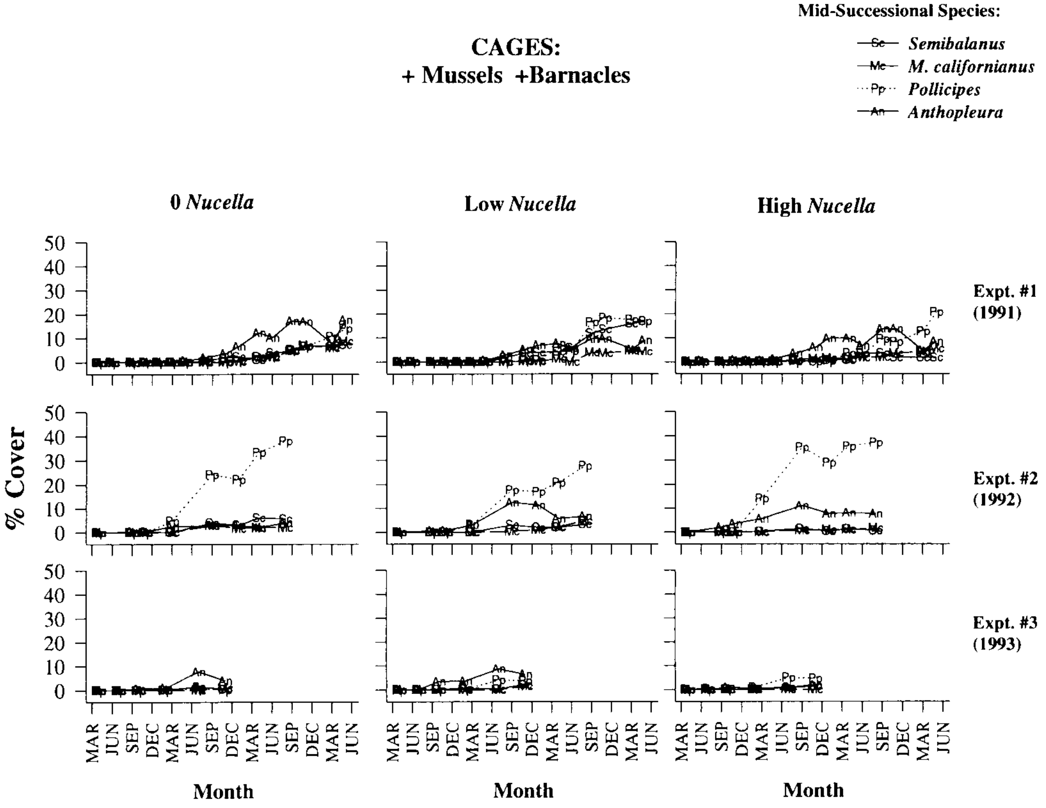
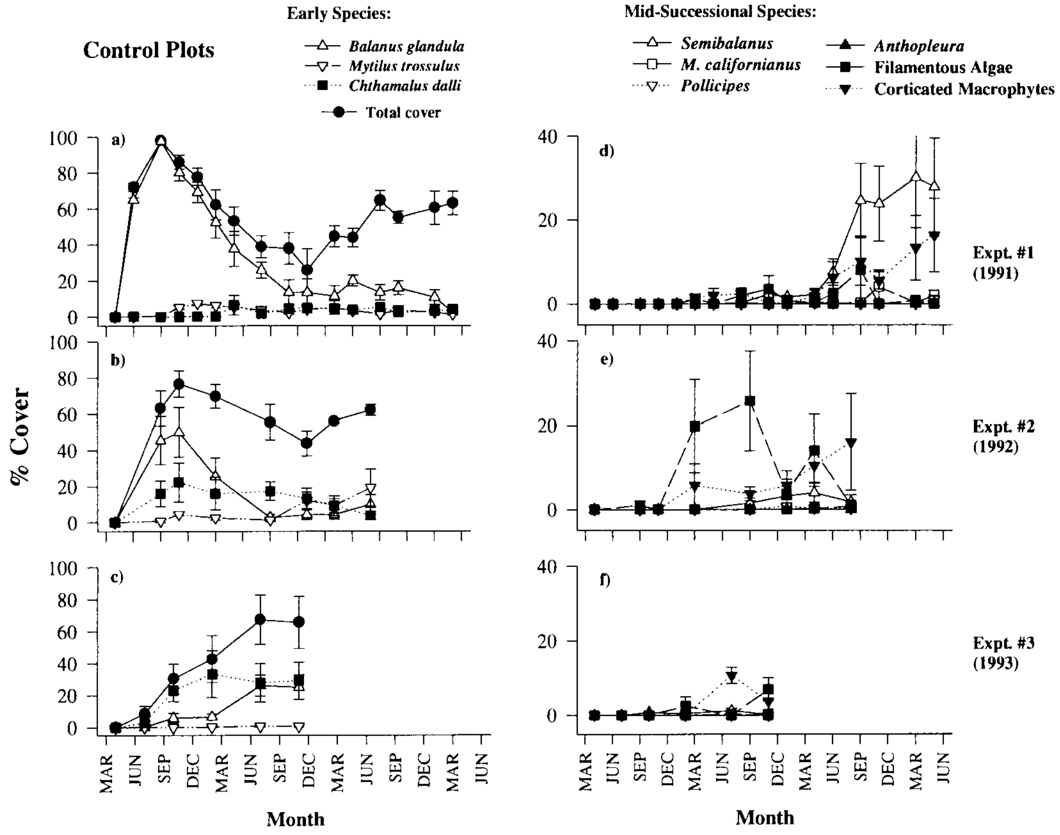


Figure IV.5. a-c) Mean (± SE) cover of B. glandula, M. trossulus, C. dalli, and all macroscopic sessile species ('Total cover') in control plots cleared at the same time as the caged plots. d-f) Mean (± SE) cover of S. cariosus, M. californianus, Pollicipes, Anthopleura, 'filamentous algae', and 'corticated macrophytes' (sensu Steneck and Dethier 1995) in control plots. See caption for Fig. 3, and see text for the definition of algal functional groups.



first year of succession, after which B. glandula slowly increased in abundance (Fig. 5e). Also similar to the cages, both B. glandula and C. dalli were consistently scarce by the middle of the third year of succession, regardless of their initial abundance (Fig. 5a and b). Similar to cages with high densities of Nucella, M. trossulus was generally rare in all control plots regardless of starting date (Fig. 5a-c). However, in Experiment #2, M. trossulus started to increase in cover at the end of the experiment (Fig 5b).

In Experiment #1 controls, like the low density Nucella cages initiated at the same time, the decline of B. glandula was followed by an increase in the cover of S. cariosus during the third year of succession (Figs. 3, 5d, and see below: Fig. 9c). This increase in S. cariosus was not observed in Experiment #2 controls of the same age or at the same point in time (Fig. 5e). M. californianus was consistently rare in all control plots during the first 2.5 years of succession (Fig. 5d-f), and only started to increase slightly in abundance at the end of the third year of Experiment#1 (Fig. 5d). Contrary to the cages, Pollicipes and Anthopleura rarely colonized any of the control plots (Fig. 5d-f). Also, macroalgae became abundant in controls in the second and third year of succession (Fig. 5d and e), while it was rare in most of the cages.

In sum, succession in the controls was characterized by an initial colonization of B. glandula and/or C. dalli, with their relative abundances and rates of colonization varying markedly between starting dates. By the end of the second year of succession, both species declined, regardless of the starting date. Subsequent species composition varied with starting date. In Experiment #1 B. glandula was replaced primarily by S. cariosus and secondarily by corticated macrophytes (Fig. 5d). In Experiment #2, B. glandula and C. dalli were replaced by a pulse of filamentous algae and then a slow increase in corticated macrophytes (Fig. 5e). In most cases, control plots of the same successional age, but different starting dates, varied considerably in species composition (Fig. 5).

III. Patterns of historic effects.

Individual sessile species responded differently to the separate and combined effects of successional age, starting date, and yearly variation. While Figure 2 provides a heuristic framework for interpreting the results, the actual patterns observed were more complicated because: 1) species abundances were not discrete values of 'high' or 'low'; 2) different attributes (e.g., peak abundance, timing of colonization, etc.) of the same species exhibited different patterns; and 3) the patterns for a given species may have varied with the presence of Nucella, mussels, and/or barnacles. Despite this complexity, some general patterns emerged:

a) 'Canalized Noise': B. glandula and Anthopleura.

Both B. glandula and Anthopleura abundances appeared partially driven by stochastic yearly variation and partially canalized into a repeatable pattern of change with successional age (Figs. 6 and 7). In neither case were stochastic differences between starting dates or years magnified into fundamentally different successional trajectories (see below).

B. glandula consistently colonized early, and consistently declined by the end of the second year (Fig. 6). However, the intensity of initial recruitment varied dramatically between starting dates (Table 1: START is significant; Fig 6: a vs. d). In Experiment #1 B. glandula rapidly reached close to 100% cover in many cages, while in Experiment #2, it trickled in more slowly and peaked at about 50% cover (Fig. 6: a vs. d, Fig. 3). Consequently, the decline in cover between Age 1 and Age 2 was more dramatic in Experiment #1 than Experiment #2 (Table 1: AGE * START is significant). The initial difference between starting dates was rapidly dampened so that, by 1992 and 1993, there were no overall differences in B. glandula cover between the two experiments in a given year (Table 2: START not significant; Fig 6: b and c vs. d and e). B. glandula in both

Figure IV.6. a-f) Mean (± SE) cover of B. glandula in the cages averaged over each year for each starting date ('Expt. #'s 1-3'). Since all plots were initiated in the spring, '1991', '1992', and '1993' represent the mean from 1991-1992, 1992-1993, and 1993-1994 respectively. '-M' = mussel recruits removed monthly; '+M' = mussels allowed to settle naturally. Other codes are the same as in Fig. 3.

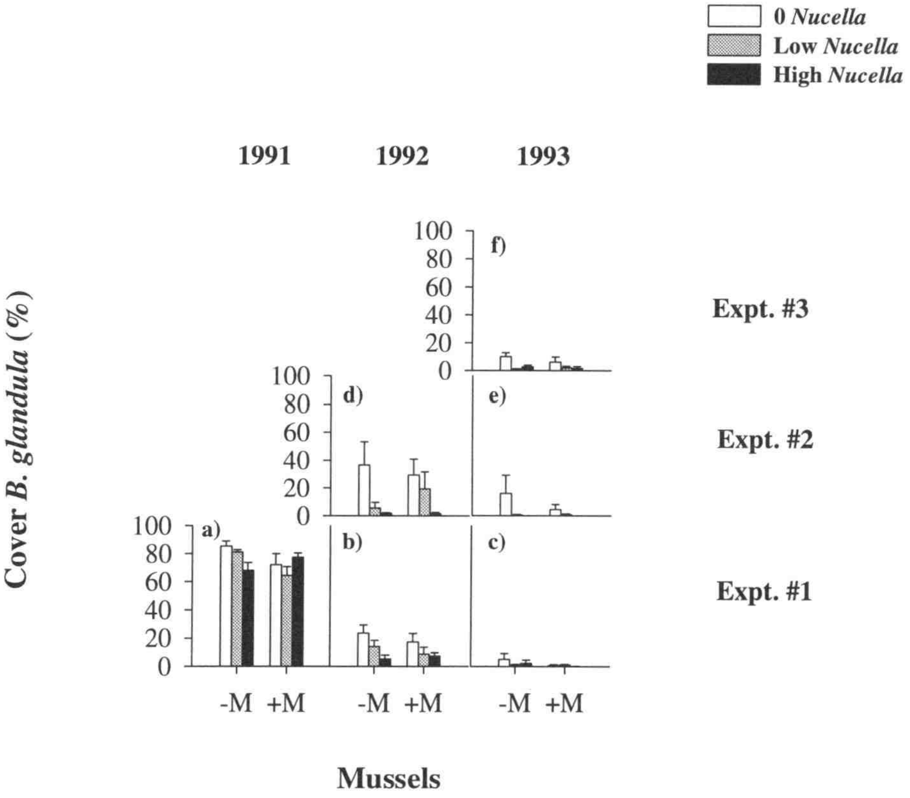
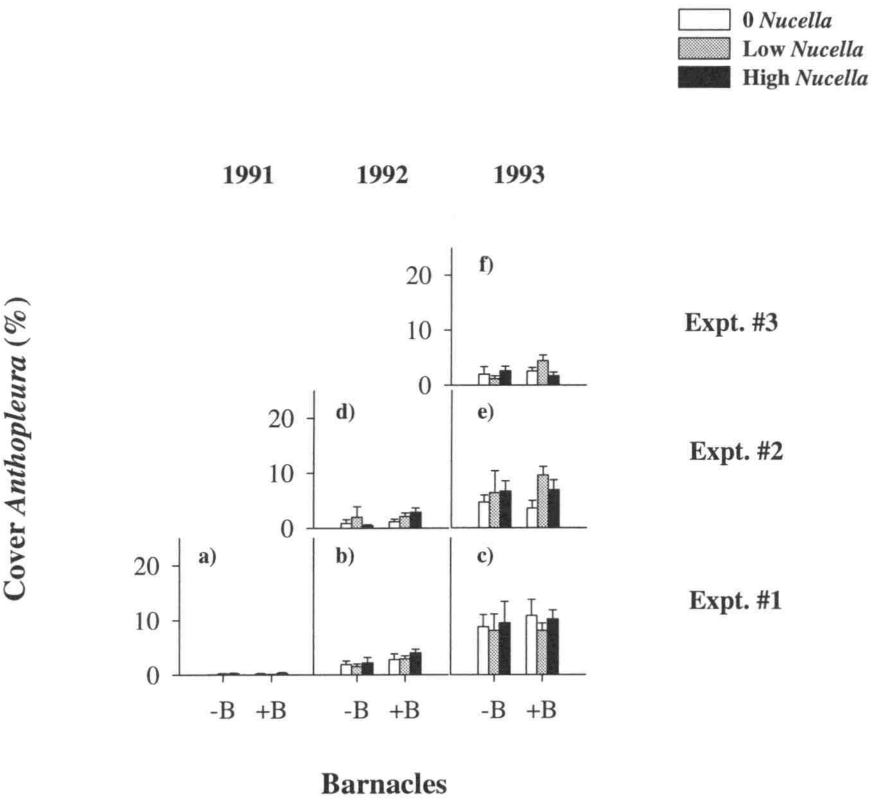


Figure IV.7. a-f) Mean (± SE) cover of Anthopleura in the cages averaged over each year for each starting date. '-B' = barnacle recruits removed monthly; '+B' = barnacles allowed to settle naturally. Data were pooled across ± mussel treatments. Other codes are the same as in Fig. 6.



experiments continued to decline in 1993 at similar rates, regardless of starting date (Table 2: YEAR is significant, YEAR * START not significant). The patterns of change with age or year were not affected by mussels or by the presence of Nucella (Table 1: AGE * NUC, and AGE * MUS not significant). Removing mussels had no overall effect on B. glandula in either experiment (Tables 1 and 2: MUS not significant; Fig 6). Predation by Nucella consistently had a negative effect on B. glandula cover, but it did not dampen or magnify initial differences between starting dates (Tables 1 and 2: NUC is significant, AGE*START*NUC and YEAR*START*NUC not significant). While the effects of Nucella on B. glandula were relatively weak in the first year of Experiment #1 relative to Experiment #2 (Berlow, Ch. 3; Fig 6: a vs. d), by 1993 the only surviving B. glandula were primarily in cages without predators, regardless of starting date (Fig. 6c and e). Thus the successional patterns of B. glandula were characterized by stochastic differences in initial colonization which was dampened by a relatively canalized decline regardless of the presence of mussels or whelks.

Anthopleura consistently colonized slowly, but its subsequent abundance at a given age varied consistently between starting dates (Fig 7: a vs. d, b vs. e; Table 3: AGE and START are significant). The cover of Anthopleura showed similar patterns of change with time for both Experiments #1 and #2, but the overall cover differed consistently between experiments (Table 3: AGE*START not significant, Table 4: YEAR and START are significant, YEAR*START not significant). Thus, initial differences between starting dates were consistently maintained through time. However, the fact that the cover of Anthopleura in the first year of succession was always relatively low, regardless of the starting date suggests that variation in Anthopleura cover was not entirely driven by stochastic differences between years. For example, the cover of Anthopleura was low in the first year of Experiment #3 relative to Experiments #'s 1 and 2 in the same year (Fig 7c, e, and f). While the effects of Nucella on Anthopleura were marginally significant in the first two years of succession (Table 3: NUC effect p = .05), the cover of Anthopleura was generally low, and the differences detected do not appear to be ecologically significant (Fig 7c and d). This is reflected in the fact that in 1992 and 1993, Nucella did not have any significant effects on Anthopleura (Table 4: NUC not significant). Similarly, removing barnacles appeared to have a significant effect overall on Anthopleura (Tables 3 and 4: BAR is significant), but a visual inspection of ± barnacle treatments in Figure 7 suggests that the effects of barnacles were not ecologically significant. In any case, the patterns of change in Anthopleura cover with successional age or year were not influenced by Nucella or barnacles (Table 3: AGE * NUC and AGE * BAR not significant; Table 4: YEAR*NUC and YEAR*BAR not significant). Similarly, neither the presence of Nucella nor the removal of barnacles played a role in dampening or magnifying stochastic variation between starting dates (Tables 3 and 4: AGE*START*NUC, AGE*START*BAR, YEAR*START*NUC, YEAR*START*BAR not significant). Thus, Anthopleura was characterized by a relatively canalized pattern of slow initial colonization with stochastic variation between years influencing its later abundance at a given age regardless of the presence of whelks or barnacles.

b) 'Consumer-Mediated Contingent Succession': C. dalli and S. cariosus

Both C. dalli and S. cariosus exhibited contingent patterns of succession which were, in turn, influenced by the presence of Nucella (Figs. 8 and 9). For C. dalli, differences between starting dates resulted in different patterns of change with time (Fig. 8; a-c vs. d-e; Tables 1 and 2: both AGE*START and YEAR*START significant). For example, in 1992, the pulse of C. dalli that recruited to newly cleared plots in Experiment #2 did not equally colonize plots of Experiment #1 that had been cleared one year earlier (Fig. 8b and d). Thus plots with different starting dates responded differently to the same externally driven event in 1992. The degree to which the successional trajectory of C. dalli was contingent on the starting date appeared to depend on the presence of Nucella (Fig. 8b and d; Table 1: AGE*START*NUC is significant). In addition, the effect of

Figure IV.8. a-f) Mean (± SE) cover of C. dalli in the cages averaged over each year for each starting date. Codes are the same as in Fig. 6.

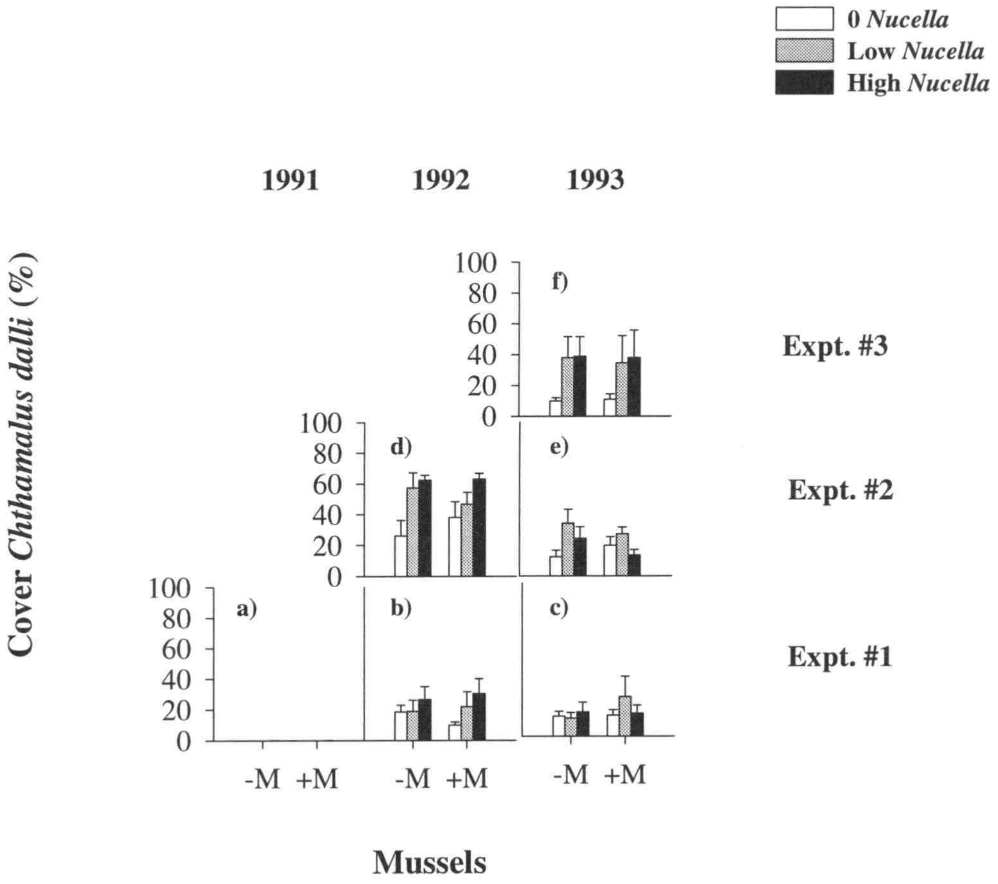
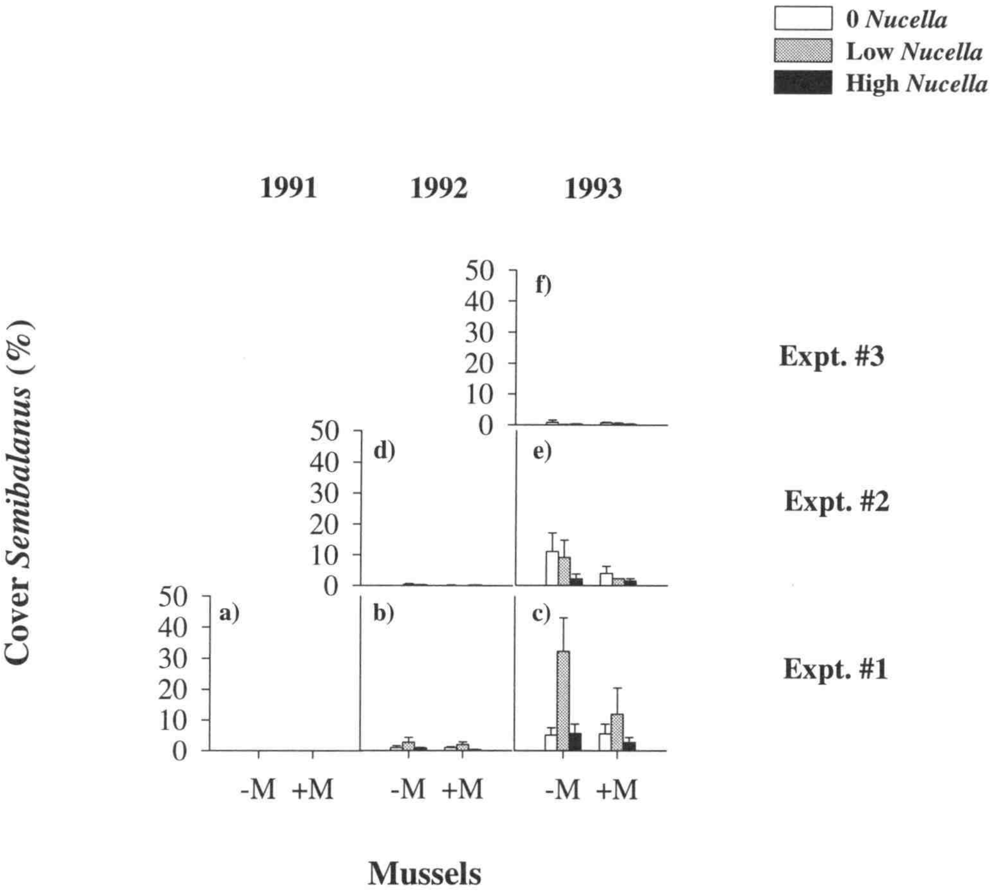


Figure IV.9. a-f) Mean (± SE) cover of Semibalanus in the cages averaged over each year for each starting date. Codes are the same as in Fig. 6.



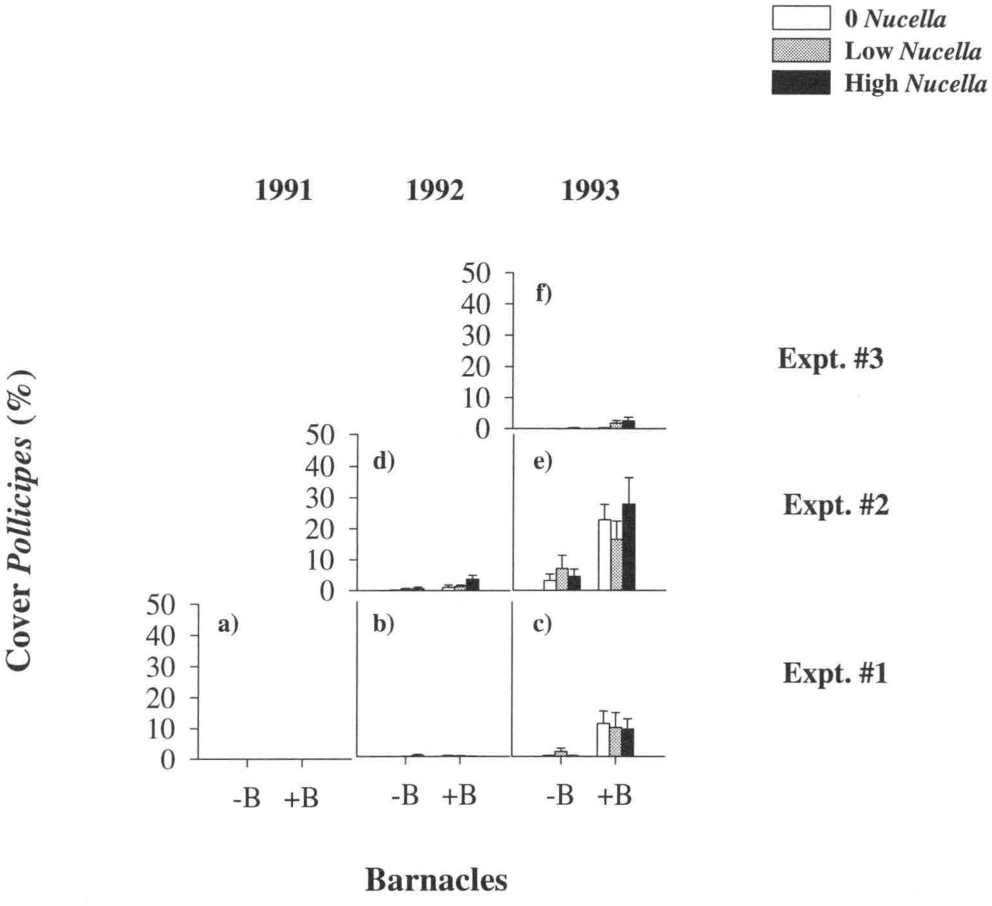
Nucella varied with the presence of mussels (Table 2: START*NUC*MUS is significant). Thus, in cages without mussels, the presence of Nucella appeared to magnify differences between starting dates and/or years. For example, in a given year (1992 or 1993), differences between experiments in the cover of C. dalli were more pronounced in cages with Nucella and without mussels (Fig. 8: b and d, c and e ('-M'). This general pattern is corroborated by the results of Experiment #3: C. dalli was more abundant overall in newly cleared plots than in older plots in the same year and the differences were greatest in cages with Nucella (Fig. 8: f vs. e, c). Thus, in the presence of Nucella, C. dalli was characterized by patterns of succession which were contingent on the starting date. Differences between plots at a given point in time could not easily be attributed to age or to simple stochastic variation between years. In the absence of Nucella, changes in C. dalli cover more closely tracked natural yearly variation, independent of successional age or the starting date.

S. cariosus exhibited similarly contingent patterns of succession (Fig. 9). Overall, changes during the first two years of succession varied with the starting date (Fig. 9: a and b vs. d and e; Table 1: AGE*START is significant). In Experiment #2 S. cariosus was more abundant by the second year than in Experiment #1 plots of the same age (Fig 9 b vs. e). Some of these differences appeared to be driven by natural variation between years, independent of starting date or successional age (Fig 9 e and c; Table 2: YEAR is significant, YEAR*START not significant). For example, 1993 was a relatively 'good' year for S. cariosus in both Experiments #'s 1 and 2 regardless of starting date. However, the degree to which S. cariosus cover tracked yearly variation depended on the density of Nucella enclosed (Table 2: YEAR*NUC and START*NUC are significant). In particular, low densities of Nucella appeared to magnify differences between experiments in a given year (Fig. 9c and e: gray bars). While mussels had a significant negative effect on S. cariosus by 1993 (Table 2: MUS is significant; Fig 9 c and e), neither the patterns of change with time, nor the way in which they were contingent on Nucella, were affected by mussels (Tables 1 and 2: none of the higher order interactions which include mussels were significant). Despite the contingent nature of S. cariosus' successional trajectory, it consistently was not abundant during the first year of succession (Fig. 9a, d, and f). Thus, despite the fact that S. cariosus was abundant in both Experiment #'s 1 and 2, it was rare in the recently cleared plots of Experiment #3. Thus, S. cariosus was characterized by a relatively canalized pattern of slow initial colonization, while its later abundance at a given age was influenced by random variation between years. The degree to which different starting dates responded differently to the same yearly variation depended on the density of Nucella.

c) 'Facilitation-Mediated Contingent Succession': Pollicipes.

Pollicipes exhibited a contingent patterns of succession which depended on the presence or absence of acorn barnacles (Figs. 8 and 9). The cover of Pollicipes was consistently low in the absence of acorn barnacles (Fig. 10). Any significant variation in the facilitation effect of barnacles (Tables 3 and 4: AGE*START*BAR, and YEAR*BAR are significant) was primarily due to the fact that, in Experiment #1, Pollicipes was rare in all cages (regardless of barnacles) until 1993 (Fig. 10a and b). When Pollicipes did colonize Experiment #1, they were more abundant in cages with barnacles (Fig. 10c). When it was present (i.e. in cages with barnacles) changes in the cover of Pollicipes with time varied with starting date (Tables 3 and 4: AGE*START and YEAR*START are significant). For example, Pollicipes was abundant in Experiment #2 by the end of the second year of succession (1993), while in Experiment #1 Pollicipes remained rare or less abundant regardless of their age or the census year (Fig 10 b and c vs. e). Thus differences in the cover of Pollicipes between Experiment #'s 1 and 2 could not be attributed simply to age or yearly variation. Different starting dates responded differently to the same natural variation between years. Despite the contingent nature of Pollicipes' successional trajectory, it consistently was not abundant during the first year of succession (Fig. 10a, d, and f). While Pollicipes was present in both Experiment #'s 1

Figure IV.10. a-f) Mean (± SE) cover of Pollicipes in the cages averaged over each year for each starting date. Data were pooled across ± mussel treatments. Codes are the same as in Fig. 6.



and 2 in 1993, it was rare in the recently cleared plots of Experiment #3. Thus, Pollicipes was characterized by a relatively canalized pattern of slow initial colonization which was consistently facilitated by barnacles however, its later abundance at a given age was contingent on the way starting date interacted with differences between years.

d) 'Facilitation-Mediated Canalized Succession': M. trossulus and M. californianus.

M. trossulus and M. californianus both exhibited relatively canalized succession in the presence of barnacles. However, where barnacles were removed, their patterns of change with time were both more variable and contingent on the starting date (Figs. 11 and 12):

Barnacles consistently facilitated M. trossulus in the first year of succession regardless of starting date (Chapter III; Fig 11a, d, and f). In the presence of barnacles, M. trossulus exhibited a relatively canalized pattern of colonization in the first year of succession and subsequent decline in years 2 and 3 (Figs 3 and 11: a and b ('+B') are similar to d and e (+B); Table 3: AGE*BAR and AGE*START*BAR are significant, Table 4: YEAR*BAR is significant). In the presence of barnacles, initial differences between starting dates in the abundance of M. trossulus (Chapter III; Fig. 11a, d, and f: ('+B')) were dampened in the second year by the canalized decline (Fig. 11b and e ('+B')) For example, differences between the first year of Experiment #'s 1 and 2 (Fig. 11a and d ('+B')) were smaller by the second year of succession in both experiments (Fig. 11b and c ('+B')). In contrast, in the absence of barnacles, differences between starting dates led to different patterns of change with time (Tables 3 and 4: AGE*START*BAR, YEAR*START, and START*BAR are all significant). In Experiment #1, M. trossulus successfully colonized cages without barnacles in the first year and increased slightly in mean cover during the second year (Fig. 11a and b ('-B')). However, in '-barnacle' plots that were cleared in 1992, M. trossulus remained scarce throughout the experiment (Fig. 11d and e '-B'). While Nucella had complex and variable effects on M. trossulus in the

Figure IV.11. a-f) Mean (± SE) cover of M. trossulus in the cages averaged over each year for each starting date. Codes are the same as in Fig. 6.

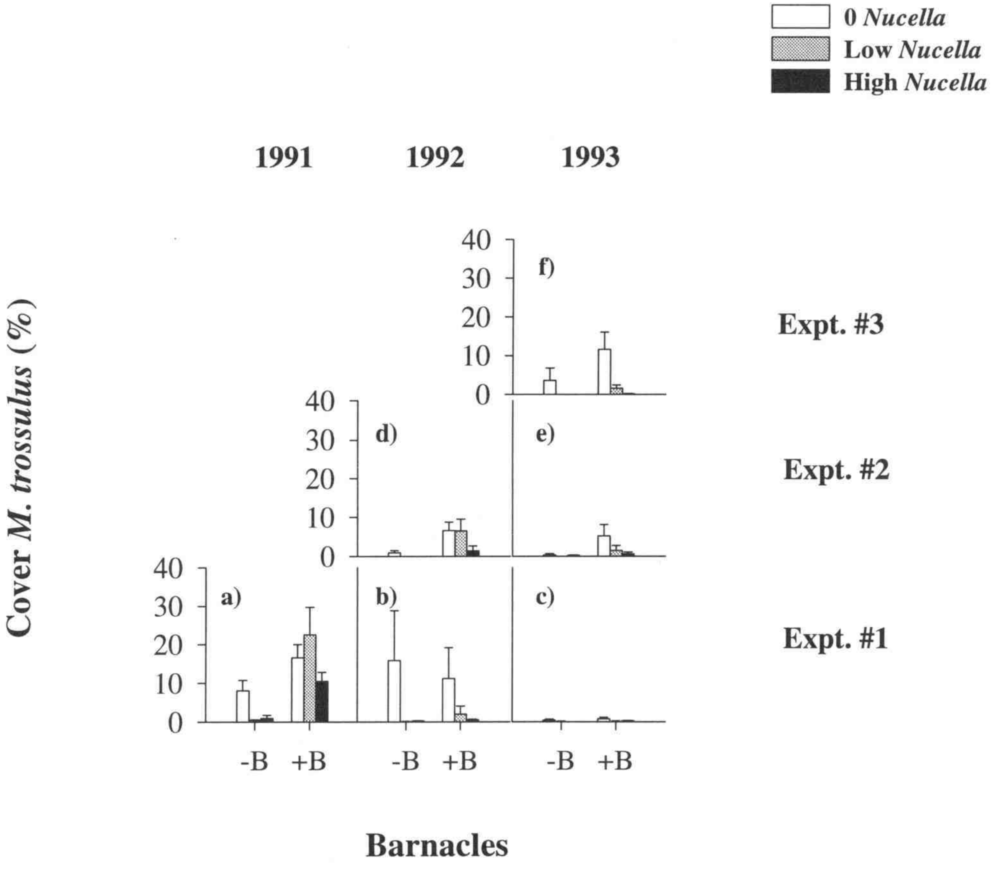
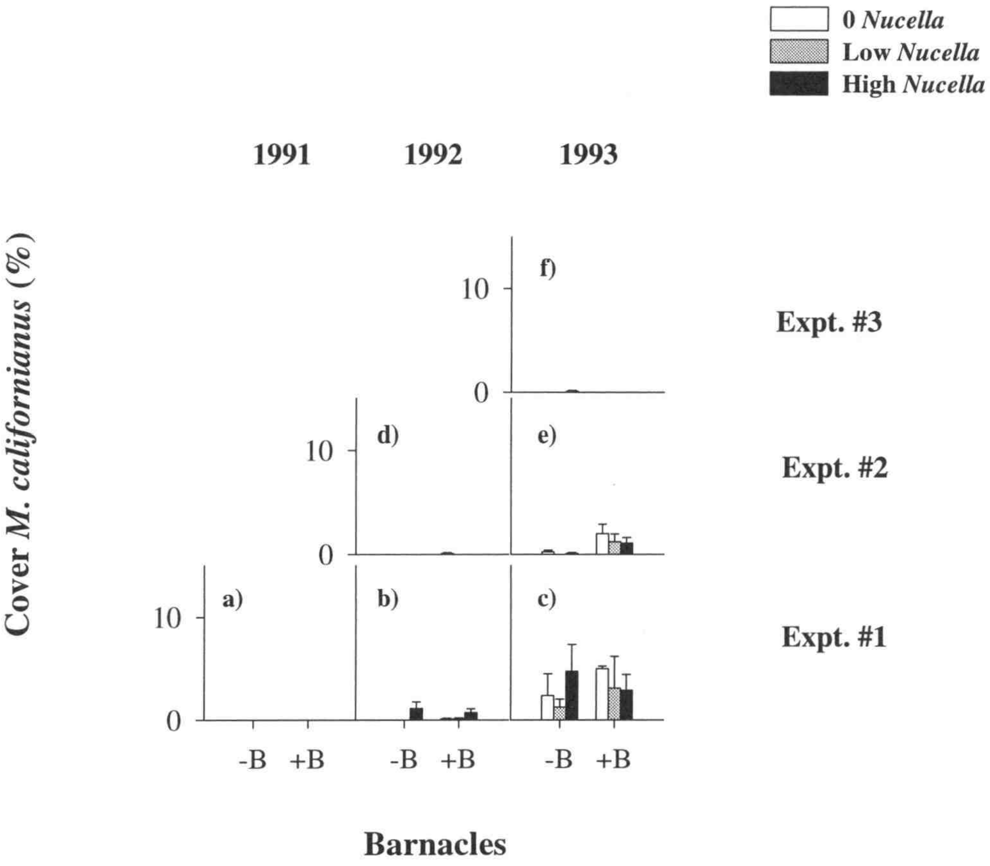


Figure IV.12. a-f) Mean (± SE) cover of M. trossulus in the cages averaged over each year for each starting date. Codes are the same as in Fig. 6.



first year of succession (Chapter III, Fig 11a, d, and f), they consistently hastened the decline of M. trossulus in year two regardless of starting date (Table 3: START*NUC, AGE*START*NUC not significant; Fig. 11b and e). Thus, by the second year of succession, M. trossulus were rare in any cages with Nucella, regardless of starting date (Fig. 11b and e). Nucella also consistently eliminated most M. trossulus in any cages where barnacles were removed (Fig. 11: all '-B' treatments). The fact that M. trossulus was more abundant in '+barnacle' cages of Experiment #3 than in older '+barnacle' plots during the same year (Fig. 11: e and c vs. f) further suggests that, in the presence of barnacles, variation in M. trossulus at a given point in time is at least partly attributable to successional age rather than to random yearly variation. Thus, in the presence of barnacles, stochastic differences between starting dates in initial abundances were dampened by a relatively consistent and repeatable pattern of early colonization and subsequent decline. In the absence of barnacles, differences between starting dates were associated with more variable and contingent successional change.

M. californianus cover remained below 10% in all experiments (Fig. 12). Therefore, many of the statistically significant effects of different treatments were the result of very small changes in M. californianus cover (e.g., from scarce or absent to rare; Fig. 12: especially a, b, d, and e). However, since M. californianus is such an important dominant species in this community, some general trends are noteworthy. In the presence of barnacles, M. californianus exhibited a relatively canalized pattern of succession which was characterized by a slow increase, regardless of starting date (Fig. 12 a-c, and d-e ('+B')). However, in the absence of barnacles, different starting dates were associated with different patterns of change with time. M. californianus managed to slowly colonize plots without barnacles that had been initiated in 1991; however, it remained rare or absent in '-barnacle' plots initiated one year later (Fig. 12b and c vs. e). Nucella had no significant effects on the later abundance of M. californianus, regardless of the presence of barnacles (Table 4: no NUC effects are significant; Fig. 12c and e). Thus, in the presence of barnacles, variation in M. californianus appeared largely attributable to differences in age alone. In the absence of barnacles, differences between starting dates were associated with more variable and contingent successional change.

Discussion

Succession in mid-intertidal patches in the mussel bed appeared to be a dialectical process in which both canalized and contingent factors operated simultaneously. The complex patterns of historic effects varied between species at the same time and between different attributes (e.g., timing of colonization, peak abundance, timing of decline) within a given species. As observed in similar systems on the Oregon coast, different mechanisms of succession appeared to be operating at different times with different species (Turner 1983a, b, Farrell 1991). The combination of these processes operating simultaneously in the same system suggests that, overall, the entire successional process in this community should be chaotic-- magnifying even the smallest stochastic variation in recruitment, disturbance events, environmental conditions, etc. (Wilson 1992, Ellner and Turchin 1995). However, despite its potential complexity, this system exhibited some consistent and repeatable patterns of succession. Understanding what forces played a role in dampening or magnifying stochastic variation may shed light on the patterns of consistency and contingency in this successional community.

I. Noise-dampening forces:

1) Constraints and tradeoffs:

Many organismal traits are ultimately based on the allocation of finite resources (Mooney 1972, Tilman 1990). Tradeoffs in allocation imply that it is usually difficult for an organism to be a 'master of all trades'. For example, in the rocky intertidal, where body size often influences competitive ability and susceptibility to predation (Wootton

1993b, Connell 1961a, b, Dayton 1971, Paine 1976, 1977, 1981), good dispersers are often poor competitors (e.g., Suchanek 1981). Thus, physiological or life-history constraints and tradeoffs can be important in making the range of probable successional pathways a small subset of what is possible (Noble and Slatyer 1980, Walker et al. 1986, Huston and Smith 1987, Halpern 1989, Tilman 1990, McCook 1994).

In mid-intertidal mussel bed patches, three species (B. glandula, C. dalli, and M. trossulus) were consistently restricted to the early stages of succession (Fig. 3). Both B. glandula and M. trossulus grew rapidly, but never were large enough to escape predation by Nucella and, in many cases, were not firmly attached to the rock (E. L. Berlow, personal observation). C. dalli escaped predation by Nucella due to its small size, but was easily overgrown by other larger species. All three species consistently declined by the middle of the second year of succession, despite the fact that some were abundant in younger, nearby plots at the same time. Thus, all three were relatively good dispersers/colonizers, but were susceptible to some combination of predation, competitive exclusion by later species, and/or physical disturbances (e.g., waves: E. L. Berlow personal observation).

At least four species (S. cariosus, M. californianus, Pollicipes, and Anthopleura) consistently did not colonize plots in the first year of succession, despite the fact that some were abundant in older, neighboring plots at the same time. These 'mid-successional' species colonized and/or grow more slowly, but are more capable of reaching a size refuge from predation (or are not eaten: e.g., Anthopleura), and are generally more robust or less susceptible to being dislodged, than the early species (Dayton 1971, Harger 1972, Suchanek 1981, 1985).

In this case, the general pattern of species replacement for the most abundant species was consistent regardless of the starting date or of variation in exact timing and relative abundances. Some of these consistencies in species replacement corroborate the idea that life-history trade-offs are important in canalizing succession (e.g., Connell and Slatyer 1977: ('tolerance model'), Tilman 1990, reviewed in McCook 1994).

2) Strong links between species:

Direct interactions between species are often not equally important; thus, the range of probable effects of a given species is usually a small subset of what is possible. Evidence from the interactions between early successional species in this community, suggests that when a direct link between two species is relatively strong, its total effect (direct + indirect) is less variable or conditional than if the link is weak (Chapter III). In the first year of succession, when the direct effect of predation by Nucella was potentially strongest, the sign of the total effect on M. trossulus and/or B. glandula was relatively consistent within and between starting dates, despite the potential complexity of indirect effects in this early successional interaction web, and despite natural variation between starting dates in the recruitment of prey, disturbance events, and environmental conditions (Chapter III). Early in succession, strong predation treatments also consistently dampened natural variation between individual replicates within a given starting date.

The longer term effects of Nucella on S. cariosus corroborate these results. Relative to the low density Nucella treatments, high densities of Nucella tended to dampen the effects of starting date or year on the final abundance of large S. cariosus (Fig. 9c and e: solid bars). In contrast, low densities of Nucella tended to magnify yearly variation in the abundance of S. cariosus (discussed below). Similar effects of strong predation have been observed in freshwater communites, where strong predation by fish and salamanders eliminated the importance of initial conditions (Morin 1984, 1995).

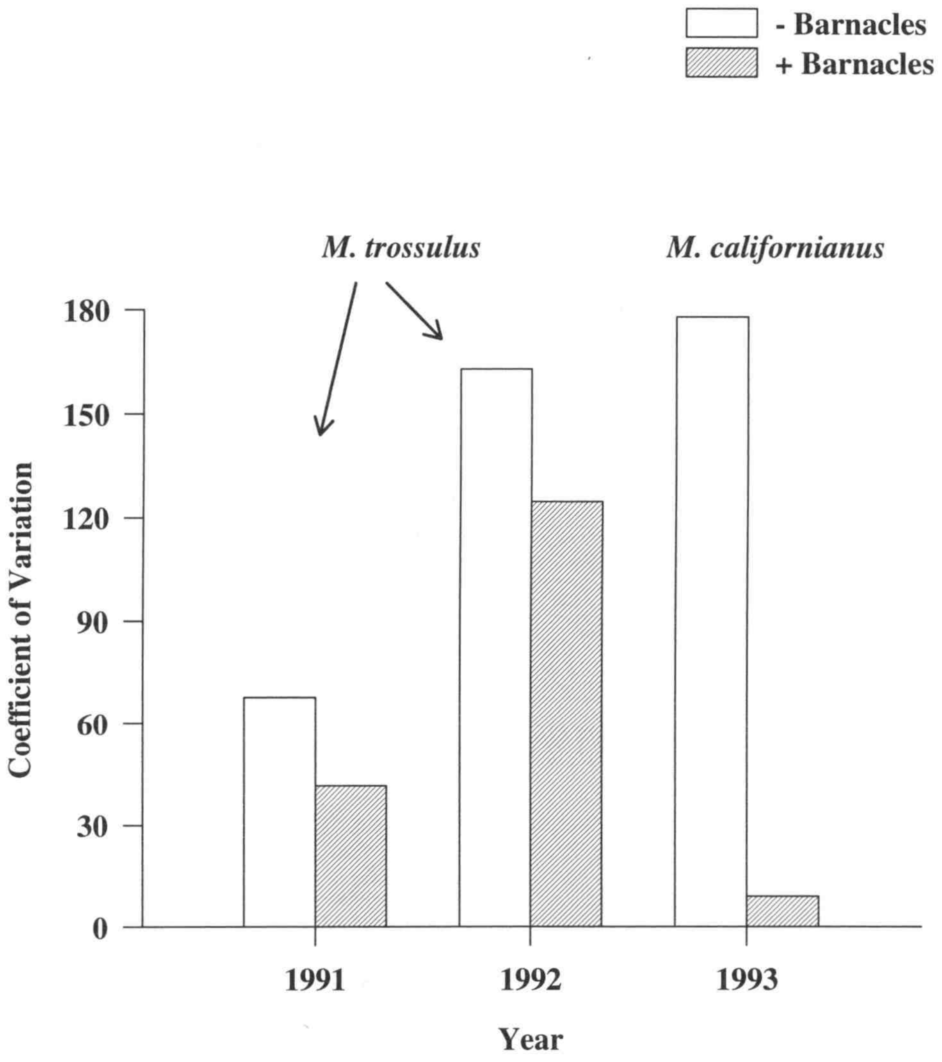
Other patterns consistent with the idea that strong links had 'noise-dampening' effects in the present study include:

a) In the absence of predation, barnacles facilitated M. trossulus, M. californianus, and Pollicipes (Figs. 10, 11, and 12: white bars). In the case of M. trossulus and M. californianus, the presence of barnacles appeared to dampen variation between years and starting dates by possibly providing a more reliable settlement substrate (Figs. 11 a vs. d, b vs. e, b vs. d; 12 c vs. e; Suchanek 1985). In Experiment #1, where mussels successfully colonized '-barnacle' cages (Figs. 11 and 12), the presence of barnacles reduced the spatial spatial variation in mussel cover between individual replicates (Fig. 13). In some plots where barnacles were removed, a few mussels successfully recruited to small crevices in the rock surface, and once established, appeared to attract more recruits to their byssal threads (Paine and Levin 1981, Suchanek 1985). In other plots, no mussels ever colonized the bare rock. This pattern of variability between replicates is consistent with the idea that 'positive-feedback switches' (sensu Wilson and Agnew 1992) can make succession variable and contingent. In contrast to the mussels, Pollicipes was reliably less abundant in barnacle removal plots than in those where barnacles were present (Fig. 10)

The facilitation effect of acorn barnacles appeared not to depend on the particular species of barnacle present. For example, while Nucella influenced the relative abundances of B. glandula and C. dalli (Fig. 3) these differences were not translated into subsequent differences in Pollicipes or M. californianus cover (Figs. 10 and 12, Table 4: no NUC effects are significant for Pollicipes or M. californianus).

b) While not explored in the present study, it has been demonstrated elsewhere that M. californianus is a strong competitive dominant in this system (Harger 1972, Paine 1974, Paine and Levin 1981, Suchanek 1985). This strong effect ultimately canalizes the endpoint of succession, regardless of the complex and conditional dynamics of the early and mid-successional stages. Early events, (e.g., predation by Nucella or birds, variable pulses of recruitment, physical disturbances, etc.) may alter the dynamics of succession, but not the endpoint (Wootton 1993b, Chapter III, this study). The eventual dominance of M. californianus is consistent enough that the general dynamics of patch creation and disappearance have been successfully modeled independent of within-patch composition (Paine and Levin 1980)

Figure IV.13. Coefficient of variation for the cover of M. trossulus in years 1 and 2 (1991 and 1992) and M. californianus in year 3 (1993) of Experiment #1 (starting date: April 1991) in predator exclusion cages. M. californianus was not abundant in 1991 or 1992. M. trossulus was not abundant in 1993 (see Figs. 11 and 12). '-Barnacles' = barnacle recruits removed monthly; '+Barnacles' = barnacles allowed to settle naturally.



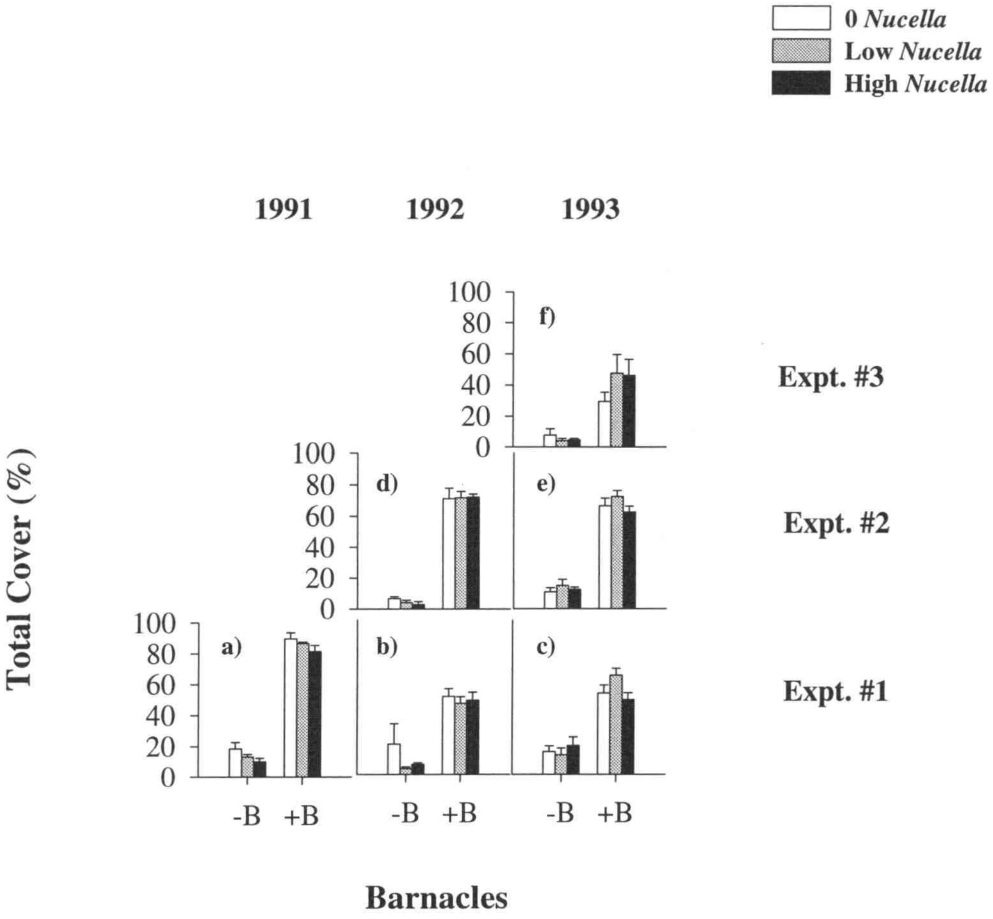
3) Diversity:

While I did not explicitly manipulate individual barnacle species or the diversity of barnacle species, the results of the present study are consistent with other evidence that species diversity can be a noise-dampening factor (McNaughton 1993, Tilman and Downing 1994, G. Allison manuscript). For example, while Nucella had significant (and variable) effects on B. glandula early in succession (Chapter III.), it had no significant effects on mid-successional species that were facilitated by the presence of barnacles (e.g., M. californianus and Pollicipes) (Figs. 10 and 12). This pattern may have been due to the fact that increases in C. dalli in the presence of Nucella compensated for the negative effects of predation on B. glandula (Fig. 3). Consequently, the total cover of sessile species (primarily barnacles: Figs. 3 and 4) in the first year of succession generally remained above 40-50% regardless of predator density (Figs 3 and 14a, d, e). Thus the effects of variation in B. glandula cover induced by Nucella could have been dampened by the compensatory response of C. dalli. Similar dampening effects due to compensatory responses appear to be common in some freshwater ecosystems (Walker 1991, Carpenter and Kitchell 1993).

II. Noise-amplifying forces: Weak effects.

While strong links between species have the potential to canalize succession, weak links, rather than being unimportant, appeared to play a role in magnifying stochastic variation between starting dates or years. This may be because the effects of weakly interacting species are more likely to be context-dependent than those of strongly interacting species (Chapter III). Some factors which appear to have contributed to the 'noise-amplifying' importance of weak effects in this system include:

Figure IV.14. a-f) Mean (± SE) cover of all macroscopic sessile species in the cages averaged over each year for each starting date. Data were pooled across ± mussel treatments. Codes are the same as in Fig. 6.



1) Indirect effects:

Indirect interactions between species occur when the effect of one species on another depends on the presence of a third species. Thus, they can be important in making the outcome of species interactions conditional on the context in which they occur (e.g., Price et al. 1980, Fairweather et al. 1984, Thompson 1988, Cushman & Whitham 1989, Cushman 1991, Steneck et al. 1991, Menge 1995, Chapter III). Some evidence suggests that when the direct link between two species is weak, indirect effects are more likely to generate variation in the total effect (direct + indirect) of one on the other than if the direct link is strong (Chapter III). For example, during the first year of succession, the total effect (direct + indirect) of 'weak' predation (low Nucella densities) on M. trossulus was more sensitive to spatial and/ or temporal variation in the indirect effect through B. glandula than was 'strong' predation (Chapter III). Consequently, the total effect (direct + indirect) of 'weak' predation on M. trossulus varied more in sign and magnitude between individual replicates, between starting dates, and between ±barnacle treatments than the effect of 'strong' predation (Chapter III; Fig. 11a, d, f). Although the resulting mean total effect of 'weak' predation was generally not significantly different from zero (Chapter III), the range of variation exceeded the magnitude of the strongest total effect observed (Chapter III).

2) Size Escapes:

When prey species are capable of attaining a size refuge from predation, spatial and/or temporal variation in predation intensity can have relatively long lasting effects on community structure (Paine 1976, 1977, Connell 1971, Lubchenco 1983, Sebens and Lewis 1985, Farrell 1988, Navarrete 1994). For example, on San Juan Island, some beds of large, adult S. cariosus which characterize the mid-intertidal landscape have been attributed to a single winter freezing event that reduced the density of Nucella 10 years earlier (Sebens and Lewis 1985). Weak predation is more likely than strong predation to magnify the importance escapes in size (e.g., Lubchenco 1983).

In the present study, the effect of low densities of Nucella on S. cariosus varied considerably between experiments in both sign and magnitude (Fig. 9c and e). High densities of Nucella apparently were more consistently successful at preventing S. cariosus from reaching a size refuge from predation, regardless of the year or starting date. Consequently low densities of Nucella magnified differences between starting dates in the cover of S. cariosus (Fig. 9c and e). As was the case with M. trossulus, the range of variation in S. cariosus under low Nucella densities was greater than the strongest effect of high Nucella densities observed (Fig. 9c and e).

3) 'Swamp' Escapes:

Even if a prey species is not capable of attaining a size escape from predation, it may be possible for it to 'swamp' the predator with sheer numbers. Thus, if a predator is not capable of eliminating a prey species throughout the natural range of variation in prey encountered, random variation in the 'supply' of prey can drive variation in the effects of predation (e.g., Fairweather 1988, Underwood and Fairweather 1989). Again, weak predation should be more likely than strong predation to magnify the importance of variation in prey supply.

In the present study, the intensity of initial colonization of B. glandula varied dramatically between starting dates (Figs. 3 and 6a, d, and f). While Nucella consistently had significant negative effect in all 3 experiments, B. glandula was so abundant in Experiment #1 that the proportional effect of predation was relatively weak (e.g., B. glandula maintained >70% cover in cages with Nucella; Fig. 6a; see Chapter III). Variation between starting dates in the strength of predation on B. glandula may have caused variation between starting dates in the indirect positive effect of Nucella on C. dalli (Fig. 8a and d; Dayton 1971, Paine 1981, Farrell 1991). While some of the differences in C. dalli cover between starting dates may have resulted from random yearly variation in recruitment, the differences appeared magnified by variation in the strength of predation on B. glandula (Figs. 3 and 8b and d). If predation by Nucella were strong enough to rapidly eliminate B. glandula even in years where they formed a dense monoculture, the indirect positive effect of Nucella on C. dalli probably would have been more consistent between starting dates and/or years (see Paine 1992, 1994 and Chapter III for a discussion of the importance of monocultures in evaluating interaction strength).

One important caveat for the 'noise-amplifying' role of weak effects is that an effect can be so weak that, even if it is extremely context-dependent, the range of variation it introduces may be ecologically trivial. Thus, weak links between species may be important to identify for at least two reasons: 1) they may play a role in making successional paths more contingent by amplifying stochastic variation, and 2) they may be so weak that they allow us to safely ignore the details of a large number of variable or conditional effects without compromising our predictive capacity.

For example, in the first year of succession, the effect of M. trossulus on B. glandula was consistently weak (Chapter III; Fig. 6a, d, and f). Thus, the potential indirect effect of Nucella on B. glandula through M. trossulus remained weak, despite a consistently strong direct link between Nucella and M. trossulus (Fig. 11: '-B' treatments; Chapter III). Much variation in the effect of Nucella on B. glandula could be explained without information about indirect effects through M. trossulus (Chapter III).

Similarly, the effects of mussels (primarily M. trossulus) on Pollicipes and Anthopleura were consistently weak and not significant (see Data Analysis). This may have been partly due to the fact that total mussel cover (M. trossulus and M. californianus) was generally low in this study (Figs. 3, 4, 11, and 12). Therefore, removing mussels had little consequence, and many potential indirect effects mediated by M. trossulus could be ignored in this study. For example, others have documented potentially strong direct facilitation of M. californianus by M. trossulus (Paine and Levin

1981, Suchanek 1985) and an indirect negative effect of Nucella on M. californianus by consuming M. trossulus (Navarrete 1994). I was not able to directly quantify these effects because I did not selectively remove each mussel species. However, in cages in the present study, strong negative effects of Nucella on M. trossulus (Figs. 3 and 11) did not result in significant effects of Nucella on M. californianus later in succession (Figs. 4 and 12c and e).

In conclusion, many landscapes are characterized by a mosaic of patches in various stages of succession (Paine and Levin 1981, Sousa 1984b, Pickett and White 1985). The degree to which succession is canalized or contingent influences the type and amount of information necessary to understand, predict, or manage variability in the landscape. Since different patterns and mechanisms of succession can be operating at different times or on different species at the same time, predictability will ultimately depend on the question of interest. However, for a given variable (e.g., a species abundance), the amount of detailed, site-specific information which can be ignored without sacrificing predictive power will depend on the relative balance of 'noise-amplifying' versus 'noise-dampening' forces operating. Some factors which appear important for determining the relative contingency of successional pathways include: 1) the importance of physiological and life-history constraints and tradeoffs (Tilman 1990, McCook 1994), 2) the potential for functionally 'redundant' species to have compensatory effects (Walker 1991, Lawton and Brown 1993, McNaughton 1993?, Tilman and Downing 1994), and 3) the distribution of interaction strengths between species (Power et. al 1995, Chapter III). All three can influence the degree to which natural variability in recruitment, disturbance, and environmental conditions alter the outcome of species interactions (e.g., through 'size escapes', 'swamp escapes',) and b) the degree to which indirect effects complicate or simplify predictability (Chapter III).

Table IV.1. Randomized block analysis of variance of the first two years of the first two experiments (starting dates) (ANOVA I, Fig. 1) to test for the effects of AGE (= experimental duration, in years), START (= experiment starting date), NUC (= *Nucella*), and MUS (= mussels) on the cover of *Balanus glandula*, *Chthamalus dalli*, *Semibalanus cariosus*. Data are arcsin(squareroot)-transformed covers averaged over each year for each experiment. df: degrees of freedom; MS: type III mean squares; F: standard F-values. Bold face p-values indicate that the factor is significant at α=0.05. Asteriks indicate that the factor is significant at α=0.025 (Bonferroni correction for performing two analyses on the same data)

ANOVA #I: 2 **I_I_**
1 **I_I_**
1 2 3

Source	df	Statistic	*B. glandula*	*C. dalli*	*S. cariosus*
BLOCK	3	MS	0.11	0.12	0.007
		F	3.87	7.41	1.18
		p	**0.01***	**0.0002***	0.33
AGE	1	MS	5.11	0.11	0.40
		F	180.73	6.49	64.25
		p	**0.0001***	**0.01***	**0.0001***
START	1	MS	5.35	3.35	0.07
		F	189.01	202.45	10.85
		p	**0.0001***	**0.0001***	**0.002***
NUC	2	MS	0.5	0.17	0.015
		F	17.74	10.48	2.41
		p	**0.0001***	**0.0001***	0.10
MUS	1	MS	0.02	0.004	0.01
		F	0.68	0.24	1.73
		p	0.41	0.63	0.19
AGE*START	1	MS	1.40	3.30	0.04
		F	49.67	199.58	5.90
		p	**0.0001***	**0.0001***	**0.02***
AGE*NUC	2	MS	0.002	0.01	0.02
		F	0.08	0.89	3.52
		p	0.92	0.41	**0.04**

Table IV.1. (continued)

Source	df	Statistic	*B. glandula*	*C. dalli*	*S. cariosus*
AGE*MUS	1	MS	0.003	0.005	0.009
		F	0.11	0.33	1.41
		p	0.74	0.57	0.24
START*NUC	2	MS	0.74	0.05	0.003
		F	2.60	2.72	0.56
		p	0.08	0.07	0.57
START*MUS	1	MS	0.02	0.0001	0.005
		F	0.82	0.01	0.82
		p	0.37	0.94	0.37
AGE*START *NUC	2	MS	0.06	0.1	0.06
		F	2.29	6.22	0.95
		p	0.11	**0.003***	0.39
AGE*START *MUS	1	MS	0.24	0.003	0.005
		F	0.83	0.16	0.85
		p	0.36	0.69	0.36
NUC*MUS	2	MS	0.05	0.01	0.002
		F	1.65	0.64	0.27
		p	0.20	0.53	0.76
AGE*NUC *MUS	2	MS	0.001	0.006	0.001
		F	0.03	0.40	0.14
		p	0.97	0.67	0.87
START*NUC *MUS	2	MS	0.6	0.05	0.004
		F	2.21	3.04	0.71
		p	0.12	**0.05**	0.50
AGE*START *NUC *MUS	2	MS	0.01	0.01	0.002
		F	0.43	0.59	0.39
		p	0.65	0.55	0.68

Table IV.1. (continued)

Source	df	Statistic	*B. glandula*	*C. dalli*	*S. cariosus*
MODEL	26	MS	0.55	0.32	0.03
		F	19.33	19.28	4.20
		p	**.0001***	**0.0001***	**0.0001***
ERROR	66	MS	0.03	0.02	0.006
R^2			0.88	0.88	0.62

Table IV.2. Randomized block analysis of variance of the second two years of experiment #1 and the first two years of the experiment #2 (ANOVA II, Fig. 1) to test for the effects of YEAR (= census year), START (= experiment starting date), NUC (= *Nucella*), and MUS (= mussels) on the cover of *Balanus glandula*, *Chthamalus dalli*, *Semibalanus cariosus*. See Table IV.1 for details.

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ANOVA #II:   2  |_|_
             1  |_|_
                 1 2 3
```

Source	df	Statistic	*B. glandula*	*C. dalli*	*S. cariosus*
BLOCK	3	MS	0.14	0.26	0.02
		F	5.10	14.51	1.26
		p	**0.003***	**0.0001***	0.30
YEAR	1	MS	1.21	0.82	0.71
		F	44.72	46.20	54.46
		p	**0.0001***	**0.0001***	**0.0001***
START	1	MS	0.00001	0.82	0.15
		F	<0.0001	46.11	11.40
		p	0.98	**0.0001***	**0.001***
NUC	2	MS	0.46	0.18	0.09
		F	17.15	9.94	7.26
		p	**0.0001***	**0.0002***	**0.001***
MUS	1	MS	0.015	0.00002	0.06
		F	0.57	<0.001	4.50
		p	0.45	0.97	**0.04**
YEAR*START	1	MS	0.002	0.32	0.0005
		F	0.06	18.09	0.04
		p	0.81	**0.0001***	0.83
YEAR*NUC	2	MS	0.07	0.10	0.04
		F	2.64	5.82	3.28
		p	0.08	**0.005***	**0.04**

Table IV.2. (continued)

Source	df	Statistic	*B. glandula*	*C. dalli*	*S. cariosus*
YEAR*MUS	1	MS	0.02	0.00003	0.04
		F	0.64	<0.001	3.31
		p	0.43	0.97	0.07
START*NUC	2	MS	0.08	0.03	0.05
		F	3.02	1.84	3.73
		p	**0.05**	0.17	**0.03**
START*MUS	1	MS	0.02	0.006	0.006
		F	0.74	0.34	0.45
		p	0.39	0.56	0.50
YEAR*START *NUC	2	MS	0.001	0.01	0.02
		F	0.04	0.65	1.58
		p	0.97	0.53	0.21
YEAR*START *MUS	1	MS	0.005	0.02	0.003
		F	0.18	1.11	0.20
		p	0.67	0.30	0.66
NUC*MUS	2	MS	0.03	0.006	0.02
		F	1.07	0.36	1.38
		p	0.35	0.70	0.26
YEAR*NUC *MUS	2	MS	0.0001	0.01	0.01
		F	<0.001	0.82	0.75
		p	0.99	0.45	0.47
YEAR*NUC* MUS	2	MS	0.03	0.06	0.01
		F	0.95	3.60	0.76
		p	0.40	**0.03**	0.47
YEAR*START *NUC *MUS	2	MS	0.02	0.001	0.01
		F	0.66	0.06	0.79
		p	0.52	0.94	0.46

Table IV.2. (continued)

Source	df	Statistic	*B. glandula*	*C. dalli*	*S. cariosus*
MODEL	26	MS	0.12	0.14	0.06
		F	4.48	8.03	4.76
		p	**0.0001***	**0.0001***	**0.0001***
ERROR	64	MS	0.03	0.02	0.01
R^2			0.65	0.77	0.66

Table IV.3. Randomized block analysis of variance of the first two years of the first two experiments (ANOVA I, Fig. 1) to test for the effects of AGE (= experimental duration, in years), START (= experiment starting date), NUC (= *Nucella*), and BAR (= barnacles) on the cover of *Mytilus trossulus*, *M. californianus*, *Pollicipes*, and *Anthopleura*. Data for *Pollicipes* and *Anthopleura* were pooled across ± mussel treatments. See Table IV.1 for details.

ANOVA #I: 2 I_I_
1 I_I_
1 2 3

Source	df	Statistic	*M. trossulus*	*M. calif.*	*Pollicipes*	*Anth.*
BLOCK	3	MS	0.05	0.004	0.08	0.03
		F	3.99	3.67	6.78	7.40
		p	**0.01***	**0.02***	**0.0003***	**0.0001***
AGE	1	MS	0.14	0.04	0.56	0.53
		F	11.16	37.21	44.56	114.01
		p	**0.001***	**0.0001***	**0.0001***	**0.0001***
START	1	MS	0.34	0.006	1.05	0.21
		F	27.51	5.11	83.51	45.03
		p	**0.0001***	**0.03**	**0.0001***	**0.0001***
NUC	2	MS	0.17	0.002	0.01	0.01
		F	14.09	1.54	0.87	3.12
		p	**0.0001***	0.22	0.42	**0.05**
BAR	1	MS	0.45	0.01	0.25	0.03
		F	36.00	11.96	20.35	5.99
		p	**0.0001***	**0.001***	**0.0001***	**0.01***
AGE*START	1	MS	0.03	0.004	3.71	0.001
		F	2.80	3.71	0.41	0.23
		p	0.10	0.06	33.17	0.63
AGE*NUC	2	MS	0.01	0.002	0.001	0.001
		F	0.95	1.62	0.07	0.25
		p	0.39	0.21	0.93	0.78

Table IV.3. (continued)

Source	df	Statistic	*M. trossulus*	*M. calif.*	*Pollicipes*	*Anth.*
AGE*BAR	1	MS	0.15	0.011	0.09	0.0001
		F	12.66	9.76	7.26	0.03
		p	**0.0007***	**0.003***	**0.008***	0.87
START*NUC	2	MS	0.03	0.004	0.01	0.007
		F	2.39	3.56	0.86	1.51
		p	0.10	**0.03**	0.43	0.22
START*BAR	1	MS	0.002	0.01	0.23	0.001
		F	0.19	7.66	18.02	0.23
		p	0.67	**0.007***	**0.0001***	0.63
AGE*START *NUC	2	MS	0.01	0.003	0.001	0.0005
		F	1.16	2.71	0.05	0.12
		p	0.32	0.07	0.95	0.89
AGE*START *BAR	1	MS	0.05	0.007	0.07	0.01
		F	3.94	5.92	5.90	2.42
		p	**0.05**	**0.02***	**0.02***	0.12
NUC*BAR	2	MS	0.03	0.006	0.01	0.005
		F	2.28	0.54	0.93	1.19
		p	0.11	0.58	0.40	0.31
AGE*NUC *BAR	2	MS	0.01	0.0005	0.009	0.006
		F	0.84	0.41	0.72	1.36
		p	0.43	0.67	0.49	0.26
START*NUC *BAR	2	MS	0.02	<0.0001	0.02	0.004
		F	1.69	0.01	1.29	0.92
		p	0.19	0.99	0.28	0.40
AGE*START *NUC *BAR	2	MS	0.002	0.0002	0.007	0.005
		F	0.13	0.15	0.61	1.04
		p	0.88	0.86	0.55	0.36

Table IV.3. (continued)

Source	df	Statistic	*M. trossulus*	*M. calif.*	*Pollicipes*	*Anth.*
MODEL	26	MS	0.07	0.005	0.15	0.04
		F	6.05	4.29	12.33	9.07
		p	**0.0001***	**0.0001***	**0.0001***	**0.0001***
ERROR	$66^{Mt,Mc}$ $114^{Pp,An}$	MS	0.01	0.001	0.01	0.005
R^2			0.70	0.63	0.74	0.67

Table IV.4. Randomized block analysis of variance of the second two years of experiment #1 and the first two years of the experiment #2 (ANOVA II, Fig. 1) to test for the effects of YEAR (= census year), START (= experiment starting date), NUC (= *Nucella*), and BAR (= barnacles) on the cover of *Mytilus trossulus*, *M. californianus*, *Pollicipes*, and *Anthopleura*. See Table IV.3 for details.

ANOVA #II: 2 I_I_
1 I_I_
1 2 3

Source	df	Statistic	*M. trossulus*	*M. calif.*	*Pollicipes*	*Anth.*
BLOCK	3	MS	0.06	0.02	0.16	0.03
		F	6.69	5.71	8.15	4..64
		p	**0.0005***	**0.002***	**0.0001***	**0.004***
YEAR	1	MS	0.14	0.16	1.16	0.63
		F	15.22	40.23	60.60	86.32
		p	**0.0002***	**0.0001***	**0.0001***	**0.0001***
START	1	MS	0.0003	0.06	0.35	0.09
		F	0.04	14.54	18.53	12.54
		p	0.85	**0.0003***	**0.0001***	**0.0006***
NUC	2	MS	0.11	0.008	0.005	0.01
		F	12.46	2.10	0.27	1.56
		p	**0.0001***	0.13	0.76	0.21
BAR	1	MS	0.12	0.02	0.60	0.03
		F	13.90	6.00	31.23	4.90
		p	**0.0004***	**0.02***	**0.0001***	**0.03**
YEAR*START	1	MS	0.04	0.01	0.10	0.001
		F	4.09	3.59	5.18	0.16
		p	**0.05**	0.06	**0.02***	0.69
YEAR*NUC	2	MS	0.03	0.004	0.003	0.0001
		F	3.75	0.92	0.14	0.01
		p	**0.03**	0.40	0.87	0.99

Table IV.4. (continued)

Source	df	Statistic	*M. trossulus*	*M. calif.*	*Pollicipes*	*Anth.*
YEAR*BAR	1	MS	0.007	0.02	0.30	0.007
		F	0.79	4.15	15.61	0.91
		p	0.38	**0.05**	**0.0001***	0.34
START*NUC	2	MS	0.01	0.01	0.02	0.01
		F	1.53	2.45	0.94	1.38
		p	0.22	0.09	0.39	0.26
START*BAR	1	MS	0.07	0.004	0.04	0.0001
		F	7.06	1.05	2.26	0.02
		p	**0.01***	0.31	0.13	0.90
YEAR*START *NUC	2	MS	0.02	0.001	0.001	0.002
		F	1.91	0.35	0.06	0.34
		p	0.16	0.70	0.95	0.71
YEAR*START *BAR	1	MS	0.007	0.005	0.001	0.0001
		F	0.78	1.18	0.04	0.02
		p	0.38	0.28	0.83	0.89
NUC*BAR	2	MS	0.009	0.005	0.02	0.008
		F	0.98	1.31	1.29	1.10
		p	0.38	0.28	0.28	0.34
YEAR*NUC *BAR	2	MS	0.005	0.002	0.02	0.005
		F	0.50	0.50	0.92	0.66
		p	0.61	0.61	0.40	0.52
START*NUC *BAR	2	MS	0.01	0.003	0.009	0.003
		F	1.19	0.63	0.48	0.40
		p	0.31	0.61	0.62	0.67
YEAR*START *NUC *BAR	2	MS	<0.0001	0.002	0.002	0.005
		F	0.01	0.57	0.10	0.65
		p	0.99	0.57	0.90	0.53

Table IV.4. (continued)

Source	df	Statistic	*M. trossulus*	*M. calif.*	*Pollicipes*	*Anth.*
MODEL	26	MS	0.04	0.02	0.15	0.04
		F	4.11	4.02	7.94	5.37
		p	**0.0001***	**0.0001***	**0.0001***	**0.0001***
ERROR	$64^{Mt,Mc}$ $112^{Pp,An}$	MS	0.009	0.004	0.02	0.007
R^2			0.63	0.62	0.65	0.55

CHAPTER V

CONCLUSIONS

The general focus of this thesis has been to understand some of the causes of variability in the outcome of species interactions and the consequences of that variability for our ability to predict the effects of perturbations to natural communities. Replicating field experiments over both space and time proved to be a valuable tool for investigating patterns of context-dependency in natural communities.

In the rocky intertidal of San Juan Island, we (Berlow and Navarrete: Chapter II) we were able to demonstrate 1) a remarkable consistency of organizing processes over time under the same environmental conditions examined previously, and 2) dramatic spatial variation in the processes structuring the same species assemblage in a different microhabitat just meters away. Many ecologists have replicated experiments spatially to explore how community organization varies across gradients of physical conditions (e.g., Dayton 1971, 1975, Menge 1976, Lubchenco and Menge 1978, Underwood 1980, Louda 1982, Lubchenco 1986, Inouye and Tilman 1988, Power 1992, Menge et al. 1994). However, repeating studies over time is much less common (Connell 1974, Elner and Vadas 1990). By repeating landmark experiments at our study site, the inferential power of our manipulations was greatly increased. The consistency between our current results and Dayton's (1971) allowed us to more confidently conclude that the spatial differences we observed between microhabitats were not confounded by potential temporal differences between the years that our work and Dayton's were conducted. In addition, information about how community organization varied spatially between microhabitats and temporally within one microhabitat offered insights into how spatial variation in community organization might, itself, vary temporally between years of low and high recruitment. Thus, the 'comparative experimental' (Menge 1991a, Underwood and Petraitis 1993) approach employed in this study allowed us to expand our conceptual model of this community and potentially increase the range of conditions over which we have predictive power.

Temporal replication of experiments in the 'simple', early-successional community on the Oregon coast revealed complex and variable direct and indirect interactions between species (Chapter III). The results of this study are consistent with the hypothesis that, all else being equal, when the direct effect of one species on another is relatively strong, the total effect (direct + indirect) is less variable or conditional than if the direct effect is weak.

When the direct effect of Nucella on a given prey species was relatively strong, its total effect was less sensitive to the presence/absence of the other prey species than when predation was weak. Consequently, the absolute change in cover attributable to indirect effects was smallest in treatments where the direct effect of predation was strongest.

Similarly, the total effect of 'strong' predation was relatively consistent within and between experiments, despite the potential complexity of indirect effects in the web examined, and despite natural variation in the recruitment of prey, disturbance events, and other environmental conditions. In contrast, the outcome of 'weak' predation was more spatially and temporally variable in sign, and whether it magnified or dampened natural differences between individual replicates varied between experiments. Since the total effect of weak predation was variable, the mean was generally not significantly different from zero (no effect). However, in some cases, the range of variation (both within and between experiments) in the total effect of weak predation exceeded the magnitude of the strongest mean total effect observed.

The direct effects of whelks were generally limited to the early successional stages (1.5 years) of this community because subsequent species which colonized either reach an effective size refuge from predation or are not eaten by whelks (e.g., anemones and algae) (Chapter IV). However, longer term effects of Nucella on the abundance of large Semibalanus which had escaped predation were consistent with the idea that weak interactions can have 'noise-amplifying' effects. Strong predation by Nucella evidently was more consistently successful than weak predation at preventing S. cariosus from reaching a size refuge from predation, regardless of the year or starting date. In contrast, weak predation by Nucella, rather than being unimportant, tended to magnify variation between starting dates or years on the final abundance of large S. cariosus. In fact, the range of variation between the different successional trajectories of S. cariosus under weak predation was greater than the largest effect of strong predation observed.

One important caveat for the 'noise-amplifying' role of weak effects is that an effect can be so weak that, even if it is extremely context-dependent, the range of variation it introduces may be ecologically trivial. For example, in the first year of succession (Chapter III), the effect of M. trossulus on B. glandula was consistently weak. Thus, the potential indirect effect of Nucella on B. glandula through M. trossulus remained weak, despite a consistently strong direct link between Nucella and M. trossulus. Much variation in the effect of Nucella on B. glandula could be explained without information about indirect effects through M. trossulus. Similarly, later in succession (Chapter IV) the effects of mussels (primarily M. trossulus) on Pollicipes and Anthopleura were consistently weak and not significant. Therefore, removing mussels had little consequence, and many potential indirect effects mediated by M. trossulus could be ignored in this study.

Thus, weak links may be especially important to identify for at least two reasons: 1) they can amplify stochastic variation over space and time by having effects which are highly context-dependent, and 2) they can be so weak that they allow us to safely ignore the details of a large number of variable or conditional effects without compromising our predictive capacity.

Both the results of early-successional species interactions and the longer term patterns of succession suggest that a knowledge of the relative strengths of direct interactions in a community may provide information about the level of certainty we can ascribe to our predictions about the consequences of a species loss or about the repeatability of successional pathways. When relatively few interactions are disproportionately strong and are all located along one main interaction chain (e.g., keystone effects and trophic cascades), we may be able to safely neglect the details of a large number of possible indirect effects without compromising our predictive capacity. In this case, identifying the species which have the strongest effects and the factors which influence variation in those effects may determine the level of uncertainty about our predictions. In contrast, if the interaction strengths are weak and more evenly distributed between species, predictions about the total effect of a species loss (or removal) may be so context-dependent that a considerable amount of detailed 'baseline' information is necessary to make even the simplest predictions.

Since the distribution of interaction strengths can vary considerably both between and within systems, critical challenge for ecologists is to develop easy, reliable techniques by which we can characterize the relative strengths of interactions in a community at a given site. The 'comparative experimental' approach used in this study proved a valuable tool for quantifying spatial and temporal variation in species interactions within the logistical limits of small scale field experiments. In addition, some potentially promising 'quick and dirty' alternatives have been proposed (e.g., Hairston 1988, Paine 1992, Menge et al 1994, Tanner et al., 1994, Wootton 1994a, b, Pfister 1995). More than one technique used simultaneously can provide complementary information, lend robustness to the interpretation of results, and still be more efficient than an exhaustive manipulation of all possible species pairs. Unfortunately, there has historically been little consensus regarding the ecological implications of different definitions of 'interaction strength' used by theorists and empiricists (McArthur 1972, Paine 1980, Yodzis 1981, 1988, Pimm et al. 1991, Lawton 1992, Wootton 1994a, c, Navarrete 1994). In addition, we are currently lacking a general theory which addresses the costs and benefits of different techniques for measuring interaction strengths in the field, the consequences of different methods for interpreting results, and the implications of different measures for integrating experiments with theory (but see Wootton 1994a, c).

With efficient and reliable field estimates of interaction strengths that are meaningful to theoreticians, predictability in ecology may then benefit enormously from methods used by meteorologists to forecast weather patterns. Historically, weather forecasting models have been plagued by higher-order interactions that result in chaotic weather patterns (Lorenz 1968, Tibbia & Anthes 1987). In this case, an important step in assessing the reliability of long-term forecasts is successfully identifying when a given weather pattern is likely to be stable or chaotic. As ecologists are increasingly being called upon to predict the outcomes of perturbations to natural communities, it is essential that we be able to assess the reliability of our predictions (Ludwig et al. 1993). One important step in that direction may involve successfully identifying situations where we can say, with confidence, that the possible outcomes are extremely context-dependent.

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