

# Multitrophic interactions mediate recruitment variability in a rocky intertidal community

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**ABSTRACT:** Environmentally induced variability in recruitment rates can result in population variability in both space and time. However, fluctuations in population sizes are also governed by species interactions. While both these processes have been widely explored, fewer efforts have been made to investigate their combined effects. The goal of this study was to investigate how environmentally induced recruitment variability combines with species interactions to influence the structure and dynamics of a simple multi-trophic rocky intertidal community. We first simulated spatial differences and temporal fluctuations in larval supply and subsequent recruitment, and found that the effects of temporal variability on community stability depended on spatial differences in mean larval supply. Next, we explored how removal of specific species influenced these patterns. These simulations showed that predatory and competitive interactions can have contrasting effects on community stability in response to recruitment variability, which depend on the life history of the predator. Our results show the difficulty of isolating questions of community response to spatial and temporal recruitment variability from each other or from a consideration of community structure in general.

**KEY WORDS:** Recruitment variability · Community variability · Community stability · Rocky intertidal

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## INTRODUCTION

Environmental factors, and therefore population dynamics, vary in both time and space, with many studies documenting substantial spatial differences and/or temporal fluctuations in population sizes in both marine (Doherty 1983, Keough 1984, Raimondi 1990) and terrestrial (Elton 1924, Lundberg et al. 2000) systems. Such environmentally induced population fluctuations may influence community stability and structure, a topic that has received increasing attention (reviewed by Loreau 2000, Schwartz et al. 2000 and many others). However, environmental variability is also mediated by species interactions (Ripa et al. 1998, Ives et al. 1999, Lehman and Tilman 2000, Ives & Hughes 2002, Doak & Marvier 2003), and considerably fewer empirical studies (Tilman 1996, Mulder et al. 2001) on this topic have yielded mixed answers; some have found that species interactions dampen the effects of environmental variability on community-level variance (Tilman & Downing 1994, Tilman 1996),

whereas others have found that interactions have no effect on community stability (Ives et al. 1999). Here we present results of a model incorporating species interactions and spatial differences and temporal variance in demographic rates for a well-understood rocky intertidal community. We use this model to explore the factors governing community structure and stability, particularly how interactions among these factors determine community patterns.

Much of the research asking if environmental variability is mediated by species interactions has either been specifically focused (Tilman & Downing 1994, Tilman 1996, Lehman & Tilman 2000) or more broadly based (Ives et al. 1999, Doak & Marvier 2003) on plant communities. Like plants, many benthic marine species are characterized by an obligate dispersive stage and a sessile adult stage. The recruitment rates of benthic nearshore organisms are one of the most striking examples of variable population processes across space and time (Caffey 1985, Connell 1985, Gaines & Roughgarden 1985, Gaines et al. 1985, Raimondi 1990,

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Sutherland 1990, Jenkins et al. 2000), thus providing an ideal system to ask questions about the influence of recruitment variability on community structure. Additionally, the composition of intertidal communities changes across large spatial scales, often as a function of upwelling intensity and other oceanographic patterns, which are strong drivers of recruitment variability (Menge et al. 1997, 1999, Connolly & Roughgarden 1998, Connolly et al. 2001).

While many fairly abstract modeling efforts have investigated the importance of environmentally driven population variation for coexistence, community productivity, or community stability (May 1973, Chesson 1983, Warner & Chesson 1985, Ives 1995, Ripa et al. 1998, Lehman & Tilman 2000, Doak et al. 1998, Yachi & Loreau 1999), very little of this work has incorporated well-understood multi-trophic species interactions, empirically parameterized vital rates, or realistic seasonal fluctuations in the life-history traits of co-occurring species. To ask how more realistic (and complex) species interactions and patterns of environmental variation influence communities, we developed a series of simple simulation models incorporating environmentally driven spatial and temporal variability in larval supply and recruitment of barnacles and limpets (the dominant space-occupiers in our system), subsequent demography, and interactions among these and other species in a high rocky intertidal community.

The rocky intertidal communities of the Pacific coast of North America are an attractive focus for this type of study for a number of reasons; the community dynamics are relatively well understood and the communities are dominated by a small number of key species. Our goal was not to build a comprehensive model for stochastic community dynamics for a full community, but rather to model the key aspects of multi-trophic interactions and environmental variability likely to govern the dynamics of this community. We parameterized multi-species difference equations with data from experiments conducted along the central California coast, along with published data from research conducted in high rocky intertidal communities. Simulation models based on these equations tracked both seasonal and annual changes in the community. We used the models to investigate (1) how mean amounts of regional and site-specific long-term limpet and barnacle recruitment (i.e. spatial variability) and temporal stochasticity in recruitment influence average community structure, (2) whether spatial and temporal variability in recruitment interact to affect community structure or stability, and (3) how important predation and competition are in mediating the effects of recruitment variation on community dynamics. While our model and results are tied to a single study system, our findings highlight general issues in the construction of

models to test effects of variability on community dynamics and how species interactions influence conclusions about community stability in the face of environmental variation.

## MATERIALS AND METHODS

**Study system.** High-intertidal communities along the Pacific coast of North America are dominated by the acorn barnacles *Balanus glandula* and *Chthamalus fissus/dalli*, which compete for space. Limpets *Macclintockia scabra* and *Collisella paradigitalis* and the algae *Endocladia muricata* and *Mastocarpus papillata* are also space competitors (Dayton 1971). The primary barnacle predators in the system are the whelks *Acanthina spirata*, *Nucella emarginata* and *N. canaliculata*. Whelks lay demersal egg masses once per year in the late spring. The seastar *Pisaster ochraceus* also consumes barnacles but, in contrast to whelks, has planktonic larvae. Several crab and bird species are common top-level predators in the system.

Fig. 1 shows the primary species interactions in this system and indicates those that we explicitly modeled. Based on past research in the high rocky intertidal zone (Connell 1985, Forde 2002), data collected in field experiments (described below), and to prevent the

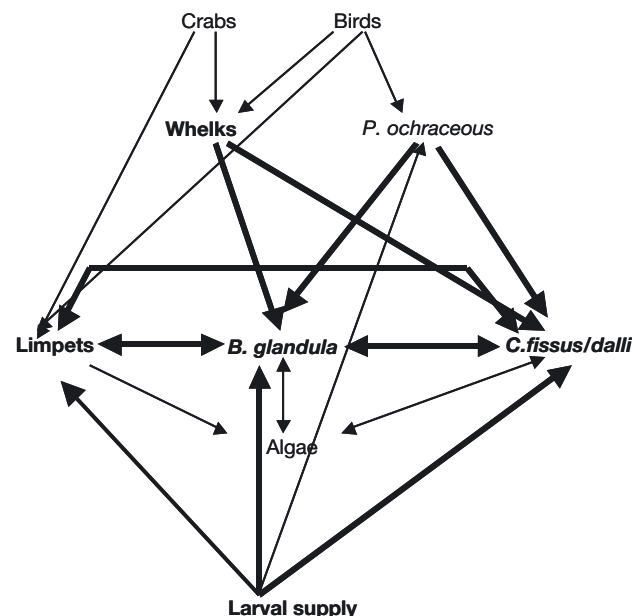


Fig. 1. Interaction webs showing competitive and predatory interactions in the rocky intertidal system. Species interactions parameterized in the model are in bold. Limpets in the community are *Macclintockia scabra* and *Collisella digitalis*. Whelks are *Acanthina punctulata/spirata* and *Nucella emarginata/canaliculata*. *B. glandula*: *Balanus glandula*; *C. fissus/dalli*: *Chthamalus fissus/dalli*; *P. ochraceus*: *Pisaster ochraceus*

model from becoming overly complex, we assumed that the interactions modeled were the most important in structuring the community. For example, although many studies have found that limpets inadvertently graze juvenile barnacles (Dayton 1971), experiments done at sites from which the majority of data were collected for this study (Forde 2002) as well as work on other coasts (e.g. Underwood et al. 1983) have shown that competition for space between limpets and barnacles can be more important than grazing to community structure. The goal of this study was to build a model that improved upon past theoretical work by incorporating biologically realistic parameters and equations, while still keeping the structure of the model relatively simple so that the results could be interpreted in a meaningful way.

The model allowed spatial differences and temporal fluctuations in larval supply and recruitment of barnacles and limpets to directly influence adult population dynamics and indirectly influence the population dynamics of predatory whelks. Recruitment of *Balanus glandula* and *Chthamalus fissus/dalli* occurs primarily in the spring and summer, although *C. fissus/dalli* recruits in very low levels throughout the rest of the year (Gaines & Roughgarden 1985, Gaines et al. 1985, Farrell et al. 1991, Grantham 1997). Limpet recruitment occurs primarily in the summer and fall (S. E. Forde unpubl. data). Recruitment can vary on the scale of days, months and years as a function of temporal fluctuations in upwelling intensity (Farrell et al. 1991, Roughgarden et al. 1991, Alexander & Roughgarden 1996, Grantham 1997, Connolly & Roughgarden 1998, 1999). During periods of upwelling, recruitment tends to be low due to offshore transport of larvae, whereas during periods of relaxation in upwelling, recruitment increases (Farrell et al. 1991, Roughgarden et al. 1991, Wing et al. 1995).

Recruitment also varies spatially along the west coast of North America. Sites in northern and central Oregon have consistently higher recruitment than sites in northern and central California due to a latitudinal gradient in upwelling intensity (Connolly et al. 2001). Similarly, sites to the north of the Monterey Bay tend to have higher long-term recruitment rates than sites to the south (Grantham 1997, Connolly & Roughgarden 1999). Recruitment also varies on a smaller spatial scale. Along the Monterey peninsula, some sites have higher mean recruitment rates than others, which can be correlated with smaller-scale oceanographic factors (Gaines et al. 1985, Grantham 1997). Thus, environmental variability, specifically upwelling dynamics, leads to both spatial and temporal variability in recruitment along the coast of the Pacific Northwest on a variety of scales. Our model was designed to realistically simulate this variability across time and space.

**Model description.** We ran simulations based on stochastic-difference equations to explore the effects of variable recruitment on a localized area of the intertidal community (e.g. 1 m<sup>2</sup> plots). The model simulates 2 sets of dynamics: the recruitment dynamics of the major space-occupiers in the community and the local competitive and predator-prey interactions. The critical local interactions are symmetric, pre-emptive competition for space between both barnacle species and limpets and predation by whelks and seastars on barnacles (Fig. 1). We describe the general structure and rationale of the model below; details of the model form are given in Appendix 1.

**Recruitment dynamics:** Variability in recruitment into a population can be divided into 2 components: (1) spatial differences in the long-term mean-recruitment rates from site to site, and (2) temporal stochasticity around the long-term mean-recruitment rate to a site. We varied the long-term mean and the variance in larval supply of barnacles and limpets in a factorial manner, with each run of the model intended to simulate the dynamics of a local intertidal community characterized by a specific long-term mean amount of larval supply (and resulting recruitment) and a specific amount of variability in larval supply/recruitment over time. Site-specific long-term means and variances were either high, medium, or low for both barnacle species and for limpets for a given model run (Table 1), reflecting oceanographically driven correlations in recruitment patterns of these species. In other words, each long-term mean represented a particular site (i.e. Site A had chronically high mean recruitment, Site B had chronically intermediate mean recruitment, and Site C had chronically low mean recruitment). The variance through time about the long-term mean in recruitment to a given site can also be high, medium or low. This model construction provided us with 9 experimental treatments with which to test the effects of spatial and temporally variability in larval supply and subsequent recruitment on community variability.

A given run of the model was simulated over 50 yr and was iterated over monthly intervals. In most marine systems, there can be substantial temporal variation both among years and among months within the recruitment season. For each year, site-specific log-normal distributions of larval supply values, based on empirically derived long-term means and variances (Table 1), were constructed separately for *Balanus glandula*, *Chthamalus fissus/dalli* and limpets (*Macclintockia sabra* and *Collisella digitalis*). To choose monthly supply, a second set of lognormal distributions of supply values were constructed for each month and each species during the recruitment season. These distributions were based on a mean value taken randomly from the yearly distribution and a constant variance

Table 1. Values used for long-term means and variances ( $10\,000\text{ cm}^{-2}$ ) of in site-specific lognormal distributions of larval supply values *Balanus glandula*, *Chthamalus fissus/dalli*, limpets and *Pisaster ochraceous*. For means, medium values are based on field data and literature, high and low values on 90% confidence intervals around these means; variances are based on coefficient of variation. To estimate realistic high and low variance values for long-term means, we calculated 90% confidence intervals around larval supply based on recruitment data from field experiments and literature (multiplied by scaling factor to estimate larval supply [Gaines & Roughgarden 1985, Grantham 1997]). Recruitment values for *P. ochraceous* were estimated from Sewell & Watson (1993). Monthly CV for *P. ochraceous* was 1.55

Mean	Variance
<i>Balanus glandula</i>	
High = 90 000	High = $9.9 \times 10^{10}$ Medium = $3.24 \times 10^{10}$ Low = $4.6 \times 10^9$
Medium = 50 000	High = $3 \times 10^{10}$ Medium = $1 \times 10^{10}$ Low = $1.41 \times 10^{10}$
Low = 6000	High = $4.41 \times 10^8$ Medium = $1.44 \times 10^8$ Low = $2.025 \times 10^7$
<i>Chthamalus fissus/dalli</i> <sup>a</sup>	
High = 70 000	High = $6 \times 10^{10}$ Medium = $1.96 \times 10^{10}$ Low = $2.75 \times 10^9$
Medium = 30 000	High = $1.1 \times 10^{10}$ Medium = $3.6 \times 10^9$ Low = $5.1 \times 10^8$
Low = 6000	High = $4.41 \times 10^8$ Medium = $1.44 \times 10^8$ Low = $2.025 \times 10^7$
Limpets	
High = 3000	High = $8.1 \times 10^7$ Medium = $2.8 \times 10^7$ Low = $3.8 \times 10^6$
Medium = 2400	High = $5.2 \times 10^7$ Medium = $1.7 \times 10^7$ Low = $2.4 \times 10^6$
Low = 200	High = $3.6 \times 10^5$ Medium = $1.2 \times 10^5$ Low = 16900
<i>Pisaster ochraceous</i>	
High = 6873	High = $1.4 \times 10^8$ Medium = $1.2 \times 10^8$ Low = $3.02 \times 10^7$
Medium = 3800	High = $4.2 \times 10^7$ Medium = $3.7 \times 10^7$ Low = $9.2 \times 10^6$
Low = 727	High = $1.5 \times 10^6$ Medium = $1.3 \times 10^6$ Low = $3.4 \times 10^5$
<sup>a</sup> Because <i>Chthamalus fissus/dalli</i> recruits in low numbers throughout the winter, mean larval supply was kept constant at 5000 and variance in larval supply was kept constant at $8.1 \times 10^7$ for October through March	

derived from the monthly coefficient of variation calculated from field data and the literature (monthly CV for barnacles = 1.8, Gaines & Roughgarden 1985, Grantham 1997; monthly CV for limpets = 1.36, this study, see 'Parameter estimation'). Monthly supply values were chosen randomly from this monthly distribution to calculate actual recruitment. Actual recruitment rates were based on larval supply for all 4 species in combination with the available free space, assuming equal proportional success of recruits from each species when space was limited, similar to a lottery model (Chesson 1983, Warner & Chesson 1985; see Appendix 1 for details). *C. fissus/dalli* recruitment occurred year-round with increased recruitment from April through September. *B. glandula* recruitment also occurred from April through September, and limpets recruited from July through September.

**Population and community interactions:** Barnacle and limpet densities in a given month were determined by the densities in the previous month, recruitment of new individuals if the month fell during the recruitment season (spring and summer for barnacles, summer for limpets), and mortality. Barnacle numbers were affected by both density-independent mortality and whelk predation. Because limpets did not suffer mortality from whelks, limpet mortality included both general density-independent and density-dependent effects (Appendix 1). During the recruitment season, larval supply rates and the amount of available free space determined recruitment. Thus, there were density-dependent effects of both larval supply and adult numbers on recruitment. Barnacles and limpets competed for free space during recruitment. The densities of barnacles and limpets in Month  $t$  and the sizes of adults and recruits determined the amount of free space available for recruitment in Month  $t+1$ . For simplicity, we assumed that a recruit grew to the size of an adult after 1 mo.

The dynamics of whelk populations were determined by constant per capita mortality rates for adults, and by recruitment, which was governed by barnacle predation rates. Whelk reproduction occurred in June of each year and fecundity was based on the average number of barnacles eaten throughout the previous 3 mo. Survivorship of new whelks was based on the number of barnacles eaten in the month they were born (Appendix 1). Whelks undergo direct development and therefore are considered a closed population (i.e. there is local feedback between reproduction and recruitment). Thus, oceanographic processes only influence whelk populations via input of prey.

**Parameter estimation.** For the most part, parameters in the model were based on species abundances, sizes, and recruitment (Table 2) measured at 4 sites along the Monterey peninsula. A detailed description of the sites and the experimental plots can be found in Forde

(2002). Briefly, sites ranged from exposed to protected. We collected data on the number of limpets and the percent cover of *Balanus glandula* and *Chthamalus fissus/dalli* on a monthly to bimonthly basis from December 1998 to November 1999. Data on limpet sizes were collected from July through September 1999. We collected data on the average size of adult barnacles in February and April 1999. Data on species abundances were collected in April 1999 and 2000. All data were averaged across sites and time to parameterize the model.

Parameters not available from field experiments were obtained from the literature (Table 2). The model was intended to investigate how temporal stochasticity and spatial differences in recruitment interact in altering the dynamics of high-intertidal communities in general. Therefore, when necessary we incorporated data from a variety of studies done in high intertidal communities, which enabled us to use field-based parameters throughout the model.

**Model runs and data analysis.** The specific questions we wanted to address were: (1) What is the relative importance of spatial differences versus temporal stochasticity in larval supply for community composition? (2) How do these 2 factors interact to influence community composition and stability? (3) Do the strengths of competition and predation change with the mean and variance in larval supply? (4) Are the effects of spatial and/or temporal variability on community stability mediated by competition and/or predation?

To address these questions, we first simulated the full model, including barnacles, limpets and whelks (Table 2) simulated 500 times over 100 yr for each of the 9 combinations of means and variances in larval supply (Table 1). For all results reported here, we used information from September of Year 50 from the model simulation to avoid any effects of initialization values. We measured stability of community structure across the replicate simulations.

Table 2. Parameters used in the model

Species Symbol	Description	Value	Source
<i>Balanus glandula</i> (B)			
$B_o$	Initial population size	4100 m <sup>-2</sup>	Forde (2002)
$S_b$	Adult survival rate	0.7 mo <sup>-1</sup>	Connolly & Roughgarden (1999)
$S_{rb}$	Recruit survival rate	0.7 mo <sup>-1</sup>	Connolly & Roughgarden (1999)
$A_b$	Average adult size	0.98 cm <sup>2</sup>	Forde (2002)
$a_b$	Average recruit size	0.03 cm <sup>2</sup>	Forde (2002)
<i>Chthamalus fissus/dalli</i> (C)			
$C_o$	Initial population size	11 000 m <sup>-2</sup>	Forde (2002)
$S_c$	Adult survival rate	0.7 mo <sup>-1</sup>	Connolly & Roughgarden (1999)
$S_{rc}$	Recruit survival rate	0.7 mo <sup>-1</sup>	Connolly & Roughgarden (1999)
$A_c$	Average adult size	0.32 cm <sup>2</sup>	Forde (2002)
$a_c$	Average recruit size	0.03 cm <sup>2</sup>	Forde (2002)
Limpets <sup>a</sup> (L)			
$L_o$	Initial population size	239 m <sup>-2</sup>	Forde (2002)
$S_l$	Adult survival rate	0.97 mo <sup>-1</sup>	Frank (1965)
$S_{rl}$	Recruit survival rate	0.88 mo <sup>-1</sup>	Frank (1965)
$A_l$	Average adult size	0.8 cm <sup>2</sup>	Forde (2002)
$a_l$	Average recruit size	0.03 cm <sup>2</sup>	Forde (2002)
$\delta$	Density-dependent parameter	-0.02	
Whelks (W)			
$W_o$	Initial population size	93 m <sup>-2</sup>	Forde (2002)
$S_w$	Adult survival rate	0.94 mo <sup>-1</sup>	Burrows & Hughes (1991)
$p$	Per capita predation rate	0.01 mo <sup>-1</sup>	Palmer (1990)
$Y$	Conversion rate <sup>b</sup>	0.01	
<i>Pisaster ochraceus</i> (P)			
$P_o$	Initial population size	1 m <sup>-2</sup>	Menge et al. (1994)
$S_p$	Adult survival rate	0.992 mo <sup>-1</sup>	Connolly & Roughgarden (1999)
$S_{rp}$	Recruit survival rate	0.998 mo <sup>-1</sup>	Connolly & Roughgarden (1999)
$p$	Per capita predation rate	0.007 mo <sup>-1</sup>	Connolly & Roughgarden (1999)

<sup>a</sup>Values used in model from field experiments were primary for *Macclintockia scabra*

<sup>b</sup>Realistic values for conversion rate of barnacle prey to whelks for field could not be found in the literature, so we considered a range of values from 0.0001 to 1 (sensu Connolly & Roughgarden 1999) and chose 0.01 because it gave realistic densities

To quantify the relative importance of spatial differences and temporal fluctuations in larval supply to the size of each population, we used the variance components from an analysis of variance (Winer et al. 1991), assuming a random design in estimating the magnitude of the effects in the model.

To investigate the effects of spatial and temporal variability in larval supply on the entire community, we first had to summarize community structure. To do so, we used canonical discriminant analysis (CDA). Population sizes for all 4 species and free space for each run of each mean/variance combination were used in the analysis. The scores from the CDA are calculated based on a linear combination of the dependent variables (Tabachnick & Fidell 2000), and therefore can be thought of as metrics describing community composition. We estimated 68% confidence ellipses around Score 1 and Score 2 from the CDA for all mean/variance combinations.

Although the CDA described the general relationship between environmentally driven variability in supply rates and community structure, we were specifically interested in the interactive effects of the mean and the variance in larval supply with the influence of species interactions in the community. To investigate these effects, we first looked for patterns in Pearson product-moment correlations in the population sizes of all species across high, medium and low mean supply. Increasingly negative correlations with increasing mean larval supply rates would indicate that, as recruitment increases, competition and/or predation exert a stronger role in influencing community structure.

Next, to investigate the extent to which community responses to recruitment variation were dampened or magnified by species interactions, we ran versions of the model without 1 of the species (i.e. predatory whelks, the dominant competitor, *Chthamalus fissus/dalli*, and the weakest competitor, limpets, as defined by larval supply values in Table 1). Deleting the interactions from the model simulated removal experiments. For each reduced model, we again ran 500 simulations of each mean/variance combination used for the original (full) model (Table 1), and used the population sizes from September of Year 50 as output.

In addition to the reduced models, we ran simulations with *Pisaster ochraceous*, which has planktonic larvae, as the top-

level predator. We were concerned that any effect of the removal of whelks could either represent the effect of the closed whelk population or the effect of predation. By comparing the results of the full model with whelks as the predator, a full model with *P. ochraceous* as the predator, and a reduced model with no predator present, we were able to disentangle the potentially confounded effects of predation and the type of life history of the predator (open or closed populations). The recruitment dynamics of *P. ochraceous* were modeled with spatial and temporal variation in recruitment from June through September, similar to the dynamics of barnacles and limpets (Table 1, Appendix 1).

We used these data for all runs of all models in a single CDA and then plotted the relationship between

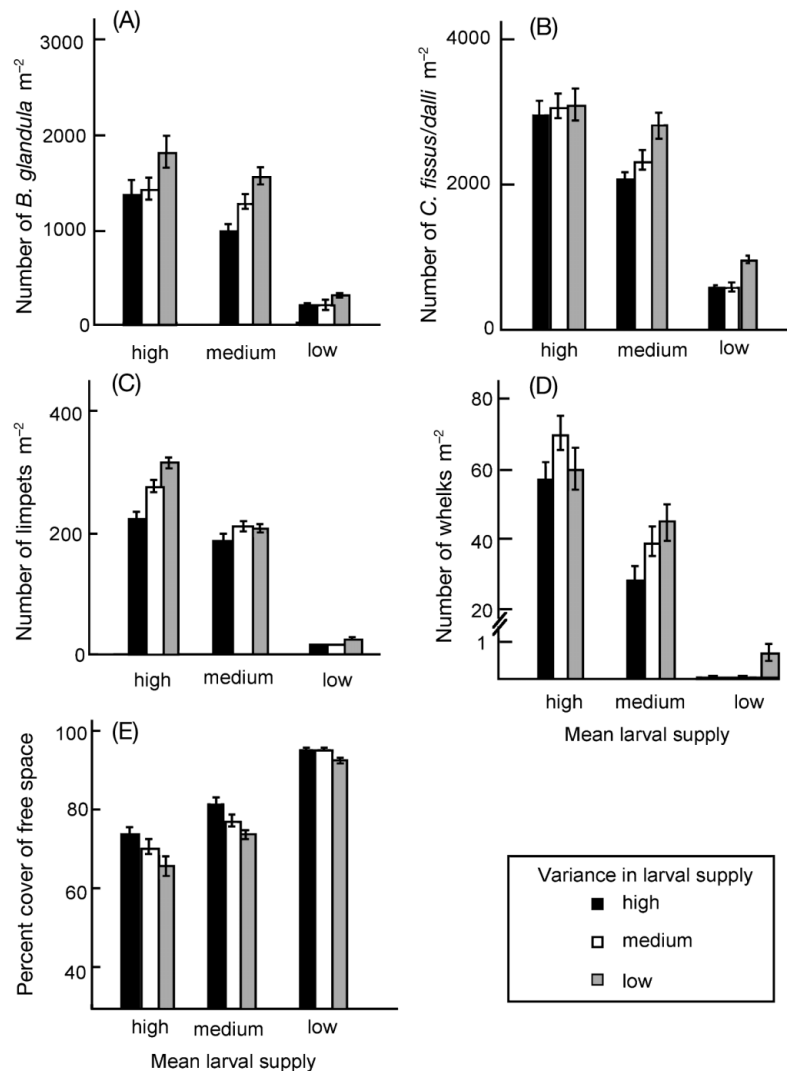


Fig. 2. (A–D) Mean population sizes ( $\pm$ SE) for (A) *Balanus glandula*, (B) *Chthamalus fissus/dalli*, (C) limpets and (D) whelks. (E) Percentage of free space, for each larval supply mean/variance combination

the variance in community structure (estimated separately as either the variance in Score 1 or the variance in Score 2 from the CDA) and the variance in *Balanus glandula* larval supply (this competitor was never removed from the model, thus the x-axis remained consistent for all comparisons of the reduced models) for the different sets of simulations. We found that as the mean of Scores 1 and 2 increased, the variance actually decreased, suggesting that scaled variance measures such as the coefficient of variation were unnecessary.

Differences in the variance in Score 1 between the full model and the reduced models could potentially be an artifact of setting the removed species' abundances to zero in the reduced models. An alternative analysis would be to do separate CDAs for each pairwise comparison. For example, a CDA would be performed on data from the full model and the reduced model without whelks. In this approach, only data on barnacles, limpets and free space would be included. We ran a series of CDAs to verify that there were no qualitative differences in the results of the model as a function of the approach used. We chose the former approach (setting the removed species abundances to zero) because this allowed for orthogonal comparisons of the results across all the reduced models. In addition, using the data from all the simulations in a single CDA guaranteed that the variance in Scores 1 and 2 scaled similarly with the means for all comparisons with and without different species.

We define community variability based on the distribution of the data in multidimensional space in a CDA, whereas past work has looked at variability in total community biomass (e.g. Ives et al. 1999) or of the combined species densities (Ives & Hughes 2002 and references therein). We use both 'community variability' and 'community stability' to describe community structure throughout the paper. For the purposes of the results presented here, an increase in community variability can be equated with a decrease in community stability.

## RESULTS

### Full-community simulations

Differences in mean larval supply and subsequent recruitment were relatively more important to population densities than was temporal variability in recruitment, as indicated by variance components analysis. Changing interannual mean supply rates (an index of spatial variability) explained about 56% of the variation in the densities of both barnacle species and of whelks, and explained 82% of the variation in the den-

sities of limpets. In contrast, temporal variability in supply among years explained only between 1 and 2% of the variation in densities of each of the 4 species. Unexplained variability, due to a combination of both inter- and intra-annual variability in larval supply and species interactions, accounted for about 42% of the variation in the densities of barnacles and whelks, and about 15% of the variation in the density of limpets.

The average density of all populations scaled with the mean amount of larval supply (Fig. 2). When mean larval supply was high, barnacle and limpet densities were about 1.5 times higher than when mean larval supply was intermediate, and 7 to 14 times higher than when mean larval was low (Fig. 2A–C). Decreasing the variance in supply rates resulted in an increase in the density of barnacles and limpets (Fig. 2A–C). When mean prey supply was high, the density of whelks was close to 1 order of magnitude greater than when the mean was low (Fig. 2D).

Changing the mean and the variance in larval supply substantially influenced community structure (Fig. 3). Confidence ellipses around the scores from the

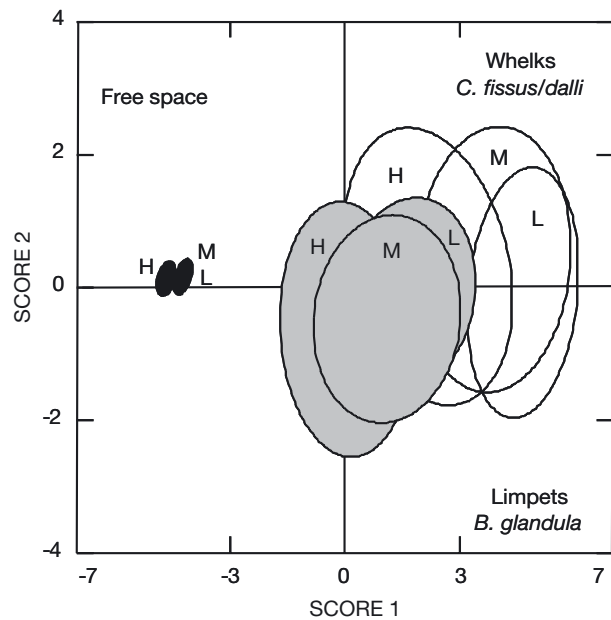


Fig. 3. 68% confidence ellipses plotted for Score 1 vs Score 2 from the canonical discriminant analysis (CDA) of population sizes of barnacles, limpets, whelks and amount of free space for each mean/variance combination of larval supply. Black ellipses indicate low mean larval supply, gray ellipses indicate intermediate mean larval supply and unfilled ellipses indicate: high mean larval supply. L, M, H are low, medium, and high variance in larval supply. Figure indicates which species abundances are highly correlated with CDA scores, e.g. communities falling in upper right-hand portion of graph (high mean larval supply) are characterized by relatively higher *Chthamalus fissus/dalli* and whelk population sizes.

Full specific names as in Fig. 1

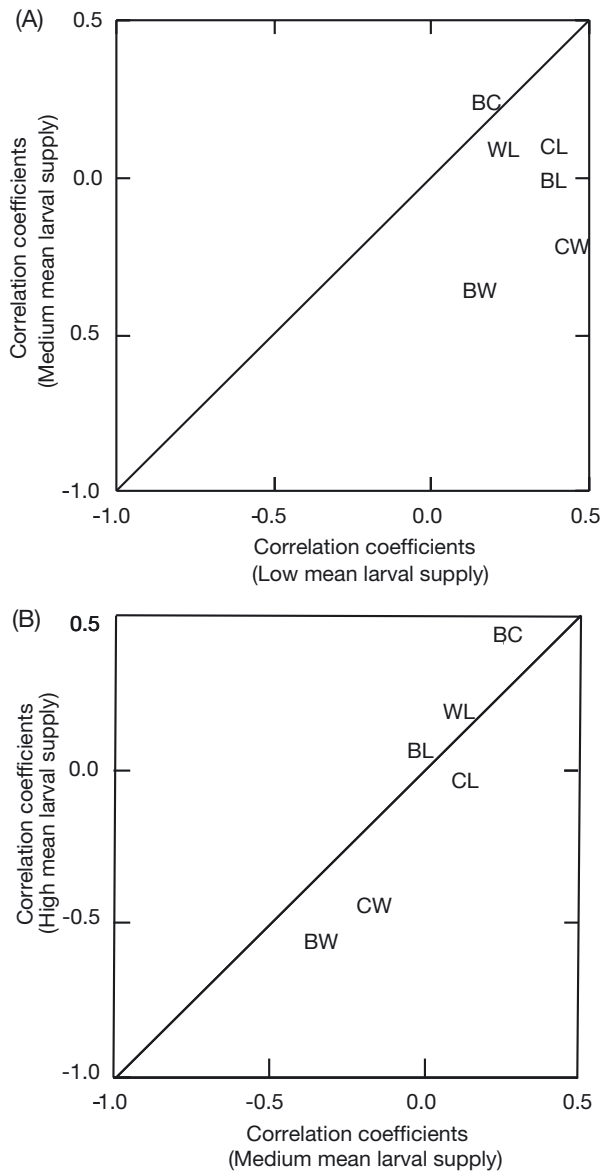


Fig. 4. Correlations among population sizes under low, medium and high mean larval supply. BC: *Balanus glandula* and *Chthamalus fissus/dalli*; BW: *B. glandula* and whelks; BL: *B. glandula* and limpets; CW: *C. fissus/dalli* and whelks; CL: *C. fissus/dalli* and limpets; WL: whelks and limpets. Points falling along 45° line indicate no change in strengths of correlations with increased mean larval supply

CDA show that communities with low mean amounts of larval supply were distinctly different from those with medium and high mean larval supply, regardless of the variance in supply rates. When mean larval supply was low, medium and low variance communities were indistinguishable from each other. Further, there was no overlap in community structure under high versus medium or low variances in supply when the mean

supply was low. When comparing communities under high and medium mean supply, less overlap in community composition was seen when the variance was low than when it was high (Fig. 3). Increasing the variance only slightly increased the unpredictability of community composition (as indicated by the size of the confidence ellipses) when mean larval supply was medium and high, and there was no increase under low mean recruitment.

The scores from the CDA can also be used to evaluate which species were driving the differences in community structure. Higher values of both Score 1 and Score 2 result from increased numbers of whelks and *Chthamalus fissus/dalli*, whereas an increase in Score 1 and a decrease in Score 2 results from higher population sizes of limpets and *Balanus glandula*. Communities with high mean larval supply had slightly higher population sizes of whelks and *C. fissus/dalli*. Not surprisingly, communities characterized by low mean supply rates were composed of more free space. Increasing the variance had the same general (but weaker) effect as decreasing the mean on community composition. In both cases, the communities shifted towards negative values of Score 1 (Fig. 3).

In general, correlations between the abundances of the different species became more negative with increasing mean supply rates (Fig. 4). There were greater but more variable changes in correlations when mean supply increased from low to medium than when supply increased from medium to high, indicated by the distance of the points relative to the 45° line in Fig. 4 (points lying along the 45° line suggest no change in the correlations with increasing mean larval supply). Correlations between both *Chthamalus fissus/dalli* and *Balanus glandula* and limpets became more negative, indicating increased competition for space with increased larval supply. Correlations between whelks and both barnacle species also became more negative with increasing larval supply, suggesting that predation intensity increased with increasing recruitment of prey.

### Reduced-community simulations

For the full community, with whelks as the top-level predator, increasing the temporal variance in larval supply resulted in only minor changes in the variance in community structure (measured as the variance in CDA Score 1, Fig. 5; all patterns were similar for the variance in Score 2). However, removal of both predators or of *Chthamalus fissus/dalli* substantially altered this relationship; there were no effects of removing limpets from the model. Under all combinations of larval supply parameters, removal of *C. fissus/dalli*



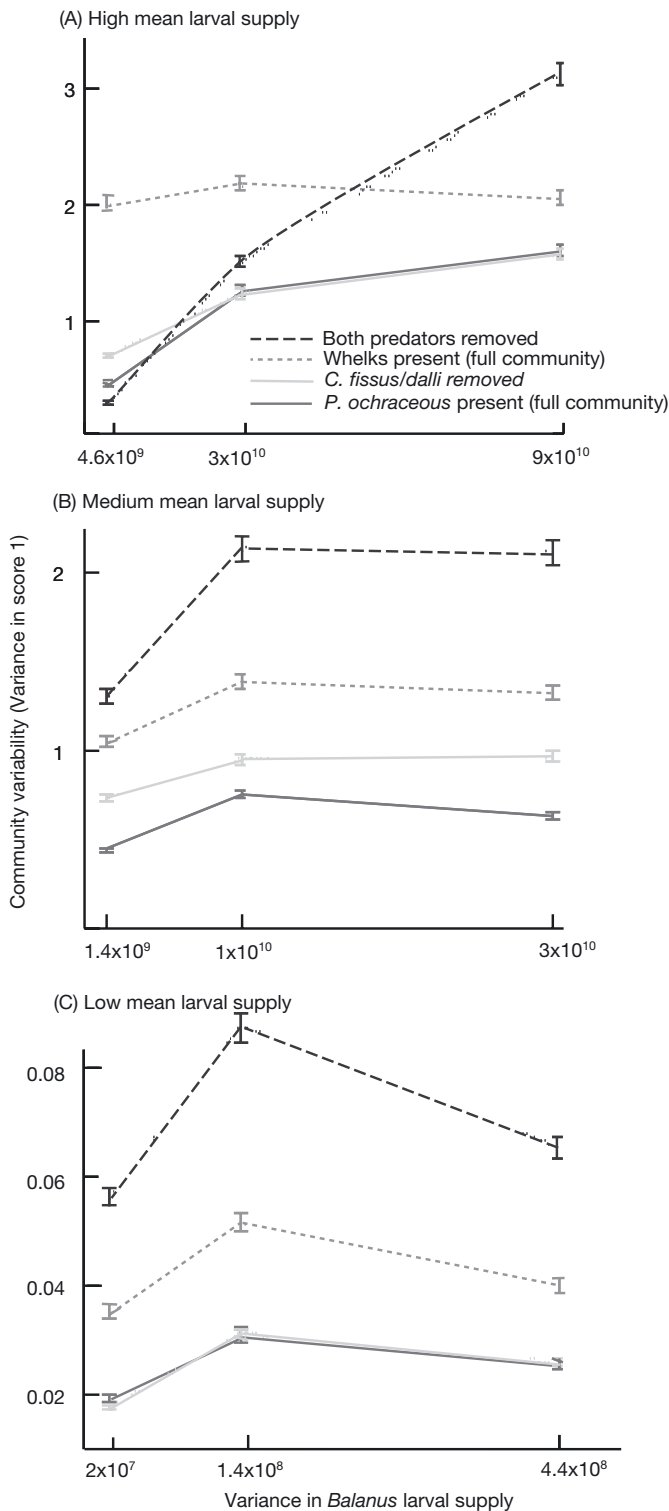


Fig. 5. Variance in Score 1 from CDA vs variance in *Balanus glandula* larval supply as a function of amount of larval supply when all species were present in the model (i.e. the full community, with either whelks or *Pisaster ochraceous* present as the top-level predator) or when the dominant competitor *Chthamalus fissus/dalli* or both predators were removed from the model. Variance in Score 2 showed similar pattern

decreased community variation compared to when whelks were present or both whelks and *Pisaster ochraceous* were removed from the model. For high and medium mean supply, removing both predators amplified environmentally driven variability more or less additively as the variance in *Balanus glandula* larval supply increased (Fig. 5A,B), while for low mean supply their effect on community variance decreased with increasing variance in larval supply (Fig. 5C).

In contrast to competitors, removal of predators resulted in strong increases in community variability, especially for medium and low mean supply rates. The effects of predators were complicated for simulations with high mean prey supply (Fig. 5A). Here, community composition was highly sensitive to increased variance in larval supply when predators were removed; community variability was actually lower when predators were removed from the community for low and medium variance in supply, whereas when the variance in prey supply rates was highest, the presence of predators again dampened variability. Interestingly, community variability was lower with *Pisaster ochraceous* (which has planktonic larvae) as the top-level predator than with whelks (a closed population) as the predator (Fig. 5).

## DISCUSSION

Spatial and temporal variability in larval supply and subsequent recruitment interacted to strongly influence community composition, with the majority of this effect resulting from differences in mean larval supply rates (spatial variability). Temporal variability and species interactions also had complex effects on community stability, which was dependent on mean supply rates. The presence of competitors magnified the influence of temporal variability on community variance, whereas predators generally dampened the translation of temporal variability into variance in community structure. Our results illustrate that the effects of environmental variability on community stability depend on the interactive effects of this variability in both space and in time, as well as the interaction between environmental variability and the species interactions structuring the community.

More general models have predicted that species interactions can produce both positive and negative feedbacks that can mediate the response of communities to environmental variability (Ives 1995, Ripa et al. 1998, Ives et al. 1999, Ives & Hughes 2002). However, the results of these models have not been constrained by key complications of real communities, such as correlations in temporal and spatial fluctuations of the demographic rates of different species or differences between differ-

ent types of species interactions. In particular, theoretical work that has incorporated multiple trophic levels has modeled relatively abstract communities (May 1973, Pimm 1979, Ives 1995). By including the idiosyncrasies of a particular community, our model is therefore not widely general, but it may nonetheless show patterns more reflective of at least some real communities. Of particular interest is our result that the effect of environmental variability is dampened by interactions between trophic levels, but amplified by competition, and that the mean recruitment into the community strongly mediates these effects.

More specifically, we found that competition by *Chthamalus fissus/dalli* and predation by whelks and *Pisaster ochraceous* have very different effects on community stability. Why did removal of *C. fissus/dalli* consistently decrease community variance? Although the correlations between barnacle species indicated that competition for space became more important with increased supply rates (as it should have, based on the model construction), the presence of *C. fissus/dalli* increased community variability regardless of mean larval supply. Thus, competition for space was not strong enough to overpower the effects of variability in larval supply on community structure, and this variability drove fluctuations in the adult populations, which ultimately increased community variability.

In contrast to removal of a competitor, removal of both predatory whelks and *Pisaster ochraceous* generally decreased community stability. More general models have yielded mixed answers; some have found that the type of interaction considered had no effect on how community stability is influenced (Ripa et al. 1998). Others have found results similar to ours, where predators dampened environmental variability and competitors enhance variability (Ives & Gilchrist 1993).

By running simulations with whelks as the top-level predators, *Pisaster ochraceous* as the predators, and a reduced model with no predator present, we were able to disentangle the potentially confounding effects of life history (closed vs open populations) and predation on community variability. The presence of both predators dampened variability, but *P. ochraceous* had a stronger effect on community variability than did whelks. In fact, community variability was often lowest in simulations with *P. ochraceous* as the predator than all other simulations, particularly at intermediate mean recruitment rates. In this model, environmental variability had direct effects on *P. ochraceous* populations, but indirect effects on the whelk populations through prey population dynamics. When mean prey supply rates were low and medium, the presence of whelks always dampened environmental variability. When prey supply rates were high, whelks dampened fluctuations only under the highest variance in supply rate.

Why do predators with open populations have a stronger effect on community variability than those with closed populations? This difference is most likely due to the fact that recruitment of *Pisaster ochraceous* occurred over a longer time period (June through September) than reproduction of whelks (June only). In addition, recruitment of *P. ochraceous* was independent of prey availability. There was a constant input of new recruits into the *P. ochraceous* population over 4 mo, and this input was not influenced by variation in the prey population. In contrast, whelk densities for a given year reflected reproductive output in only 1 mo, and reproductive output depended on prey availability over the entire year. Clearly, these results reflect how *P. ochraceous* recruitment was parameterized in our model. One can imagine a community characterized by very low and/or variable *P. ochraceous* recruitment and relatively high and constant whelk densities through time. In this case, it is likely that whelks would have a stronger influence on community variability than *P. ochraceous*. Regardless, our results emphasize the importance of incorporating this kind of realistic biological information into models in order to understand the potentially complicated relationships between environmental variability, life history and different types of species interactions, which can result in complex effects on the stability of natural communities.

There is always a tradeoff between obtaining biologically meaningful insights from the model results and the ability to generalize to other systems. We chose to take a highly empirically based approach in the work discussed here. However, to keep the model from becoming overly complex, we omitted various biological processes, that if included, might have influenced the results of our model. For example, we assumed that there was no density-dependence in barnacle mortality via hummocking (Gaines & Roughgarden 1985) and that there were no asymmetries of interactions related to size-dependence (i.e. size-dependent predation or competition). In addition, we did not include differences in predation rates on *Balanus glandula* and *Chthamalus fissus/dalli* or asymmetries in competition between barnacles (Connell 1961). Including these interactions in the model would have approximated the natural history of the system more closely, but also would have decreased our ability to interpret the results in a meaningful way.

Thus, there is a balance between incorporating biological realism and the ability to generalize the results of models to other communities. Although it is likely that the specific results presented here may only pertain to the rocky intertidal communities, some of our general conclusions and the approach we use should be applicable to communities comprised of organisms

with similar life histories, such as some plant communities. For example, regional patterns in seedling recruitment may depend on site-specific mean rainfall (Enright & Lamont 1993). It is likely that there is also temporal variability about this mean on a seasonal, monthly, or daily basis. Environmentally induced variability in seedling recruitment may then be mediated by herbivory or competition on a local scale (Tilman 1996). Thus, similar patterns to those resulting from the model presented here may be seen in plant communities if site-specific mean differences in seedling recruitment are relatively more important to population dynamics and community structure than temporal fluctuations. Similarly, if recruitment of competitors is affected by environmental variability in a correlated manner (i.e. both species germinate with increased rainfall), as are barnacles and limpets in our model, then removing 1 of the competitors from the community may actually decrease community variability. Finally, one can imagine herbivory dampening the influence of environmental variability on community stability.

Some of the differences in our results compared to past work examining stability–diversity relationships might be due to our definition of community variability. As mentioned earlier, we defined community variability as the results of a CDA, whereas past work has looked at variability of total community biomass (e.g. Ives et al. 1999) or of the combined species densities (Ives & Hughes 2002 and references therein). In addition, most community models have explored questions about stability for closed communities, whereas we incorporated open populations into our model. Thus, both our definition of community variability and the incorporation of open-population dynamics into the model probably explain some of the differences in our conclusions compared to those of previous models.

The general results of our model add to our understanding of how regional and local processes interact to structure communities: large-scale differences in input of individuals (seeds, larvae, zooplankton) are the ‘raw materials’ with which local interactions have to work (Connolly & Roughgarden 1998, Shurin 2000, Shurin & Allen 2001). The results of our model indicate that removal of either competitor or predator species can substantially alter the response of the community to variability in input rates. Removal of predators, in particular, greatly increased the response of the community to changes in input variation through time, effectively destabilizing the local assemblage of species. More empirically based research and modeling must be done before we can evaluate how common these patterns may be across systems.

*Acknowledgements.* We are particularly grateful to P. Raimondi for his insights. We also thank P. Armsworth, B. Bohannan, J. Brown, E. Danner, B. Kerr and C. Syms for comments on previous versions of the manuscript. We thank the Monterey Bay National Marine Sanctuary, the California Department of Fish and Game, and the California Department of Parks and Recreation for permission to conduct the field work. This research was supported in part by the David and Lucille Packard Foundation, the Friends of Long Marine Laboratory, the Meyers Oceanographic Trust, an NSF Graduate Research Training grant (GER-9553614), and a Sigma Xi Grant-In-Aid of Research to S.E.F. This is contribution number 157 of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO): a long-term ecological consortium funded by the David and Lucille Packard Foundation.

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**Appendix 1.** Details of model form

Potential recruitment, or larval supply, is defined by the number of possible recruits that can fit into the community based on the amount of free space and the average size of a recruit, along with the number of potential settlers in the water column. For each recruitment month ( $t$ ), potential recruitment ( $\mathcal{L}$ ) to the rock of a Species  $x$  (barnacles or limpets) is calculated as

$$\mathcal{L}_x(t) = \left( \frac{F(t-1)}{A_x} \right) \left[ 1 - \exp(-a_x I_x / F(t-1)) \right] \quad (1)$$

where  $F(t-1)$  equals the amount of free space on the rock available in Month  $t-1$ ,  $A_x$  is the average size of an adult of Species  $x$ ,  $a_x$  is the average size of a recruit, and  $I_x$  is the number of settling larvae of Species  $x$ . Due to density dependence, as the number of larvae ( $I_x$ ) increases, the proportion of space filled by new recruits increases, but can never increase above what is available. Thus, potential recruitment is limited by the number of settlers in the water column when larval supply is low, and by free space when larvae are abundant, with considerable interference between larvae when abundant at intermediate densities.

Potential recruitment for each species, independent of all other species in the model, is calculated in each month of the recruitment season. However, the actual number of larvae that recruit to the adult population depends in part on the larvae of other species also attempting to recruit due to preemptive competition for space. We calculated actual recruitment as proportional to each species potential recruitment rate, so that

$$R_x(t) = \left( \frac{FS(t-1)}{\mathcal{L}_x A_x + \mathcal{L}_y A_y + \dots \mathcal{L}_z A_z} \right) \mathcal{L}_x \quad (2)$$

where  $\mathcal{L}_x$  is the potential number of recruits of Species  $x$ ,  $\mathcal{L}_y$  is the potential number of recruits of Species  $y$ , and so on, similar to a lottery model.

Eqs. (1) & (2) are used in tandem in the simulations, allowing for both intra- and interspecific density-dependence. However, we also ran a series of simulations that incorporated interspecific density-dependence into potential recruitment (Eq. 1). This resulted in a slight decrease in actual recruitment and community variability, but the qualitative results of the model did not change.

The actual number of recruits of Species  $x$  is then used in conjunction with the preexisting adult population to calculate population size at Time  $t$ .

For both barnacle species, population sizes are calculated as

$$X(t) = S_x(1-pW(t-1))(X(t-1)) + S_{rx}R_x(t) \quad (3)$$

where  $S_x$  is the survivorship (before whelk predation) of Barnacle Species  $x$ ,  $p$  is the encounter rate of barnacles by whelks,  $W(t-1)$  is the whelk population size in the previous month and  $X(t-1)$  is the *Balanus glandula* or *Chthamalus fissus/dalli* population size in the previous month.  $S_{rx}$  is the survivorship of recruits of Species  $x$  and  $R_x(t)$  is the number of actual recruits of barnacle Species  $x$  (Eq. 2). We assumed that barnacle mortality is density-independent, except in the case of predation by whelks.

Limpet population sizes were calculated as

$$L(t) = S_l L(t-1) + S_{il} R_l(t) \partial^{L(t-1)} \quad (4)$$

The symbols represent the same parameters as for the barnacle species, but values used in the model were specific to limpets.  $\partial$  incorporates density-dependence into the limpet population (due to predation, which is not explicitly included in the population equations).

Whelk population size was calculated as

$$W(t) = W(t-1) \frac{\exp(-5.6p[B(t-\tau) + C(t-\tau)])}{1 + \exp[-5.6p[B(i) + C(i)]]} + R_w(t) \quad (5)$$

where  $R_w$  is whelk recruitment. This equation models whelk survivorship as a logistic function of the number of barnacles eaten, where the value  $-5.6$  determines the shape of the function.  $p(B(t-\tau) + C(t-\tau))$  is the measure of food intake, where  $\tau = 1$  during the barnacle recruitment season (which begins in April or Month 1). Because whelks can survive without food for days to months (Perry 1983, Burrows & Hughes 1991), we assumed that in winter, prey availability during the prey-recruitment season was more likely to influence whelk survivorship than prey availability during the winter. Therefore, for Months 7 to 12 (October to March),  $\tau = 6$  (i.e. survivorship in November was based on the number of barnacles eaten in May).

Whelk recruitment was calculated once a year in the model (in June), and the number of whelk offspring was calculated as

$$R_w = \left[ \text{mean}(C(1:3)) + \text{mean}(B(1:3)) \right] \times 3pY(W(t-1)) \times [(B(3) + C(3))] \quad (6)$$

where  $B(1:3)$  and  $C(1:3)$  are the average number of *Balanus glandula* and *Chthamalus fissus/dalli* from April through June (i.e. the months prior to reproduction), and  $Y$  is the conversion rate of barnacles eaten into new whelks (Table 2). We assumed that survivorship of new whelks depended on the amount of food available when they were born [ $B(3)$  and  $C(3)$ ]. To incorporate density-dependent fecundity and offspring survivorship, if  $R_w$  was greater than or equal to 90, a value of 90 was used in Eq. (6).

*Pisaster ochraceus* population sizes were calculated as

$$P(t) = S_p P(t+1) + S_{ip} R_p(t) \quad (7)$$

where the symbols represent the same parameters as for the barnacle and limpet species, but the values used were specific to *P. ochraceus*. We assumed that seastar settlement does not require free space (sensu Connolly & Roughgarden 1999), so Eqs. (1) & (2) were not used to calculate  $R_p$ . Population size is not dependent on the prey population because of the lack of feedback between reproductive output at time  $t$  and recruitment at Time  $t+1$  in populations with planktonic larvae. The maximum density was set at  $6 \text{ m}^{-2}$  (Menge et al. 1994). Free space was calculated at the end of each month as

$$F(t) = T - (B(t)A_b + C(t)A_c + L(t)A_l) \quad (8)$$

where  $T$  is total area,  $B(t)$  is the population size of *Balanus glandula*,  $A_b$  is the average size of an adult *B. glandula*,  $C(t)$  is the population size of *Chthamalus fissus/dalli*,  $A_c$  is the average size of an adult *C. fissus/dalli*,  $L(t)$  is the population size of limpets, and  $A_l$  is the average size of an adult limpet.