

Experimental species removal alters ecological dynamics in a natural ecosystem

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Abstract. Theory predicts that species extinction or invasion can affect the temporal dynamics of ecological communities by altering feedback patterns and by damping or amplifying environmental variation via changes in the network of species interactions, but because of the logistical challenges of investigating temporal dynamics, evidence from natural ecosystems is lacking. In a long-term experimental manipulation of a rocky intertidal community on Tatoosh Island, Washington, USA, chronic removal of the dominant species *Mytilus californianus* altered the dynamics of the system, causing reductions in the temporal variability of three subdominant species but no consistent change in the spectral characteristics or the order of density dependence across experimental replicates. This pattern of results suggests that *Mytilus californianus* impacted the temporal dynamics by amplifying environmental stochasticity, rather than by changing feedback pathways as is emphasized in most theoretical predictions and laboratory studies. Hence, further investigation of the mechanisms and implications of transmission of environmental stochasticity in natural ecosystems is merited.

Key words: environmental stochasticity; extinction; interaction network; intertidal zone; *Mytilus californianus*; order of density dependence; population dynamics; spectral analysis; time series; variance amplifier.

INTRODUCTION

Ecologists have long been intrigued by the often dramatic causes of, and differences in, dynamic fluctuations of plant and animal populations (Volterra 1926, Elton 1927, Andewartha and Birch 1954). Explanations for population fluctuations have generally been attributed to two forces: (1) variation in environmental conditions, which may cause stochastic fluctuations in populations over time, or even somewhat predictable fluctuations because of environmental autocorrelation (Andewartha and Birch 1954), and (2) nonlinearities and time lags arising from biological interactions, which can generate deterministic fluctuations in populations (Volterra 1926, May 1973, May and Oster 1976, Schaffer 1985, Hastings and Powell 1991, Turchin 2003, Ims et al. 2008, Jiang et al. 2009). Although deterministic, the latter can generate high-dimensional cycles or chaotic behavior, which may have the appearance of stochastic fluctuations generally attributed to variation in environmental conditions. Theory predicts that changing biodiversity can alter population dynamics by changing feedback pathways (Schaffer 1985, Hastings and Powell 1991, Bjørnstad et al. 2001, Turchin 2003, Jiang et al. 2009) or by affecting the network that transmits environmental stochasticity through ecosystems (Ives 1995, Forde and Doak 2004).

Although laboratory experiments with simplified communities under highly controlled conditions provide some evidence supporting this prediction (Gause 1934, Luckinbill 1973, 1979, Lawler and Morin 1993, Bjørnstad et al. 2001, Jiang et al. 2009), it has not been evaluated in real ecosystems because appropriate data from long-term experiments are scarce.

With the discovery that chaotic dynamics may potentially occur in even simple ecological systems (May 1974), there has been much recent interest in identifying the role of intrinsic biological processes vs. extrinsic stochastic processes in generating fluctuations of populations in the field (Schaffer 1985, Morris 1990, Ellner and Turchin 1995, Turchin 2003, Ims et al. 2008). The primary method for probing these roles has been to develop long time series of population size data, to use these data to parameterize models incorporating biological interactions involving nonlinearities and time lags, and to evaluate the models to determine whether they exhibit deterministic fluctuations. Although recent progress has been made (Ellner and Turchin 1995, Turchin 2003), this method has been difficult to fully implement because of the long time series required, the absence of knowledge of which specific model forms are appropriate (Morris 1990), and the presence of measurement error in the datasets, which can produce apparent density dependence in time series data (Dennis and Taper 1994). An alternative approach is to experimentally change key parameters or manipulate species composition, and determine whether such a

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manipulation changes the dynamic characteristics of the system. This approach has been carried out in a few laboratory microcosms (Gause 1934, Luckinbill 1973, 1979, Lawler and Morin 1993, Bjørnstad et al. 2001, Jiang et al. 2009), but these studies evaluate situations with unnaturally low levels of environmental stochasticity and species richness. Although field experiments manipulating species composition in natural communities are now quite common, few studies have imposed a consistent field manipulation for sufficient time to evaluate the dynamical consequences to the system and then evaluated the consequences of these manipulations on the dynamical patterns of an ecological community (Cottingham et al. 2001). Here I explore the changes in community dynamics in a natural, rocky-intertidal community following a long-term, experimental removal of the dominant species, the mussel *Mytilus californianus*, relative to unmanipulated controls. The goal of this study is to explore whether there is empirical evidence that local extinction can change dynamical characteristics of a natural community, rather than to confirm a particular class of models that make specific assumptions such as closed population dynamics.

METHODS

Experimental and census methods

To explore the effects of extinction on ecological dynamics, I implemented a long-term species manipulation in the rocky intertidal community of Tatoosh Island, Washington, USA (48°24' N, 124°44' W). The middle intertidal zone here is dominated by a band of the mussel *Mytilus californianus* containing interspersed gaps occupied by other species (Paine and Levin 1981, Wootton 2001a). Data were collected from four sites, which contained gently sloping rock benches that were subject to relatively high wave exposure and that exhibited strong patterns of vertical zonation. In 1993, I established 14 permanent unmanipulated plots of 60 × 60 cm dimension in the middle intertidal zone. In 1994, I established another two unmanipulated plots and ten 60 × 60 cm plots in which *Mytilus californianus* were continually removed by hand as they entered for the duration of the study. These plots were located immediately adjacent to unmanipulated plots. Another five plots in which mussels were chronically removed were established in 1997. Mussel removals were carried out opportunistically whenever *M. californianus* were observed in plots, but limited visits to the study site and hazardous conditions during winter months allowed some mussel accumulation during this time period, primarily around the very edges of the plots where unmanipulated mussel beds could encroach. Censuses prior to spring mussel removal indicate that mussel populations were on average >90% lower than controls throughout the year. All plots were censused annually in late May–early June for the percentage cover of all macroscopic sessile species with the aid of a quadrat subdivided into 121 squares by monofilament lines. Percent cover was used as the

measure of abundance because it best accounts for the fact that most organisms in this community exhibit indeterminate growth, and hence a wide range of sizes. Censusing of the plots and treatment maintenance continues to present; the data reported here were collected through June 2007, hence span 10–15 years, depending on the plot. Further details of these plots and the mean responses of species abundance to the manipulation are outlined elsewhere (Wootton 2001a, b, 2004, 2005) (see Plate 1).

Statistical analysis

To explore whether community dynamics were affected by species interactions, I compared three different aspects of the dynamics in these plots: temporal variability, spectral patterning, and the order of density dependence. None of these methods make specific assumptions about the form of equations underlying community dynamics, such as whether the system is open or closed to immigration. I focused my analysis on the three subdominant species in the community: the articulated coralline alga *Corallina vancouveriensis*, the acorn barnacle *Semibalanus cariosus*, and the goose barnacle *Pollicipes polymerus*.

First, I compared plots with and without *Mytilus californianus* present to look for systematic deviations from the general relationship between temporal variance and mean abundance of each species. I accounted for the effect of mean abundance on variability because temporal variance generally scales with mean abundance owing to the impossibility of negative abundance, and because the goal of this analysis was to identify changes in dynamic characteristics induced by the experiment rather than the previously documented strong changes in mean abundance of species (Wootton 2004, 2005). For each species, I first generated a relationship between the mean cover and temporal variance using linear regression on log-transformed variables, which generated linear relationships with well-behaved residuals. This analysis provides a more flexible approach than comparing coefficients of variation, which assume a very specific functional relationship between mean and variance that may not be empirically correct (Gaston and McArdle 1994, Cottingham et al. 2001). I then tested whether residuals varied systematically from this relationship between treatments by scoring whether a residual fell above (high variance) or below (low variance) the best-fit regression line using chi-square tests.

Second, I performed spectral analysis (Bloomfield 1976, Denny et al. 2004) on each replicate time series of *C. vancouveriensis*, *S. cariosus*, and *P. polymerus* to determine whether the pattern of dynamics, as assessed by the relative contribution of sine/cosine functions of different frequencies (one cycle per decade, two cycles per decade, and so on) to describing the dynamics, changed systematically with the presence or absence of *Mytilus californianus*. Some combination of trigonometric functions might be expected to describe well the dynamics of

ecological time series because ecological feedbacks often produce cyclical dynamics and because negative feedbacks arising over various temporal scales can generate complex behavior arising from the interaction of multiple cycles (Volterra 1926, Hastings and Powell 1991). If experimental extinction of *M. californianus* caused a change in the dynamic characteristics of the system, then the relative magnitude of the contribution of functions with different periods should change systematically across replicate time series. To perform the analysis, I first standardized each time series by removing any linear trend and dividing by the standard deviation of the resulting residuals, because I was interested in dynamical effects independent of differences in mean abundance, and because trends in the data can cause spurious signals at low frequencies (Bloomfield 1976). I next applied a Fourier analysis to each time series and analyzed the relative magnitude of contributions of the component functions of different frequencies by scaling the sum of the magnitudes of all period components to one. To insure comparability, I only analyzed spectra of length 10 years, which corresponds to the shortest time series. For time series replicates longer than 10 years, I analyzed each possible block of 10 sequential observations and then averaged the results to obtain a replicate-specific estimate. I tested whether the standardized spectra varied between treatments for each species using multivariate analysis of variance (MANOVA), because the proportional contributions of each frequency in the analysis are not independent of the others.

Third, I used nonparametric, nonlinear analysis of the order of density dependence using cross-validation methods (Cheng and Tong 1992, Bjørnstad et al. 2001) to estimate the imbedding dimension, or order, of the dynamics of each replicate time series, and to test whether this varied with local mussel extinction. This analysis explores relationships between observed abundance at one point in time to abundances at different time lags in the past, which theoretically can induce strong dynamical fluctuations. To carry out the method, I again standardized the time series by detrending the data and dividing by the standard deviation of the residuals. Then I analyzed the order of the standardized time series using the nonlinear time series package (NLT) for R software (Bjørnstad et al. 2001). I analyzed the data for evidence of first to fifth-order lags by subtracting the lowest cross-validation errors for each plot from all the errors for that plot, which scales the best-fitting order to 0, and then analyzing these results with MANOVA.

Evaluation of statistical methods

The lengths of the data series in this study (10–15 years) are shorter than those used in many prior studies applying spectral analysis and order determination (e.g., Bjørnstad et al. 2001), and these methods provide reliable information only for short-period lags when they are applied to a single time series. To overcome this problem, I analyzed

replicated time series with the goal of increasing reliability of longer-period estimates. Therefore, it was important to verify that the methods could successfully distinguish replicated time series with different underlying dynamics over these time spans. I did this by simulating first- through fourth-order systems and applying the same analyses used on my empirical data. The model took the following general Ricker-like form:

$$N_t = I + N_{t-1} \exp(r - \alpha_1 N_{t-1} - \alpha_2 N_{t-2} - \alpha_3 N_{t-3} - \alpha_4 N_{t-4} + \varepsilon_p)$$

$$N_{\text{obs},t} = N_t + \varepsilon_m$$

where I is an outside immigration term, N_t is the population size at time t , r is the intrinsic rate of increase, α_n is an n th order density dependent term, ε_p is normally distributed process error, $N_{\text{obs},t}$ is the observed population size, and ε_m is normally distributed measurement error. Parameters I , ε_p , and ε_m were included to inject a realistic component to the dynamics that could provide a challenge for the methods, and their values were chosen to reflect those expected from the empirical data series, with ε_p tuned to generate simulated results with temporal coefficients of variation that were similar to those observed in the series (≈ 1). In all runs, $I = 0.2$, $\varepsilon_p = 0.7$, $\varepsilon_m = 0.05$, $\alpha_n = 1$, and $r = 2.1$. I added immigration and error terms to the standard Ricker formulation to include in the simulations aspects of population biology that were present within the study system. For the parameter values I used, the deterministic version of the first order model exhibited four-point cycles, the second order model attained a stable equilibrium, and third and fourth order models generated apparently chaotic dynamics (Appendix: Figs. A1 and A2). These dynamics confirm that systems open to immigration are capable of generating complex dynamics. Stochastic versions of the simulations for all models exhibited strong fluctuations (Appendix: Fig. A2).

Each model was simulated 15 times. For each run, the model was iterated 1000 times, after which the model parameters were switched to the other parameter set and the simulation run an additional 15 time steps to simulate a series of transient dynamics following imposition of an experimental manipulation. Analysis was carried out on both the last 10 and 14 iterations of the long-term segment and on the first 10 and 14 iterations of the transient dynamic segments, using methods identical to those used for the empirical dataset, and the mean and variance across the runs was calculated as a weighted sum of those for the two segment lengths (one-third weight to the 10 iteration segments, two-thirds to the 14 iteration segments). The replication level and fraction of time series lengths that I used in the analysis represent the worst-case situation for my empirical data (the experimental extinction series); using the higher replication and time series length of the empirical controls would increase the chances of finding a difference between treatments.

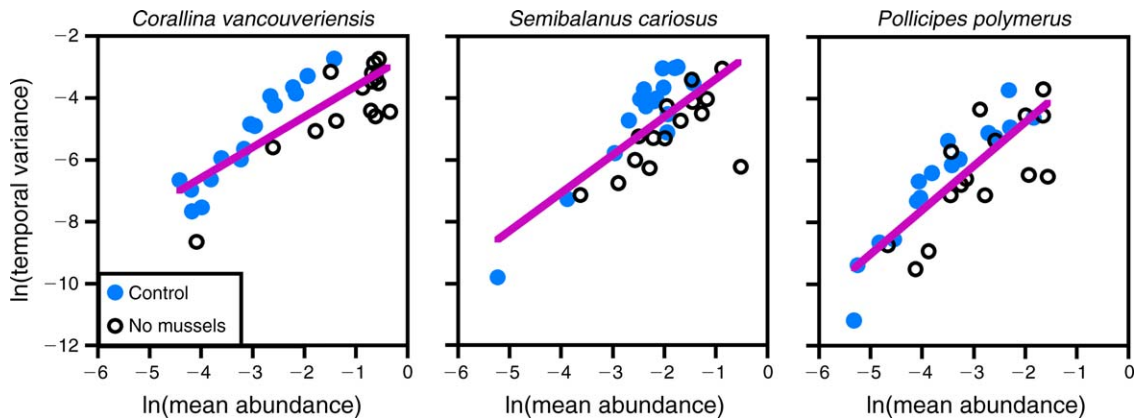


FIG. 1. The relationship between temporal variance in abundance and mean abundance for coralline algae *Corallina vancouveriensis*, the acorn barnacle *Semibalanus cariosus*, and the goose barnacle *Pollicipes polymerus* in the presence (solid blue circles, $n = 16$) and absence (open circles, $n = 15$) of the mussel *Mytilus californianus*. The lines presented are best-fit lines from linear regression for all plots combined.

RESULTS

Deleting mussels from the community caused strong effects on some aspects of temporal dynamics exhibited by other community members (e.g., Fig. A3). For all three focal species, plots of different treatments deviated systematically from the general relationship between mean and temporal variance in cover (Fig. 1); in all cases, plots with *M. californianus* present exhibited significantly higher temporal variance relative to their mean cover than in plots with mussels experimentally removed (Fig. 1, all $P < 0.04$).

Analyses of temporal patterning in the data provided no evidence that it consistently shifted with mussel extinction. Spectral characteristics in Fourier analyses were similar between treatments for all three species (Fig. 2; MANOVA, $F_{4,26} < 1.3$, all $P > 0.3$), suggesting

no consistent change in the patterning of the dynamics through time with the extinction of mussels. Long period components tended to dominate in both treatments.

Like the spectral analyses, the best estimate of the order of density dependence of each replicate time series did not change consistently with treatment (Fig. 3; Kolmogorov-Smirnov [K-S] tests, all $P > 0.8$), nor did the average cross validation error for each order evaluated (Fig. 3; MANOVA, $F_{5,25} < 1.9$, all $P > 0.1$). There was also no strong indication that any particular order consistently described the dynamics for particular species and treatment combinations (Kolmogorov-Smirnov Test vs. uniform distribution, all $P > 0.1$), although a first-order pattern was suggested when all species and treatments were pooled into a single analysis (K-S test vs. uniform distribution, $P < 0.001$).

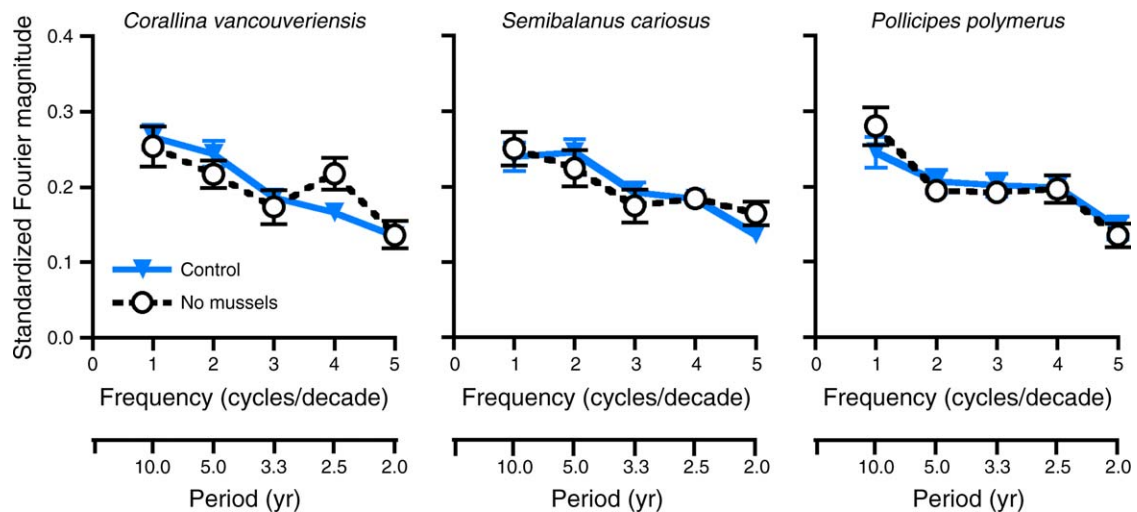


FIG. 2. The proportional contribution of different spectral components from Fourier analysis (mean \pm SE) describing the abundance dynamics of *C. vancouveriensis*, *S. cariosus*, and *P. polymerus* in the presence (blue triangles, blue line, $n = 16$) and absence (open circles, dashed line, $n = 15$) of *M. californianus*.

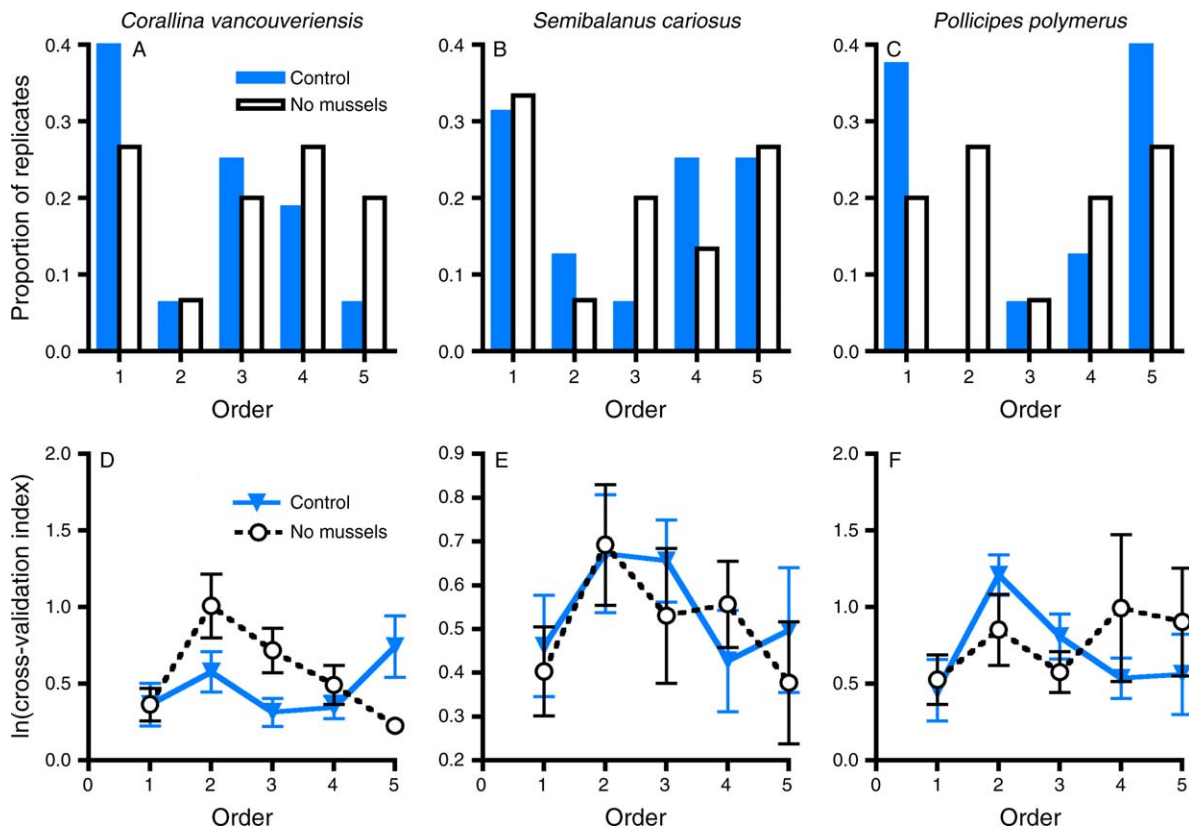


FIG. 3. (A–C) Frequency distribution of the best-fitting order of density dependence and (D–F) the average cross-validation error (mean \pm SE) of each order tested for the abundance dynamics of (A, D) *C. vancouveriensis*, (B, E) *S. cariosus*, and (C, F) *P. polymerus* in the presence (blue symbols, $n = 16$) or absence (open symbols, $n = 15$) of *M. californianus*. Note that lower average cross-validation error indicates better performance of a particular order.

Analysis of simulated data demonstrated that, like traditionally analyzed closed systems, systems open to outside immigration can exhibit complex dynamics arising from feedbacks. It also demonstrated that spectral analysis is capable of detecting differences in dynamics for the time span and number of replicates used in this study. Spectral analysis detected a significant difference among models (MANOVA, $F_{12,140.5} = 10.648$, $P < 0.0001$), with higher order models exhibiting higher relative power at progressively lower frequencies (Appendix: Fig. A4). Results obtained for the transient dynamics exhibited similar patterns to non-transient dynamics in the spectral analysis (Appendix: Fig. A4). Differences among model dynamics in the order of density dependence analysis were marginally nonsignificant (MANOVA, $F_{15,143.9} = 1.733$, $P = 0.051$), and did not correctly predict the actual order of the underlying model (Appendix: Fig. A4). Hence, results of the order analysis on the experimental data should be treated with caution, but are presented for completeness.

DISCUSSION

Understanding the contribution that biological interactions play in ecological dynamics has been a long-standing challenge to ecologists. While initial discussion

framed the question as whether extrinsic environmental factors or intrinsic biological factors drive population dynamics, more recent perspectives have recognized that both are likely to play a role. Given this viewpoint, one approach has tried to extract the independent role of biological interactions from external perturbations using time-series modeling (Ellner and Turchin 1995, Turchin 2003). Often these analyses focus on single species, with the expectation that important effects of species interactions will be revealed by non-linear temporal lags that correspond to delayed feedback as chains of species interactions play themselves out. An alternative approach recognizes that biological interactions can also act to alter the impact of extrinsic environmental stochasticity, either by damping or amplifying external variation (Ives 1995). In this approach, multispecies models must be parameterized and analyzed to determine how external impacts and internal feedback loops play themselves out. These models are often challenging to parameterize, and an estimate of how environmental fluctuations differentially impact species is required. The study reported here offers a direct empirical approach to the question of whether interactions among species change the dynamic character of communities.

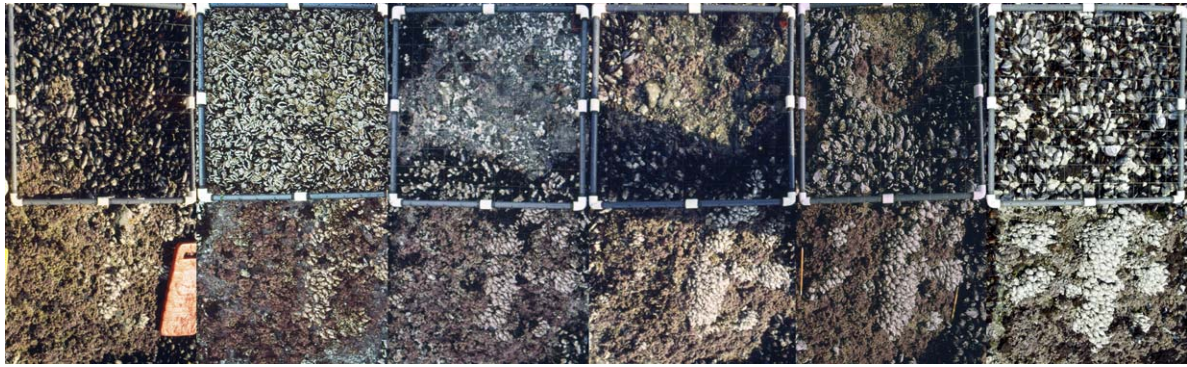


PLATE 1. Series of photographs through time showing relative patterns of change in cover in controls (top) and mussel removal (bottom) plots. Note the relative stasis of pink coralline algae (primarily *Corallina vancouveriensis*) and white goose barnacle (*Pollicipes polymerus*) populations in experimental removal areas relative to controls, reflecting the change in system dynamics arising from the absence of *Mytilus californianus*, which acts as a strong transmitter of environmental stochasticity arising from wave disturbance. Photo credits: J. T. Wootton.

The experimental results demonstrate that *M. californianus* affects the dynamic character of this intertidal community, consistent with expectations of theory and laboratory studies. By examining three components of system dynamics, variability, spectral composition, and temporal order of the time series, the results also provide some insight into the likely mechanistic basis of this change. *M. californianus* extinction caused significant declines in temporal variability of subdominant species, but no significant change in the spectral composition or order of their population dynamics through time. This pattern suggests that changes in system dynamics were primarily the result of *M. californianus* amplifying stochastic environmental noise rather than through changes in the lengths of feedback cycles. *M. californianus* appears to be relatively susceptible to wave disturbance (Paine and Levin 1981, Wootton 2001b), and interacts strongly with other species (Paine 1966, Paine and Levin 1981, Wootton 2004), which would predispose it to be an amplifier of environmental variance. Changes in feedback could be expected because acorn barnacles (e.g., *S. cariosus*) promote mussel recruitment (Berlow 1999) and *C. vancouveriensis* may also do so because its branched morphology traps water at low tide, ameliorating physical conditions. Both of these mechanisms could generate lagged negative feedback via increased competition for space from *M. californianus* with increasing abundance. Furthermore, *C. vancouveriensis* becomes dominant in the absence of *M. californianus* (Wootton 2004; Fig. 1) and its recruits are derived locally (Dethier et al. 2003) hence the removal of *M. californianus* might enhance the strength of feedback loops via local reproduction. The importance of feedback mechanisms might be reduced, however, because planktonic *M. californianus* larvae recruit from areas outside the impact of local interactions among species, competitive interactions among mussels and other species seem very asymmetric (Paine 1966, Wootton 2001a), and *M. californianus* interacts with a wide

spectrum of species (Paine 1966, Wootton 2001a), which may preclude strong feedback signals of a given order (Bjørnstad et al. 2001, Murdoch et al. 2002). Hence, the development of additional feedback-driven changes in dynamics cannot be excluded over longer time frames or manipulations at much larger scales.

Long-term species manipulations can provide insight into the effects of ecological interactions on dynamics by directly perturbing biological aspects of the system while making minimal model assumptions. Furthermore, in contrast to laboratory studies, field experiments can probe the role of species in altering system dynamics through amplifying or damping stochasticity, because they expose study units to natural levels of environmental variation. My results suggest that the role of species in affecting ecosystem dynamics by mediating the impact of environmental variation may be underemphasized in current ecological theory, and further highlight the need for long-term field experiments to be carried out as an essential component to understanding how ecosystems respond to environmental change.

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APPENDIX

Dynamics of replicated open population models with process and measurement error, and examples of empirical dynamics (*Ecological Archives* E091-005-A1).