2000

The consequences of variable recruitment of prey for predators

Evie Ann Wieters
San Jose State University

Follow this and additional works at: https://scholarworks.sjsu.edu/etd_theses

Recommended Citation

Wieters, Evie Ann, "The consequences of variable recruitment of prey for predators" (2000). *Master's Theses*. 2028.

DOI: <https://doi.org/10.31979/etd.ud63-2yjx>
https://scholarworks.sjsu.edu/etd_theses/2028

This Thesis is brought to you for free and open access by the Master's Theses and Graduate Research at SJSU ScholarWorks. It has been accepted for inclusion in Master's Theses by an authorized administrator of SJSU ScholarWorks. For more information, please contact scholarworks@sjsu.edu.

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

**Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600**

UMI[®]

**THE CONSEQUENCES OF VARIABLE RECRUITMENT OF PREY FOR
PREDATORS**

**A Thesis Presented to the Faculty
of
San Jose State University
through
Moss Landing Marine Laboratories**

**In Partial Fulfillment
of the Requirements for the Degree
Master of Science in Marine Science**

**By
Evie Ann Wieters**

May, 2000

UMI Number: 1399832

UMI[®]

UMI Microform 1399832

Copyright 2000 by Bell & Howell Information and Learning Company.

All rights reserved. This microform edition is protected against
unauthorized copying under Title 17, United States Code.

Bell & Howell Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

© 1999

Evie Ann Wieters

ALL RIGHTS RESERVED

APPROVED FOR THE DEPARTMENT OF MARINE SCIENCE

A handwritten signature in black ink, appearing to read "Michael S. Foster", written over a horizontal line.

Dr. Michael S. Foster, Professor
San Jose State University

A handwritten signature in black ink, appearing to read "Steven D. Gaines", written over a horizontal line.

Dr. Steven D. Gaines, Professor
University of California, Santa Barbara

A handwritten signature in black ink, appearing to read "James T. Harvey", written over a horizontal line.

Dr. James T. Harvey, Professor
San Jose State University

APPROVED FOR THE UNIVERSITY

A handwritten signature in black ink, appearing to read "William Fish", written over a horizontal line.

ABSTRACT

THE CONSEQUENCES OF VARIABLE RECRUITMENT OF PREY FOR PREDATORS

by Evie Ann Wieters

Among sites along the central coast of California, densities of the whelk *Nucella emarginata*, a direct developer, were tightly correlated with prey recruitment, while densities of the seastar *Pisaster ochraceus*, which has pelagic larvae, were not. Reciprocal transplant of whelks between two sites of similar habitat characteristics but different levels of prey recruitment showed that whelks in the high prey recruitment site maintained higher densities and higher survival, but the mechanisms leading to these results differed between species. By manipulating the abundance and seasonal timing of new barnacle recruits entering whelk habitat at a given site, I was able to quantify and separate the effects of recruitment intensity and frequency. Responses of predatory whelks varied among species, and those species that did respond displayed changes in movement, feeding, growth, and mortality. Frequent barnacle recruitment produced different responses by *Ocenebra circumtexta* than those produced by a single barnacle recruitment event.

ACKNOWLEDGMENTS

Many people contributed to this thesis, either directly or indirectly, and their help and support is deeply appreciated.

It is a pleasure to thank my advisor Mike Foster for his encouragement and patience. Mike challenged me to look at my research from a different perspective, and his flexibility allowed me to more easily mesh my personal life with my scientific aspirations (even when they took me to Chile).

It is impossible for me to fully express here my deep appreciation for the constant support and endless generosity of Steve Gaines, without whom I would not have been able to complete this thesis. He cheerfully offered help and advice on many aspects of my education. Steve also provided the practical support needed to do intertidal field research: lab space, use of field equipment, undergraduate field assistants, etc.

I am grateful to Jim Harvey for quickly producing constructive comments on my thesis.

I am in debt to Sergio Navarrete for his candid advice, guidance, and patience. Discussions with Sergio were probably the most educational and formative, and his comments on my thesis were invaluable. Sergio added realism to my often unrealistic plans and expectations, as well as pointed-out the detour route when I began to “go down that road”.

I am grateful to John Steinbeck and Jay Carrol at Tenera, who “bent-over-backwards” to facilitate my access to research sites at Diablo Canyon.

I thank the Moss Landing PIGS and members of the Gaines lab group for their help in the initial stages of this thesis. Special thanks to friends Ron Walder, Ross Clark and Kate Stanbury. Conversations with Ron were some of my most enjoyable moments at Moss Landing. Ross reminded me not to take myself too seriously, showed me how to take advantage of the free food at Happy Hour when I was too poor to feed myself, and

begrudgingly watched Basketball with me. Kate listened patiently for hours while I rambled on-and-on, challenged my ideas, celebrated my successes, and supported me through the difficult times. Kate often provided me with a home away from home.

Many undergraduate students helped me with field work at painfully early hours of the morning. I would especially like to thank Tiffany Jenkins, without whom I would not have been able to complete field work. I cannot count the number of times Tiffany stayed up all night to endure the often cold and windy night/dawn hours just to help me set-up and monitor experiments at frighteningly wave-exposed sites. I am also grateful to Suzanne Hebert, Randy Finke, Chris Krenz, and Zahna Naskouwi.

I thank the people of the Estacion Costera Investigaciones Marinas (ECIM) in Chile for their support. Discussions with Ruben Soto during the writing of this thesis helped to clarify my thoughts. Bernardo Broitman happily volunteered, on several occasions, to monitor my ongoing field experiments in Chile while I completed the writing of this thesis.

Finally, I express my gratitude to those that unconditionally offer their support and love: Sergio Navarrete, Zahna Naskouwi, my parents Bob and Jane Wieters, and my sister Julie. Zahna reminded me to always have fun.

The research was funded by grants from the Dr. Earl H. and Ethel M. Myers Oceanographic and Marine Biology Trust and the David and Lucille Packard Foundation.

TABLE OF CONTENTS

	<u>Page</u>
CHAPTER I. GENERAL INTRODUCTION.....	1
CHAPTER II. AMONG-SITES PREDATOR-PREY CORRELATIONS: BOTTOM-UP EFFECTS OF PREY RECRUITMENT VARY WITH PREDATOR LIFE HISTORY.....	7
Abstract.....	7
Introduction.....	9
Methods.....	11
Results.....	15
Discussion.....	17
References.....	21
Tables.....	26
Figures.....	27
CHAPTER III. VARIATION IN THE MOVEMENT, DIET, GROWTH, AND ABUNDANCE OF INTERTIDAL WHELKS BETWEEN HIGH AND LOW PREY RECRUITMENT SITES.....	31
Abstract.....	31
Introduction.....	33
Methods.....	36
Results.....	43
Discussion.....	50
References.....	59
Tables.....	64
Figures.....	67
CHAPTER IV. CONSEQUENCES OF VARIATION IN RECRUITMENT OF PREY <i>BALANUS GLANDULA</i> FOR PREDATORY WHELKS.....	77
Abstract.....	77
Introduction.....	79
Methods.....	84
Results.....	94
Discussion.....	106
References.....	119
Tables.....	126
Figures.....	131

TABLE OF CONTENTS (Continued)

CHAPTER V. GENERAL CONCLUSIONS.....	143
BIBLIOGRAPHY.....	148

LIST OF TABLES

<u>Table</u>	<u>Page</u>
II.1. Spatial correlations between densities of a) whelks, <i>Nucella emarginata</i> , and b) seastars, <i>Pisaster ochraceus</i> , and their prey.....	26
III.1. Regressions between shell length and wet weight of <i>Nucella emarginata</i> sampled at Arroyo Hondo and Diablo.....	64
III.2. Regressions between shell length and wet weight of <i>Acanthina spirata</i> sampled at Arroyo Hondo and Diablo.....	65
III.3. Two-way analysis of variance for the effect of site and whelk origin on distances moved by <i>Nucella emarginata</i> after 44 days from release in autumn 1996. One-way analysis of variance of the effect of site on distances moved by <i>Acanthina spirata</i> after 56 days from release in autumn 1996.....	66
IV.1. Contingency tables and ChiSquare analyses of the number of <i>Nucella emarginata</i> , <i>Nucella canaliculata</i> , and <i>Ocenebra circumtexta</i> observed on feeding area or sheltering habitats (crevice, pool) during low tide periods. Observed and expected values (in parenthesis) are reported for each treatment by habitat combination.....	126
IV.2. Contingency tables and ChiSquare analyses of diet composition of <i>Nucella emarginata</i> , <i>Nucella canaliculata</i> , and <i>Ocenebra circumtexta</i> . Data based on observed diet during low tide periods. Observed and expected values (in parenthesis) are reported for each treatment by prey type combination. Here, mussels are <i>Mytilus californianus</i> and barnacles are <i>Balanus glandula</i>	127
IV.3. Repeated measures analysis of variance of the effects of barnacle recruit additions on densities of <i>Nucella emarginata</i> . Since only two levels of time (periods) were considered, data conformed to assumptions of univariate split-plot ANOVA and only these results are presented for within subject effects (see text).....	128
IV.4. Repeated measures analysis of variance of the effects of barnacle recruit additions on densities of <i>Nucella canaliculata</i> . Since only two levels of time (periods) were considered, data conformed to assumptions of univariate split-plot ANOVA and only these results are presented for within subject effects (see text).....	129

LIST OF TABLES (Continued)

<u>Table</u>	<u>Page</u>
IV.5. Repeated measures analysis of variance of the effects of barnacle recruit additions on densities of <i>Ocenebra circumtexta</i> . Since only two levels of time (periods) were considered, data conformed to assumptions of univariate split-plot ANOVA and only these results are presented for within subject effects (see text).....	130

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
II.1. Map of central California showing location of study sites.....	27
II.2. A) Mean prey recruitment ($\pm$ SE) per site expressed as number of barnacle settlers per 100 cm ² (top left panel) and number of <i>Mytilus</i> settlers per 100 cm ² of mesh (bottom left panel, see Methods). B) Percent cover of adult barnacles (top right panel) and mussels (bottom right panel) at each study site. n.d. = no data available.....	28
II.3. Mean density ($\pm$ SE) of whelks <i>Nucella emarginata</i> (top panel) and seastars, <i>Pisaster ochraceus</i> (bottom panel), at each study site. n.d. = no data available.....	29
II.4. Correlation between mean barnacle and <i>Mytilus</i> recruitment (ranking of sites) and mean whelk (top panel) and seastar (bottom panel) densities.....	30
III.1. Mean ($\pm$ SE) percent cover of A) barnacles and B) mussels in Arroyo Hondo and Diablo Canyon during late summer 1996. Barnacles are presented as occupiers of primary space (top panel) and secondary space (inset top panel).....	67
III.2. A) Mean ($\pm$ SE) monthly recruit densities of mussels and B) barnacles attached to artificial collectors (see Methods) in the mid intertidal zones of Arroyo Hondo and Diablo Canyon. C) Density of whelks <i>Nucella emarginata</i> and <i>Acanthina spirata</i> at Arroyo Hondo and Diablo Canyon. P are the probability values associated to the one-way ANOVA F ratios for the between site comparisons.....	68
III.3. Size structure (shell length) of <i>Nucella emarginata</i> at A) Arroyo Hondo and B) Diablo Canyon. Mean $\pm$ 1 standard error of the mean and sample size are given in each panel. Logarithm of wet weight (WW) regressed on logarithm of shell length (SL) for whelks originating from Arroyo Hondo and Diablo Canyon are also presented (inset).....	69
III.4. Size structure (shell length) of <i>Acanthina spirata</i> at A) Arroyo Hondo and B) Diablo Canyon. Mean $\pm$ 1 standard error of the mean and sample size are given in each panel. Logarithm of wet weight (WW) regressed on logarithm of shell length (SL) for whelks originating from Arroyo Hondo and Diablo Canyon are also presented (inset).....	70

LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
III.5. Diet of small and large <i>Nucella emarginata</i> based on low tide observations at Arroyo Hondo and Diablo Canyon. Sample size is given for each whelk size by site combination.....	71
III.6. Diet of <i>Acanthina spirata</i> based on low tide observations at Arroyo Hondo and Diablo Canyon. Sample size for each site is given. Small and large whelks are combined.....	72
III.7. Frequency distribution of growth rates for marked native and transplanted <i>Nucella emarginata</i> whelks at Arroyo Hondo and Diablo Canyon. Mean (thin arrow) and median (thick arrow) growth rates and sample size are given in each panel.....	73
III.8. Frequency distribution of growth rates for marked native <i>Acanthina spirata</i> at Arroyo Hondo and Diablo Canyon. Mean (thin arrow) and median (thick arrow) growth rates and sample size are given in each panel.....	74
III.9. Median distances moved by <i>Nucella emarginata</i> and <i>Acanthina spirata</i> at each sampling period in autumn 1996 at Arroyo Hondo and Diablo Canyon. Upper panels show whelks in their native sites and the lower panel shows whelks transplanted to non-native sites (see Methods). There is no data for transplanted <i>Acanthina</i>	75
III.10. Survivorship of marked native <i>Nucella emarginata</i> and <i>Acanthina spirata</i> at Arroyo Hondo and Diablo Canyon after 50 days from release. Estimates of percentage of population alive is adjusted to account for those hidden during censuses (see Methods).....	76
IV.1. Sketch of the experimental design. Barnacle recruitment was manipulated by transplanting small barnacle recruits atop valves of mussel shells either once (Early) or twice (Frequent) during the main barnacle settlement season. To control for artifacts of the transplanting method itself, clean mussel valves were transplanted to 'shells only' treatments. The 'Control' treatment refers to plots that were left undisturbed for the duration of the experiment. See text for details.....	131
IV.2. Mean ($\pm$ SE) percent cover of mussels and barnacles at Diablo Canyon during late summer 1996. Insert shows barnacle cover on mussel shells....	132

LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
IV.3. Mean ($\pm$ SE) percent cover of small barnacle prey in experimental blocks at Diablo Canyon during late summer 1996.....	133
IV.4. Mean ($\pm$ SE) densities of whelks a) <i>Nucella emarginata</i> , b) <i>Nucella canaliculata</i> , c) <i>Ocenebra circumtexta</i> , and d) <i>Acanthina spirata</i> in experimental blocks at Diablo Canyon.....	134
IV.5. Density of <i>Nucella emarginata</i> , <i>Nucella canaliculata</i> , <i>Ocenebra circumtexta</i> , and <i>Acanthina spirata</i> on the study bench at Diablo Canyon. Each bar is the mean ($\pm$ SE) of 20 0.25m ² quadrats regularly positioned along two permanently marked transects in the mid zone of the experimental platform.....	135
IV.6. Variance in the density of <i>Nucella emarginata</i> , <i>Nucella canaliculata</i> , and <i>Ocenebra circumtexta</i> at different quadrat spacings (distance between quadrats along 20m transects), using the paired-quadrats variance method (see text).....	136
IV.7. Mean ($\pm$ SE) growth rates of marked juvenile a) <i>Nucella emarginata</i> and b) <i>Ocenebra circumtexta</i> experiencing different prey recruitment treatments (see text). Hatched bars represent mean growth rates for those marked whelks moving long distances outside of experimental plots.....	137
IV.8. Density of a) <i>Nucella emarginata</i> , b) <i>Nucella canaliculata</i> , c) <i>Ocenebra circumtexta</i> , and d) <i>Acanthina spirata</i> in experimental plots before and after the second pulse of barnacle recruitment. Each bar is the mean ($\pm$ SE) of average densities for 5 months monitoring periods before September (addition 1) and after September (addition 2). Densities for <i>A. spirata</i> are presented for the only block in which this species was observed.....	138
IV.9. Mean ($\pm$ SE) movement rate of marked individual <i>Nucella emarginata</i> , <i>Nucella canaliculata</i> , and <i>Ocenebra circumtexta</i> under natural conditions at Diablo Canyon.....	139
IV.10. Mean ($\pm$ SE) frequency at which a marked individual a) <i>Nucella emarginata</i> , b) <i>Nucella canaliculata</i> , and c) <i>Ocenebra circumtexta</i> was observed within control, early, and frequent prey recruitment plots.....	140

LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
IV.11. Percent of marked <i>Nucella emarginata</i> , <i>Nucella canaliculata</i> , and <i>Ocenebra circumtexta</i> whose empty shells were recovered (dead whelks).....	141
IV.12. Survivorship of transplanted barnacle recruits in predator exclusion (open circles), early (filled squares), and frequent (filled triangles) barnacle addition treatments.....	142

CHAPTER I

GENERAL INTRODUCTION

Many marine invertebrates have a life history that includes a planktonic larval stage, which remains in the water column from hours to months (Moran 1994; Strathmann 1987; Wray 1995). During this time, larvae are subject to processes acting on the water column and are often carried great distances from their parents before settlement occurs (Scheltema 1971). The process of settlement and recruitment links planktonic larvae with their benthic adult life history stage, thereby setting the initial abundances available to post-recruitment processes that influence juvenile and adult populations (e.g. competition, predation, physical disturbance). Therefore, variations in recruitment can be an important cause of variability in these “open” populations, and this source of variation has been advocated as a major determinant of community structure on rocky shores (Underwood and Denley 1984; Lewin 1986; Young 1987; Underwood and Fairweather 1989).

Studies on the temporal and spatial scales of recruitment have revealed great variability, but some consistencies do occur and have provided important insight into the causes of variable recruitment. Large-scale spatial variability (between regions, among sites kilometers or more apart) has largely been attributed to physical transport processes altering larval distributions and rates of arrival of larvae to the shore, including currents, wind patterns, tides, and shoreline topography (see review by Shanks 1995). Settlement, as well as recruitment, also varies among areas within a site (localities 10's of meters

apart), as there appears to be a gradient from high to low settlement along a decreasing gradient of wave-exposure. Such gradients in recruitment can at least in part be due to the fact that settlement can act as a “drain” on larval concentrations as a water mass passes over successive sites (Gaines and others 1985). Thus, both localities and areas within localities can often and consistently be ranked as receiving relatively higher or lower abundances of recruits (Sutherland 1990; Menge 1992; Menge and others 1994; Robles and others 1995; Farrell and others 1991; Caffey 1985; Wethey 1986; Pineda 1994).

Large variation in recruitment also occurs over small spatial scales (patches 10's - 100's of centimeters apart, see review by Crisp 1976) and appears primarily due to suitable settlement substrate (Denley and Underwood 1979; Gaines and Roughgarden 1985; Minchinton and Scheibling 1993), larval behavior (Strathmann and others 1981; Keough and Downes 1982; Raimondi 1991) and micro-hydrodynamic processes (Ekman 1983; Butman 1987). Although the nature of recruitment variation occurring over tens of centimeters is poorly understood, data suggest variability is negatively correlated with larval abundance (Underwood and others 1983; Underwood and Denley 1984; Gaines and Roughgarden 1985; Judge and others 1988).

Large within year (seasonal) and between years variability in settlement and recruitment also occurs and is generally associated with processes that alter the concentration of larvae in the water column, such as the timing of reproductive output by adults (Connell 1961; Christy 1982; Christy and Stancyk 1982; Geraci and Romairone 1982), changes in larval mortality rates (Gaines and Roughgarden 1987), as well as hydrodynamic factors (see references above).

Since variability can be observed at all scales of space and time, quantification of patterns of variation as well as identification of their causes and consequences requires the use of different approaches and techniques suited to address similar questions at different scales (Levin 1989, 1992). While each technique has its limitation, a combination of approaches can expand understanding, put results into context, and offer important insight into the scale-dependency of processes. Over large spatial and temporal scales, correlation is the primary tool for detection and characterization of patterns of variation, but they are generally weak approaches in terms of determining causes of variation (Diamond 1986; Lubchenco and Real 1991). On the other hand, field experiments are the most powerful tool ecologists have to determine causes of variation in natural communities, but are also necessarily limited in 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 and others 1984; Diamond 1986; Underwood and Petraitis 1993). Comparisons of processes acting among locations or initial sets of conditions have helped to refine hypotheses and expand the conditions under which experimental results are applicable (Berlow and Navarrete 1997). In this thesis, I have used these three tools to examine potential consequences of variable recruitment rates of prey on predators.

Despite the prominent role that predator-prey and plant-herbivore interactions have played in the study of marine communities (Underwood and Denley 1984; Menge and Sutherland 1987; Lubchenco and Real 1991), little attention has been given to the

theoretical and empirical study of the consequences of variable recruitment rates for predator-prey interactions (but see Fairweather 1988a; Gaines and Lafferty 1995; Robles and others 1995). Some experimental evidence has shown that variation in the availability of different potential prey in rocky intertidal habitats can greatly affect predation on them. Therefore, in conditions where the availability of prey varies via settlement of their larvae and their recruitment as juveniles, variation in recruitment of particular prey species may also influence the outcome of predatory interactions.

Theory (Getz 1984; Fretwell 1987; Arditi and Ginzburg 1989) predicts that greater prey production (recruitment) can support greater predator biomass, and in turn, greater predator density can cause higher mortality of local prey. Indeed, experimental field studies have seen that the intensity of the total effects of predators on prey does increase with increasing levels of prey recruitment (Robles 1997; Menge and others 1994). Correlated changes in local population sizes of predators and their prey are often considered evidence that prey can control predators and vice versa. In marine systems, however, the sign and intensity of these correlations are expected to change over temporal and spatial scales (Hastings 1977; McCauley and others 1993; Rose and Leggett 1990), as well as with the life history attributes of the species involved. Predators with direct development are expected to track among-site variability in prey productivity more closely than predators with pelagically dispersed larvae, which cannot develop typical numerical responses. In chapter II, I studied the relationships between local predator population size and local prey abundance or local prey recruitment rates for two predators with different modes of reproduction. Because I was interested in correlations that could be attributed

to population level responses (i.e. numerical) rather than behavioral changes (i.e. functional and aggregation responses), I examined changes that could be evaluated at scales of several hundred meters within a given site and compared them to sites tens of kilometers down the coast.

As mentioned above, field experiments have shown that variation in prey recruitment can greatly affect the pattern and intensity of predation on them. However, while there is a wealth of information on the effects of predators on prey, there is little evidence of the effects of prey on predators. The mechanisms by which individual predators adjust to differences in prey recruitment, and whether or not these responses ultimately influence predator population structure (abundance, size frequency distribution), remain largely unknown. In chapter III, I examined the potential short-term responses of two marine intertidal predators with direct development to natural large-scale variation in recruitment of their prey. Because large and consistent variability in recruitment occurs over relatively large spatial scales, I compared whelk behavior between two sites of similar habitat characteristics but with different levels of prey recruitment.

Large variability in prey recruitment is not only observed at large spatial scales, but also at local scales within a site. At these scales, experimental determination of the causes and consequences of variation is not only possible but necessary if community ecology is going to become a predictive science (Dayton 1971; Lubchenco and others 1993; Berlow and Navarrete 1997; but see Peters 1991). In chapter IV, I experimentally investigated the consequences of variable recruitment rates of barnacle prey within a given site, at scales of meters, on short and longer-term responses of predatory whelks. By

manipulating the abundance and seasonal timing of new barnacle recruits entering whelk habitat, I was able to quantify and separate the effects of recruitment intensity and frequency.

CHAPTER II

AMONG-SITES PREDATOR-PREY CORRELATIONS: BOTTOM-UP EFFECTS OF PREY RECRUITMENT VARY WITH PREDATOR LIFE HISTORY

Abstract

Theory predicts that greater prey production can support greater predator biomass, and in turn, greater predator density can cause higher mortality of local prey. Therefore, negatively correlated changes in populations of predators and their prey were evidence of "top-down" control of prey populations, whereas positive correlations were considered evidence of "bottom-up" influences of prey on predators. In marine systems, these correlations are expected to change over time and spatial scales, and with the life history attributes of the species involved. Predators with direct development are expected to track among-site variability in prey productivity more closely than predators with pelagically dispersed larvae which cannot develop typical numerical responses. In this study I looked at spatial correlations between local prey abundance, local prey recruitment rates, and the mean abundance of two types of predators over sites tens of kilometers apart along the coast of southern California. Predators were the whelk *Nucella emarginata*, a species with direct development, and the seastar *Pisaster ochraceus*, a species with pelagic larvae. My results indicate that a) densities of the predatory whelk *N. emarginata* are correlated with prey recruitment across sites tens of kilometers apart, b)

neither whelk nor seastar densities were correlated with local adult prey abundances across these same sites, and c) unlike whelks, seastars did not seem to track prey recruitment over space at these scales.

Greater prey production (recruitment) is correlated with higher densities of whelks but not seastars in central California, and the difference may be due to their different modes of reproduction. In contrast to my results, previous studies conducted in separate regions found that mean seastar density and recruitment of mussels were positively correlated among sites (Menge 1992; Robles and others 1995). The ability of predators with open populations to track prey productivity over large spatial scales is probably related to the degree of coupling between the larvae of these prey and predators, and to the way they respond to different oceanographic transport processes. Apparent regional differences in among site predator-prey correlations could thus be the result of regional differences in transport processes. Most existing predator-prey theory can be relevant for predators that have essentially closed population structure, but it is largely inappropriate for predators with open life history characteristics.

Introduction

The interaction between top-down (e.g. herbivory, predation) and bottom-up (e.g. nutrients) effects in the regulation of trophic levels within natural communities has received considerable conceptual and theoretical treatment (Oksanen and others 1981; Carpenter and Kitchell 1984, 1987; Carpenter and others 1985; Fretwell 1987; Oksanen 1988; Persson and others 1988; Menge and Olson 1990; Power 1990, 1992; Menge 1992; Strong 1992). In marine communities, numerous studies have indicated the strong top-down effects of herbivores and predators on their prey, but the paucity of studies on the bottom-up effects of nutrients or prey on predators is notorious (but see Fairweather 1988a; Menge 1992; Menge and others 1995; Robles and others 1995; Leonard and others 1998). Theory (Getz 1984; Fretwell 1987; Arditi and Ginzburg 1989) predicts that greater prey production can support greater predator biomass, and in turn, greater predator density can cause higher mortality of local prey. Following this line of argument, negatively correlated changes in the populations of predators and their prey were evidence of "top-down" control of prey populations, whereas positive correlations were considered evidence of "bottom-up" influences of prey on predators (Fairweather 1988a, b; Menge and others 1994; Robles and others 1995; Robles 1997). Because predators and prey can respond in diverse ways to changes in abundance of the other, the intensity and sign of these correlations are expected to change across temporal and spatial scales (Hastings 1977; Rose and Leggett 1990; McCauley and others 1993). In marine systems, these correlations also are expected to change with the life history attributes of the species

involved.

The life history of many marine invertebrates and fishes includes a planktonic larval stage, which remains in the water column from hours to months (Strathmann 1987; Moran 1994; Wray 1995). During this stage, larvae are subject to local and regional oceanographic conditions that can determine whether and where they return to suitable habitats used by adults (Roughgarden and others 1988; Pineda 1994). Depending to a great extent on the duration of the larval stage, the products of fertilization may be carried great distances away from their parents before settlement occurs (Scheltema 1971), and the juveniles that recruit to a given local population are likely to be immigrants from distant populations. These characteristics produce an 'open-population' type of dynamics, in which population size is largely independent of local adult reproduction (Underwood and Denley 1984; Gaines and Roughgarden 1985; Roughgarden and others 1985; Sale 1990). In contrast, organisms with direct development produce juveniles that are born and usually grow in the same habitat of the adults. These life-history characteristics produce a 'closed-population' in which local population size is more dependent on local demographics, and therefore, on local environmental conditions. Predator species with these different types of life history respond differently to variability in among-sites productivity of prey. Beyond the spatial scale of behavioral changes (e.g. aggregation), predators with direct development can increase local reproduction at high prey productivity sites (Spight 1974). Species with open populations lack this ability and therefore, all else being equal, are expected to track variation in prey productivity across sites less closely than direct developers. In this study, I tested these simple predictions in

predator-prey systems along the coast of central California.

I examined predator-prey correlations that can be attributed to population level responses (i.e. numerical responses) rather than behavioral changes (i.e. functional responses). I evaluated these correlations at scales of several hundred meters within a given site and compared them to sites tens of kilometers away. Specifically, I asked 1) do predator population sizes correlate with local prey abundance and/or with prey recruitment rates, and 2) do predators with different modes of reproduction show similar correlations with prey over these scales?

Methods

The system

Mussels and barnacles are dominant components of rocky, mid intertidal communities on the Pacific coast of North America. The most common mussels, *Mytilus californianus*, *M. trossulus*, *M. galloprovincialis*, and barnacles, *Balanus glandula*, *Chthamalus* spp., have pelagically dispersed larvae. Several studies have documented large spatial variation in settlement across tidal elevation and among sites within the same region (Dayton 1971; Connell 1985; Gaines and others 1985; Roughgarden and others 1988; Menge 1992; Menge and others 1994; Robles and others 1995; Connolly and Roughgarden 1998). However, individual sites can often be consistently ranked as receiving relatively high or low recruitment (Gaines and Roughgarden 1985; Menge 1992; Connolly and Roughgarden 1998).

Whelks (*Nucella emarginata*, *N. canaliculata*, *Acanthina* spp.) and seastars (*Pisaster ochraceus*) are common predators along the California coast, but marked differences in their abundances occur among sites (Foster 1990; Menge and others 1994). Both *Pisaster* and *Nucella* feed mostly on mussels and barnacles in the mid and low intertidal zones (Feder 1970; Palmer 1984; Robles and others 1995; Wieters and Navarrete 1998), while *Acanthina* spp. have a broader diet that frequently includes littorine snails and can be observed feeding in the mid and high intertidal zones (Menge 1974; see chapter II). Whelks are direct developers that lay benthic egg capsules from which small juveniles crawl-away. Numerical (Spight 1982) and behavioral (Dayton 1971; Navarrete 1996; Navarrete and Menge 1996) changes in populations of *N. emarginata* occur in response to changes in food supply, indicating that food can be a controlling factor for this predator species (Spight 1982). Growth rates of whelks (*Nucella* spp.) change with local food supplies (Spight 1982), and because clutch size increases with growth, an individual whelk can be more fecund when food is more abundant (Spight and Emlen 1976). Additionally, *N. emarginata* spawn more frequently during the year when prey are more abundant (Spight 1981).

The seastar, *Pisaster ochraceus*, has broadly dispersed pelagic larvae. Larvae are planktotrophic and spend between 75 and 230 days in the water column (Strathmann 1987). Based on empirical evidence from field experiments, predation by seastars on mussels is strongest where prey and predator abundances are greatest (Menge 1992; Menge and others 1994; Robles and others 1995). At scales of tens to hundreds of meters, changes in food supply produce rapid changes in seastar densities because

behavioral mechanisms, particularly aggregation, permit predators to concentrate in areas of high prey recruitment (Robles and others; 1995).

I chose eight rocky intertidal sites, similar in wave exposure and assemblage composition, distributed along 250 km of coastline around Point Conception, central California (Fig. 1). Point Conception represents a break between regions that differ in oceanographic conditions, including general circulation pattern and mean surface water temperature (Mackas and others 1992). To examine predator-prey relationships at these spatial scales, I sampled density and size structure of whelks, *N. emarginata*, and seastars, *P. ochraceus*, and local abundance and monthly recruitment of their prey, mussels and barnacles. Due to logistic constraints, sampling of monthly recruitment started irregularly among sites (see below).

Prey and predator abundance

To determine the local abundance of prey and predators at each site, I used the transect-quadrat method. Percent cover of mussels and barnacles within 10-12 0.25m² quadrats, with 81-100 systematically marked points, were sampled at one to two meter intervals along a transect line stretched parallel to the shore at the low, mid and high intertidal zones. Both primary and secondary covers of mussels and barnacles were recorded because barnacles that had settled atop secondary substrates (e.g. mussel shells) also are exposed to predators. Two rocky benches, tens of meters apart, were sampled at each site during autumn, 1996. Whelks were counted in each quadrat. To obtain an estimate of percent cover and whelk density at each site, samples were averaged across

tidal heights and benches.

Seastar densities were measured in three to five 50m² rectangular plots placed haphazardly along the lower shore at each site in August, 1997. Plots were determined by stretching a 25 meter tape horizontal to the shore and counting the number of seastars in a 2m wide strip along the tape.

Prey recruitment.

Mussel recruit density was estimated by monthly counts of the number of mussels settling on plastic mesh scrubbing pads (“Tuffies”). Mussel larvae attach to filamentous algae (Bayne 1964; Paine 1974) and these pads mimicked the natural substrata. Beginning in October 1995 (mainland sites) and February 1996 (island sites, Fig. 1), five tuffies were replaced each month in the mid-zone of each site. Monthly abundances were expressed as the mean number of mussels per 100 cm² of mesh. Because *Mytilus californianus* and *M. galloprovincialis* could not be distinguished when <2 mm long, they were lumped together in my estimates of recruitment. The only other mussel recruiting to my sites was *Septifer bifurcatus*, which is easily distinguished from *Mytilus* spp. at all sizes.

Barnacle recruitment was estimated by monthly counts of the number of barnacles, *Balanus glandula* and *Chthamalus fissus*, settling on 10x10 cm plexiglass plates fastened to the substratum. Each plate was covered with a no-slip adhesive tape (Safety Walk®) that mimicked the rough and pitted heterogeneity of the rock surface. Five plates were replaced each month in the mid zone beginning in June 1996 (Mussel Shoals, Arroyo, Diablo) and January 1997 (all other sites). Monthly densities were expressed as the mean

number per 100 cm² of plate.

Results

Small, post-recruit mussels (0.5-1 cm long) were seen primarily intermixed among adults, but also in patches and at margins of mussel beds. Abundances of small mussels in the field varied greatly from site-to-site, but mirrored my estimates of mussel recruitment made from monthly counts of mussels settling in tuffies. Those sites that ranked high in recruitment had massive amounts of small mussels forming dense patches that often covered large areas of the shore after approximately one month from the time that appreciable recruitment was observed in tuffies. Recruitment of *Mytilus* spp. was highest at the two most southern sites (Arroyo Hondo and Mussel Shoals) and similarly low across sites north of Arroyo Hondo. *Septifer bifurcatus* was absent north of Point Conception (Diablo and Lompoc), and recruitment was low relative to *Mytilus* spp. at all other sites, with the highest recruitment occurring at Arroyo Hondo (Fig. 2a).

No significant correlation was found between *Mytilus* spp. recruitment and local abundance of adult mussels (> 4 cm shell length) (Spearman Rho = 0.20, P = 0.7471). Sites with a wide range of recruitment rates had similar adult *Mytilus* cover. For example, mean monthly mussel recruit density at Mussel Shoals was over five times greater than at either Lompoc or Diablo, but local abundance of adult mussels at these sites was similar (55-60% cover, Figs. 2a,b). This appears to be partially explained by the accumulation of past settlement events at those sites with low recruitment rates; large (> 10 cm long) *M.*

californianus composed much of the mussel cover at Diablo, whereas mussels > 7 cm were rare at Mussel Shoals (*pers. obs.*). These results suggest that mussel mortality is greater at sites receiving higher mussel recruitment rates.

The barnacles *Balanus glandula* and *Chthamalus fissus* settled on plates from late spring to late autumn. Field observations confirmed that those sites with relatively high barnacle densities on plates also had dense patches of small barnacle recruits on adjacent rock surfaces or on shells of large *M. californianus*. *Balanus glandula* recruitment was low at all sites, and this apparently accounts for the general scarcity of adults of this barnacle in the mid zone (Fig. 2 a,b). Recruitment of *C. fissus* was overall greater than *B. glandula* and greatest at Jalama, Alegria, and Mussel Shoals. The general agreement of patterns of *C. fissus* recruitment (Figs. 2a) and local adult abundance (Fig. 2b) indicated that the higher abundance of this barnacle at southern sites is a result of higher recruitment levels (Spearman Rho = 0.9, P= 0.0374).

Given that all prey species in this study have pelagically dispersed larvae, I also examined among-site patterns of barnacle recruitment and mussel recruitment. There was a significant correlation between recruitment rates of *Mytilus* spp. and *C. fissus* across sites (Fig. 2a, Spearman Rho = 0.7143, P=0.0465), suggesting these larvae respond similarly to similar transport processes (Pineda 1994). Recruitment of *B. glandula* was too rare to make comparisons.

Mean densities of the whelk *N. emarginata* varied greatly among sites, ranging from 75.5 individuals/m² at Jalama to a low of 9.4 individuals/m² at Willows (Fig. 3). Similarly, densities of *Pisaster* varied an order of magnitude among sites, from 8

individuals to less than 0.5 per 50 m² in Lompoc and Diablo, respectively (Fig. 3). The correlation between *Pisaster* and *Nucella* densities among sites was non significant (Spearman Rho = 0.3214, P = 0.4821).

Neither seastar nor whelk densities correlated with local abundance of adult mussels or barnacles (Figs. 3a, 2a,b; Table 1). In addition, there was no correlation between barnacle or mussel recruitment and density of seastars among sites (Figs. 4, Table 1). However, the number of whelks occupying a site was significantly related to *Mytilus* recruit density, and there was a striking positive correlation between recruitment rates of barnacles (*C. fissus*) and whelk density (Fig. 4, Table 1). Most of the variation in density of *N. emarginata* was explained by a simple measure of the average monthly number of new prey that arrive to a site; where recruitment of *Mytilus* and/or *C. fissus* was high, densities of *N. emarginata* were high, and vice versa.

Discussion

I emphasize three major points. First, densities of the predatory whelk *N. emarginata* seem tightly correlated with prey recruitment across sites tens of kilometers apart. Second, neither whelks nor seastar densities were correlated with local adult prey abundances among these same sites. Third, unlike whelks, seastars did not seem to track prey recruitment over space at these scales.

These results suggest that availability of small prey (new recruits) for juvenile and hatchling whelks acts as a bottleneck for whelk population size. Whereas adult *N.*

emarginata prey upon all sizes of barnacles and eat large mussels up to 12 cm in length (*pers. obs.*), whelk hatchlings and juveniles are restricted to smaller individuals of the same prey species (Hart and Palmer 1987). Smaller prey are more likely consumed than larger ones because of differential attack success (Palmer 1984). Therefore, new prey recruits are essential for survival of juvenile and hatchling whelks, and I suggest survival of juvenile whelks may be determined by nearshore oceanographic factors affecting the frequency and intensity of prey supply. Spight (1975) also suggested food supply for juvenile whelks limits the size of populations on San Juan Islands, Washington. He found that the number of barnacle recruits were positively correlated with size of the yearling crop of *N. emarginata*.

Further evidence of the importance of small prey recruits for whelk populations comes from examining local prey abundance among sites. My sites with low recruitment rates and correspondingly low whelk densities (e.g. Diablo, Lompoc) had high percent cover of adult mussels. These older, larger prey, however, are available only to adult whelks. Since whelk density was independent of local adult prey abundance, prey for adult whelks does not seem to limit *N. emarginata* population size.

The case of the seastar *Pisaster ochraceus* is different. Seastar density did not correlate with prey recruitment rates nor with local prey abundance, suggesting prey does not limit the population size of *P. ochraceus* along the coast of central California. Because *P. ochraceus* has an open life history with pelagically dispersed larvae, I suspected that settlement of seastars was highly variable and could be a controlling factor of local population size. As stated earlier, this openness in population precluded true numerical

responses by seastars to within site changes in prey abundance. The ability of seastars to track prey population changes over scales of kilometers is thus probably related to the degree to which larvae of predators and prey are affected by similar transport processes. Therefore, it is interesting to note that conditions that lead to higher settlement of prey did not seem to lead to higher settlement of seastars. Of course, other factors such as differential mortality may be responsible for the lack of correlation among sites.

These results differ from those of other studies conducted over different regions. Comparing differences in long-term records of predators and prey among two sites 80 kilometers apart on the Oregon coast, Menge (1992) found that areas of higher *Mytilus* spp. recruitment had higher *P. ochraceus* density (see also Navarrete and Menge 1996). Similarly, Robles and others (1995) found that mean seastar density and recruitment of *Mytilus* were positively correlated among three sites separated by hundreds to thousands of meters, on the west coast of Vancouver Island. I suspect that the ability of open-population predators to track prey over large-spatial scales will vary across regions according to regional variation in transport processes (e.g. Connolly and Roughgarden 1998). Such regional differences may also be responsible for the apparently much lower overall densities of *Pisaster* in all my sites as compared to those on the outer coast of Vancouver Island, Washington and Oregon (Menge and others 1994; Robles and others 1995). However, scientists are clearly just starting to elucidate regional as well as within site transport mechanisms.

Robles and others (1995) showed that seastars move up into higher intertidal habitats to feed during advancing tides and then move down to lower habitats during low

tide. My estimates of seastar density were made during low tide and so may be inaccurate if large proportions of seastar populations move to subtidal habitats. Such behavior would produce a bias in my results only if vertical movement patterns differed among sites, and I have no evidence suggesting that such differences occur. Additionally, I feel my estimates of local density of seastars are accurate because physical site characteristics make interchange between intertidal and subtidal habitats difficult for seastars. Most sites were surrounded by sandy beaches that would preclude alongshore as well as vertical migration of seastars beyond the very shallow subtidal zone.

Greater prey production (recruitment) appears to maintain higher densities of whelks but not seastars, and I suggest the variation among predators is due to their different modes of reproduction. Results from this study suggest that classic predator-prey theory (Rosenzweig and MacArthur 1963; Rosenzweig 1971). can be relevant for predators that have essentially closed population structure, but it is largely inappropriate for predators with open life history characteristics (Gaines and Lafferty 1995). Determination of the mechanisms enabling or precluding open-population predators to track prey over large spatial scales awaits further studies.

References

- Arditi, R., Ginzburg L. R. 1989. Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology* 139:311-326.
- Bayne, B. L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology* 33:513-523.
- Carpenter, S. C., Kitchell J. F. 1984. Plankton community structure and limnetic primary production. *American Naturalist* 124:159-172.
- Carpenter, S. C., Kitchell J. F. 1987. The temporal scale of variance in limnetic interactions and lake productivity. *American Naturalist* 129:417-433.
- Carpenter, S. C., Kitchell J. F., Hodgson P. A. 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35:634-639.
- Connell, J.H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93:11-45.
- Connolly, S. R., Roughgarden J. 1998. A latitudinal gradient in northeast Pacific intertidal community structure: Evidence for an oceanographically based synthesis of marine community theory. *American Naturalist* 151:311-326.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41:351-389.
- Fairweather, P. G. 1988a. Correlations of predatory whelks with intertidal prey at several scales of space and time. *Marine Ecology Progress Series* 45:237-243.
- Fairweather, P. G. 1988b. Predation can increase variability in the abundance of prey on seashores. *Oikos* 53:87-92.
- Feder, H. M. 1970. Growth and predation by the ochre sea star *Pisaster ochraceus* (Brandt) in Monterey Bay, California. *Ophelia* 8:161-185.
- Foster, M. S. 1990. Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia* 192:21-33.

- Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology. *Oikos* 50:291-301.
- Gaines, S., Brown S., Roughgarden J. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267-272.
- Gaines, S., Roughgarden J. 1985. Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences USA* 82:3707-3711.
- Gaines, S. D., Lafferty K. D. 1995. Modeling the dynamics of marine species: The importance of incorporating larval dispersal. Pages 389-412 *in* McEdward L., editor. *Ecology of Marine Invertebrate Larvae*. Boca Raton, FL: CRC Press.
- Getz, W. M. 1984. Population dynamics: a per capita resource approach. *Journal of Theoretical Biology* 108:623-643.
- Hart, M.W., Palmer A. R. 1987. Stereotypy, ontogeny, and heritability of drill site selection in thaidid gastropods. *Journal of Experimental Marine Biology and Ecology* 107:101-120.
- Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. *Theoretical Population Biology* 12:37-48.
- Leonard, G. H., Levine J. M., Schmidt P. R., Bertness M. D. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79:1395-1411.
- Mackas, D., Strub T., Hunter J. (eds.). 1992. Report on Climate Change and the California Current Ecosystem, Eastern Boundary Current Program, U.S. GLOBEC, Global Ocean Ecosystems Dynamics, Rep. 7. Scientific Steering Committee Coordinating Office, Univ.Of Calif., Davis.
- McCauley, E., Wilson W. G., de Roos A. M.. 1993. Dynamics of age-structured and spatially structured predator-prey interactions: individual-based models and population-level formulations. *American Naturalist* 142:412-442.
- Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755-765.
- Menge, B. A., Olson A. M. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* 5:52-57.

- Menge, B. A., Berlow E. L., Blanchette C., Navarrete S. A., Yamada S. B. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249-286.
- Menge, B. A., Daley B., Wheeler P. A. 1995. Control of interaction strength in marine benthic communities. Pages 258-274 *in* Polis, G. and K. O. Winemiller, editors. *Food Webs: Integration of Patterns and Dynamics*. New York: Chapman & Hall.
- Menge, J. L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. *Oecologia* 17:293-316.
- Moran, N. A. 1994. Adaptation and constraint in the complex life cycles of animals. *Annual Review of Ecological Systematics* 25:573-600.
- Navarrete, S. A. 1996. Variable predation: Effects of whelks on a mid intertidal successional community. *Ecological Monographs* 66:301-322.
- Navarrete, S. A., Menge B. A. 1996. Keystone predation: interactive effects of two predators on their main prey. *Ecological Monographs* 66:409-429.
- Oksanen, L. 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for coexistence? *American Naturalist* 131:424-444.
- Oksanen, L., Fretwell S. D., Arruda J., Niemela P. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240-261.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93-120.
- Palmer, A.R. 1984. Prey selection by thaidid gastropods: some observational and experimental field test of foraging models. *Oecologia* 62:162-172.
- Persson, L., Andersson G., Hamrin S. F., Johansson L. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. Pages 45-65 *in* Carpenter S. C., editor. *Complex interactions in lake communities*. New York: Springer-Verlag.
- Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Marine Ecology Progress Series* 107:125-138.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250:811-814.

- , 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733-746.
- Robles, C., Sherwood-Stephens R., Alvarado M. 1995. Responses of a key intertidal predator to varying recruitment of its prey. Ecology 76:565-579.
- Robles, C.D. 1997. Changing recruitment in constant species assemblages: implications for predation theory in intertidal communities. Ecology 78:1400-1414.
- Rose, G. A., Leggett W. C. 1990. The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. Ecology 71:33-43.
- Rosenzweig, M. L. 1971. The paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171:385-387.
- Rosenzweig, M. L., MacArthur R. H. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist 97:209-223.
- Roughgarden, J., Gaines S. D., Possingham H. 1988. Recruitment dynamics in complex life cycles. Science 241:1460-1466.
- Roughgarden, J., Iwasa Y., Baxter C. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology 66:54-67.
- Sale, P. F. 1990. Recruitment of marine species: Is the bandwagon rolling in the right direction? Trends in Ecology and Evolution 5:25-27.
- Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. Biological Bulletin 140:284-322.
- Spight, T. M. 1974. Sizes of populations of a marine snail. Ecology 55:712-729.
- , 1975. On a snail's chances of becoming a year old. Oikos 26:9-14.
- , 1981. How three rocky shore snails coexist on a limited food resource. Resource Population Ecology 23:245-261.
- , 1982. Population sizes of two marine snails with a changing food supply. Journal of Experimental Marine Biology and Ecology 57:195-217.
- Spight, T. M., Emlen J. M. 1976. Clutch sizes of two marine snails with a changing food supply. Ecology 57:1162-1178.

- Strathmann, M. F. 1987. Reproduction and development of marine invertebrates of the northern Pacific coast. Seattle: University of Washington Press.
- Strong, D.R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747-754.
- Underwood, A. J., Denley E. J. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151-180 in Strong D. R., Simberloff D., Abele L. G., Thistle A. B., editors. *Ecological Communities: Conceptual Issues and the Evidence*. Princeton: Princeton University Press.
- Wieters, E. A., Navarrete S. A. 1998. Spatial variation in feeding preferences of the rocky intertidal whelks *Nucella canaliculata* and *N. emarginata*. *Journal of Experimental Marine Biology and Ecology* 222:133-148.
- Wray, G.A. 1995. Evolution of larval and developmental modes. Pages 413-437 in McEdward L., editor. *Ecology of Marine Invertebrate Larvae*. Boca Raton, FL: CRC Press.

Table II.1. Spatial correlations between densities of a) whelks, *Nucella emarginata*, and b) seastars, *Pisaster ochraceus*, and their prey.

Correlation	n	Spearman Rho	P
<u>N. emarginata</u> vs. adult <u>Mytilus</u> abundance	6	0.2000	0.7471
<u>N. emarginata</u> vs. adult barnacle abundance	6	-0.1000	0.8729
<u>N. emarginata</u> vs. <u>Mytilus</u> recruitment	8	0.7619	0.0280
<u>N. emarginata</u> vs. barnacle recruitment	8	0.8333	0.0102
<u>P. ochraceus</u> vs. adult <u>Mytilus</u> abundance	6	0.3000	0.6238
<u>P. ochraceus</u> vs. adult barnacle abundance	6	0.1000	0.8729
<u>P. ochraceus</u> vs. <u>Mytilus</u> recruitment	7	0.4286	0.3374
<u>P. ochraceus</u> vs. barnacle recruitment	7	0.5357	0.2152

Figure II.1. Map of central California showing location of study sites.

Figure II.2. A) Mean prey recruitment ($\pm$ SE) per site expressed as number of barnacle settlers per 100 cm² (top left panel) and number of *Mytilus* settlers per 100 cm² of mesh (bottom left panel, see Methods). B) Percent cover of adult barnacles (top right panel) and mussels (bottom right panel) at each study site. n.d. = no data available.

Figure II.3. Mean density ($\pm$ SE) of whelks *Nucella emarginata* (top panel) and seastars, *Pisaster ochraceus* (bottom panel), at each study site. n.d. = no data available.

Figure II.4. Correlation between mean barnacle and *Mytilus* recruitment (ranking of sites) and mean whelk (top panel) and seastar (bottom panel) densities.

CHAPTER III

VARIATION IN THE MOVEMENT, DIET, GROWTH, AND ABUNDANCE OF INTERTIDAL WHELKS BETWEEN HIGH AND LOW PREY RECRUITMENT SITES

Abstract

Field experiments have shown that variation in prey recruitment can greatly affect the pattern and intensity of predation on them. However, the mechanisms by which individual predators adjust to differences in prey recruitment, and whether or not these responses ultimately influence predator population structure, are likely to differ according to the life history characteristics of the predator. I examined the potential short-term responses of two marine intertidal predators with direct development, the whelks *Nucella emarginata* and *Acanthina spirata*, to natural large-scale variation in recruitment of their prey (mussels and barnacles). Because large variability in recruitment occurs over relatively large spatial scales, I compared whelk behavior between two sites of similar habitat characteristics but with contrasting levels of prey recruitment. My results show that whelks in the high prey recruitment site (AH) maintain higher densities and higher survival rates, but the mechanisms leading to these results differed between species. Where prey recruitment was low, *N. emarginata* moved more to presumably capture enough food for growth. However, associated with the higher movement rates was an increased risk to other stresses (e.g. wave forces) which resulted in higher mortality. In contrast, the relatively low density of *A. spirata* at the low prey recruitment site (DC) appeared to be a

direct consequence of food limitation. Here, whelks completely preyed upon a different prey item, but did not obtain enough energy to sustain comparable body mass, as whelks of similar size were thinner at DC than at AH and had negative growth rates.

Additionally, *A. spirata* did not appear to have reproduced during 1996 at the low prey recruitment site.

Introduction

To explain differences in population and community structure between sites and/or geographic regions, marine ecologists are trying to integrate processes operating on large spatial scales with those occurring on the much better studied local scales. Increasing focus on large-scale processes arises from the want to understand the causes and consequences of variation in recruitment to “open” populations of marine organisms (Underwood and Denley 1984; Lewin 1986; Young 1987; Menge and Sutherland 1987; Underwood and Fairweather 1989; Menge 1992). Further, understanding how pre-juvenile (e.g. larval production, settlement and recruitment density) and post-juvenile factors (predation, competition, environmental stress) interact and influence each other, and what mechanisms underlie variation in each, could offer important insight into the multi-factorial nature of population and community regulation, as well as help develop more realistic fishery and management models (Tegner and Dayton 1977; Pfister and Bradbury 1996).

Studies of “supply-side” ecology are now a major subject of attention by marine ecologists (Sale 1990; Fairweather 1991). Most of this theoretical and empirical research has been directed toward understanding the causes of recruitment variation and its consequences on the population dynamics of selected species (e.g. Caffey 1985; Connell 1985; Gaines and Roughgarden 1985; Roughgarden and others 1988; Raimondi 1990; Sutherland 1990; Bertness and others 1992; Rodríguez and others 1993; Carr 1994; Possingham and others 1994; McEdward 1995), on the final composition of assemblages

(e.g. Petraitis 1991; Menge 1991; Menge and others 1993; Underwood and Anderson 1994) or on the interspecific interactions within trophic levels (i.e. competition, facilitation; Underwood 1978; Schmitt 1985; Sutherland and Ortega 1986; Navarrete and Castilla 1990; Schmitt and Holbrook 1990). Considerably less attention has been given to the consequences of variable recruitment rates for predator-prey interactions (but see Fairweather 1988; Gaines and Lafferty 1995; Robles and others 1995; Robles 1997), despite the prominent role that predator-prey interactions have played in the study of marine communities (Underwood and Denley 1984; Menge and Sutherland 1987; Lubchenco and Real 1991; Gaines and Lafferty 1995).

Recent experimental field studies have shown that the pattern and intensity of predation on prey species can be strongly influenced by variation in prey recruitment (Menge and others 1994; Robles and others 1995; Robles 1997). However, the effect of differences in prey recruitment on predator populations is largely unknown. The few field data available suggest that higher prey recruitment leads to greater abundances of predators (Menge and others 1994; Robles 1997; see chapter II). Yet, the mechanisms by which individual predators adjust to differences in prey recruitment, and whether or not these responses ultimately influence predator population structure (i.e. abundance, size frequency distribution), are unknown and likely to differ according to the life history characteristics of the predator. In one of the first studies attempting to relate densities of prey recruits to their predators, Fairweather (1988) simulated failure of recruitment by an abundant intertidal barnacle (*Tesseropora rosea*) into areas with and without predators (the muricid whelk *Morula marginalba*). He found that whelks responded readily and

negatively to experimentally induced variation in recruitment of barnacles; whelks avoided the areas that simulated failures of barnacle recruitment. More recently, Robles and others (1995) investigated how a key intertidal predator, the seastar *Pisaster ochraceus*, responded to differences in the availability of its main prey, *Mytilus californianus*, by experimentally reducing or augmenting mussel recruitment. They found that sea star aggregations formed in a matter of days in the recruitment augmentation experiment, whereas mean total densities of seastars became significantly lower on the recruitment reduction treatments. Both of these insightful studies underscore the importance of predator behavioral responses to small-scale spatial variation in prey recruitment, as well as the need for incorporating recruitment as an explicit variable in experimental and theoretical treatments of biological interactions and demographic models. However, these studies do not provide information on population responses of predators.

Two species of intertidal whelks, *Nucella emarginata* and *Acanthina spirata*, are conspicuous predators of barnacles and mussels in wave-exposed habitats along the central California coast (Menge 1974; West 1986; chapter II). Large-scale spatial variation (sites kilometers or more apart) in settlement of mussels and barnacles is common and has been attributed to factors altering larval distribution, including currents, wind patterns, shoreline topography, and regional differences in larval mortality (Boicourt 1982; Hawkins and Hartnoll 1983; Gaines and Bertness 1992, 1993; Shanks 1995; Bertness and others 1996; Connolly and Roughgarden 1998). In general, sites within a region can often consistently be ranked as receiving relatively higher or lower abundance of recruits (Connell 1985; Gaines and others 1985; Sutherland 1990; Menge 1992; Menge

and others 1994; Robles and others 1995; Robles 1997; Connolly and Roughgarden 1998). I used these types of temporally consistent, between-site differences in prey recruitment to examine the long-term consequences of differences in prey availability on *Nucella* and *Acanthina* whelk populations.

Previous studies have documented short-term responses of *Nucella* to variation in prey abundance over scales of few to tens of meters (Menge and others 1994; Wootton 1994; Navarrete 1996; Navarrete and Menge 1996). Other studies have looked at how local populations of *Nucella* can track changes in prey availability over time (Spight and Emlen 1976; Spight 1981, 1982). In this study, I look at the potential responses of *Nucella* and *Acanthina* species to natural variation in prey recruitment between two sites tens of kilometers apart, to answer four simple questions: Do whelks in a high prey recruitment habitat have 1) higher densities, 2) larger body sizes, 3) higher survival and 4) smaller foraging ranges than whelks in a recruitment-poor habitat? Although my study was conducted in only two sites and effects of prey recruitment could be confounded with other between-site differences, I believe my results, in conjunction with a previous, more extensive geographic survey (see chapter II), provide mechanistic insight into the consequences of variation in prey recruitment for predators with direct development.

Methods

Study Sites - Studies were done between January, 1996 and January, 1997 at two sites along the central coast of California, Diablo Canyon and Arroyo Hondo. Both of

these sites were part of a previous study of eight sites on a larger geographic scale (see chapter II). Diablo Canyon lies within a 20 km expansion of rocky shore within Pacific Gas & Electric's Diablo Canyon Nuclear Power Plant north of San Luis Bay. At this site, experiments were conducted on a broad, flat mid-intertidal rocky platform approximately 1,500m² in area that terminates abruptly at the seaward end in a vertical wall. Waves pound the seaward end of the platform and rapidly cover the entire platform at high tides. Here, the low zone is restricted to broad shallow channels dominated by a multispecies mosaic of seaweeds. The mid-zone is dominated by mussel beds of *Mytilus californianus*, bare rock patches, and large barnacles (mostly *Tetraclita rubescens* and *Semibalanus cariosus*, but also *Pollicipes polymerus*, *Balanus glandula*, and *Chthamalus fissus*). The upper zone is restricted to tops of small rocky outcrops and is dominated by bare space, the red alga *Endocladia muricata*, and sparse barnacles.

Arroyo Hondo is a series of narrow, flat mudstone benches that lie linearly along the shore approximately 125 km south of DC. This site experiences moderate to high wave forces and preliminary measurements from maximum wave force dynamometers (Bell and Denny 1994) suggest forces are similar to those at DC (author's unpublished data). The mid-zone is formed of flat benches covered with 1-2 layer deep mussel beds and patches of colonial anemones (*Anthopleura elegans*). Benches are less extensive than at DC and sand covers most of the low zone at the seaward edge and the high zone on the landward edge.

Despite similarities in wave exposure and general topography, mid-zone community structure varied between the two sites in subtle ways. At DC, mussel beds

occurred in monolayered patches, had high levels of unoccupied space ($\approx 35\%$), and consisted of seemingly old (highly eroded shells) and large (>12 cm) individual *Mytilus californianus*. At AH, a mixture of mussel species (*M. californianus*, *M. galloprovincialis* (= *M. edulis*, McDonald and Kohen 1988), and *Septifer bifurcatus*) formed dense patches of mostly small (< 3 cm long), young (clean, dark shells with no erosion) individuals stacked 2-3 layers deep. While scarce at DC, small barnacles (*B. glandula* and *C. fissus*) were more abundant at AH, often found in dense patches and attached to the top surfaces of mussel shells. I used the transect-quadrat method to quantify these differences. Percent cover of all sessile organisms occurring within 10-12 0.25m^2 quadrats, under 100 intersection points, was sampled at regular intervals along a transect line. Four to five transects were stretched horizontally along the mid-intertidal zone at each site, and transects were pooled to provide an estimate of mean prey abundance.

Prey Recruitment - I measured mussel recruitment from monthly counts of the number of mussels settling on plastic mesh scrubbing pads ("Tuffies"). These pads mimic the natural filamentous substrata to which mussel larvae are attached (see Menge and others 1994). Beginning in January 1996, five tuffies were placed in the mid-zone of each site, where prey abundance was sampled with quadrats, and replaced each month. Monthly field observations determined if high recruit densities counted in tuffies were eventually (within 2-3 mos.) reflected in the appearance of small mussels on natural substrata along the shore. Mean monthly recruitment rates were expressed as the mean number of individuals per 100 cm^2 of mesh and compared using ANOVA with site as a

fixed factor. after checking that assumptions of normality and homogeneity of variances were met.

Barnacle recruitment was estimated from monthly counts of the number of barnacles settling on 10x10 cm plexiglass plates fastened to the substratum with stainless-steel screws. Because barnacles avoid settling on smooth surfaces, each plate was covered with a no-slip adhesive (Safety Walk®) that mimics the roughened and pitted heterogeneity of the rock surface (Menge and others 1994). Five plates were placed in the mid-high intertidal zone beginning in June, 1996 and replaced each month. Barnacle plates were spaced throughout the area sampled by transects. Mean monthly densities were expressed as the mean number of individuals per 100 cm² of plate per month. Data were analyzed with a one-way ANOVA, with site as a fixed factor.

Whelk populations - At DC and AH, predatory whelks are the most abundant and conspicuous predators of mussels and barnacles in the mid-zone. Four species of whelks are present at DC, *Nucella canaliculata*, *Ocenebra circumtexta*, *Nucella emarginata*, and *Acanthina spirata*, whereas only the latter two species are present at AH. Predatory seastars, *Pisaster ochraceus*, are scarce at both sites (see chapter II) and are naturally absent from the mid-zone. Birds are present at these sites, but differ in abundance and species composition (see Discussion). In this study, I concentrate on the whelks *Nucella emarginata* and *Acanthina spirata* because they are the most common and abundant species along the central California coast, present north and south of Point Conception, (see chapter II) and at both AH and DC.

I estimated the density of all whelk species at low tide by counting the number of

whelks occurring in the 0.25m² area quadrats used in the prey abundance transects. In addition, to obtain diets of different size *Nucella emarginata* and *Acanthina spirata* in the field, I recorded shell length (apex to tip of siphonal canal), activity (see below), and, if a whelk was eating, the identity and size of its prey for each whelk encountered. Each whelk was then collected and taken to the lab, where wet weight and shell length were measured. Wet weight (in grams) was measured using a digital scale; shell lengths were measured to the nearest 0.1 mm using vernier calipers. Sample sizes per transect were small, so samples from different transects were pooled to provide single representations of size structure and density for each of the two sites. To compare relationships between shell length and body mass between sites, wet weight was regressed on shell length. ANCOVA with whelk shell length as the covariate was used to determine if regressions of wet weight on shell length differed between AH and DC. Data were Log transformed before regression.

A limited number of high tide observations of whelk activity and diet were also conducted on unusually calm days using a mask and snorkel. Sampling methods were similar to those described above for low tide observations.

Experimental Design

To look at differences in predator growth, movement, and mortality rates between sites, I conducted a replicated, reciprocal transplant experiment of marked whelks during late summer to early winter (July to January). Individuals of *N. emarginata* and *A. spirata* were collected from the low recruitment (DC) and the high recruitment (AH) sites. In the

lab, each shell was lightly filed near the lip to create a smooth surface, painted with white correction fluid ('Wite-Out'), and given a number or name that was written on the white surface with black India Ink. Tags were then coated with fast-drying Superglue® to reduce erosion. Once tags were dry, shell length was measured, and individual whelks were weighed and released. To reduce crowding when releasing whelks, two nearby areas were marked with stainless-steel screws placed at one-meter intervals along a five-meters stretch in the mid-intertidal zone. Whelks were released at the mid point section of both areas, which were similar in topography and wave exposure. Treatments included: (a) individual whelks from AH or DC released at marked release points at their original sites and (b) whelks from AH released in DC and *vice versa*. The re-introductions to the original sites served as a control for potential artifacts of experimental handling and for potential differences between sites in physical conditions.

Released marked whelks were surveyed every two days for the first week and then every 2-4 weeks for six months. A thorough systematic search was conducted along the length of the marked area and four meters to each side. A second search was then conducted along the entire bench. Searches included turning urchins, probing anemones, and using a light source to see within crevices and between mussels. In order not to disturb a whelk found deep within a crevice, a hand mirror was utilized to determine its identity. Between three and three and one-half hours of search were dedicated to each transect at each site. When a marked whelk was encountered, its tag number, species, shell length, position relative to release point (x-y coordinates), activity (see below), microhabitat (pool, crevice, flat rock, on mussel, under anemone, etc.), and, if the whelk

was eating, the identity of its prey species were recorded. Whelks were left in the position in which they were found. Shell length was not recorded until two months after release because growth rates were slow, and I did not want to excessively disturb whelks. Activity was described as either feeding (only those whelks observed drilling or with proboscis inserted in prey), searching (moving), mating, or inactive.

Observations on field diet of marked whelks were pooled with those obtained in the transect-quadrat samplings described above. For marked whelks encountered two or more times on different monitoring dates, only the observation for the first encounter was used so that observations were independent.

Growth - Mean growth rates of *N. emarginata* and *A. spirata* were calculated for each site x predator origin combination. Because of the presence of extreme values, the assumptions of normality and particularly homogeneity of variances were violated and could not be met by transforming data. I thus only report median and mean growth rates, as well as growth frequency distributions.

Movement - Median and mean distance displaced from the initial release point by *N. emarginata* and *A. spirata* was calculated for each time period x predator origin combination. The mean distances displaced after 44 days were then analyzed using a two-way ANOVA with site and predator origin as fixed factors. Distances were transformed to logarithms before analysis in order to meet assumptions of normality and homogeneity of variances. A time of 44 days was chosen for comparisons because this was the only time in which weather allowed both sites to be sampled so that the number of days since whelk release were equivalent.

Survival- The percentage of whelks seen alive at each successive monitoring date provided an estimate of survival rates. I considered a whelk as dead if all successive searches, conducted up to six months following release, failed to find the marked individual. The time to death was then the time elapsed from release to a day after the last date seen in a census. Death thus included whelks that emigrated beyond the searched area, whelks hidden in deep crevices for long periods of time (several months), whelks that completely lost their tags, and those whelks that actually died. I produced more conservative estimates of whelk mortality in two manners. First, I calculated the percentage of whelks that, after failing to appear in a given census, were observed again after two to three months. This percentage provided an estimate of my inability to observe live whelks present in the area but temporarily hidden and was then discounted from the mortality estimates. Secondly, in many cases I was able to find marked shells of dead whelks, which had been taken up by hermit crabs. Thus, the number of hermit crabs with tag whelk shells provided an extremely conservative estimate of whelk mortality.

Results

Prey abundance in the field - As mentioned earlier, mussel and barnacle prey abundance differed between the two sites (Fig. 1). Overall, barnacle cover was low at both sites (<10%), but it was over five times higher at AH than DC for both *C. fissus* and *B. glandula* (Fig. 1a). At both sites, barnacles were more abundant atop mussel shells (secondary cover) than on rock substrate (Fig. 1a insert). Although overall cover of mussels was similar between sites, the smaller *Mytilus galloprovincialis* was abundant at

AH and virtually absent from DC (Fig. 1b).

Prey recruitment - Recruitment rates of mussels, *Mytilus* spp. and *Septifer bifurcatus*, were significantly higher at AH than at DC (Fig. 2a). Mean monthly recruitment rates of *Mytilus* spp., averaged over the year, were two times greater than those of *S. bifurcatus* at AH, and five times higher than at DC. Recruitment of *S. bifurcatus* was zero at DC. Dense recruitment of *Mytilus* spp. generally occurred between May and June (peaked in June and then quickly dropped) at AH, whereas DC received almost no mussel settlement except for a small pulse during March. Recruitment of *S. bifurcatus* occurred as three small pulses in June, August, and October at AH. Additional data for 1995 and 1997-1998 (see chapter II, author's unpublished data) suggests that differences in mussel recruitment between sites are consistent among years.

Similarly, recruitment rates of barnacles, *Cthamalus fissus* and *Balanus glandula*, were significantly higher at AH than at DC (Fig 2b,). At AH, *C. fissus* monthly recruitment rates were six times higher than those of *B. glandula*. Recruitment of both species peaked in September and October. At DC, recruitment rates of *C. fissus* were low and virtually zero for *B. glandula* throughout the year. Although the monthly measurements of barnacle recruitment are limited (the first set of plates were installed in June), field observations were consistent with these patterns. At DC, virtually no new barnacles were observed during 1996; whereas at AH, dense patches of small barnacle recruits developed atop shells of large mussels and new recruits were seen on rock surface patches within the mussel bed.

Whelk population size and structure - Differences in predatory whelk densities

between sites were striking. *Nucella emarginata* were more abundant at AH than at DC and relatively more abundant than *Acanthina spirata* at both sites (Fig. 2c). Densities of *Nucella canaliculata* and *Ocenebra circumtexta* were low (5.9 ± 1.4 and 8 ± 1.2 individuals/m², respectively) year-round at DC and both species were absent from AH. Mean sizes and size frequency distributions of *N. emarginata* were similar between sites (Fig. 3). A tendency to bimodal size frequency distributions was observed in both sites, suggesting that whelks live roughly two years. The relation between shell length and body mass (wet weight) also appeared to be similar between sites (Fig. 3a insert, slopes and intercepts of log-log regressions did not differ significantly, Table 1), and no other morphological differences were apparent (i.e. similar shell thickness, shoulder widths, etc.).

Acanthina spirata was also significantly less abundant at DC compared to AH (Fig. 2c). Additionally, whelks of this species were on average larger at DC than at AH (Fig. 4). However, differences in mean size were primarily produced by the presence of more small individuals (<10 mm in length) at AH than at DC, rather than by whelks being larger overall at DC (Fig. 4). Hatchlings and small juveniles were never seen at DC in 1996 (*pers. obs.*). The overall relation between shell length and body mass (wet weight) also differed significantly between sites, even when the small individuals (<10 mm SL) at AH were dropped from the analysis (Table 2, Fig. 4a insert).

Whelk Diet - The proportion of *Nucella emarginata* found feeding when observations were made differed between sites. At AH, most (> 60%) of small (< 20 mm SL) and approximately half (48%) of large whelks examined at low tide were found

feeding. At DC, only 31% of small and 28% of large whelks were observed feeding during low tide. Observations made during high tides suggest that the percentages do not change substantially between low and high tide. The sole exception may be small *N. emarginata* at AH, which seemed more active at low than high tide. Although 50% of large (n = 10) and 21% of small (n = 73) whelks were observed feeding during high tide at AH, only 32% (n = 40) were found feeding during high tide at DC. High tide observations were made on unusually calm days and are restricted by sample size, but they tend to confirm my personal observations that whelks were actively feeding at both low and high tides, although searching behavior (movement) was only observed during high tide.

A total of five prey species (*B. glandula*, *C. fissus*, *M. californianus* at both sites, plus *M. galloprovincialis* and the polychaete *Phragmatapoma californica* at AH) were observed in the diet of *N. emarginata*. Of these, barnacles and mussels composed 99 % of the diet. At AH, the diet of juveniles (whelks < 20 mm) differed from that of adults (Fig. 5). Juvenile *N. emarginata* preyed almost exclusively upon barnacles (primarily *B. glandula* but also *C. fissus*), whereas adult whelks preyed predominantly upon mussels (*M. californianus* and *M. trossulus*). By contrast, at DC, both small and large *N. emarginata* preyed upon the mussel *M. californianus*, probably as a result of the scarcity of barnacles and small mussels.

The diet of *Acanthina spirata* also differed between sites (Fig. 6). At AH, the majority of whelks (70%) were found feeding, and all but two individuals were eating barnacles (*B. glandula* and *C. fissus*). The low frequency of mussels in the diet was

surprising because previous studies reported that the diet of this species included barnacles and mussels (Murdoch 1969). At DC, 49% of *A. spirata* were found feeding, but most of these ($\approx 75\%$) were eating the periwinkle *Littorina planaxis* (Fig. 6). Barnacles (mostly *Tetraclita rubescens*, but also *C. fissus* and *B. glandula*) composed the rest of the diet. One individual was found drilling a small chiton. Although I could find no other reports of *A. spirata* feeding on littorines, the higher intertidal species *A. punctulata* selectively preys on littorines (*L. planaxis* and *L. scutulata*) and barnacles (*B. glandula* and *C. fissus*) (Menge 1974). Because of small sample size for juvenile *A. spirata* at both sites (AH $n = 10$, DC $n = 5$), I was not able to evaluate whether juvenile and adult whelks differed in diet.

Experimental Marking Results- Marked whelks released at the beginning of the low tide seemed to have fully recovered before they were covered by water from the incoming tide. They re-attached and moved to a nearby crevice. Surveys were conducted as regularly as possible at both sites, but a combination of weather conditions and logistical conflicts did not allow me to survey both sites at similar time intervals beyond 50-60 days from initiating the experiment. Most whelks retained tags for up to six months, up to the conclusion of the experiment (see also Menge 1974; Spight 1982). Portions of a few tags peeled off after four months, but the shells retained the roughened file marks and recognizable tag remains.

Whelk growth - No differences in *N. emarginata* growth rates were detected between sites (Fig. 7a,b), suggesting that differences in prey recruitment do not correlate with differences in whelk growth during late summer and autumn when growth rates were

measured. Growth rates did not change in response to site of origin or when whelks were transplanted to opposite sites (Fig. 7c,d). The frequency distributions of growth rates are similar among all whelks, regardless of site or whelk origin (Fig. 7)

Growth rates of *A. spirata*, on the other hand, varied with site (Fig. 8). Whelks at the high prey recruitment site (AH) grew on average six times faster than whelks at the low prey recruitment site (DC). Further, *A. spirata* at DC exhibited mostly negative growth rates, suggesting that their energy expenditure was greater than their food intake, at least during late summer and autumn. I was not able to make repetitive observations on marked *A. spirata* transplanted to opposite sites.

Whelk Movement - Whelks exhibited different rates of movement at AH and DC (Fig. 9, Table 3: significant main effect of "Site"). Regardless of site of origin, *N. emarginata* moved much greater distances at DC than at AH. The difference between sites remained similar over time (Fig. 9a). Whelks originating from DC decreased their movement rates when placed at AH, and the mean distances traveled were similar to those of whelks native to AH (compare Fig. 9a and b). Further, whelks originating from AH moved little when placed back at AH, but moved great distances when placed at DC (Fig. 9b). However, increased movement rates of AH whelks at DC did not reach the high rates of DC whelks at their own site over the 44 days used in the analyses (Table 3, significant "Site x Predator origin" interaction).

Because the probability of finding marked whelks decreases the further whelks move from the release point, the data are conservative estimates of total distances traveled by whelks. Note that in some cases mean distance traveled appeared to decrease over

time beyond 50 days (Fig. 9), which is probably the result of increasing difficulty of finding whelks that have moved greater distances from the release point. Additionally, I looked at movement patterns of those whelks that were found on three to five consecutive monitoring dates and found that an individual whelk might make a long or short move at any time after release. This suggests that whelks did not initially move more or less in response to handling.

Like *N. emarginata*, significant differences in movement rates of *A. spirata* were observed between DC and AH (Fig. 9, Table 3: significant main effect of "Site").

Acanthina spirata in the low prey recruitment site (DC) moved greater distances than those whelks in the high prey recruitment site (AH). Too few observations were available for whelks transplanted to non-native sites to make reliable comparisons. Analysis was thus restricted to comparisons between sites.

Whelk Survival - More native *N. emarginata* and *A. spirata* survived at the high prey recruitment site (AH) than at the low prey recruitment site (DC) (Fig. 10). Judging by the number of whelks that were not seen in a survey but were found on successive dates, less than five percent of the whelk population was hidden at one time during the study. This suggests that my census efficiency was similar between sites and hidden whelks did not bias mortality estimates unequally among sites or predator treatments. These proportional differences in survivorship between sites were maintained when I compared only the number of tagged shells recovered (shells without the live animal). At DC, 13% (29 of 230) of tagged *N. emarginata* shells were found with hermit crabs in them. At AH, only 1 empty *N. emarginata* shell of 310 tagged whelks was found,

apparently trapped by byssal threads of mussels.

Discussion

With a few notable exceptions (see below), the impact of prey recruitment variation on predator populations has been largely ignored in most marine predator-prey studies due to the relatively large temporal and spatial scales over which prey affect predator population dynamics. To look at the effects of prey variation that occurs between sites tens of kilometers apart, I compared the responses of two predatory whelk species. Because the study sites were over 100 km apart (preventing exchange of individuals), and because both whelk species are direct developers which lack a swimming larva, individual and population differences between sites are expected to reflect more tightly within site conditions than broadcaster species (Spight 1981; see chapter II). My results showed that whelks in the high prey recruitment site had higher densities and had higher survival, but the apparent mechanisms that lead to these results differed for the two whelk species. In what follows, I discuss the main insights gained through these comparisons and experiments, as well as the limitations of my conclusions.

Diet - The feeding observations at AH provide strong evidence that, where recruitment of both mussels and barnacles is high, *N. emarginata* shift diet from barnacles to mussels as they progress from juvenile to adult. Although such shifts in diet have not been previously reported for *N. emarginata*, other thaid species (*N. lapillus*) are known to display similar changes with an increase in body size (Hughes and others 1992). This

apparent ontogenetic change in foraging behavior may likely be due to an increasing energy demand as the body grows and changes in the relative offer of larger prey. Through a series of detailed field observations and experiments, Palmer (1984) revealed that *N. emarginata* behavior is consistent with a prey-selection decision based on energetic considerations. Whelks appeared to discriminate not only among prey species, but also among different sized individuals of the same prey species. Additionally, Palmer (1983) found that *N. emarginata* smaller than 20 mm (Palmer's small- and medium-sized whelks) grew more rapidly on a diet of barnacles (*B. glandula*) than on a diet of mussels (*M. edulis*), particularly when the mussels were rather large (50 mm). Meanwhile, for those whelks larger than 20 mm, larger barnacles were increasingly more valuable than smaller ones and small (20 mm) mussels were similar in value to the large *B. glandula*. Because mussels grow considerably larger than barnacles, my observed change in diet is consistent with energy-maximizing behavior: small whelks prey mostly on small barnacles when available, as whelks grow there is an increase in prey size which eventually 'forces' them to switch to the larger mussels.

Unlike whelks at AH, whelks at DC did not display a size-related shift in diet composition. The majority of both small and large whelks fed on mussels (Fig. 5). This is likely because barnacles were scarce at DC (Figs. 1 and 2b) and small whelks must feed on whichever small prey they encounter first. Interestingly, diet of *N. emarginata* from another high prey recruitment site, Mussel Shoals, about 60 km south of AH (author's unpublished data), also shows a shift in diet with whelk size similar to that seen at AH (author's unpublished data). At Mussel Shoals, 82% of small whelks found feeding were

consuming barnacles, while 81% of large whelks were preying on mussels. These observations suggest that a change in diet of *N. emarginata* with increasing size may be a general pattern at those sites with high barnacle and mussel recruitment.

It appears that *A. spirata* responds more opportunistically to changing levels of prey recruitment. Where barnacle recruitment was relatively high (AH), 98% of those whelks found eating were preying upon barnacles. Where barnacle recruitment was low (DC), 70% of whelks were found preying upon the periwinkle snail, *Littorina planaxis*. The different diets are likely explained by differences in relative abundance between sites: littorines are almost absent at AH (*pers. obs.*) and barnacles are scarce at DC. Without further experiments, it is difficult to know whether prey preferences are different between whelks of different sites, or if in fact they simply feed on the most abundant prey species. Whatever the mechanism, it is clear that these whelks are able to utilize other prey when recruitment of mussels and barnacles is low.

Surprisingly, *A. spirata* rarely (only 2 individuals) preyed upon mussels at either site. Previous laboratory feeding experiments (Murdoch 1969) showed that these whelks readily consumed mussels as much as barnacles. It is possible that, when given a choice, *A. spirata* prefers littorines over large mussels. Another potential explanation for the low representation of mussels in the diet of this whelk species is that some competitive interaction between *N. emarginata* (which prey heavily on mussels) and *A. spirata* exist. My field observations do not tend to support this latter hypothesis.

Differences in handling times for different prey types may bias the characterization of diet based on feeding observations (Fairweather and Underwood 1983). Although *N.*

emarginata and *A. spirata* were rarely found actively searching during low tide, neither whelk species can capture and consume either barnacles, mussels or littorines during one high tide and, therefore, prey consumption continues during low tide. Such long handling times for all prey species probably decrease the potential bias in these estimates. While within-site comparisons may be more susceptible to bias due to different handling times, I believe that diet differences between small and large whelks at AH are real. It is unlikely that small whelks would have eaten mussels at high tide and not remained with a mussel into the following low tide.

Movement – Movement rates were clearly different between sites. At DC where prey recruitment was low, both *N. emarginata* and *A. spirata* moved surprisingly long distances (several meters in few days). The difference between DC and AH could very well be a response to prey density produced by differences in prey recruitment, but because prey (primarily mussels) also provide habitat structure for whelks, differences in whelk movement may also result from smaller distances traveled due to a more heterogeneous environment. However, overall cover of large mussels was similar at both AH and DC (Fig. 1), suggesting gross habitat characteristics were similar. Spight (1981) also observed that whelks moved minimally during a year of high food supply in one site on the Washington coast.

My reciprocal transplants support the idea that differences in movement rates are produced by differences in prey recruit densities. Whelks displaced from their native habitats and introduced to one with a different level of prey availability quickly changed movement patterns according to expectations based on prey recruitment. *Nucella*

emarginata from DC stopped moving when placed into AH, while whelks from AH began moving long distances when placed in DC, where prey recruitment was lower. Because the different responses were almost immediate, such behavior also likely occurs among patches of high and low prey recruit densities within a habitat. If true, changes in movement rates alone may account for observed aggregations reported by other authors (Berlow 1995; Navarrete 1996; Menge and others 1994; Wootton 1994).

Growth - Differences in prey recruitment rates and whelk movement did not translate into measurable differences in growth rates of *N. emarginata* between sites during the months of August to January. Although I do not have growth rates for other times of the year, I expected any growth differences between sites to be maximum during late summer and autumn because mussel recruitment in AH peaked at the end of June and the new settlers had grown to edible sizes by the end of August (*pers. obs.*). In addition, peaks in barnacle recruitment occurred in autumn (September-October). When food is available, *Nucella* are known to behave opportunistically by feeding more frequently regardless of season (Spight 1981; Wieters and Navarrete 1998).

To determine whether growth rates differed between seasons at DC (no comparable data for AH), I estimated growth of *N. emarginata* between spring and late summer by calculating the change in mean size of modal size-classes. Whelks of 13 mm shell length by the first of April 1996 had grown to 20 mm by late September (0.039 mm/day) and were 24 mm at the end of the year (0.04 mm/day) (author's unpublished data). While these estimates of growth rates are slightly higher than my estimates following marked individuals, they suggest that growth rates at DC are consistent

throughout the year. It is unlikely that large changes in growth rates between sites occurred from late January to March, as whelks commonly are less active during this time (Spight 1981). Spight (1981) also found temporally consistent, low growth for *N. emarginata* at sites where food was poor (Shady Cove) and suggests that “seasonality” should be less evident where prey abundance is more uniform throughout the year.

Why are growth rates of *N. emarginata* similar at AH and DC, despite large differences in prey recruitment? I suspect that this is partially explained by the high movement rates at DC. Whelks move great distances and this appears to pay-off in obtaining enough food to maintain similar growth rates. However, higher moving rates mean higher locomotion costs and thus AH whelks should have more surplus energy to direct to reproduction. This is consistent with the much higher *Nucella* densities observed at AH and the higher density of egg capsules observed at this site. Unfortunately, I do not have the appropriate data on *per capita* fecundity rates to test this proposition. Absence of between-site differences in growth rates seem to explain the lack of differences in shell length-body weight relationships.

Unlike *N. emarginata*, obvious differences in growth did occur for *A. spirata* (Fig. 8). Where prey recruitment was low (DC), whelks not only did not grow but they decreased in size. Where prey recruitment was high, *A. spirata* grew at rates similar to *N. emarginata*. Evidently, whelks at DC, feeding mostly on littorines, were not able to capture enough energy to sustain body mass, producing between-site differences in shell length -body weight allometries (Table 2). This suggests that a diet of littorines provides less energy than a diet of barnacles. However, Menge (1972) reports that a similar

Littorina species contain more calories than *B. glandula* (5.7 compared to 5.1 kcal/ash-free gram dry weight), so capturing and handling costs must be higher for littorines than barnacles for this explanation to hold truth.

Survival - *Nucella emarginata* and *A. spirata* show similar patterns of survival among sites (Fig. 10). Mortality appears high at both sites, but it was strikingly higher where prey recruitment was low (DC). Stresses during low tide periods are often the major cause of non-predatory mortality for whelks (Spight 1981), and this may explain in part why mortality was high at both sites during late summer and autumn. In central California, the lowest tides are during night and early morning hours throughout spring and summer and then change to late afternoons in autumn. However, it is difficult to imagine that physical stresses alone are so different so as to account for the large differences in mortality rates between sites.

The mechanism causing a higher mortality rate of *N. emarginata* at the site with low prey recruitment (DC) does not appear to be related to starvation. Whelks at DC grew at rates similar to those at AH and exhibited a similar body mass for a given shell length. Also, similar size frequency distributions for the two populations suggest that the factor of mortality between sites is not size-selective. I suspect that the answer lies in a combination of higher movement rates and higher exposure to multiple stresses at DC. For instance, both study sites are exposed to high wave forces during high tide when *N. emarginata* are active, but whelks at DC spend more time moving over the heterogeneous rock surface of the bench in search for food, and thus likely experience a higher risk of dislodgment by waves. Similarly, higher movement rates during low tides would expose

whelks to higher desiccation stress. This explanation is supported by the transplant of whelks originating from AH to DC. These whelks moved less and survived better than DC whelks in their native site.

The cause of higher mortality of *A. spirata* at DC does seem to be related to starvation. Apparently, whelks at DC are not able to eat enough to compensate for the greater movement rates. Other whelks are known to decrease movement when food is poor in order to save energy (Spight 1981), but this strategy should be expected only when prey replenishment occurs relatively frequently.

Other potential sources of differential mortality between sites were difficult to determine. Predatory seastars and crabs were essentially absent from both sites. Small octopuses were relatively common in tidepools at DC, but no marks (drill holes, chips, etc.) were apparent upon inspection of recovered whelk shells. Additionally, surveys of stomach contents of large anemones (*Anthopleura xanthogrammica*) were conducted at DC, and while several whelks were found inside stomachs and attached to the outer surfaces of anemones, this could not explain differences in whelk mortality rates between sites. Differences in seabird populations between sites did occur. A large (1000+ individuals) population of resident gulls is present year-round at AH, whereas a variety of seabirds nest atop a rock adjacent to the study bench at DC. The effect of bird foraging at both sites was addressed experimentally in a separate study (author's unpublished data), but results indicate that birds have no strong effects on whelk densities.

Because of logistical and funding constraints, there is always a trade off between the scope and depth of ecological studies. Here I concentrated on several aspects of

whelk behavior and population structure, but compromised the number of high and low prey recruitment sites to one each. This means that my interpretation of between-sites differences must be tempered by potentially confounding factors (Underwood 1997). However, in conjunction with a previous study conducted over 13 sites along the coast of California (see chapter II), the data presented here support the hypothesis that large-scale variation in prey recruitment has important direct and indirect effects on whelks' behavior and this in turn affects overall population abundances. The two predatory whelks, *Nucella emarginata* and *Acanthina spirata* respond behaviorally different to this variation, but in both cases it may lead to lower population abundances in a site with lower prey recruitment.

References

- Bayne, B. L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology* 33:513-523.
- Bell, E. C., Denny M. W. 1994. Quantifying 'wave exposure': A simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* 181: 9-29.
- Berlow, E. L. 1995. Patterns and dynamics of context-dependency in the marine rocky intertidal. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.
- Bertness, M. D., Gaines S. D., Stephens E. G., Yund P. O. 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 156:199-215.
- Bertness, M. D., Gaines S. D., Wahle R. A. 1996. Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series* 137:103-110.
- Boicourt, W. C. 1982. Estuarine larval retention mechanisms on tow scales. Pages 445-457 in Kennedy V. S., editor. *Estuarine Comparisons*. Proceeding of the Sixth Biennial International Estuarine Reserve Conference. New York: Academic Press.
- Caffey, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* 55:313-332.
- Carr, M. H. 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75:1320-1333.
- Connell, J. H. 1985. The consequences of variation in initial settlement versus post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93:11-45.
- Connolly, S. R., Roughgarden J. 1998. A latitudinal gradient in northeast Pacific intertidal community structure: Evidence for an oceanographically based synthesis of marine community theory. *American Naturalist* 151: 311-326.
- Fairweather, P. G. 1988. Consequences of supply-side ecology: manipulating the recruitment of intertidal barnacles affects the intensity of predation upon them. *Biological Bulletin* 175:349-354.
- Fairweather, P. G. 1991. Implications of 'supply-side' ecology for environmental assessment and management. *Trends in Ecology and Evolution* 6:60-63.
- Fairweather, P.G., Underwood A. J. 1983. The apparent diet of predators and biases due

- to different handling times. *Oecologia* 56:169-179.
- Foster, M. S. 1990. Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia* 192:21-33.
- Gaines, S., Brown S., Roughgarden J. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267-272.
- Gaines, S., Roughgarden J. 1985. Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences USA* 82:3707-3711.
- Gaines, S. D., Bertness M. D. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360:579-580.
- Gaines, S. D., Bertness M. D. 1993. The dynamics of juvenile dispersal: why field ecologists must integrate. *Ecology* 74:2430-2435.
- Gaines, S. D., Lafferty K. D. 1995. Modeling the dynamics of marine species: The importance of incorporating larval dispersal. Pages 389-412 in McEdward, L., editor. *Ecology of Marine Invertebrate Larvae*. Boca Raton, FL: CRC Press.
- Hawkins, S. J., Hartnoll R. G. 1983. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977-1981). *Journal of Experimental Marine Biology and Ecology* 62: 271-283.
- Hughes, R. N., Burrows M. T., Rogers H. H. 1992. Ontogenetic changes in foraging behaviour of the dogwhelk *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* 155:199-212.
- Hughes, R. N., Dunkin S de B. 1984. Effect of dietary history on selection of prey, and foraging behaviour among patches of prey, by the dogwhelk, *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* 79:159-172.
- Lewin, R. 1986. Supply-side ecology. *Science* 234:25-27.
- Lubchenco, J., Real L. A. 1991. Experimental manipulations in lab and field systems. Pages 715-7133 in Real, L. A. and J. H. Brown, editors. *Foundations of Ecology*. Chicago: The University of Chicago Press.
- McDonald, J. H., Kohen R. K. 1988. The mussels (*Mytilus galloprovincialis* and *Mytilus trossulus*) on the coast of North America. *Marine Biology* 99:111-118.

- McEdward, L., editor. 1995. Ecology of marine invertebrate larvae. Boca Raton, FL: CRC Press.
- Menge, B. A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecological Monographs* 42:25-50.
- Menge, B. A. 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* 146:69-100.
- Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755-765.
- Menge, B. A., Sutherland J. P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130:730-757.
- Menge, B. A., Farrell T. M., Olson A. M., van Tamelen P., Turner T. 1993. Algal recruitment and the maintenance of plant mosaic in the low intertidal region on the Oregon coast. *Journal of Experimental Marine Biology and Ecology* 170:91-116.
- Menge, B. A., Berlow E. L., Blanchette C., Navarrete S. A., Yamada S. B. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249-286.
- Menge, J. L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. *Oecologia* 17:293-316.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39:335-354.
- Navarrete, S. A. 1996. Variable predation: Effects of whelks on a mid intertidal successional community. *Ecological Monographs* 66:301-322.
- Navarrete, S. A., Castilla J. C. 1990. Resource partitioning between intertidal predatory crabs: interference and refuge utilization. *Journal of Experimental Marine Biology and Ecology* 143:101-129.
- Navarrete, S. A., Menge B. A. 1996. Predation and interaction strength: Interactive effects of two predators on their main prey. *Ecological Monographs* 66:409-429.
- Palmer, A. R. 1983. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. *Journal of Experimental Marine Biology and Ecology* 73:95-124.
- , 1984. Prey selection by thaidid gastropods: some observational and experimental field test of foraging models. *Oecologia* 62:162-172.

- Petraitis, P. S. 1991. Recruitment of the mussel *Mytilus edulis* L. on sheltered and exposed shores in Maine, USA. *Journal of Experimental Marine Biology and Ecology* 147:65-80.
- Pfister, C. A., Bradbury A. 1996. Harvesting red sea urchins: recent effects and future predictions. *Ecological Applications* 6:298-310.
- Possingham, H. P., Tuljapurkar S., Roughgarden J., Wilks M. 1994. Population cycling in space-limited organisms subject to density-dependent predation. *American Naturalist* 143:563-582.
- Raimondi, P. T. 1990. Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecological Monographs* 60:283-309.
- Robles, C., Sherwood-Stephens R., Alvarado M. 1995. Responses of a key intertidal predator to varying recruitment of its prey. *Ecology* 76:565-579.
- Robles, C. D. 1997. Changing recruitment in constant species assemblages: implications for predation theory in intertidal communities. *Ecology* 78: 1400-1414.
- Rodríguez, S. R., Ojeda F. P., Inestrosa N. C. 1993. Settlement of benthic marine invertebrates. *Marine Ecology Progress Series* 97:193-207.
- Roughgarden, J., Gaines S. D., Possingham H. 1988. Recruitment dynamics in complex life cycles. *Science* 241:1460-1466.
- Sale, P. F. 1990. Recruitment of marine species: Is the bandwagon rolling in the right direction? *Trends in Ecology and Evolution* 5:25-27.
- Schmitt, R. J. 1985. Competitive interactions of two mobile prey species in a patchy environment. *Ecology* 66:950-958.
- Schmitt, R. J., Holbrook S. J. 1990. Contrasting effects of giant kelp on dynamics of surfperch populations. *Oecologia* 84:419-429.
- Shanks, A. L. 1986. Tidal periodicity in the daily settlement of intertidal barnacle larvae and a hypothesized mechanism for the cross-shelf transport of cyprids. *Biological Bulletin* 170: 429-440.
- Shanks, A. L. 1995. Mechanisms of cross-shelf dispersal of larval invertebrates and fish. Pages 323-367 in McEdward, L. R., editor. *Ecology of Marine Invertebrate Larvae*. Boca Raton, FL: CRC Press.
- Spight, T. M. 1981. How three rocky shore snails coexist on a limited food resource. *Resource Population Ecology* 23:245-261.

- , 1982. Population sizes of two marine snails with a changing food supply. *Journal of Experimental Marine Biology and Ecology* 57:195-217.
- Spight, T.M., Emlen J. M. 1976. Clutch sizes of two marine snails with a changing food supply. *Ecology* 57:1162-1178.
- Sutherland, J. P. 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology* 71:955-972.
- Sutherland, J. P., Ortega S. 1986. Competition conditional on recruitment and escape from predators on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* 95:155-166.
- Tegner, M. J., Dayton P. K. 1977. Sea urchin recruitment patterns and implications of commercial fishing. *Science* 196:324-326.
- Underwood, A. J. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia* 33:185-202.
- , 1997. *Experiments in ecology*. Melbourne: Cambridge University Press, 504 pages.
- Underwood, A. J., Anderson M. J. 1994. Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. *Journal of the Marine Biological Association UK* 74:563-584.
- Underwood, A. J., Denley E. J. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Pages 171-180 in Strong, D. R., Simberloff D., Abele L. G., Thistle A. B., editors. *Ecological Communities. Conceptual Issues and the Evidence*. Princeton: Princeton University Press.
- Underwood, A. J., Fairweather P. G. 1989. Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution* 4(1):16-20.
- West, L. 1986. Interindividual variation in prey selection by the snail *Nucella* (= *Thais*) *emarginata*. *Ecology* 67:798-809.
- Winters, E. A., Navarrete S. A. 1998. Spatial variation in feeding preferences of the rocky intertidal whelks *Nucella canaliculata* y *N. emarginata*. *Journal of Experimental Marine Biology and Ecology* 222: 133-148.
- Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75:151-165.
- Young, C. M. 1987. Novelty of "Supply-Side Ecology". *Science* 235:415-416.

Table III.1. Regressions between shell length and wet weight of *Nucella emarginata* sampled at Arroyo Hondo and Diablo.

Site	Regression	R ²	n	P	X mass (g)	X shell length (mm)
AH	log wet weight = -3.487 + 2.816 log shell length	0.89	363	<0.0001	1.79	20.12
DC	log wet weight = -3.122 + 2.526 log shell length	0.81	122	<0.0001	1.77	20.87

ANCOVA (Ho: regression slopes are equal)					
Source	df	MS	F	P	R ²
Site (AH vs. DC)	1	0.015	1.36	0.243	
Shell length (covariate)	1	34.00	3023.87	<0.0001	
Site x shell length	1	0.012	1.10	0.296	
Error	481	0.011			0.877

Table III.2. Regressions between shell length and wet weight of *Acanthina spirata* sampled at Arroyo Hondo and Diablo.

					X mass (g)	X shell length (mm)
Site	Regression	R ²	n	P		
AH	log wet weight = -3.391 + 2.692 log shell length	0.88	155	<0.0001	1.08	17.83
DC	log wet weight = -2.827 + 2.290 log shell length	0.70	107	<0.0001	1.24	18.64

ANCOVA (Ho: regression slopes are equal)					
Source	df	MS	F	P	R ²
Site (AH vs. DC)	1	0.047	5.86	0.0162	
Shell length (covariate)	1	11.186	1396.58	<0.0001	
Site x shell length	1	0.039	4.88	0.0281	
Error	259	0.008			<0.0001

Table III.3. Two-way analysis of variance for the effect of site and whelk origin on distances moved by *N. emarginata* after 44 days from release in autumn 1996. One-way analysis of variance of the effect of site on distances moved by *A. spirata* after 56 days from release in autumn 1996.

Whelk Species	Source	df	MS	F	P
<u>N. emarginata</u>	Site (AH vs. DC)	1	1.279	17.80	<0.0001
	Whelk origin	1	0.787	10.98	0.0012
	Site x Whelk origin	1	0.609	8.48	0.0042
	Error	127	0.072		
<u>A. spirata</u>	Site (AH vs. DC)	1	0.918	9.088	0.0046
	Error	38	0.101		

Figure III.1. Mean ($\pm$ SE) percent cover of A) barnacles and B) mussels in Arroyo Hondo and Diablo Canyon during late summer 1996. Barnacles are presented as occupiers of primary space (top panel) and secondary space (inset top panel).

Figure III.2. A) Mean ($\pm$ SE) monthly recruit densities of mussels and B) barnacles attached to artificial collectors (see Methods) in the mid intertidal zones of Arroyo Hondo and Diablo Canyon. C) Density of whelks *Nucella emarginata* and *Acanthina spirata* at Arroyo Hondo and Diablo Canyon. P are the probability values associated to the one-way ANOVA F ratios for the between site comparisons.

Figure III.3. Size structure (shell length) of *Nucella emarginata* at A) Arroyo Hondo and B) Diablo Canyon. Mean $\pm$ 1 standard error of the mean and sample size are given in each panel. Logarithm of wet weight (WW) regressed on logarithm of shell length (SL) for whelks originating from Arroyo Hondo and Diablo Canyon are also presented (inset).

Figure III.4. Size structure (shell length) of *Acanthina spirata* at A) Arroyo Hondo and B) Diablo Canyon. Mean $\pm$ 1 standard error of the mean and sample size are given in each panel. Logarithm of wet weight (WW) regressed on logarithm of shell length (SL) for whelks originating from Arroyo Hondo and Diablo Canyon are also presented (inset).

Figure III.5. Diet of juvenile and adult *Nucella emarginata* based on low tide observations at Arroyo Hondo and Diablo Canyon. Sample size is given for each whelk size x site combination.

Figure III.6. Diet of *Acanthina spirata* based on low tide observations at Arroyo Hondo and Diablo Canyon. Sample size for each site is given. Small and large whelks are combined.

Figure III.7. Frequency distribution of growth rates for marked native and transplanted *Nucella emarginata* whelks at Arroyo Hondo and Diablo Canyon. Mean (thin arrow) and median (thick arrow) growth rates and sample size are given in each panel.

Figure III.8. Frequency distribution of growth rates for marked native *Acanthina spirata* at Arroyo Hondo and Diablo Canyon. Mean (thin arrow) and median (thick arrow) growth rates and sample size are given in each panel.

Figure III.9. Median distances moved by *Nucella emarginata* and *Acanthina spirata* at each sampling period in autumn 1996 at Arroyo Hondo and Diablo Canyon. Upper panels show whelks in their native sites and the lower panel shows whelks transplanted to non-native sites (see Methods). There is no data for transplanted *Acanthina*.

Figure III.10. Survivorship of marked native *Nucella emarginata* and *Acanthina spirata* at Arroyo Hondo and Diablo Canyon after 50 days from release. Estimates of percentage of population alive is adjusted to account for those hidden during censuses (see Methods).

CHAPTER IV

CONSEQUENCES OF VARIATION IN RECRUITMENT OF PREY *BALANUS GLANDULA* FOR PREDATORY WHELKS

Abstract

Despite the suggestion that variation in recruitment can be an important determinant of many ecological patterns and that this variability can be the main factor driving the dynamics of interspecific interactions in open systems (organisms with long distance dispersal), explicit experimental manipulations of recruitment to look at predator-prey dynamics are few. A common scenario in marine communities is one in which the income (settlement, recruitment) of prey species with long dispersal is not greatly affected by local conditions. Yet, their predators can be direct developers (no free-swimming larval stages), potentially affected and dependent on the local abundance of prey. Rocky intertidal muricid gastropods (direct developers) feeding on barnacle prey (pelagic dispersers) is just such a system, with the great quality of being amenable to experimental manipulation. In this study, I experimentally investigated the consequences of variable recruitment rates of barnacle prey within a given site, at scales of meters, on short and longer-term responses of whelks. By manipulating the abundance and seasonal timing of new barnacle recruits entering into whelk habitat, I was able to quantify and separate the effects of recruitment intensity and frequency. My results show that responses of predatory whelks were complex and varied among whelk species. Those species that did respond displayed a complex pattern of changes in movement, feeding rates, growth rates,

and mortality. Surprises from this study included 1) large differences in responses of *Nucella emarginata* and *N. canaliculata* and 2) high spatial variation in *Ocenebra circumtexta* responses over what appeared to be homogeneous habitat. Furthermore, frequent recruitment of barnacles into whelk habitat produced different responses by *O. circumtexta* than those produced by a single barnacle recruitment event, suggesting that the frequency of recruitment may play an important role in whether or not prey effects translate into long-term responses by this species.

Introduction

Variation in the influx of new members to local benthic communities is an important cause of variability in "open" populations of marine organisms. Indeed, this source of variation has been advocated as a major determinant of community structure on rocky shores (Underwood and Denley 1984; Lewin 1986; Underwood and Fairweather 1989). The process of settlement and recruitment links planktonic larvae with their benthic adult life history stage, thereby setting the initial conditions (e.g. abundance) for post-recruitment factors that influence juvenile and adult populations. Understanding the interplay between pre-recruitment and post-recruitment effects could offer important insight into the multi-factorial nature of population and community regulation, as well as develop more realistic fishery and management models (e.g. Tegner and Dayton 1977; Pfister and Bradbury 1996).

Many studies have demonstrated that larval settlement, and their subsequent recruitment to juvenile and adult populations, is highly variable over most spatial and temporal scales (e.g. Hawkins and Hartnoll 1983; Gaines and others 1985; Gaines and Roughgarden 1987). However, recent studies have shown that some consistent patterns in recruitment variation do occur. Large-scale spatial variability in settlement (sites kilometers or more apart) has been widely attributed to oceanographic transport processes that alter larval distributions (see references in Shanks 1995). Settlement, as well as recruitment, also varies within a site (e.g. tens of meters) according to small-scale changes in the physical and biological environment, and their interplay with larval behavior (Gaines

and others 1985; Denley and Underwood 1979; Gaines and Roughgarden 1985; Minchinton and Scheibling 1993; Strathmann and others 1981; Keough and Downes 1982; Raimondi 1990). Thus, both sites and habitats within sites can often be ranked consistently as receiving relatively higher or lower abundances of recruits (Menge 1976; Caffey 1985; Sutherland 1990; Menge 1992; Menge and others 1994; Robles and others 1995; Wetthey 1986; Pineda 1994; see chapter II).

Large within year (seasonal) and between years variability in recruitment also occurs and is generally associated with processes that alter the supply of larvae in the water column, such as the timing of reproductive output by adults (Connell 1961; Christy 1982; Christy and Stancyk 1982; Geraci and Romairone 1982), changes in larval mortality rates (Gaines and Roughgarden 1987), and changes in physical transport processes (see references in Shanks 1995). Thus, while recruitment can usually be considered a highly stochastic process (Hanski 1991; Haydon and others 1993), at other scales variation in recruitment can be very predictable (Caffey 1985; Sutherland 1990; Menge in press).

The consequences of such variation for the ecology of populations and communities has received a great deal of recent attention. Tailored theoretical models and careful experimental studies on the consequences of recruitment variability on the population dynamics of selected species (e.g. Caffey 1985; Connell 1985; Gaines and Roughgarden 1985; Roughgarden and others 1988; Raimondi 1990; Sutherland 1990; Bertness and others 1992; Rodríguez and others 1993; Carr 1994; Possingham and others 1994), on the final assemblages of species (e.g. Petraitis 1991; Menge and others 1993; Underwood and Anderson 1994; Foster and others, in prep.), and on interspecific

interactions within trophic levels (i.e. competition, facilitation; Underwood 1978; Schmitt 1985; Sutherland and Ortega 1986; Navarrete and Castilla 1990; Schmitt and Holbrook 1990) are now mounting. In contrast, only a handful of studies have looked at the consequences of variable recruitment rates for predator-prey interactions (but see Fairweather 1988; Gaines and Lafferty 1995; Robles and others 1995), despite the prominent role that predator-prey and herbivore-plant interactions have played in the study of marine communities (Underwood and Denley 1984; Menge and Sutherland 1987; Lubchenco and Real 1991).

Several possible responses of predators to varying recruitment of their prey include numerical responses (changes in death as well as birth rate of a predator, Holling 1959; Valiela 1984), functional responses (changing diet or consumption rates, Murdoch 1969; Morgan and others 1997), aggregation responses, and developmental responses (e.g. changes in body size for species with indeterminate growth, Murdoch 1971). These mechanisms interact in complex ways and not all mechanisms are important everywhere, nor are they and their interactions constant over time.

The most direct tests of whether variation in recruitment interacts with predation would include manipulation of the number and/or the timing of the arrival of recruits to population of prey and subsequent monitoring of predator movement, density, foraging rates, diet, and reproductive success. In one of the first attempts to relate densities of recruits and their predators, Fairweather (1988) simulated failure of recruitment by an abundant intertidal barnacle (*Tessieropora rosea*) into areas with and without predators (the muricid whelk *Morula marginalba*). He found that whelks responded readily and

negatively to experimentally induced variation in barnacle recruitment: whelks avoided the areas that simulated failure of recruitment. Recently, Robles and others (1995) investigated how a key intertidal predator, the sea star *Pisaster ochraceus*, responded to differences in the availability of its main prey, *Mytilus californianus*, by experimentally reducing or augmenting natural mussel recruitment. They found that sea star aggregations formed in a matter of days in the recruitment augmentation experiment, whereas mean total densities of sea stars became significantly lower on the recruitment reduction treatments. While both of these insightful studies manipulated recruitment variation over small spatial scales, they underscore the need for incorporating recruitment as an explicit variable in experimental and theoretical treatments of biological and demographic models.

The timing can be as important in many systems as the cumulative intensity (density) or rate of arrival of propagules. Different temporal patterns of recruitment include seasonality (time of the year) and frequency (number of pulses of recruitment per time period) in which recruits are added. Frequency can vary among species and between years for a single species, from brief irregular pulses (resembling a rapid "spike" in prey abundance) to numerous small asynchronous pulses (change occurs over longer time periods). Because different temporal patterns of recruitment can cause prey to fluctuate greatly or fluctuate less, individual predators may respond to different temporal patterns by adjusting the amount of time spent detecting, pursuing, capturing, and handling prey. In this way recruitment variations through time may enhance differences in the pattern and duration of predation, and may ultimately determine whether and how the predator regulates the prey population (Hassell and May 1974; Murdoch and Oaten 1975; Murdoch

and Bence 1987; Hassell 1978; Hassell and May 1990). However, whether or not different temporal patterns of recruitment contribute to temporal or spatial variability in predator responses, and whether or not these then influence predator population structure remain open questions.

To look at the consequences of variable recruitment rates on predator populations, I used organisms whose ecology has been well studied and whose life history combinations have the greatest potential for long-term changes in predator population structure. I focused on the effects of barnacles (*B. glandula*), which have broadly dispersing larvae, on one of their most important predators, predatory whelks (*Nucella* spp., but also *Ocenebra circumtexta*). Whelks are direct developers with juveniles that grow and live in the same general habitat as adults, and therefore local population fluctuations are dependent to some extent on the local conditions that affect adult reproduction. Among sites 10's to 100's of kilometers apart, whelk densities are significantly, positively correlated with barnacle and mussel recruitment rates (but not local abundance; see chapter II). Thus, at least at large spatial scales, higher prey recruitment may lead to larger predator populations, suggesting whelks can respond numerically to high prey productivity. Within a site, both long term (numerical) and short term (aggregation, functional) responses have been documented in whelks. Numerical (Spight 1982a) and behavioral (Menge and others 1994; Wootton 1994; Navarrete and others, in press) changes in populations of *Nucella* are known to correspond to changes in food supply, implying food can be a controlling factor.

In this study, I experimentally investigate the consequences of variable recruitment

rates of barnacle prey at scales of tens of meters on short-term responses of an assemblage of four whelk species with direct development. By manipulating the abundance and seasonal timing that new barnacle recruits entered into whelk habitat, I was able to quantify and separate the effects of recruitment intensity and frequency. My results suggest that direct and indirect influence of prey recruitment varies greatly among whelk species, and the frequency of recruitment may play an important role in whether prey effects translate into long-term responses by predators.

Methods

Study Site

The study was conducted between February 1996 and January 1997 on a broad, flat mid intertidal rocky platform at Diablo Canyon, a site approximately 30 km north of San Luis Bay, on the central coast of California. Recruitment of *B. glandula* occurs during a broad temporal window in central California, with pulses occurring as early as March, but generally is greatest from late summer through late autumn (Gaines and Roughgarden 1985; Judge and others 1988; Pineda 1994; author's unpublished data). Here, a given site can receive anywhere from one to six pulses of recruitment per year in the main settlement season. During a year with relatively high recruit densities, settlement pulses appear as spikes of rapid increases and decreases separated by periods of low settlement. In contrast, years with relatively low recruitment are often characterized by barnacles "trickling-in" throughout the settlement season. Within a habitat at a specific

wave-exposure, densities of *B. glandula* recruits often show a clumped distribution over scales of 10's to 100's of centimeters (Judge and others 1988). I purposely selected Diablo Canyon as a study site because prior data on mussel and barnacle recruitment revealed that this bench received consistently low mussel and barnacle recruitment (see chapter II, J. Carroll, *pers. communication*), much lower than many other sites in California (e.g. Gaines and others 1985; Gaines and Roughgarden 1985; Farrell and others 1991; Judge and others 1988; Connolly and Roughgarden 1999; see chapter II), and I thought it would be under these conditions that predators would more rapidly respond to changes in prey abundance.

The experimental bench consisted of a 100 x 150m platform directly exposed to ocean swell that abruptly ended in a vertical wall at the ocean side. The often pounding wave forces experienced at this site did not appear to diminish greatly as water washed over the length of the bench due to the flat, seemingly homogenous topography. The expansive mid zone was dominated by a patchy, single-layer mussel bed composed of large, adult california mussels (*Mytilus californianus*, 10-15 cm in length), bare space, and large barnacles (mostly *Tetraclita rubescens*, but also *Pollicipes polymerus*). The most common invertebrate predators in the mid zone consisted of four species of whelks, *Nucella emarginata*, *N. canaliculata*, *Ocenebra circumtexta*, and *Acanthina spirata*, all of which were found at low densities relative to other sites (see chapter II). The large size of mussels and barnacles made them virtually immune to whelk predation (Dayton 1971; Palmer 1984; Navarrete 1996). Initial field observations suggested that *A. spirata* was found on only one small section of the study site where slightly higher rock surfaces could

be easily accessed by whelks. Additionally, Diablo Canyon lies at the southern tip of the geographic distribution limit for *N. canaliculata*. The seastar *Pisaster ochraceus* was naturally absent from the mid zone and was rarely seen at lower tidal levels at this site. Herbivores, mostly small limpets, but also the large limpet *Lottia gigantea*, were found in patches among the mussel bed but did not appear to be very abundant. Littorines (*Littorina* sp.) were common in upper portions of the mid zone at the landward edge of the platform. Other predators often found feeding on the bench during low tide included a variety of seabirds, mostly the Black Oystercatcher (*Haematopus bachmani*) and gulls (*Larus* spp.), that nested atop a neighboring rocky outcrop.

Abundance and Distribution of predators and prey

In order to estimate the temporal and spatial variation in the abundance of prey and predators, fixed quadrats were sampled on a bi-monthly basis from June 1996 to January 1997. It was not always possible to monitor abundances with this frequency as the limited time available to work during low tides was dedicated to monitoring the experimental plots (see below). Predator densities were monitored four times during eight months. The fixed, 50 x 50 cm quadrats were located every meter along two ten meter long transects that were laid horizontally along the shore. One transect was placed at the northern edge of the bench, while a second transect was placed in the area of shore where *A. spirata* were also present. On this second transect, I could quantify variation in the abundance of *A. spirata* as well as *N. emarginata*. Positions of fixed quadrats were marked with marine epoxy. All whelks found within the quadrats were identified, counted, and measured to

the nearest millimeter using vernier calipers. Percent cover of all sessile organisms occurring within quadrats, under 100 intersection points, was also recorded. On each monitoring date, quadrats from the two transects were averaged to provide estimates of predator abundance. To characterize the spatial pattern of variation in prey and predator abundance in greater detail, three additional transects, with 10-12 quadrats each, were sampled in December 1996. Quadrats sampled about 30% of the total mid zone bench surface.

Correlation coefficients were calculated to determine the degree of association among whelk species over time and space. Similar analyses were used to determine spatial correlation between whelk densities and cover of mussel and barnacle prey. In all cases, the Spearman Rank correlation was used because data were not normally distributed. To determine the size of whelk aggregations and if the aggregation level changed over time, plots of variance versus quadrat spacing were used for each whelk species (Ludwig and Reynolds 1988; see Navarrete 1996).

Effects of prey recruitment on predators

To determine the effects of barnacle recruitment on predator behavior, I conducted a recruitment augmentation experiment that emulated small-scale spatial variation in barnacle recruitment and then monitored the responses of whelks. From a separate site approximately 120 km north of Diablo Canyon, near Point Sur, I collected mussel shells with small (2-3 mm basal diameter) individuals of the barnacle *B. glandula* that had naturally settled atop them. Shells were then transplanted into 1m x 1m

experimental plots in the mid-intertidal zone by gluing the valves of the mussel shells to the rock surface using a non-toxic submarine epoxy (Z-spar). Similar epoxy products have been used by others with no noticeable negative effects (Palmer 1984; Wieters and Navarrete 1998), and field observations confirmed that the epoxy had no visible effects on behavior of whelks, as individuals were commonly found crawling over, resting on, and eating atop the epoxy. I took great care to transplant the shells to bare rock patches that naturally existed among large *M. californianus* within the plots, so that I did not alter greatly the habitat. Individual plots were marked by placing stainless steel screws at each corner. In each experimental plot I either 1) added small barnacles provided on mussel shells, 2) added mussel shells that had been cleaned of any epifauna, to control for changes in substrate heterogeneity caused by the mussel shell transplants themselves, or 3) left the plot in its natural condition as an unmanipulated control. Additionally, in order to control for the timing in which barnacle recruits might enter into whelk habitat, I either added barnacles once a year ('Early' treatment) or added barnacles twice a year ('Frequent' treatment). Five replicates of the four treatments (+ barnacles once (Early), + barnacles twice (Frequent), + Shells Only, Control) were assigned to plots according to a complete randomized block design (Fig.1). The effectiveness of barnacle recruit additions was assessed by estimating percent cover of *B. glandula* in all experimental plots at the beginning of the experiment in May 1996.

To look at differences in predator growth, movement, and mortality, individually marked *N. emarginata*, *N. canaliculata*, and *O. circumtexta* were released at the center of each plot at the beginning of the experiment and monitored every two to four weeks.

Individual whelks were collected and taken to the lab where each shell was lightly filed near the lip to create a smooth surface, painted with white correction fluid ('Wite-Out'), and given a number that was written on the white surface with black India Ink. Tags were then coated with fast-drying Superglue® to reduce erosion. Once tags were dry, shell length and wet weight were measured. Marked whelks were separated into two size categories, juveniles (10-20 mm) and adults (>20 mm), and released in densities that coincided with the upper level of ambient density of each size category and species combination. A total of 60 marked whelks (three species pooled) were released in each plot at the beginning of the experiment. The spatial distribution of plots was probably not adequate to evaluate responses of *A. spirata* because this species was limited to one area of the bench. Thus, I look at the response of this species in the 'blocks' that overlap with its distribution.

During each monitoring, the numbers of each species of marked or unmarked ('new') whelks within the plots were recorded and the size (shell length), activity (feeding, searching, resting), prey item if eating, and microhabitat (crevice, pool, bare substrate) of each individual whelk was noted. Additional searches for marked individuals were conducted outside of each plot. Care was taken not to disturb the whelks during monitoring. They were not picked-up from the substratum for measurement. When a marked whelk was encountered inside or outside the plot, its position on a permanently marked x-y grid was also noted. The x-y axes were marked by stretching two measuring tapes between points that had been permanently marked using marine epoxy and stainless steel screws. The two measuring tapes crossed at the center of each plot, which was also

permanently marked with marine epoxy, and designated the coordinates at which whelks were released (0,0).

Whelk Diet – Diet of marked and unmarked whelks was characterized through field observations collected during regular monitoring of the experiment. For marked whelks encountered two or more times on successive monitoring dates, only the observation for the first encounter was used. Percentages of whelks found feeding at low tide were calculated for each species for each treatment.

Because whelks search and begin feeding during high tide periods, direct observations of whelks still feeding at low tide might underestimate foraging activity in the different treatments. Thus, I used a second method to estimate feeding frequency among treatments. Those whelks found on flat, unprotected rock surfaces next to prey items were considered to have been foraging during the previous immersion period. Those whelks found in crevices, small pools, and hiding places contiguous with flat rock surfaces were not considered to be on the feeding area. Similar methods have been utilized by other authors to characterize whelk feeding activity (Spight 1982b). Contingency tables and chi-square tests (Sokal and Rohlf 1981) were used to compare feeding frequency and diet composition of whelks.

Whelk Growth - Mean daily growth rates (changes in shell length) of marked *N. emarginata* and *O. circumtexta* were calculated for each treatment. Too few data were available to reliably estimate growth of *N. canaliculata* and *A. spirata* in the different treatments (see Results). I restricted growth rate comparisons to juveniles (whelks less than 20 mm) in order to avoid complications due to reproductive output. Additionally,

only those juvenile whelks that were continuously found within experimental plots for at least ten weeks were used in treatment comparisons to be certain that individuals had experienced the specified prey recruitment treatment. To assess the impact of movement rates on whelk growth rates, I included in comparisons growth rates of marked whelks continuously found outside of experimental plots. These whelks were known to move long distances in habitat and prey availability similar to control plots. Because sample sizes were small for *N. emarginata*, I combined data for control and manipulation control treatments (“no barnacle additions”) and early and frequent treatments (“+ barnacle recruits”). For clarity, data presented in figures are mean growth rates for each treatment. Treatments were not combined for *O. circumtexta*. Data were compared using one-way ANOVA. No transformations were necessary to meet assumptions of normality and homogeneity of variances.

Whelk Densities - Because the ‘Frequent’ barnacle recruitment treatment was not applied until September, density data were divided into two time intervals that coincided with before and after the second barnacle recruit addition. Within the two periods, data were averaged across time to analyze the mean response of whelks to barnacle manipulations. The first time period measured the effect of ‘Early’ barnacle recruit additions (versus control and manipulation control). The second time period also contrasted the effect of ‘Early’ versus ‘Frequent’. Since the same plots were followed over the two periods, they were not completely independent, and so were analyzed statistically using a split-plot, repeated measures ANOVA design (replicated plots were ‘split’ into two time periods). As only two time periods were analyzed, the assumption of

spherecity was met for all analyses (von Ende 1993). Assumptions of normality and homoscedasticity were assessed by visual inspection of residual plots and normal probability plots of the residuals. Data were log transformed to meet model assumptions. For easy interpretation, data presented in figures are the untransformed means $\pm$ SE for each effect.

Whelk Movement - Movement rates of marked whelks were estimated by determining the minimum distance (diagonal formed by x,y coordinates) between points of recapture and then dividing by the number of days between sightings. Mean movement rates were then constructed for each individual. Spatial variation in natural movement rates of *N. emarginata* and *O. circumtexta* was determined by comparing mean movement rates of whelks consistently found outside of experimental plots. Differences among experimental blocks were analyzed using a one-way ANOVA. No transformation of data was necessary to meet assumptions of normality and homogeneity of variances. To compare natural movement rates among species, data were pooled across space.

To determine whether residence time of an individual in the plots varied among prey recruitment treatments, I calculated the frequency (number of monitoring events after release) at which an individual was observed within experimental plots throughout the experiment. Data for each treatment were pooled and compared using Kruskal-Wallis tests. Non-parametric tests were used because data were not normally distributed and transformation techniques did not resolve the problem. No data were available for *A. spirata*.

Whelk Mortality - In addition to the regular monitoring, systematic searches for

marked shells of dead whelks were conducted each month. These additional searches included surveys of 1) hermit crabs found on the bench and in small pools 2) stomach contents of large anemones (*Anthopluera xanthogrammica*) and 3) sea bird regurgitates and foraging remains found along nearby cliffs. All recovered shells were inspected for damage. The percentage of marked whelks found dead provided a conservative estimate of whelk mortality for each species.

Additional estimates of mortality were obtained from the regular whelk monitoring (described above) by calculating the percentage of whelks seen alive at each successive monitoring date. A whelk was considered dead on the last date seen in a census if all successive searches failed to find that marked individual. Thus, “death” as defined here includes whelks hidden and whelks that completely lost their tags (small fraction), as well as those whelks that actually died.

Effects of Predators on Prey Transplants - To estimate the effects of whelk predation on barnacle survival, I conducted a cage exclusion experiment that prevented access by whelks and other predators to transplanted barnacles. Barnacle recruits were transplanted to small plots, using the same methods as described above, and covered with 10 x 10 x 5 cm stainless steel mesh cages fixed to the rock with stainless steel screws. A piece of silicone tubing was attached around the bottom rim of the cages to provide a better fit to the irregular rock surface. Barnacle survival in the presence of whelks was monitored in two 10 x 10 cm permanently marked areas within each of the large 1m² plots. Additionally, to evaluate whether predation intensity by whelks in prey addition plots differed according to distance from the edge, one barnacle survival area was placed in the

center and one at the edge of each plot. Every month, all areas were photographed and the number of live barnacles was counted. Individual barnacles were identified and followed through time so as to distinguish between original barnacle recruits (that I had added) and any new recruitment that could potentially occur after the transplant manipulation. Plots in the presence of predators were monitored from the start of the experiment in May 1996 to the end of the experiment in January 1997 or until all barnacles had been eaten. Cages were installed in July 1996 and monitored monthly until the experiment was terminated or until whelks had invaded the cages, rendering the treatment ineffective.

The average percentage of transplanted barnacles alive in the Early, Frequent, and predator exclusion plots were calculated for each time period. Barnacle survival in the presence of whelks was similar with respect to location within plots (center vs. edge), so subplots were averaged to provide an estimate for each main experimental plot. The mean percentages alive after 100 days were then analyzed using a one-way ANOVA with prey treatment as a fixed factor. The period of 100 days was chosen for comparisons because this was the only time when weather conditions and logistics allowed all treatments to be sampled so that the number of days was equal.

Results

Abundance and Distribution of Predators and Prey

Bare space and large individual *M. californianus* dominated the mid shore, while

large barnacles (*T. rubescens* and *P. polymerus*) were sparsely distributed among gaps within the mussel zone (Fig. 2). Adults of the smaller species of acorn barnacles, *B. glandula* and *C. fissus*, were scarce within the site and occurred as small patches of epifauna on *M. californianus* (Fig. 2, insert). Within the experimental blocks, covers of *B. glandula* and *C. fissus* were similarly low (Fig. 3).

Whelks were distributed throughout the mid-low to mid-high zones of the shore, and three of the four species overlapped throughout their tidal range. The exception was *A. spirata*, which was present only on a small area of the bench where individuals could access a slightly higher portion of the shore (Fig. 4d, block 4). Overall, densities of whelks were low and similar among species, with *N. emarginata* observed at slightly greater abundance (Fig. 4). Although the magnitude of variation in densities of each species was generally small, the portion of the bench that exhibited the highest/lowest abundances varied among species. With the exception of the most landward edge of the bench, *N. emarginata* showed relatively even distribution among experimental blocks (panel 4a), while densities of *N. canaliculata* were slightly higher along the northern edges of the platform (panel 4b, blocks 1 and 5), and *O. circumtexta* were most abundant near the center of the bench (panel 4c, blocks 2 and 4).

Densities of whelks in the study site fluctuated little between June 1996 and January 1997 (Fig. 5). Although overall changes in density were small, whelk densities did display a seasonal pattern that was roughly similar among species, and different from the seasonal pattern observed in Oregon and Washington for the same species (Connell 1970; Spight and Emlen 1976; Spight 1982a; Navarrete and Menge 1996; Navarrete

1996). In general, whelk densities were highest in late spring and winter months and decreased in summer and fall months, but the time at which the highest densities were observed varied slightly among species. Densities of *O. circumtexta* were highest at the beginning of the experiment in late May and early June, while *N. emarginata* and *N. canaliculata* densities peaked in January. Densities of *A. spirata* were higher in October than in June.

Mean densities of *N. emarginata* and *N. canaliculata* were highly correlated over time when using the mean density observed in 50 x 50 cm quadrats (Spearman Rho = 1.00, $P < 0.0001$, $n = 3$, Fig. 5), but not significantly correlated over space (Spearman Rho = 0.20, $P = 0.167$, $n = 50$). Additionally, *N. emarginata* and *A. spirata* were highly, negatively correlated across the bench (Spearman Rho = -0.54, $P < 0.0001$, $n = 50$), but the correlation was caused by *N. emarginata* being similarly abundant at all areas of the bench except at the upper mid-shore section where *A. spirata* occurred (Fig. 4 a,d). No other whelk species were correlated across space or through time ($P > 0.05$). Thus, at least at the low densities observed in the study site, there was no evidence of small-scale negative association among species.

None of the whelk densities were significantly correlated to the cover of large mussels (*M. californianus*, $P > 0.05$). However, densities of *N. emarginata* were positively correlated with the gooseneck barnacle *P. polymerus* (Spearman Rho = 0.5, $P = 0.001$, $n = 50$) and densities of *N. canaliculata* were weakly positively correlated with the large acorn barnacle *T. rubescens* (Spearman Rho = 0.33, $P = 0.0365$, $n = 50$). Since these species are too large to be eaten by whelks, significant correlations probably reflect

microhabitat rather than food preferences.

The degrees of aggregation of whelks in the study site were overall low and similar among whelk species, but varied with season of the year (Fig. 6). In figure 6, a relatively flat curve or one with peaks and troughs, but not a clearly defined peak, represents a relatively random distribution of whelks over space. A peaked curve represents an aggregated distribution in which the position of the peak indicates the average size of the aggregation and the "steepness" of the peak is the aggregation intensity (see Ludwig and Reynolds 1988). In late spring and winter, *N. emarginata* and *N. canaliculata* tended to be randomly distributed across the study site, but formed small aggregations of low intensity in the fall. Similarly, small aggregations of *O. circumtexta* that occurred in late spring increased in size (5 meters in diameter) towards fall, and then disappeared in winter. Therefore, while the overall mean density of whelks in the study site decreased slightly toward fall, the magnitude of the decrease with respect to late spring and winter months varied over space because whelks aggregated more in small areas of the bench.

Effects of barnacle recruitment on whelks

Barnacle recruitment manipulations successfully increased the abundance of small barnacles, from an average 1.8% in control plots to 20% + in barnacle addition plots. The transplanting method worked well. Despite occasional pounding by high wave forces, only one transplanted shell was dislodged during the course of the experiment. Eleven months after the beginning of the experiment, surviving transplanted barnacles were still firmly attached, were seen filter feeding when covered by the incoming tide, and had

grown considerably (*pers. obs.*).

Marked whelks released at the beginning of a low tide seemed to recover quickly as they re-attached and moved to nearby crevices before being covered by the incoming tide. Most whelks retained tags up to the conclusion of the experiment (approx. 8 months; see also Menge 1974; Spight 1982a). Portions of a few tags peeled off after nine months, but the shells retained the roughened file marks, smoothened surface, and recognizable tag remains. Less than 2% of total marked whelks (1200 individuals) were re-captured with damaged tags.

The experiment was monitored as regularly as possible, (every two weeks for first two months and then once every month), but rough seas and bad weather prevented me from monitoring the experiment in October and December. However, I was able to make rapid visual observations on each plot during these months to determine if any major change had occurred.

Diet - The proportions of whelks found feeding when observations were made were low for both small and large whelks of each species and similarly low among all three species of whelks under natural conditions (20 – 23 % of 320 observations in controls). In addition, the proportion of whelks observed feeding during low tide did not appear to change substantially among barnacle treatments. The greatest difference among treatments was for *O. circumtexta*, in which a greater percentage of the whelks was found feeding in areas where barnacle recruits were added (39 % of 1031 observations) than in areas where shells without barnacles had been added (29 % of 84 observations) or in controls (23 % of 105 observations).

The proportion of whelks found 'foraging' (on open areas with prey) at low tide differed among prey recruitment treatments and the pattern of difference was similar among whelk species (Table 1). Where barnacle recruitment was augmented, whelks were more frequently found foraging. In contrast, whelks were more often found in crevice and pool habitats in plots where barnacle recruits had not been added (Table 1).

Diet width varied among whelk species and ranged between three and eight prey items. No differences in diet composition were found between juvenile and adult whelks, therefore data were pooled. *Nucella canaliculata* had a narrow diet, preying predominantly on *M. californianus* (92% of 23 observations) and occasionally on *C. fissus* and *B. glandula*. *Nucella emarginata* showed a similarly narrow diet of mussels (80% of 46 observations) and barnacles (16%). In over a year of observations at this site, only one individual *N. emarginata* was found eating *T. rubescens* and one individual found eating a limpet. In contrast, the diet of *O. circumtexta* frequently included limpets (21% of 42 observations) and to a lesser extent the littorine snail *Littorina planaxis*, the turban snail *Tegula funabralis*, the barnacle *T. rubescens*, and even the claw remains of the shore crab *Pachygrapsus crassipes* (< 5% combined). No data were available for *A. spirata* because too few individuals were found in control plots (see Results), but results from a separate study conducted at this site (see chapter III) show that these whelks prey predominantly upon littorine snails at slightly higher shore levels.

The frequency of different prey items in the diet of all three whelk species significantly differed with barnacle treatments (Table 2). Where barnacle recruits were added, whelks preyed more on *B. glandula* and less on alternative prey items (mussels and

limpets) than in those areas where barnacle recruits had not been added. The magnitude of the change in diet appeared largest for *O. circumtexta*, which increased its consumption of barnacles by 54 percent. As mentioned above, too few data were available for *A. spirata* in the various treatments to make comparisons, but observations suggested that this whelk shifted from eating predominantly littorine snails under natural unmanipulated conditions (see above, chapter III) to eating predominantly barnacle recruits where barnacles were added (83% of 23 observations).

Growth - Few tagged juvenile whelks were found within experimental plots on consistently consecutive monitoring dates, thereby limiting my ability to detect differences in individual growth rates among treatments. Exceptions were for *O. circumtexta* and to a lesser extent *N. emarginata*, for which several individuals (3-9 per treatment) stayed within the experimental plots long enough so that I was confident that changes in measured shell length occurred under the treatment conditions (more than 10 weeks). Too few data were available to obtain growth estimates of *N. canaliculata*.

Growth rates of juvenile *N. emarginata* differed significantly among treatments ($df=2$, $F = 8.3168$, $P = 0.0018$), but Tukey-Kramer post-hoc tests revealed the difference was complex (Fig. 7a). Those whelks consistently found in experimental plots grew similarly regardless of the presence of barnacle recruit additions (Fig. 7a, '- barnacles' vs. '+ barnacles' not significant).

To evaluate the effect of movement rates on growth, I compared growth rates of those whelks that moved great distances in unmanipulated habitat outside of experimental plots to those whelks moving little but in similar habitat and prey availability within control

plots, and found no significant differences (Fig. 7a, ‘- barnacles’ vs. ‘Outside’ not significant). The treatment effect was significant because those whelks that both moved relatively little and experienced barnacle recruit additions grew faster than those whelks that moved great distances in unmanipulated habitat outside of experimental plots (Fig 7a, ‘+ barnacles’ vs. ‘Outside’ significantly different).

Despite the small sample sizes, there was a significant effect of barnacle recruits on growth of *O. circumtexta*. Those individuals that experienced two additions of barnacle recruits within the year (‘Frequent’ treatment) grew significantly more than whelks in control, "shells only", and single barnacle addition (‘Early’) treatments (Fig. 7b, $df=4$, $F=2.9759$, $P=0.0378$).

Density - The effect of barnacle recruits on whelk density varied among species. *Nucella emarginata* showed a strong response to treatments, which was consistent through time periods (Fig. 8a, Table 3, significant between subjects main effect, no significant Period interactions). The transplant of mussel shells itself had a significant impact on whelk densities, which varied in sign according to the presence or absence of barnacle recruits. The addition of mussel shells without barnacles had a significant negative effect on *N. emarginata* densities (Table 3, contrasts C vs. MC), while the addition of mussel shells with barnacle recruits produced a significant positive effect (Table 3, contrasts C_MC vs E_F). Therefore, the increased densities observed in the barnacle addition treatments are a result of two counter-acting effects and suggest that the overall positive effect of barnacle recruits on density of *N. emarginata* is stronger than the negative effect of shell transplants. The frequency of barnacle recruitment did not affect

densities of *N. emarginata*, as densities of whelks remained similarly high in areas that received either one or two pulses of recruitment (Table 3, no Period x Treatment interaction).

In contrast to *N. emarginata*, *N. canaliculata* did not respond to treatments (Fig. 8b, Table 4, no significant between subjects effects). Regardless of experimental treatment, densities decreased over time periods (Table 4, significant Period effect) and significantly varied across the bench (Table 4, significant Block effect), as expected by natural variation in temporal and spatial patterns of abundance (see Figs. 4b and 5).

Density of *O. circumtexta* generally decreased over time periods but the magnitude of decrease varied across the bench (Fig. 8c, Table 5, significant Period x Block interaction). Superimposed on the temporal changes in densities were significant treatment effects (Fig. 8c, Table 5). The addition of barnacle recruits had a large, positive impact on *O. circumtexta*, which was consistent through time period (Table 5, significant main effect of treatment and significant contrasts between C_MC vs E_F). However, the response was highly variable over space (Table 5, significant Block effect). In two of the five experimental blocks (four and five), *O. circumtexta* quickly (few days) aggregated to prey addition plots (reaching 81 individuals/m²) and were observed eating transplanted barnacle recruits (author's personal observations). Although still significant, responses of whelks in the remaining three experimental blocks were much slower (several weeks to months) and overall weaker relative to blocks four and five (reaching densities of only 15 individuals/m²). In contrast, whelk density rapidly declined, remained low, and was less variable over space on areas where no barnacle recruits were available as prey ('Control'

and 'Shells Only', Fig. 8c).

The frequency of barnacle recruitment additions produced important changes in *O. circumtexta* densities in some areas but not in others, rendering the Period x Treatment interaction non-significant. Where individual whelks quickly located barnacle addition plots, densities showed two obvious peaks that coincided with the first and then second pulses of barnacle recruit additions. Where whelks responded more slowly and with lesser intensity, densities were not altered by the second addition of prey recruits, apparently because barnacle depletion occurred more slowly in these experimental blocks. Overall, no significant differences were found between Early and Frequent prey treatments (Table 5, no sig. Treatment x Period effect).

Acanthina spirata showed a strong response to treatments (Fig. 8d), but results are only suggestive due to lack of true replication for this species, which was naturally present only in one area of the bench (Fig. 4d). *Acanthina spirata* aggregated to prey addition treatments and the strength of the aggregation increased with time periods until all barnacles were eaten, at which time whelks rapidly moved away from plots. Densities of *A. spirata* were consistently low in areas where no barnacle recruits were added. An indication of the degree of spatial variability in *A. spirata* responses can be seen by comparing the Early and Frequent treatment plots, especially during the first half of the experiment when these two treatments were essentially equivalent (Fig. 8d). In the Frequent treatment plot, whelks rapidly found barnacle recruits and densities increased exponentially with the second "pulse" of recruitment. In contrast, *A. spirata* responses were slower in the Early treatment plot, where whelk densities did not substantially

increase until more than four months after the start of the experiment.

Movement - All species of whelks moved similarly long distances under natural, unmanipulated conditions (Fig. 9, $df = 2$, $F = 1.683$, $P = 0.1906$). Because the probability of recapturing marked whelks is lower for those whelks that move relatively longer distances, the values in figure 9 are a conservative estimate of the actual distance traveled in a month.

The frequency at which an individual whelk was found within the experimental plot in which it was initially released varied among species (Fig. 10). Generally, an individual *O. circumtexta* spent a greater amount of time within an experimental plot than either *N. emarginata* or *N. canaliculata*. Additionally, the residence time of an individual *N. emarginata* and *O. circumtexta* varied significantly among prey treatments (Fig. 10, *N. emarginata*: $df = 2$, $\chi^2 = 12.7306$, $P = 0.0017$, *O. circumtexta*: $df = 2$, $\chi^2 = 6.2202$, $P = 0.0446$). Those individuals that experienced the barnacle addition treatment were more frequently found within the plot than whelks that did not experience the treatment (Fig. 10). Residence time of an individual *N. canaliculata* was consistently low among treatments (Fig. 10, $df = 2$, $\chi^2 = 2.4858$, $P = 0.2885$).

Mortality - The majority of marked shells recovered from dead whelks had been taken up by hermit crabs (78% from 32 recovered shells). Only two shells were found in association (in stomachs or attached to sides) with anemones, one whelk shell had been trapped by byssal threads of mussels, and no whelk shells (marked or not) were found in bird regurgitates. Inspection of recovered shells found no evidence of predation by crabs, other whelks, or octopuses, as shells were clean of any marks, chips, or drill holes. These

results suggest that whelks may have died from physiological or physical stress, a common cause of whelk deaths at other sites (Spight 1982b; Dayton 1971).

Mortality of whelks, estimated as recovered shells, varied among species, and these differences became apparent during the first three months after marked whelks were released. Generally, fewer *N. canaliculata* survived relative to *N. emarginata* and *O. circumtexta*, with the latter showing the highest survivorship (Fig. 11). These proportional differences in survivorship among species were maintained when I compared the percentages of marked whelks seen alive from the whelk census data.

I could not obtain reliable estimates of whelk mortality among prey recruitment treatments using census data. Such estimates confounded effects of movement and mortality because the probability of recapture was negatively correlated to distance traveled. When data were restricted to only those whelks known to be dead (found shells), no consistent differences were found among treatments for *N. emarginata* (5-9% mortality across treatments) nor *N. canaliculata* (10-18%). However, data suggest that mortality of *O. circumtexta* may have differed among prey treatments, as fewer dead whelks were recovered from those that had originally been released in areas that received two pulses of barnacle recruitment (2%) than in control, shells only, or single barnacle additions (5-9%)

Barnacle Survival - Transplanted barnacles survived well in the absence of whelks (Fig. 13). Whelks had an overall significant, negative (main) effect on barnacle survival ($df = 2$, $F = 9.6689$, $P = 0.0133$) and the effect was similar for both Early and Frequent barnacle additions through time (Fig. 12). Since there are no other important predators of

barnacles, these results suggest that whelks found the barnacle recruits and ate.

Additionally, these results suggest that whelks can have important, significant effects on the abundance of barnacles at this site.

Discussion

I showed that, as predator-prey models would predict, prey additions at a site with consistently low prey influx lead to short and longer-term responses by the resident predatory whelk populations. However, not all whelk species responded to the ten-fold increase in prey, and those species that did respond displayed a complex pattern of changes in diet, movement, feeding rates, growth rates and mortality. Similarly, the temporal pattern of prey additions, either once a year or twice a year, had effects only on those whelk species that had the ability to switch between barnacle and limpet prey resources. In what follows, I discuss in some detail the observed responses among whelk species, their potential consequences for the populations, and the possible causes for the lack of changes in some. I argue that a better understanding of the diverse mechanisms by which predators can adjust to variability in prey recruitment will be necessary to understand how recruitment and predation effects interact and influence each other, and thereby offer important insight into the multi-factorial nature of population and community regulation.

Responses Among Whelk Species

Short-term behavioral responses of *N. emarginata* differed among prey recruitment treatments in a regular manner. Where barnacle recruitment was augmented, individuals appear to have quickly located plots, stopped moving and stayed for a relatively longer period of time, leading to significantly higher densities in these areas. The magnitude of aggregation appeared to be limited by the rate at which whelks moved away from experimental plots. During each monitoring period, aggregations of *N. emarginata* in recruitment augmentation plots were composed primarily of newly immigrated, unmarked whelks that moved in from unmanipulated areas without prey recruits. Although emigration rates were significantly lower in areas where prey recruitment was augmented than in control areas, individuals still left prey addition plots too fast to allow larger aggregations to form.

It is not clear why whelks did not remain longer in prey addition plots when small barnacle prey were still available. I have shown elsewhere that *N. emarginata* transplanted to high prey recruitment sites significantly reduce movement to the low levels of the local population (see chapter III). Their inability to stay within the plots is probably related to the high mortality rates and the microhabitat structure of the experimental plots. When creating treatments, the rock spaces among the large California mussels were covered with mussel shells in the barnacle addition and manipulation control treatments, which created a rather bare, unprotected, smooth surface area within the plots. As shown here, the addition of mussel shells without barnacle recruits had significant negative effects on whelk density, as whelks quickly dispersed away from plots

and few new individuals immigrated into areas where only shells were added. Thus, although experimental plots provided refuge in the matrix of large mussels while foraging on transplanted shells, whelks had to manage the conflicting demands of feeding and seeking refuge. This is not entirely an artifact of the manipulations since under natural conditions whelks will be faced with similar trade-offs (Burrows and Hughes 1991; Hughes and Burrows 1991; Berlow and Navarrete 1997). Only when barnacles recruit on the mussel matrix can whelks find food and refuge at the same time (but see Day and others 1991).

Therefore, short-term responses of *N. emarginata* to the barnacle addition treatments appear to be a result of both bottom-up factors due to increased prey availability and the counter-acting factors associated with a decrease in habitat heterogeneity. The overall positive effect suggests that prey recruitment was relatively more important than the decrease in habitat heterogeneity, and that only a naturally occurring, patchy influx of new barnacle recruits onto the matrix of large mussels at this site would likely produce even larger changes in *N. emarginata* distribution than those seen in this experiment.

Potential long-term responses by *N. emarginata* to variable barnacle recruitment rates were assessed by measuring growth rates of juveniles. It has been shown that short-term rates of growth are correlated with fitness attributes for *Nucella* when no energy is committed to reproduction (Palmer 1983). Despite an increase in the proportion of whelks on the feeding area and an increase in the proportion of barnacles in the diet of whelks, growth rates of juvenile *N. emarginata* were similar among prey recruitment

treatments when whelks moved little. Because growth rate estimates were restricted to those individual whelks that were continuously found within experimental plots for at least ten weeks, movement rates were similar and assumedly low relative to individuals moving outside of experimental plots. Therefore, any differences in growth likely represent differences in diet. Since regular feeding by a juvenile is always accompanied by shell growth (Spight 1972; Palmer 1983), these data imply that large mussels and small barnacles are of similar value to medium-size (13-17 mm), juvenile *N. emarginata* when whelks move little. Palmer (1983) also found that small and medium-sized *N. emarginata* grew similarly on barnacles and mussels.

The naturally high movement rates of whelks at this site did not appear to have an important effect on growth rates of *N. emarginata* under natural, low prey recruitment conditions. Whelks moving long distances outside of experimental plots grew similarly to those whelks with similar diets but moving little, spending relatively long periods of continuous time in plots where barnacle recruits had not been added. Evidently, whelks moving long distances are able to find enough food to maintain growth. Although growth rate estimates were based on only a few individuals, the values are consistent with those found in a separate study where growth rates of *N. emarginata* at Diablo were similar to those at a different site that received naturally high recruitment rates of prey (mean growth = 0.02-0.03 mm/day at both sites, see chapter III). The lack of differences in growth of individuals that either move great distances or move very little in similar habitat over the short-term is perplexing, but suggests that consumption rates of moving whelks were higher. Unfortunately, I do not have adequate data on individual consumption rates

as it was impossible to follow individuals during high tide periods, when whelks were most actively feeding.

In this experiment, the two *Nucella* species responded with clearly different intensities to manipulations of barnacle recruitment. Unlike *N. emarginata*, *N. canaliculata* appeared largely unaffected by the presence of barnacle recruits. The differences in responses between the two *Nucella* species are rather surprising because both feed almost exclusively on mussels and barnacles, and previous experiments have shown that prey preferences and diet conditioning are similar (Palmer 1984; Wieters and Navarrete 1998). Also, the spatial and temporal pattern of variation in abundance are remarkably similar between these species (Navarrete 1996; Spight 1972; this study). It is possible that the differential response could be due to slight differences in the way the two *Nucella* species use microhabitat.

Working in Oregon, Navarrete and others (in press) found that *Nucella* were primarily limited by prey and that the two whelk species responded to mussel manipulations with slightly different intensities, which the authors attributed to differences in the value of mussel beds as microhabitat for the species. In contrast to my results, the positive bottom-up effect of mussel prey removal was greater for *N. canaliculata* than for *N. emarginata*. Such contrasting results between these studies is actually expected if *N. canaliculata* is more dependent on microhabitat structure because while I added prey, I also reduced microhabitat heterogeneity (see above). However, in a separate experiment conducted at this site (author's unpublished data), addition of mussel recruits (*Mytilus galloprovincialis*) to 1m² experimental plots did not result in increased *N. canaliculata*

densities with respect to unmanipulated control plots. Apparently, *N. canaliculata* was not limited by recruitment of either mussels or barnacles at this site.

A more likely explanation for the lack of response by *N. canaliculata* is the fact that Diablo Canyon lies at the southern edge of its geographic range (Morris and others 1992). Which are the specific controlling factors is not clear, but mortality rates for *N. canaliculata* were consistently high across all size classes and clean shells with no apparent chips, marks, or drill holes were recovered, suggesting that individuals may have been physiologically stressed. Indeed, individuals transplanted to a site further south, beyond the distribution limit for *N. canaliculata*, died within a couple of weeks (author's unpublished data).

Like *N. emarginata*, *O. circumtexta* responded to barnacle recruitment treatments by increasing aggregation to prey addition plots. However, the magnitude of the response was highly variable across space, a surprising and difficult to explain result. Abundances and size frequency distributions of *O. circumtexta* were similar across the bench. Potential competitive interactions with other whelk species also did not seem plausible, as the abundances of *N. emarginata*, *N. canaliculata*, or *A. spirata* did not significantly correlate with *O. circumtexta* at the scale of 50 x 50 quadrats, nor with the magnitude of aggregative response by *O. circumtexta* across experimental blocks. As mentioned earlier, spatial variation in protective habitat can also amplify or weaken predator responses, but habitat characteristics at Diablo Canyon were seemingly homogeneous, as percentage cover of crevice, pool, bare rock, and large mussel habitat were similar among experimental plots. Preliminary data from wave meters that register

maximum wave forces (Bell and Denny 1994) also suggests that wave forces did not differ dramatically across the bench, at least during late autumn.

In addition to the spatial variation in the overall magnitude of aggregation in barnacle recruitment augmentation plots, the rate of density build-up also varied among experimental blocks. Where density responses were relatively weak, peak abundances did not occur until after five months from the start of the experiment. In contrast, increases in whelk abundance were fast (days) where density responses were stronger. I suspect that some of this spatial variation is explained by the fact that whelks naturally formed aggregations in small areas of the bench under unmanipulated conditions during fall, and thereby may have indirectly dampened or magnified whelk responses to barnacle recruitment augmentation over different areas of the bench. Under a suite of micro-scale conditions, aggregations are formed and probably food abundance is only one of such conditions. The extent to which seasonal changes in whelk distribution interacted with whelk responses to barnacle recruitment remains for future study.

Effects of temporal pattern of recruitment

Frequent recruitment of barnacles into whelk habitat at Diablo Canyon produced different responses by *O. circumtexta* and apparently *A. spirata*, but not *Nucella spp.*, than those produced by a single barnacle recruitment event. Where barnacle recruits were added both early and late in the main settlement season, individual whelks moved less and spent a consistently greater amount of time feeding. Spight (1982b) also observed whelks more often on feeding areas in years with relatively more frequent settlement of barnacles.

The frequency of prey recruitment events appears to be most important for long-term responses of *O. circumtexta*, and thus has the most potential for impacting population structure of this whelk species. Those individuals that experienced pulses of recruitment both early and late during the settlement season grew relatively faster and appear to have survived longer than those whelks that experienced only one or no pulses of barnacle recruitment. These results suggest that temporally variable recruitment in combination with recruitment intensity can differentially affect predator responses.

Although *A. spirata* were distributed over such a small portion of the bench that it was not possible to replicate experimental treatments for this species, results suggest that variation in barnacle recruitment can have important consequences for at least short-term behavior and distribution of this predator. Where barnacle recruitment was augmented, whelks formed aggregations that continued to increase in size over time. However, like *O. circumtexta*, the magnitude of aggregation seemed to be highly variable over space (see Results). In the case of *A. spirata*, part of this variation is likely because the 'Early' barnacle recruitment plot was, by necessity (lack of space) closer to the edge of the natural distribution of *A. spirata* at this site. The 'Control', 'Shells only', and 'Frequent' treatment plots were all located near the center. Interestingly, there appeared to be a temporal delay in *A. spirata* responses to barnacle recruit additions, as densities in both barnacle addition treatments increased rapidly in late fall (after September). This suggests that *A. spirata* may be foraging more actively in the mid intertidal in late fall and winter than in spring and summer. Indeed, *A. spirata* densities were naturally slightly higher during fall than summer on this section of the shore. Partial explanation for the

delay in aggregation response may be related to seasonal variation in stresses at low tide. Under unmanipulated conditions at this site, *A. spirata* preys largely upon littorine snails, which are found at slightly higher shore levels (see chapter III). Here, too, stresses due to temperature and desiccation are probably higher, but may not become important for whelks until September, when low tides switch from night and early morning hours to mid- and late afternoon hours. Therefore, it is possible that whelks shift the relative amount of time spent foraging at higher sections of the shore in response to seasonal differences in risks associated with low tides. Unfortunately, results for *A. spirata* are only speculative at this point.

Overall, whelk responses to ten-fold increase in prey recruitment appeared rather weak when compared to predator responses documented in other similar studies (Fairweather 1988; Robles and others 1995; Navarrete and others, in press). All of these authors observed rapid, large changes in local predator abundance in response to either the removal or augmentation of small prey recruits. However, unlike these other studies, I selected a site where predator abundances were naturally low and therefore potential for large changes in total predator density is expected to be lower. Therefore comparisons of the strength of predator responses among sites should be considered in light of local predator population sizes. Indeed, when *per capita* density responses of predators are compared, the aggregative responses of whelks in this study are relatively similar (*N. emarginata*) or stronger (*O. circumtexta* and presumably *A. spirata*) than observed changes in densities of seastars (Robles and others 1995; Navarrete and others, in press) or whelks (Fairweather 1988; Navarrete and others, in press) to prey manipulations at

sites with relatively high predator abundances.

The use of relatively small experimental plots in the field allowed me to vary the timing and abundance of prey recruits entering into whelk habitat. In a similar way, Robles and others (1995) studied the strong aggregative response of a keystone predator, the seastar *Pisaster ochraceus*, to variable recruitment of its main mussel prey, *Mytilus californianus*. Mean seastar densities were lower in areas where small mussels were removed and increased rapidly (matter of days) in areas where mussel recruits were added. However, such dramatic local re-distribution of seastars has limited potential consequences for long-term changes in population levels. Unlike whelks, the life history of *Pisaster* includes a pelagic larval stage and thus these predators do not have a mechanism (i.e. via differential fecundity) to increase population size as a direct response to local prey abundances. Indeed, *Pisaster* densities are de-coupled from both local prey abundance and prey recruitment rates across sites 10's -100's of kilometers apart in central and southern California (see chapter II). Whelks, on the other hand, are direct developers where juveniles are born and grow in the same habitat as adults, and therefore can respond numerically to differences in prey recruitment by increasing local reproduction. Careful consideration should be given to the different modes of reproduction when interpreting predator responses to variability in prey, as responses should vary according to different life history characteristics (see chapter II).

Although the different whelk species in this study are all direct developers, the mechanisms by which whelks responded to small patches of barnacle additions differed among species and therefore potential consequences for numerical responses also varied.

Because of the usually longer temporal scale over which prey affect predator population dynamics, previous studies assumed that population level responses followed trends of short-term aggregative responses (Robles and others 1995; Navarrete and others, in press). However, results from this study show that the reasonableness of this assumption is dependent upon the diverse mechanisms by which predators respond to varying rates of prey recruitment. For example, both *N. emarginata* and *O. circumtexta* formed aggregations in areas where barnacle recruitment was augmented, but long-term changes were likely for only *O. circumtexta* (see above).

In this experiment, barnacle manipulations emulated small-scale spatial variation in barnacle recruitment, where changes in barnacle recruit abundance occurred as patches within whelk habitat. Although the nature of recruitment variation occurring over tens of centimeters to meters is poorly understood, data suggest variability is negatively correlated with larval abundance (Underwood and others 1983; Underwood and Denley 1984; Gaines and Roughgarden 1985; Judge and others 1988). Therefore, the results of this experiment may be more characteristic of processes occurring at naturally low prey recruitment sites than at sites normally receiving relatively high rates of barnacle recruitment.

Because various responses of predators to varying recruitment of their prey interact in complex ways and the mechanisms are likely to vary across space, the scale of prey recruitment is important. Increasing the abundance of food in patches within the predator's habitat may elicit different responses by a predator than increasing food abundances across the entire environment (see Morgan and others 1997 for discussion of

changes in predator's functional response at varying spatial scales of resource abundance). Identifying which predator responses vary with scale, and how, may give insight into the applicability of "scaling-up" interpretation of local, small-scale experimental results. Insight into the degree to which results in this study are dependent on the small-size (1m^2) of the recruitment patches can be gained by comparing responses of *N. emarginata* in this study to those observed in a separate study, where variation in prey recruitment occurred over the scale of an entire bench (see chapter III). In both studies, individual whelks responded to changes in prey recruitment (high or low) by shifting diets and altering movement, but did not appear to adjust growth rates. Whelk survival, on the other hand, varied greatly over the scale of a bench but didn't appear to change when barnacle recruitment varied among local patches. Differential survival was apparently caused by greater risks associated with higher movement rates, and was likely a major factor leading to the larger whelk populations observed at benches receiving higher prey recruitment. In this study, whelks only temporarily stopped moving upon discovering patches of relatively high barnacle recruit abundance (see above), and whereas this lead to the formation of small aggregations, it is not likely that short-term change in movement rates substantially reduced risks of mortality. Therefore, survival and, to some degree, movement appears to occur over the scale of a bench and probably prevents *N. emarginata* from realizing true population changes to barnacle availability when recruitment occurs as patches within whelk habitat.

An important message from this study is that variable prey recruitment regimes can have important consequences for predators and the traditional protocols of

incorporating recruitment variation as either great or small may obscure effects, as the timing and frequency of recruitment can have important effects on predator populations. The mechanisms by which individual predators adjust to variable prey recruitment, and whether or not these responses ultimately influence predator population structure, can offer important insight into how recruitment and predation processes interact.

References

- Bell, E. C., Denny M. W. 1994. Quantifying 'wave exposure': A simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* 181: 9-29.
- Berlow, E. L. 1995. Patterns and dynamics of context-dependency in the marine rocky intertidal. Ph.D. Dissertation. Oregon State University, Corvallis, Oregon.
- Berlow, E. L., Navarrete S. A. 1997. Spatial and temporal variation in rocky intertidal community organization: Lessons from repeating field experiments. *Journal of Experimental Marine Biology and Ecology* 214:195-229.
- Bertness, M. D., Gaines S. D., Stephens E. G., Yund P. O. 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 156:199-215.
- Burrows, M. T., Hughes R. N. 1991. Variation in foraging behaviour among individuals and populations of dogwhelks, *Nucella lapillus*: natural constraints on energy intake. *Journal of Animal Ecology* 60:497-514.
- Caffey, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* 55(3):313-332.
- Carr, M. H. 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75:1320-1333.
- Christy, J. H. 1982. Adaptive significance of semilunar cycles of larval release in fiddler crabs (Genus *Uca*): test of an hypothesis. *Biological Bulletin* 163:251-263.
- Christy, J. H., Stancyk S. E. 1982. Timing of larval production and flux of invertebrate larvae in a well-mixed estuary. Pages 489-503 in Kennedy V. S., editor. *Estuarine Comparisons. Proceedings of the Sixth Biennial International Estuarine Research Conference*. New York: Academic Press.
- Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* 31:61-104.
- . 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs* 40:49-78.
- . 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93:11-45.

- Connolly, S. R., Roughgarden J. 1999. Increased recruitment of northeast Pacific barnacles during the 1997 El Nino. *Limnology and Oceanography* 44:466-469.
- Day, R. W., Barkai A., Wickens P. A. 1991. Trapping of three whelks by two species of mussel. *Journal of Experimental Marine Biology and Ecology* 149:109-122.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41:351-389.
- Denley, E. J., Underwood A. J. 1979. Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. *Journal of Experimental Marine Biology and Ecology* 36:269-293.
- Fairweather, P. G. 1988. Consequences of supply-side ecology: manipulating the recruitment of intertidal barnacles affects the intensity of predation upon them. *Biological Bulletin* 175:349-354.
- Farrell, T. M., Bracher D., Roughgarden J. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnology and Oceanography* 36:279-288.
- Foster, M. S., Nigg E. W., Kiguchi L. M., Hardin D. D., Pearse J. S. in prep. Temporal variation and succession in an algal-dominated high intertidal assemblage.
- Gaines, S., Brown S., Roughgarden J. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267-272.
- Gaines, S., Roughgarden J. 1985. Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. *Proceeding of the National Academy of Sciences USA* 82:3707-3711.
- Gaines, S. D., Lafferty K. D. 1995. Modeling the dynamics of marine species: The importance of incorporating larval dispersal. Pages 389-412 in McEdward L., editor. *Ecology of marine invertebrate larvae*. Boca Raton, FL: CRC Press.
- Gaines, S. D., Roughgarden J. 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science* 235:479-481.
- Geraci, S., Romairone V. 1982. Barnacle larvae and their settlement in Genoa Harbor (North Tyrrhenian Sea). *Marine Ecology* 3:225-232.

- Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models, and observations. *Biological Journal of the Linneological Society* 42:17-38.
- Hassell, M. P., editor. 1978. *The dynamics of arthropod predator-prey systems*. Princeton: Princeton University Press.
- Hassell, M., May R. M. 1974. Aggregation in predators and insect parasites and its effect on stability. *Journal of Animal Ecology* 43:567-594.
- Hassell, M. P., May R. M., editors. 1990. *Philosophical Transactions of the Royal Society of London: population regulation and dynamics*. Volume 330. Royal Society, London, England.
- Hawkins, S. J., Hartnoll R. G. 1983. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977-1981). *Journal of Experimental Marine Biology and Ecology* 62:271-283.
- Haydon, D., Radtkey R. R., Pianka E. R. 1993. *Experimental Biogeography: interactions between stochastic, historical, and ecological processes in a model archipelago*. Pages 117-130 *in* Ricklefs R. E., Schluter D., editors. *Species Diversity in Ecological Communities: historical and geographical perspectives*. Chicago: The University of Chicago Press.
- Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine saw fly. *Canadian Entomologist* 91:293-320.
- Hughes, R. N, Burrows M. T. 1991. Diet selection by dogwhelks in the field: an example of constrained optimization. *Animal Behaviour* 42:47-55.
- Judge, M. L., Quinn J. F., Wolin C. L. 1988. Variability in recruitment of *Balanus glandula* (Darwin, 1854) along the central California coast. *Journal of Experimental Marine Biology and Ecology* 119:235-251.
- Keough, M. J., Downes B. J. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54:348-352.
- Lewin, R. 1986. Supply-Side Ecology. *Science* 234:25-27.
- Lubchenco, J., Real L. A. 1991. Experimental manipulations in lab and field systems. Pages 715-733 *in* Real L. A., Brown J. H., editors. *Foundations of Ecology*. Chicago: The University of Chicago Press.
- Ludwig, J. A., Reynolds J. F. 1988. *Statistical Ecology. A primer on Methods and Computing*. New York: John Wiley & Sons.

- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* 46:355-393.
- . 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755-765.
- Menge, B. A. in press. Relative importance of recruitment and post-recruitment processes in determining barnacle abundance in rocky intertidal communities. *Ecology*.
- Menge, B. A., Berlow E. L., Blanchette C., Navarrete S. A., Yamada S. B. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249-286.
- Menge, B. A., Farrell T. M., Olson A. M., van Tamelen P., Turner T. 1993. Algal recruitment and the maintenance of plant mosaic in the low intertidal region on the Oregon coast. *Journal of Experimental Marine Biology and Ecology* 170:91-116.
- Menge, B. A., Sutherland J. P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130:730-757.
- Menge, J. L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. *Oecologia* 17:293-316.
- Minchinton, T. E., Scheibling R. S. 1993. Free space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. *Marine Ecology Progress Series* 95:233-244.
- Morgan, R. A., Brown J. S., Thorson J. M. 1997. The effect of spatial scale on the functional response of fox squirrels. *Ecology* 78:1087-1097.
- Morris, R. H., Abbott D. P., Haderlie E. C. 1992. *Intertidal Invertebrates of California*. Stanford: Stanford University Press.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39:335-354.
- Murdoch, W. W. 1971. The developmental responses of predators to changes in prey density. *Ecology* 52:132-137.
- Murdoch, W. W., Bence J. 1987. General predators and unstable prey populations. Pages 17-30 in Kerfoot W. C., Sih A., editors. *Predation*. Hanover, NH: University of New England Press.
- Murdoch, W. W., Oaten A. 1975. Predation and population stability. *Advances in*

Ecological Research 9:1-131.

- Navarrete, S. A. 1996. Variable predation: Effects of whelks on a mid-intertidal successional community. *Ecological Monographs* 66(3):301-321.
- Navarrete, S. A., Castilla J. C.. 1990. Resource partitioning between intertidal predatory crabs: interference and refuge utilization. *Journal of Experimental Marine Biology and Ecology* 143:101-129.
- Navarrete, S. A., Menge B. A. 1996. Keystone predation and interaction strength: Interactive effects of predators on their main prey. *Ecological Monographs* 66:409-429.
- Navarrete, S. A., Menge B. A., Daley B. A. in press. Species interactions in a rocky intertidal food web: prey or predation regulation of intermediate predators? *Ecology*.
- Palmer, A. R. 1983. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. *Journal of Experimental Marine Biology and Ecology* 73:95-124.
- . 1984. Prey selection by thaidid gastropods: some observational and experimental field test of foraging models. *Oecologia* 62:162-172.
- Petratits, P. S. 1991. Recruitment of the mussel *Mytilus edulis* L. on sheltered and exposed shores in Maine, USA. *Journal of Experimental Marine Biology and Ecology* 147:65-80.
- Pfister, C. A., Bradbury A. 1996. Harvesting red sea urchins: Recent effects and future predictions. *Ecological Applications* 6:298-310.
- Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Marine Ecology Progress Series* 107:125-138.
- Possingham, H. P., Tuljapurkar S., Roughgarden J., Wilks M. 1994. Population cycling in space-limited organisms subject to density-dependent predation. *American Naturalist* 143:563-582.
- Raimondi, P. T. 1990. Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecological Monographs* 60:283-309.
- Robles, R., Sherwood-Stephens R., Alvarado M. 1995. Responses of a key intertidal predator to varying recruitment of its prey. *Ecology* 76:565-579.
- Rodríguez, S. R., Ojeda F. P., Inestrosa N. C. 1993. Settlement of benthic marine invertebrates. *Marine Ecology* 97:193-207.

- Roughgarden, J., Gaines S., Possingham H. 1988. Recruitment dynamics in complex life cycles. *Science* 241:1460-1466.
- Sale, P. F. 1990. Recruitment of marine species: is the bandwagon rolling in the right direction? *Trends in Ecology and Evolution* 5:25-27.
- Schmitt, R. J. 1985. Competitive interactions of two mobile prey species in a patchy environment. *Ecology* 66:950-958.
- Schmitt, R. J., Holbrook S. J. 1990. Contrasting effects of giant kelp on dynamics of surfperch populations. *Oecologia* 84:419-429.
- Shanks, A. L. 1995. Mechanisms of cross-shelf dispersal of larval invertebrates and fish. Pages 323-367 *in* McEdward L. R., editor. *Ecology of Marine Invertebrate Larvae*. Boca Raton, FL: CRC Press.
- Sokal, R. R., Rohlf F. J. 1981. *Biometry*. second edition. New York: W. H. Freeman and Company.
- Spight, T. M. 1972. Patterns of change in adjacent populations of an intertidal snail, *Thais lamellosa*. Ph.D. Dissertation. University of Washington, Seattle, Washington, USA.
- . 1981. How three rocky shore snails coexist on a limited food resource. *Researches on Population Ecology* 23:245-261.
- . 1982a. Population sizes of two marine snails with a changing food supply. *Journal of Experimental Marine Biology and Ecology* 57:195-217.
- . 1982b. Risk reward, and the duration of feeding excursions by a marine snail. *Veliger* 24:302-308.
- Spight, T. M., Emlen J. M. 1976. Clutch sizes of two marine snails with a changing food supply. *Ecology* 57:1162-1178.
- Strathmann, R. R., Branscomb E. S. 1979. Adequacy of cues to favorable sites used by settling larvae of two intertidal barnacles. *in* Stancyk S. E., editor. *Reproductive Ecology of Marine Invertebrates*. Columbia, SC: University of South Carolina Press.
- Strathmann, R. R., Branscomb E. S., Vedder D. 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia* 48:13-18.
- Sutherland, J. P. 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology* 71:955-972.
- Sutherland, J. P., Ortega S. 1986. Competition conditional on recruitment and

- temporary escape from predators on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* 95:155-166.
- Tegner, M. J., Dayton P. K. 1977. Sea urchin recruitment patterns and implications of commercial fishing. *Science* 196:324-326.
- Underwood, A. J. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia* 33:185-202.
- Underwood, A. J., Anderson M. J. 1994. Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. *Journal Marine Biological Association, U.K.* 74:563-584.
- Underwood, A. J., Denley E. J. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151-180 *in* Strong D. R., Simberloff D., Abele L. G., Thistle A. B., editors. *Ecological Communities: Conceptual Issues and the Evidence*. Princeton: Princeton University Press.
- Underwood, A. J., Denley E. J., Moran M. J. 1983. Experimental analyses of the structure of midshore rocky intertidal communities in New South Wales. *Oecologia* 56:202-219.
- Underwood, A. J., Fairweather P. G. 1989. Supply-side Ecology and Benthic Marine Assemblages. *Trends in Ecology and Evolution* 4:16-20.
- Valiela, I. 1984. *Marine ecological processes*. New York: Springer-Verlag.
- von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113-137 *in* Scheiner S. M., Gurevitch J., editors. *Design and analysis of Ecological Experiments*. London: Chapman & Hall.
- Wethey, D. S. 1984. Spatial pattern in barnacle settlement: day to day changes during the settlement season. *Journal Marine Biological Association, U.K.* 64:687-698.
- Wethey, D. S. 1986. Local and regional variation in the settlement and survival in the littoral barnacle *Semibalanus balanoides* (L.): patterns and consequences. Pages 194-202 *in* Moore, P.G., Seed, R., editors. *The ecology of rocky coasts*. New York: Columbia University Press.
- Wieters, E. A., Navarrete S. A. 1998. Spatial Variability in Prey Preferences of the Intertidal Whelks *Nucella canaliculata* and *Nucella emarginata*. *Journal of Experimental Marine Biology and Ecology* 222:133-148.
- Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75:151-165.

Table IV.1. Contingency tables and ChiSquare analyses of the number of *Nucella emarginata*, *Nucella canaliculata*, and *Ocenebra circumtexta* observed on feeding area or sheltering habitats (crevice, pool) during low tide periods. Observed and expected values (in parentheses) are reported for each treatment by habitat combination.

	<i>N. emarginata</i>			<i>N. canaliculata</i>			<i>O.circumtexta</i>		
	crevice	pool	foraging	crevice	pool	foraging	crevice	pool	foraging
Control	51 (29.8)	35 (17.0)	110 (149.2)	83 (41.4)	18 (24.3)	45 (80.3)	114 (55.9)	65 (54.6)	95 (163.5)
Shells	20 (11.4)	3 (6.5)	52 (57.1)	19 (27.8)	27 (16.3)	52 (53.9)	22 (30)	27 (29.3)	98 (87.7)
Early	65 (66.1)	36 (37.8)	334 (331)	45 (46.5)	20 (27.3)	99 (90.1)	150 (114)	78 (111)	331 (333)
Frequent	18 (46.7)	14 (26.7)	275 (234)	13 (44.3)	29 (26)	114 (85.7)	54 (140)	162 (137)	471 (410)
ChiSquare	84.259			103.312			189.523		
P	<0.0001			<0.0001			<0.0001		

Table IV.2. Contingency tables and ChiSquare analyses of diet composition of *Nucella emarginata*, *Nucella canaliculata*, and *Ocenebra circumtexta*. Data based on observed diet during low tide periods. Observed and expected values (in parentheses) are reported for each treatment x prey type combination. Here, mussels are *Mytilus californianus* and barnacles are *Balanus glandula*.

	<i>N. emarginata</i>		<i>N. canaliculata</i>		<i>O.circumtexta</i>	
	Barnacle	Mussel	Barnacle	Mussel	Barnacle	Mussel
No Barnacle	7	45	5	33	21	27
Recruits	(23.2)	(28.8)	(9.5)	(28.5)	(46.5)	(6.5)
Added						
+ Barnacle	64	43	10	12	307	19
Recruits	(47.8)	(59.2)	(5.5)	(16.5)	(281.5)	(39.5)
ChiSquare	33.328		7.571		73.623	
P	<0.0001		0.0059		<0.0001	

Table IV.3. Repeated measures analysis of variance of the effects of barnacle recruit additions on densities of *Nucella emarginata*. Since only 2 levels of time were considered, data conformed to assumptions of univariate split-plot ANOVA and only these results are presented for within subject effects (see text).

Between Subjects

Source	df	MS	F	P
Treatment	3	0.785	8.48	0.0027
Block	4	0.182	1.97	0.1641
Error	12	0.092		
Contrasts				
Shells vs. Control	1	0.858	9.27	0.0102
Shells_Control vs. Early_Frequent	1	1.254	13.57	0.0031
Early vs. Frequent	1	0.242	2.61	0.1319

Within Subjects

Source	df	MS	F	P
Period	1	0.141	3.51	0.0854
Period x Treatment	3	0.018	0.45	0.7223
Period x Block	4	0.010	0.25	0.9021
Error	12	0.040		
Contrasts				
Period*Shells vs. Control	1	0.003	0.08	0.7879
Period*Shells_Control vs. Early_Frequent	1	0.00002	0.001	0.9833
Period*Early vs. Frequent	1	0.051	1.27	0.2814

Table IV.4. Repeated measures analysis of variance of the effects of barnacle recruit additions on densities of *Nucella canaliculata*. Since only 2 levels of time were considered, data conformed to assumptions of univariate split-plot ANOVA and only these results are presented for within subject effects (see text).

Between Subjects

Source	df	MS	F	P
Treatment	3	0.025	1.02	0.4166
Block	4	0.669	27.65	0.0001
Error	12	0.024		
Contrasts				
Shells vs. Control	1	0.045	1.87	0.1965
Shells_Control vs. Early_Frequent	1	0.029	1.19	0.2972
Early vs. Frequent	1	0.0003	0.01	0.9128

Within Subjects

Source	df	MS	F	P
Period	1	0.348	16.11	0.0017
Period x Treatment	3	0.021	0.97	0.4372
Period x Block	4	0.037	1.69	0.2159
Error	12	0.022		
Contrasts				
Period*Shells vs. Control	1	0.053	2.46	0.1429
Period*Shells_Control vs. Early_Frequent	1	0.009	0.43	0.5266
Period*Early vs. Frequent	1	0.0008	0.04	0.8503

Table IV.5. Repeated measures analysis of variance of the effects of barnacle recruit additions on densities of *Ocenebra circumtexta*. Since only 2 levels of time were considered, data conformed to assumptions of univariate split-plot ANOVA and only these results are presented for within subject effects (see text).

Between Subjects

Source	df	MS	F	P
Treatment	3	0.433	4.40	0.0262
Block	4	0.616	6.26	0.0058
Error	12	0.098		
Contrasts				
Shells vs. Control	1	0.084	0.85	0.3745
Shells_Control vs. Early_Frequent	1	1.183	12.02	0.0047
Early vs. Frequent	1	0.034	0.34	0.5702

Within Subjects

Source	df	MS	F	P
Period	1	0.165	9.59	0.0092
Period x Treatment	3	0.002	0.13	0.9374
Period x Block	4	0.145	8.40	0.0018
Error	12	0.017		
Contrasts				
Period*Shells vs. Control	1	0.002	0.10	0.7609
Period*Shells_Control vs. Early_Frequent	1	0.002	0.11	0.7476
Period*Early vs. Frequent	1	0.003	0.20	0.6635

Figure IV.1. Sketch of the experimental design. Barnacle recruitment was manipulated by transplanting small barnacle recruits atop valves of mussel shells either once (Early) or twice (Frequent) during the main barnacle settlement season. To control for artifacts of the transplanting method itself, clean mussel valves were transplanted to 'shells only' treatments. The 'Control' treatment refers to plots that were left undisturbed for the duration of the experiment. See text for details.

Figure IV.2. Mean ($\pm$ SE) percent cover of mussels and barnacles at Diablo Canyon during late summer 1996. Insert shows barnacle cover on mussel shells.

Figure IV.3. Mean ($\pm$ SE) percent cover of small barnacle prey in experimental blocks at Diablo Canyon during late summer 1996.

Figure IV.4. Mean ($\pm$ SE) densities of whelks a) *Nucella emarginata*, b) *Nucella canaliculata*, c) *Ocenebra circumtexta*, and d) *Acanthina spirata* in experimental blocks at Diablo Canyon.

Figure IV.5. Density of *Nucella emarginata*, *Nucella canaliculata*, *Ocenebra circumtexta*, and *Acanthina spirata* on the study bench at Diablo Canyon. Each bar is the mean ($\pm$ SE) of 20 0.25m² quadrats regularly positioned along two permanently marked transects in the mid zone of the experimental platform.

Figure IV.6. Variance in the density of *Nucella emarginata*, *Nucella canaliculata*, and *Ocenebra circumtexta* at different quadrat spacings (distance between quadrats along 20m transects), using the paired-quadrats variance method (see text).

Figure IV.7. Mean ($\pm$ SE) growth rates of marked juvenile a) *Nucella emarginata* and b) *Ocenebra circumtexta* experiencing different prey recruitment treatments (see text). Hatched bars represent mean growth rates for those marked whelks moving long distances outside of experimental plots.

Figure IV.8. Density of a) *Nucella emarginata*, b) *Nucella canaliculata*, c) *Ocenebra circumtexta*, and d) *Acanthina spirata* in experimental plots before and after the second pulse of barnacle recruitment. Each bar is the mean ($\pm$ SE) of average densities for 5 months monitoring periods before September (addition 1) and after September (addition 2). Densities for *A. spirata* are presented for the only block in which this species was observed.

Figure IV.9. Mean ($\pm$ SE) movement rate of marked individual *Nucella emarginata*, *Nucella canaliculata*, and *Ocenebra circumtexta* under natural conditions at Diablo Canyon.

Figure IV.10. Mean ($\pm$ SE) frequency at which a marked individual a) *Nucella emarginata*, b) *Nucella canaliculata*, and c) *Ocenebra circumtexta* was observed within control, early, and frequent prey recruitment plots.

Figure IV.11. Percent of marked *Nucella emarginata*, *Nucella canaliculata*, and *Ocenebra circumtexta* whose empty shells were recovered (dead whelks).

Figure IV.12. Survivorship of transplanted barnacle recruits in predator exclusion (open circles), early (filled squares), and frequent (filled triangles) barnacle addition treatments.

CHAPTER V

GENERAL CONCLUSIONS

The general focus of this thesis has been to understand some of the consequences of variability in prey recruitment rates for predators. By using a combination of correlation, comparison, and field experiments, I was able to investigate short-term and potential long-term patterns of predator responses to prey recruitment over several spatial scales. Together, these different methods have proved to be useful in expanding the range of predictive power by providing insight into scale-dependency of predator responses.

As a first step to determine if population sizes of predators were linked to prey recruitment and/or local prey abundance, I examined predator-prey correlations over large spatial scales (among sites 10's - 100's kilometers apart). In chapter II, I hypothesized that such large-scale correlations would vary according to the combination of life-history attributes of the species involved. Predators with pelagic larvae that disperse long distances away from adults have "open" population dynamics in which population size is largely independent of local adult reproduction. In contrast, predators with direct development have juveniles that are born and usually grow in the same habitat as adults, producing a "closed" population type of dynamics where population size is more dependent on local adult reproduction. Because predators with these different types of life history differ in their ability to respond numerically to persistent differences in local prey productivity across sites, correlations beyond the spatial scale of behavioral changes (aggregation) were expected to be strongly positive for the whelk *Nucella emarginata*

(direct developer) and less tight for the seastar *Pisaster ochraceus* (pelagic larvae).

Patterns of numerical abundance of whelks varied similarly with prey recruitment among sites, but not with local prey abundance. These results suggest that availability of small prey (new recruits) for juvenile and hatchling whelks acts as a bottleneck for whelk population size. Seastars, on the other hand, did not seem to track prey recruitment or local prey abundance over space at these scales, suggesting prey does not limit the population size of this species along the coast of central California.

I concluded from this study that, although limited in determining causation, greater prey production (recruitment) may be a necessary factor to maintain higher densities of whelks but not seastars, and I suspected that the variation between predators is due to their different modes of reproduction. Further study of predators with direct development at sites experiencing persistently different levels of prey recruitment should prove fruitful and help provide insight into mechanisms that lead to such large-scale correlations.

In chapter III, I compared short-term behavior of two predator species with direct development, the whelks *Nucella emarginata* and *Acanthina spirata*, between two sites with similar habitat characteristics but with naturally contrasting levels of prey recruitment. Both of the sites were part of the study in Chapter II that covered a larger geographic scale, and were chosen as typical representatives of sites that had consistently received either relatively high (Arroyo Hondo) or relatively low (Diablo Canyon) recruitment of mussels and barnacles prey. To look at differences in predator diet, growth, movement, and mortality rates between sites, I conducted a replicated, reciprocal transplant experiment of marked whelks during late summer to early winter (July to

January), when prey recruitment was at its peak.

My results showed that whelks in the high prey recruitment site maintained higher densities and higher survival, but the apparent mechanisms that led to these results differed between the two whelk species. Where prey recruitment was low, *N. emarginata* foraged over a broader area and captured enough food to maintain growth rates. However, higher movement rates appeared to increase exposure to multiple stresses (e.g. wave forces) which resulted in higher mortality. In contrast, the relatively low density of *A. spirata* at the low prey recruitment site appeared to be a direct consequence of food limitation. Here, whelks preyed upon an alternative prey item, but did not seem to obtain enough energy to sustain comparable body mass, as whelks of similar size weighed less and had negative growth rates.

The results of between-site comparisons led me to conclude that behavior of predatory whelks with direct development differed greatly between sites, and prey recruitment was the most likely explanation for these differences. Potential alternative explanations based on other relatively slight physical and biological differences between the two sites did not seem plausible, as results were opposite those predicted by these alternative explanations. Although I compromised the number of study sites to concentrate on several aspects of whelk behavior and population structure, data are consistent with previous work and support the hypothesis that large-scale variation in prey recruitment can have important direct and indirect effects on whelk behavior and this in turn affects overall population abundances.

In chapter IV, I tested whether variable recruitment rates of prey cause important short-term and/or long-term responses by predators. I experimentally manipulated small-scale spatial variation (meters) in barnacle recruitment and monitored responses of four species of whelks with direct development. I augmented barnacle recruitment in 1 x 1 meter experimental plots at Diablo Canyon (DC, a consistently low prey recruitment site) by transplanting small barnacles that had, at a separate site north of DC, naturally settled atop mussel shells. Valves of mussel shells were glued to the rock surface using a non-toxic submarine epoxy. By manipulating the abundance and seasonal timing that the new barnacle recruits entered into whelk habitat, I was able to quantify and separate the effects of recruitment intensity and frequency. Five replicates of prey recruitment treatments were assigned to plots according to a complete randomized block design. In addition, individually marked whelks were released at the center of each plot at the beginning of the experiment and monitored every two to four weeks to examine differences in predator growth, movement, and mortality.

Results of the experiment, which was monitored for nine months, showed that addition of prey recruits to a site with consistently low prey influx leads to short and long term responses by the resident predatory whelk populations. However, not all whelk species responded to the ten-fold increase in prey, and those species that did respond displayed a complex pattern of changes in movement rates, feeding, growth, and mortality. Furthermore, frequent recruitment of barnacles into whelk habitat produced different responses by one whelk species, *Ocenebra circumtexta*, than those produced by a single barnacle recruitment event. These results suggest that the temporal pattern of recruitment

may lay an important role in whether or not prey effects translate into long-term responses by this species.

BIBLIOGRAPHY

- Arditi, R., Ginzburg L. R. 1989. Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology* 139:311-326.
- Bayne, B. L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology* 33:513-523.
- Bell, E. C., Denny M. W. 1994. Quantifying 'wave exposure': A simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* 181: 9-29.
- Bender, E. A., Case T. J., Gilpin M. E. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1-13.
- Berlow, E. L. 1995. Patterns and dynamics of context-dependency in the marine rocky intertidal. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.
- Berlow, E. L., Navarrete S. A. 1997. Spatial and temporal variation in rocky intertidal community organization: Lessons from repeating field experiments. *Journal of Experimental Marine Biology and Ecology* 214:195-229.
- Bertness, M. D., Gaines S. D., Stephens E. G., Yund P. O. 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 156:199-215.
- Bertness, M. D., Gaines S. D., Wahle R. A. 1996. Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series* 137:103-110.
- Boicourt, W. C. 1982. Estuarine larval retention mechanisms on tow scales. Pages 445-457 in Kennedy V. S., editor. *Estuarine Comparisons*. Proceeding of the Sixth Biennial International Estuarine Reserve Conference. New York: Academic Press.
- Burrows, M. T., Hughes R. N. 1991. Variation in foraging behaviour among individuals and populations of dogwhelks, *Nucella lapillus*: natural constraints on energy intake. *Journal of Animal Ecology* 60:497-514.
- Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanography and Marine Biology Annual Review* 25:113-165.

- Caffey, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* 55:313-332.
- Carpenter, S. C., Kitchell J. F. 1984. Plankton community structure and limnetic primary production. *American Naturalist* 124:159-172.
- Carpenter, S. C., Kitchell J. F. 1987. The temporal scale of variance in limnetic interactions and lake productivity. *American Naturalist* 129:417-433.
- Carpenter, S. C., Kitchell J. F., Hodgson P. A. 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35:634-639.
- Carr, M. H. 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75:1320-1333.
- Christy, J. H. 1982. Adaptive significance of semilunar cycles of larval release in fiddler crabs (Genus *Uca*): test of an hypothesis. *Biological Bulletin* 163:251-263.
- Christy, J. H., Stancyk S. E. 1982. Timing of larval production and flux of invertebrate larvae in a well-mixed estuary. Pages 489-503 in Kennedy V. S., editor. *Estuarine Comparisons. Proceedings of the Sixth Biennial International Estuarine Research Conference*. New York: Academic Press.
- Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* 31:61-104.
- . 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs* 40:49-78.
- . 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93:11-45.
- Connolly, S. R., Roughgarden J. 1998. A latitudinal gradient in northeast Pacific intertidal community structure: Evidence for an oceanographically based synthesis of marine community theory. *American Naturalist* 151: 311-326.
- Connolly, S. R., Roughgarden J. 1999. Increased recruitment of northeast Pacific barnacles during the 1997 El Nino. *Limnology and Oceanography* 44:466-469.
- Crisp, D. J. 1976. Settlement responses in marine organisms. Pages 83-124 in Newell R. C., editor. *Adaptation to environment: essays on the physiology of marine animals*. London: Butterworths.

- Day, R. W., Barkai A., Wickens P. A. 1991. Trapping of three whelks by two species of mussel. *Journal of Experimental Marine Biology and Ecology* 149:109-122.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41:351-389.
- Denley, E. J., Underwood A. J. 1979. Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. *Journal of Experimental Marine Biology and Ecology* 36:269-293.
- Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 in Diamond J., Case T. J., editors. *Community Ecology*. New York: Harper & Row.
- Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. *Limnological Oceanography* 28:241-257.
- Fairweather, P. G. 1988a. Consequences of supply-side ecology: manipulating the recruitment of intertidal barnacles affects the intensity of predation upon them. *Biological Bulletin* 175:349-354.
- . 1988b. Correlations of predatory whelks with intertidal prey at several scales of space and time. *Marine Ecology Progress Series* 45:237-243.
- . 1988c. Predation can increase variability in the abundance of prey on seashores. *Oikos* 53:87-92.
- . 1991. Implications of 'supply-side' ecology for environmental assessment and management. *Trends in Ecology and Evolution* 6:60-63.
- Fairweather, P.G., Underwood A. J. 1983. The apparent diet of predators and biases due to different handling times. *Oecologia* 56:169-179.
- Farrell, T. M., Bracher D., Roughgarden J. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnology and Oceanography* 36:279-288.
- Feder, H. M. 1970. Growth and predation by the ochre sea star *Pisaster ochraceus* (Brandt) in Moterey Bay, California. *Ophelia* 8:161-185.
- Foster, M. S. 1990. Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia* 192:21-33.

- Foster, M. S., Nigg E. W., Kiguchi L. M., Hardin D. D., Pearse J. S. in prep. Temporal variation and succession in an algal-dominated high intertidal assemblage.
- Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology. *Oikos* 50:291-301.
- Gaines, S., Brown S., Roughgarden J. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267-272.
- Gaines, S., Roughgarden J. 1985. Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences USA* 82:3707-3711.
- Gaines, S. D., Bertness M. D. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360:579-580.
- Gaines, S. D., Bertness M. D. 1993. The dynamics of juvenile dispersal: why field ecologists must integrate. *Ecology* 74:2430-2435.
- Gaines, S. D., Lafferty K. D. 1995. Modeling the dynamics of marine species: The importance of incorporating larval dispersal. Pages 389-412 in McEdward L., editor. *Ecology of Marine Invertebrate Larvae*. Boca Raton, FL: CRC Press.
- Gaines, S. D., Roughgarden J. 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science* 235:479-481.
- Geraci, S., Romairone V. 1982. Barnacle larvae and their settlement in Genoa Harbor (North Tyrrhenian Sea). *Marine Ecology* 3:225-232.
- Getz, W. M. 1984. Population dynamics: a per capita resource approach. *Journal of Theoretical Biology* 108:623-643.
- Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models, and observations. *Biological Journal of the Linnean Society*. 42:17-38.
- Hart, M.W., Palmer A. R. 1987. Stereotypy, ontogeny, and heritability of drill site selection in thaidid gastropods. *Journal of Experimental Marine Biology and Ecology* 107:101-120.
- Hassell, M. P., editor. 1978. *The dynamics of arthropod predator-prey systems*. Princeton: Princeton University Press.

- Hassell, M., May R. M.. 1974. Aggregation in predators and insect parasites and its effect on stability. *Journal of Animal Ecology* 43:567-594.
- Hassell, M. P., May R. M., editors. 1990. *Philosophical Transactions of the Royal Society of London: population regulation and dynamics*. Volume 330. Royal Society, London, England.
- Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. *Theoretical Population Biology* 12:37-48.
- Hawkins, S. J., Hartnoll R. G. 1983. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977-1981). *Journal of Experimental Marine Biology and Ecology* 62:271-283.
- Haydon, D., Radtkey R. R., Pianka E. R. 1993. Experimental Biogeography: interactions between stochastic, historical, and ecological processes in a model archipelago. Pages 117-130 in Ricklefs R. E., Schluter D., editors. *Species Diversity in Ecological Communities: historical and geographical perspectives*. Chicago: The University of Chicago Press.
- Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine saw fly. *Canadian Entomologist* 91:293-320.
- Hughes, R. N., Burrows M. T. 1991. Diet selection by dogwhelks in the field: an example of constrained optimization. *Animal Behaviour* 42:47-55.
- Hughes, R. N., Burrows M. T., Rogers H. H.. 1992. Ontogenetic changes in foraging behaviour of the dogwhelk *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* 155:199-212.
- Hughes, R. N., Dunkin SdeB. 1984. Effect of dietary history on selection of prey, and foraging behaviour among patches of prey, by the dogwhelk, *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* 79:159-172.
- Judge, M. L., Quinn J. F., Wolin C. L. 1988. Variability in recruitment of *Balanus glandula* (Darwin, 1854) along the central California coast. *Journal of Experimental Marine Biology and Ecology* 119:235-251.
- Keough, M. J., Downes B. J. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54:348-352.
- Leonard, G. H., Levine J. M., Schmidt P. R., Bertness M. D. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79:1395-1411.

- Levin, S. A. 1989. Challenges in the development of a theory of community and ecosystem structure and function. Pages 242-255 in Roughgarden J., May R. M., Levin S. A., editors. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- . 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.
- Lewin, R. 1986. Supply-side ecology. *Science* 234:25-27.
- Lubchenco, J., Real L. A. 1991. Experimental manipulations in lab and field systems. Pages 715-7133 in Real, L. A., Brown J. H., editors. *Foundations of Ecology*. Chicago: The University of Chicago Press.
- Lubchenco, J. A., Navarrete S. A., Tissot B. N., Castilla J. C. 1993. Possible ecological responses to global climate change: nearshore benthic biota of Northeastern Pacific coastal ecosystems. Pages 147-166 in Mooney H. A., Fuentes E. R., Kronberg B. I., editors. *Earth Systems Responses to Global Climate Change. Contrasts Between North and South America*. San Diego: Academic Press.
- Ludwig, J. A., Reynolds J. F. 1988. *Statistical Ecology. A primer on Methods and Computing*. New York: John Wiley & Sons.
- Mackas, D., Strub T., Hunter J. (eds.). 1992. Report on Climate Change and the California Current Ecosystem, Eastern Boundary Current Program, U.S. GLOBEC, Global Ocean Ecosystems Dynamics, Rep. 7. Scientific Steering Committee Coordinating Office, Univ. Of Calif., Davis.
- McCauley, E., Wilson W. G., de Roos A. M. 1993. Dynamics of age-structured and spatially structured predator-prey interactions: individual-based models and population-level formulations. *American Naturalist* 142:412-442.
- McDonald, J. H., Kohen R. K. 1988. The mussels (*Mytilus galloprovincialis* and *Mytilus trossulus*) on the coast of North America. *Marine Biology* 99:111-118.
- McEdward, L., editor. 1995. *Ecology of marine invertebrate larvae*. Boca Raton, FL: CRC Press.
- Menge, B. A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecological Monographs* 42:25-50.
- . 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* 46:355-393.

- . 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* 146:69-100.
- . 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755-765.
- . in press. Relative importance of recruitment and post-recruitment processes in determining barnacle abundance in rocky intertidal communities. *Ecology*.
- Menge, B. A., Olson A. M. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* 5:52-57.
- Menge, B. A., Berlow E. L., Blanchette C., Navarrete S. A., Yamada S. B. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249-286.
- Menge, B. A., Daley B., Wheeler P. A. 1995. Control of interaction strength in marine benthic communities. Pages 258-274 in Polis, G., Winemiller K. O., editors. *Food Webs: Integration of Patterns and Dynamics*. New York: Chapman & Hall.
- Menge, B. A., Farrell T. M., Olson A. M., van Tamelen P., Turner T. 1993. Algal recruitment and the maintenance of plant mosaic in the low intertidal region on the Oregon coast. *Journal of Experimental Marine Biology and Ecology* 170:91-116.
- Menge, B. A., Sutherland J. P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130:730-757.
- Menge, J. L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. *Oecologia* 17:293-316.
- Minchinton, T. E., Scheibling R. S. 1993. Free space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. *Marine Ecology Progress Series* 95:233-244.
- Moran, N. A. 1994. Adaptation and constraint in the complex life cycles of animals. *Annual Review of Ecological Systematics* 25:573-600.
- Morgan, R. A., Brown J. S., Thorson J. M. 1997. The effect of spatial scale on the functional response of fox squirrels. *Ecology* 78:1087-1097.
- Morris, R. H., Abbott D. P., Haderlie E. C. 1992. *Intertidal Invertebrates of California*. Stanford: Stanford University Press.

- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39:335-354.
- . 1971. The developmental responses of predators to changes in prey density. *Ecology* 52:132-137.
- Murdoch, W. W., Bence J. 1987. General predators and unstable prey populations. Pages 17-30 in Kerfoot W. C., Sih A., editors. *Predation*. Hanover, NH: University of New England Press.
- Murdoch, W. W., Oaten A. 1975. Predation and population stability. *Advances in Ecological Research* 9:1-131.
- Navarrete, S. A. 1996. Variable predation: Effects of whelks on a mid intertidal successional community. *Ecological Monographs* 66:301-322.
- Navarrete, S. A., Castilla J. C. 1990. Resource partitioning between intertidal predatory crabs: interference and refuge utilization. *Journal of Experimental Marine Biology and Ecology* 143:101-129.
- Navarrete, S. A., Menge B. A. 1996. Keystone predation: interactive effects of two predators on their main prey. *Ecological Monographs* 66:409-429.
- Navarrete, S. A., Menge B. A., Daley B. A. in press. Species interactions in a rocky intertidal food web: prey or predation regulation of intermediate predators? *Ecology*.
- Oksanen, L. 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for coexistence? *American Naturalist* 131:424-444.
- Oksanen, L., Fretwell S. D., Arruda J., Niemela P. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240-261.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93-120.
- Palmer, A. R. 1983. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. *Journal of Experimental Marine Biology and Ecology* 73:95-124.
- . 1984. Prey selection by thaidid gastropods: some observational and experimental field test of foraging models. *Oecologia* 62:162-172.

- Persson, L., Andersson G., Hamrin S. F., Johansson L. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. Pages 45-65 in Carpenter S. C., editor. Complex interactions in lake communities. New York: Springer-Verlag.
- Peters, R. H. 1991. A Critique for Ecology. Cambridge: Cambridge University Press.
- Petraitis, P. S. 1991. Recruitment of the mussel *Mytilus edulis* L. on sheltered and exposed shores in Maine, USA. Journal of Experimental Marine Biology and Ecology 147:65-80.
- Pfister, C. A., Bradbury A. 1996. Harvesting red sea urchins: recent effects and future predictions. Ecological Applications 6:298-310.
- Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a southern california rocky shore. Marine Ecology Progress Series 107:125-138.
- Possingham, H. P., Tuljapurkar S., Roughgarden J., Wilks M. 1994. Population cycling in space-limited organisms subject to density-dependent predation. American Naturalist 143:563-582.
- Power, M. E. 1990. Effects of fish in river food webs. Science 250:811-814.
- , 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733-746.
- Raimondi, P. T. 1990. Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. Ecological Monographs 60:283-309.
- Robles, C., Sherwood-Stephens R., Alvarado M. 1995. Responses of a key intertidal predator to varying recruitment of its prey. Ecology 76:565-579.
- Robles, C. D. 1997. Changing recruitment in constant species assemblages: implications for predation theory in intertidal communities. Ecology 78: 1400-1414.
- Rodriguez, S. R., Ojeda F. P., Inestrosa N. C. 1993. Settlement of benthic marine invertebrates. Marine Ecology Progress Series 97:193-207.
- Rose, G. A., Legget W. C. 1990. The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. Ecology 71:33-43.
- Roughgarden, J., Iwasa Y., Baxter C. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology 66:54-67.

- Roughgarden, J., Gaines S. D., Possingham H. 1988. Recruitment dynamics in complex life cycles. *Science* 241:1460-1466.
- Rosenzweig, M. L. 1971. The paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385-387.
- Rosenzweig, M. L., MacArthur R. H. 1963. Graphical representation and stability conditions of predator-prey interactions. *American Naturalist* 97:209-223.
- Sale, P. F. 1990. Recruitment of marine species: Is the bandwagon rolling in the right direction? *Trends in Ecology and Evolution* 5:25-27.
- Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin* 140:284-322.
- Scheltema, R. S. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bulletin of Marine Science* 39:290-322.
- Schmitt, R. J. 1985. Competitive interactions of two mobile prey species in a patchy environment. *Ecology* 66:950-958.
- Schmitt, R. J., Holbrook S. J. 1990. Contrasting effects of giant kelp on dynamics of surfperch populations. *Oecologia* 84:419-429.
- Shanks, A. L. 1986. Tidal periodicity in the daily settlement of intertidal barnacle larvae and a hypothesized mechanism for the cross-shelf transport of cyprids. *Biological Bulletin* 170: 429-440.
- Shanks, A. L. 1995. Mechanisms of cross-shelf dispersal of larval invertebrates and fish. Pages 323-367 in McEdward, L. R., editor. *Ecology of Marine Invertebrate Larvae*. Boca Raton, FL: CRC Press.
- Sokal, R. R., Rohlf F. J. 1981. *Biometry*. second edition. New York: W. H. Freeman and Company.
- Spight, T. M. 1972. Patterns of change in adjacent populations of an intertidal snail, *Thais lamellosa*. Ph.D. Dissertation. University of Washington, Seattle, Washington, USA.
- . 1974. Sizes of populations of a marine snail. *Ecology* 55:712-729.
- . 1975. On a snail's chances of becoming a year old. *Oikos* 26:9-14.

- . 1981. How three rocky shore snails coexist on a limited food resource. *Researches on Population Ecology* 23:245-261.
- . 1982a. Population sizes of two marine snails with a changing food supply. *Journal of Experimental Marine Biology and Ecology* 57:195-217.
- . 1982b. Risk reward, and the duration of feeding excursions by a marine snail. *Veliger* 24:302-308.
- Spight, T.M., Emlen J. M. 1976. Clutch sizes of two marine snails with a changing food supply. *Ecology* 57:1162-1178.
- Strathmann, M. F. 1987. *Reproduction and development of marine invertebrates of the northern Pacific coast*. University of Washington Press, Seattle.
- Strathmann, R. R., Branscomb E. S. 1979. Adequacy of cues to favorable sites used by settling larvae of two intertidal barnacles. *in* Stancyk S. E., editor. *Reproductive Ecology of Marine Invertebrates*. Columbia: University of South Carolina Press.
- Strathmann, R. R., Branscomb E. S., Vedder D. 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia* 48:13-18.
- Strong, D.R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747-754.
- Sutherland, J. P. 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology* 71:955-972.
- Sutherland, J. P., Ortega S. 1986. Competition conditional on recruitment and escape from predators on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* 95:155-166.
- Tegner, M. J., Dayton P. K. 1977. Sea urchin recruitment patterns and implications of commercial fishing. *Science* 196:324-326.
- Underwood, A. J. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia* 33:185-202.
- . 1997. *Experiments in ecology*. Melbourne: Cambridge University Press, 504 pages.
- Underwood, A. J., Anderson M. J. 1994. Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. *Journal of the Marine Biological Association UK* 74:563-584.

- Underwood, A. J., Denley E. J. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151-180 in Strong D. R., Simberloff D., Abele L. G., Thistle A. B., editors. Ecological Communities: Conceptual Issues and the Evidence. Princeton: Princeton University Press.
- Underwood, A. J., Denley E. J., Moran M. J. 1983. Experimental analyses of the structure of midshore rocky intertidal communities in New South Wales. *Oecologia* 56:202-219.
- Underwood, A. J., Fairweather P. G. 1989. Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution* 4(1):16-20.
- Underwood, A. J., Petraitis P. S. 1993. Structure of intertidal assemblages in different locations: how can local processes be compared? Pages 39-51 in Ricklefs R. E., Schluter D., editors. Species Diversity in Ecological Communities. Historical and Geographical Perspectives. Chicago: The University of Chicago Press.
- Valiela, I. 1984. Marine ecological processes. New York: Springer-Verlag.
- von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113-137 in Scheiner S. M., Gurevitch J., editors. Design and analysis of Ecological Experiments. London: Chapman & Hall.
- West, L. 1986. Interindividual variation in prey selection by the snail *Nucella* (= *Thais*) *emarginata*. *Ecology* 67:798-809.
- Wetthey, D. S. 1984. Spatial pattern in barnacle settlement: day to day changes during the settlement season. *Journal Marine Biological Association, U.K.* 64:687-698.
- Wetthey, D. S. 1986. Local and regional variation in the settlement and survival in the littoral barnacle *Semibalanus balanoides* (L.): patterns and consequences. Pages 194-202 in Moore, P.G., Seed, R., editors. The ecology of rocky coasts. New York: Columbia University Press.
- Wieters, E. A., Navarrete S. A. 1998. Spatial variation in feeding preferences of the rocky intertidal whelks *Nucella canaliculata* and *N. emarginata*. *Journal of Experimental Marine Biology and Ecology* 222:133-148.
- Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75:151-165.

Wray, G.A. 1995. Evolution of larval and developmental modes. Pages 413-437 *in* L. McEdward, editor. Ecology of Marine Invertebrate Larvae. Boca Raton, FL: CRC Press.

Young, C. M. 1987. Novelty of "Supply-Side Ecology". Science 235:415-416.