FROM CANALIZATION TO CONTINGENCY: HISTORICAL EFFECTS IN A SUCCESSIONAL ROCKY INTERTIDAL COMMUNITY

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Abstract. Many landscapes are characterized by a mosaic of patches in various stages of succession. Whether successional paths dampen, track, or magnify extrinsic variation in initial conditions influences how much historical and site-specific detail is required to explain variation in patch composition. I investigated the patterns and importance of historical effects in a successional marine rocky intertidal community on the central coast of Oregon, USA. Patches in the mid-intertidal mussel bed (*M. californianus*) were manually cleared in a way that mimicked natural disturbances. In four separate blocks (large patches ~9 m²), three sets of plots were initiated with their starting dates staggered by one year. Within each set of plots, I manipulated the presence/absence of two groups of early successional sessile species under each of three predator densities. This design allowed me to address the following general questions: (1) What are the separate and interactive effects of successional age, yearly variation, and initial conditions on the temporal changes observed after disturbance? (2) When do interactions between early species act to dampen or magnify natural variation between years or starting dates?

Succession in mid-intertidal patches in the mussel bed displayed complex patterns of historical effects, which varied among species and between different stages of succession. Embedded in this potential complexity were some consistent and repeatable successional trends. Some potentially important canalizing, or ''noise-dampening'' forces in this system included: (1) physiological and/or life history trade-offs between dispersal ability and competitive ability, (2) strong direct biotic interactions, which buffer environmental variability, and (3) compensatory (''buffering'') responses of species within an important functional group. ''Noise-amplifying'' forces included: (1) variable indirect effects of predators, (2) prey size escapes, and (3) predator saturation (or prey ''swamp'' escapes). Understanding the patterns and causes of consistency or contingency in succession will be critical for managing variability in landscapes that are increasingly dominated by anthropogenic disturbance regimes.

Key words: context dependency; disturbance, community response to; Oregon; patch dynamics; predation; predictability of patterns; rocky intertidal; succession, historical effects during; temporal variation; whelks.

INTRODUCTION

Ecological succession consists of the sequence of changes in community structure that occur after a site has been disturbed (Connell and Slatyer 1977, Pickett et al. 1987, Farrell 1991, McCook 1994). Because succession is inherently a historical process, studies of succession have long been focused on the importance of past events in shaping current variation in community structure and organization (Clements 1916, 1928, Gleason 1926, Egler 1952, reviewed in Mac-Mahon 1980). For a given temporal scale of observation, historic effects, which influence variation in successional patterns, can include both physical events in history (e.g., disturbance events, environmental conditions, recruitment/dispersal events, and other events)

and/or past biological interactions, which are not currently measurable, but which have lasting effects (e.g., facilitation/inhibition by early species, consumption of early species, competition among early species, and other effects) (e.g., Connell 1980, Lubchenco 1982, 1983, Sousa 1984b, McCune and Allen 1985, Franklin 1989, Farrell 1991, Hixon and Brostoff 1996). Since the outcome of species interactions often varies with the local setting, or conditions (e.g., Dayton 1971, Menge 1976, Fairweather et al. 1984, Thompson 1988, Cushman 1991, Power 1992, Carpenter and Kitchell 1993, Wedin and Tilman 1993, Menge et al. 1994), historical events can also strongly influence current processes by shaping the context in which they occur (Wilbur and Alford 1985, Robinson and Edgemon 1988, Drake 1990, 1991).

Given the potential importance of these interactions among past events and current processes, the patterns and mechanisms by which communities change during succession can be tremendously variable, complex, and context-dependent (Connell and Slatyer 1977, Catte-

lino et al. 1979, Paine and Levin 1981, Turner 1983*a*, *b*, Sousa 1984*b*, Connell et al. 1987, Pickett et al. 1987, Dudley and D'Antonio 1991, McCook 1994). In this light, it is notable that many empirical ecologists have also documented or inferred remarkably regular and repeatable patterns of change through time (e.g., Clements 1928, Odum 1969, Paine and Levin 1981, Paine 1984, Farrell 1989, 1991, McCook 1994). Thus, a critical challenge for the successful application of basic ecological theory is to determine not *if* succession can be variable and contingent, but *when* (Walker and Chapin 1987, Grover and Lawton 1994).

Understanding the way in which successional paths depend on historical events has important consequences for the types and amount of information necessary to develop predictive models and natural resource management strategies (Colwell 1974, Franklin 1989, Pickett 1989, Drake 1990, 1991, Facelli and Pickett 1990). Here I outline three patterns of historical effects and their consequences to represent a continuum in the degree to which successional changes dampen, track, or magnify extrinsic variation during the course of succession.

1. *Canalized succession.*—If early species have strong and consistent effects on later species, the community may follow deterministic, repeatable patterns of change over time (Fig. 1a, e.g., Clements 1928, Egler 1952: relay floristics, Odum 1969, Connell and Slatyer 1977: facilitation and inhibition models, Lubchenco 1983, Farrell 1991). In this case, consistent effects of early events canalize subsequent successional changes. Succession can also be highly regular if recruitment patterns are consistent over time. In either case, much of the current variation in community structure can be explained by the length of time since the last disturbance in combination with either empirically derived models of transition probabilities, or mechanistic models that incorporate strong interactions among species (Botkin et al. 1972, Horn 1975, Usher 1979, Noble and Slatyer 1980, Greene and Schoener 1982, Huston and Smith 1987, Tilman 1990, McCook 1994).

2. *Externally driven succession.*—If extrinsic events override the effects of deterministic species interactions, variation in successional pathways may be driven "externally" by stochastic variation in environmental conditions, recruitment, propagule availability, disturbance, and other events (Fig. 1b, e.g., Gleason 1926, Egler 1952: initial floristic composition, Connell and Slatyer 1977: tolerance model, Sale 1977: lottery hypothesis, Sousa 1984*a*, *b*, Gaines and Roughgarden 1985, Chesson and Case 1986, Hubbell and Foster 1986, Fastie 1995). Current variation in community structure may be better explained by a combination of site characteristics, both current (e.g., position relative to propagule sources) and historic (e.g., initial conditions), and models of external driving variables, which do not depend on a detailed knowledge of the mechanisms of species interactions.
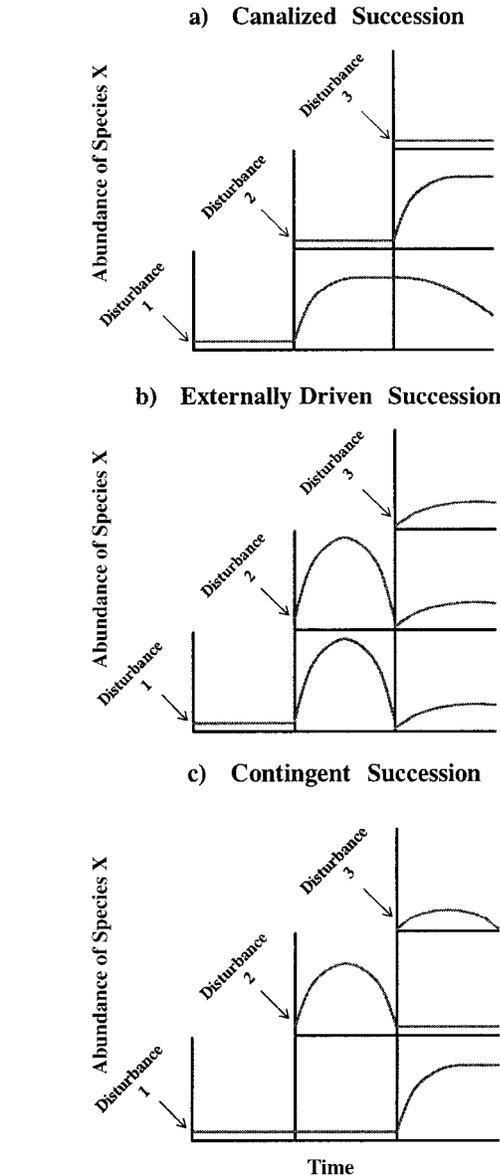

FIG. 1. Examples of the patterns of change with time in the abundance of a given species (species X) following a disturbance (indicated by the arrows) for three disturbance patches for (a) canalized, (b) externally driven, and (c) contingent succession.

3. *Contingent succession.*—If the sign and magnitude of species interactions depend strongly on the context in which they occur, the interaction between stochastic and deterministic processes may result in highly contingent, rarely repeatable patterns of succession (Fig. 1c, e.g., Cattelino et al. 1979: multiple pathways, Drake 1990, 1991: assembly rules, Sutherland 1974: alternative stable states, Paine 1977: priority effects, Franklin 1989: biological legacies, Wilson and Agnew 1992: positive-feedback switches). Current variation in community structure can only be explained by a detailed knowledge of species interactions and the way

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

Many studies of successional processes involve either the reconstruction of historical species abundances at a site or the use of spatial chronosequences (Pickett 1989, McCook 1994). The latter attempts to substitute space for time by interpreting sites of different ages as different points in time for a single site. Neither of these allows for a rigorous evaluation of the causal processes regulating succession, and chronosequences necessarily confound the effects of site age with historic or stochastic differences among sites (Pickett 1989). Field experiments have proven to be one of the most powerful tools to elucidate the causal mechanisms of succession (Connell and Slatyer 1977, Paine 1977, Lubchenco and Menge 1978, Hils and Vankat 1982, Lubchenco 1983, Sousa 1984*a*, Connell et al. 1987, Farrell 1991, McCook 1994, Hixon and Brostoff 1996), but individual experiments are often necessarily limited in their spatial and temporal extent (Bender et al. 1984, Diamond 1986, Underwood and Petraitis 1993). However, by replicating small-scale experiments over space and/or time, the site-specific nature of field experiments can itself be a powerful tool for characterizing contingencies and patterns of variation in successional processes (Dayton 1971, Menge 1991, Menge et al. 1994, Berlow and Navarrete 1997).

I used this comparative experimental approach (sensu Menge 1991) to investigate factors that influence whether successional changes dampen or magnify variation in initial conditions. In a marine rocky intertidal community, I experimentally cleared plots and manipulated the presence/absence of two groups of early successional species under each of three predator densities. Three identical, fully replicated, runs, had starting dates staggered by one year. This design allowed me to explore the following questions:

1) When are differences between plots at a given point in time attributable to successional age, independent of the starting date? (In other words, is succession canalized?)

2) When do differences over time track extrinsic yearly variation independent of successional age? (Is succession externally driven?)

3) When do different starting dates lead to fundamentally different patterns of change over time? (Is succession contingent on the starting date?)

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

In this study, I focus on the patterns of variation in succession among adjacent plots that differed primarily in their starting dates.

DISTINGUISHING HISTORICAL EFFECTS

One primary objective of this study was to tease apart the separate and interactive effects of successional age, starting date, and census year (Fig. 2):

1) Successional age (or AGE) refers to the time elapsed since a plot was cleared, or initiated. If two plots that started at different times follow the same deterministic pattern of change over time, then differences between them at a given point in time will be primarily a function of AGE.

2) Starting date (or START) refers to the actual year that a plot was cleared. Hereafter, I use run to refer to a set of plots initiated at a given starting date. Thus, this study consisted of three identical runs with starting dates staggered by one year (Runs 1, 2, and 3). I also use initial conditions to refer to conditions at a given starting date. Because all the plots were cleared in the same fashion and at the same time of year, differences in initial conditions among runs were assumed to be due to natural variation among years in recruitment, environmental conditions, and other variables.

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

The design of this study is inherently complicated by the fact that it is impossible to have different starting dates at the same time (Fig. 2). Thus one cannot design a completely orthogonal experiment to measure how the effect of successional age varies with starting date independent of stochastic variation between census years, or how the variation between census year varies with starting date independent of successional age. If two runs are initiated one year apart, one can compare the first two years of each to explore the interaction between age and starting date; however, the effects of starting date per se are confounded with the effect of census year (Fig. 2: ANOVA 1). For example, if the patterns of change with age differ between runs (ANOVA 1: AGE × START is significant), it could be because different initial conditions result in different successional trajectories (e.g., Fig. 1c), or because both runs are similarly tracking the same stochastic variation between years (e.g., Fig. 1b). Similarly, one can measure the interaction between starting date and census year by comparing census years two and three for both runs (Fig. 2: ANOVA 2). However, in this case, the effect of starting date is confounded with successional age. For example, if difference between census years varies between runs (ANOVA 2: YEAR × START is significant), it could be because different starting dates lead to different successional paths (e.g., Fig. 1c), or
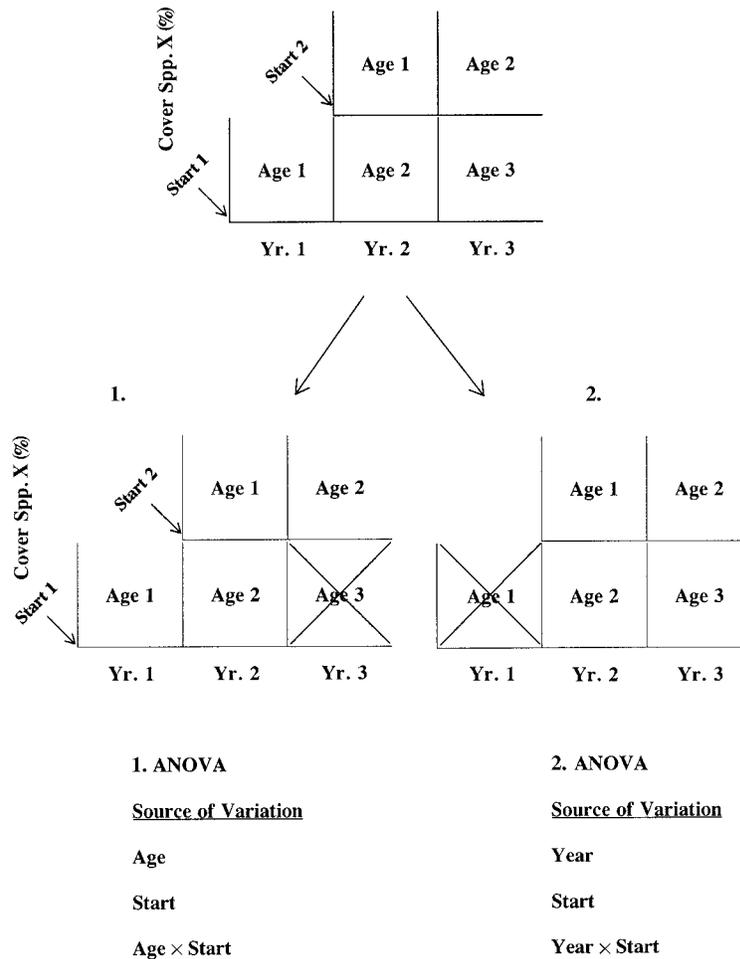
FIG. 2. Experimental design for quantifying the separate and interactive effects of successional age (AGE), run starting date (START), and census year (YEAR). Because the full design was inherently not orthogonal, two separate factorial analyses of variance (ANOVAs 1 and 2) were used to measure AGE × START and YEAR × START interactions. Information provided by both analyses can be combined to resolve some of the confounding factors present in each individual analysis. See *Distinguishing historical effects* for details.

because both runs are following the same, repeatable successional path, which is staggered by one year (e.g., Fig. 1a).

Information provided by both analyses can be combined to resolve some of these confounding factors. For example, in Fig. 2, if AGE × START is significant in ANOVA 1 *and* only the main effect of YEAR is significant in ANOVA 2, it is likely that both runs are similarly tracking the same stochastic variation between census years, regardless of successional age (i.e. Externally Driven Succession, Fig. 1b). If the YEAR × START interaction is significant in ANOVA 2 *and* only the main effect of AGE is significant in ANOVA 1, it is likely that both runs are following the same repeatable path of succession, regardless of starting date (i.e., Canalized Succession, Fig. 1a). If both the AGE × START *and* YEAR × START interactions are significant, this suggests that runs initiated in different years responded differently to the same stochastic vari-

ation between census years, resulting in different patterns of change with age (i.e., Contingent Succession, Fig. 1c).

The above examples provide a heuristic framework for interpreting the results of the experiment and inferring whether the successional patterns were canalized, stochastic, or contingent. However, in some cases, more information is required to distinguish between alternative patterns (either a longer time series, more starting dates, or information about specific causal mechanisms), and in other cases, more than one pattern could be occurring simultaneously (e.g., relatively canalized timing of colonization with some stochastic variation in the peak abundance). In the following section I describe some of the biology of this system to aid interpretation of statistical results.

THE SYSTEM

This study was conducted in the rocky intertidal zone at Fogarty Creek Point (44°51′ N, 124°03′ W), ~2 km

north of Boiler Bay State Park, in the central coast of Oregon, USA. The zonation of intertidal organisms at this site is similar to that described for Boiler Bay by Menge et al. (1994). A more detailed description of the Fogarty Creek site is provided by Farrell (1991) and Navarrete (1996). Characteristics relevant to the current study are described in the following section.

Much of what we know about the details of succession in mid-intertidal mussel beds in the Pacific Northwest comes from the work of Paine and colleagues in Washington State (e.g., Levin and Paine 1974, Paine and Levin 1981, Paine 1984, Suchanek 1986, Wootton 1993*b*, 1994*a*). On wave-exposed shores of Washington, the mussel *Mytilus californianus* is the dominant competitor for primary space and has the potential to form extensive monocultures in the mid-intertidal zone in the absence of disturbance (Paine 1974, Paine and Levin 1981). The cycle of disturbance, succession, and re-establishment of *M. californianus* typically takes ~7 yr for patches >3 m² (Paine and Levin 1981). In the interim, the substrate is colonized by a suite of competitively subordinate sessile invertebrates and algae (Paine and Levin 1981, Wootton 1993*b*).

Succession tends to proceed from small-bodied to large-bodied species (Wootton 1993*b*), and exhibits an early peak in diversity followed by a decline in species number (Paine and Levin 1981). However, details of the early and midsuccessional dynamics can be complex and variable. In Washington, the initial patterns of patch occupancy depended on patch size and the season of patch creation (Paine and Levin 1981). In addition, species composition was a poor predictor of patch age due to high between-patch variability among patches of the same age (Paine and Levin 1981).

Experiments for the present study in Oregon were carried out in a mid-intertidal zone consisting of a smooth, basaltic, gently sloping, moderately wave-exposed bench. This area was characterized by an extensive bed of large California mussels, *M. californianus.* As in Washington (Paine and Levin 1981), patches of bare rock of varying sizes are continually created by waves dislodging the mussels or by a combination of freezing events and wave stress (Brosnan 1994).

The most abundant predators in the midzone patches in this study were whelks (*Nucella emarginata* and *Nucella canaliculata*) and birds (mostly Black Oystercatchers, *Hematopus bachmani,* and gulls, *Larus* spp.). The abundance of whelks varies seasonally, with peak abundances occurring during the summer months (Navarrete 1996, E. L. Berlow, *unpublished data*). Adult predatory starfish, *Pisaster ochraceus,* are scarce in this area, occurring primarily below the lower limit of the mussel bed. The smaller, brooding starfish, *Leptasterias hexactis,* and recruits and juveniles (<3 cm total diameter) of *Pisaster ochraceus,* were seasonally abundant, although they were generally restricted to the edges of new patches and to refuges within older patches

provided by tufts of algae, crevices in the rock, or spaces among large barnacles.

Early successional species and young individuals of some later species are susceptible to consumers. Limpets (*Lottia* spp.) graze algae and can have important negative effects on recruits of some acorn barnacles, especially *Balanus glandula* (Dayton 1971, Paine 1981, Farrell 1991, Berlow and Navarrete, 1997). *Nucella* can be important predators on *B. glandula* and small mussels, *Mytilus trossulus,* which are common in the first year after patch formation (Connell 1970, Dayton 1971, Palmer 1983, Wootton 1993*b*, Navarrete and Menge 1996); however, the strength (and even the sign) of their effect at this site is variable (Berlow 1995, Navarrete 1996). The other common early-colonizing acorn barnacle, *Chthamalus dalli,* is less vulnerable to predation by whelks or limpets (includes bulldozing) due to its small size and flat morphology (Dayton 1971, Paine 1981, Farrell 1991, Navarrete 1996). Birds can also have important negative effects on *M. trossulus,* small *M. californianus,* and the gooseneck barnacle, *Pollicipes polymerus* (Marsh 1984, 1986, Wootton 1992, 1993*a, b*, 1994*a*, Meese 1993). The direct effects of predation by *Nucella* are restricted to the first few years of succession. The later successional species they consume (e.g., large acorn barnacles, *Semibalanus cariosus*; gooseneck barnacles, *Pollicipes polymerus*; and the competitive dominant mussel, *M. californianus*) eventually achieve a size refuge from predation (Connell 1970, Dayton 1971, Palmer 1984, Navarrete 1996).

Many interactions between early species and later sessile species have been documented. Some of these interactions that potentially affect the dynamics of succession in midzone patches include: (1) *B. glandula* outcompete the smaller acorn barnacle, *C. dalli* for space, and (2) predation on *B. glandula* and small *S. cariosus* (including limpet ''bulldozing'') can indirectly facilitate *C. dalli* (Dayton 1971, Paine 1981, Farrell 1991, Navarrete 1996). (3) Several species of acorn barnacles, can facilitate the recruitment of mussels by providing an irregular surface, which offers protection from predation and/or desiccation (Dayton 1971, Suchanek 1978, 1986). (4) *B. glandula* (but not *C. dalli*) also facilitate the recruitment of algae (Farrell 1991). (5) *M. trossulus* and *S. cariosus* can potentially outcompete *B. glandula* for space by growing on top of them or undercutting them (Dayton 1971, Suchanek 1986). (6) Both *M. trossulus* and filamentous algae facilitate the recruitment of *M. californianus* (Paine and Levin 1981, Sousa 1984*a*, Suchanek 1986, Navarrete 1996).

Variation in recruitment of planktonic larvae can influence the patterns and importance of interactions between the species inhabiting mid-intertidal patches (Paine and Levin 1981). While reproductive periodicity is common in many sessile intertidal species and settlement patterns can be influenced by larval preferences (e.g., Wethey 1986, Raimondi 1988, Johnson and

Strathmann 1989), the timing and intensity of recruitment and colonization can be characterized by much variability over a wide range of spatial and temporal scales (Paine and Levin 1981, Sousa 1984b, Roughgarden et al. 1988, Lively et al. 1993).

In sum, the early and midsuccessional dynamics of this community are characterized by much variability on the level of individual species, with some coarser trends that are relatively consistent, and repeatable. Many potentially complex and variable direct and indirect interactions between successional species have been documented, and stochastic variation in the timing and intensity of disturbance and recruitment can be important forces. This study attempts to capitalize on the wealth of information available for this system, and its amenability to experimental manipulation, to explore some of the factors involved in dampening or magnifying variation in successional trajectories.

Methods

The general experimental design was similar to that illustrated in Fig. 2 except that a third set of plots, which ran for ~1.5 yr, were initiated in year 3. To evaluate whether interactions between early and midsuccessional species influence the patterns of historical effects, in each run I manipulated the abundance of whelks (*N. emarginata*), acorn barnacles (primarily *B. glandula, S. cariosus,* and *C. dalli*), and mussels (*M. trossulus* and *M. californianus*) in nine separate $20 \times 20 \text{ cm}^2$ plots (Fig. 3a). Within each run all nine treatments were replicated in four separate blocks, or large patches (~9 m²) in the bed of *M. californianus* that were partially created by a recent physical disturbance and partially expanded by manually removing additional *M. californianus.* Thus, the plot locations were determined in part by locations already receiving some natural disturbance. Within each run, all nine treatments were randomly assigned to plots within each disturbance patch, and successive runs were installed in the same four patches (Fig. 3b). The locations of plots for successive runs were chosen haphazardly, without preconceived bias, depending on the availability of space within each patch. I expanded each patch laterally in the second year to make room for the plots of Run 2, while those for Run 3 managed to fit in the space available among the existing runs. This resulted in Runs 1 and 2 being spatially segregated within a given patch, while plots from Run 3 were interspersed among them (Fig. 3). While small-scale (within-patch) spatial variation in microsite characteristics for each run could have confounded differences among starting dates, many important stochastic events (e.g., recruitment pulses) were spatially, relatively homogeneous within a given patch and more visibly variable on the among-patch scale. In addition, all runs had a similar number of plots in the center vs. the edge of the patch. The mean inter-patch distance was ~25 m.

Within each patch, plots were spaced, on average, ~20 cm apart.

There were three levels of whelk densities (none, low, and high), and two levels of both barnacles and mussels (present/absent) (Fig. 3a). The design for Run 1 was initally completely orthogonal, but since treatments where both mussels and barnacles were removed monthly remained essentially bare, they were eliminated after the first year to make the installation and monitoring of subsequent runs more logistically feasible. Thus, the design for each run was not completely orthogonal (i.e., there were no ''−mussel, −barnacles'' treatments). Stainless steel mesh cages $20 \times 20 \times 5$ cm in size (mesh size = 18 gauge [0.12 cm thickness], 0.32 cm space between mesh, 51.6% of surface area open) were used to manipulate the density of whelks. Cages either excluded whelks or enclosed two or six whelks (15–22 mm in length from apex to siphonal canal), corresponding to densities of 0, 50, and 150 whelks/m², respectively. *Nucella* often form dense aggregations, which at this site can be >500 whelks/m² (Navarrete 1996); thus the manipulated densities in this experiment were well within the natural range for *Nucella.* However, while the abundance of *Nucella* at a given location is normally quite variable over time (Navarrete 1996), in this experiment *Nucella* densities were maintained at constant levels. Cages also excluded birds, and any small sea stars (*Leptasterias* and juvenile *Pisaster* <1.5 cm total diameter), which crawled under the mesh were removed during monthly censusing.

All plots were initially cleared of macroscopic invertebrates and algae with a paint scraper and wire brush. Scraping, like natural disturbances in the mussel bed, left areas with algal crusts and byssal threads of *M. californianus.* The subsequent colonization by acorn barnacles (three species) and mussels (two species) was manipulated by either allowing them settle naturally (present) or removing the newly colonized individuals on a monthly basis (absent). Thus, while the predator treatments were maintained at a constant density throughout the experiment, the +barnacle and +mussel treatments varied naturally with recruitment and mortality (independent of predation and interspecific competition). Hereafter, I use barnacle to refer to acorn barnacles.

To compare treatments in the caged plots with successional patterns naturally occurring in the patches, each patch contained three (one for each run) 20×20 cm unmanipulated plots (controls) marked with four screws and three roofs, which allowed the passage of *Nucella,* to evaluate artifacts introduced by the cages themselves. The comparisons of roofs against marked, unmanipulated, control plots, showed the effects of cages per se and bird predation, but these two factors could not be separated. Unfortunately, by the second year of each run, most of the roofs were destroyed by severe wave action. On this short time scale, the roofs did not differ significantly from the controls (Berlow
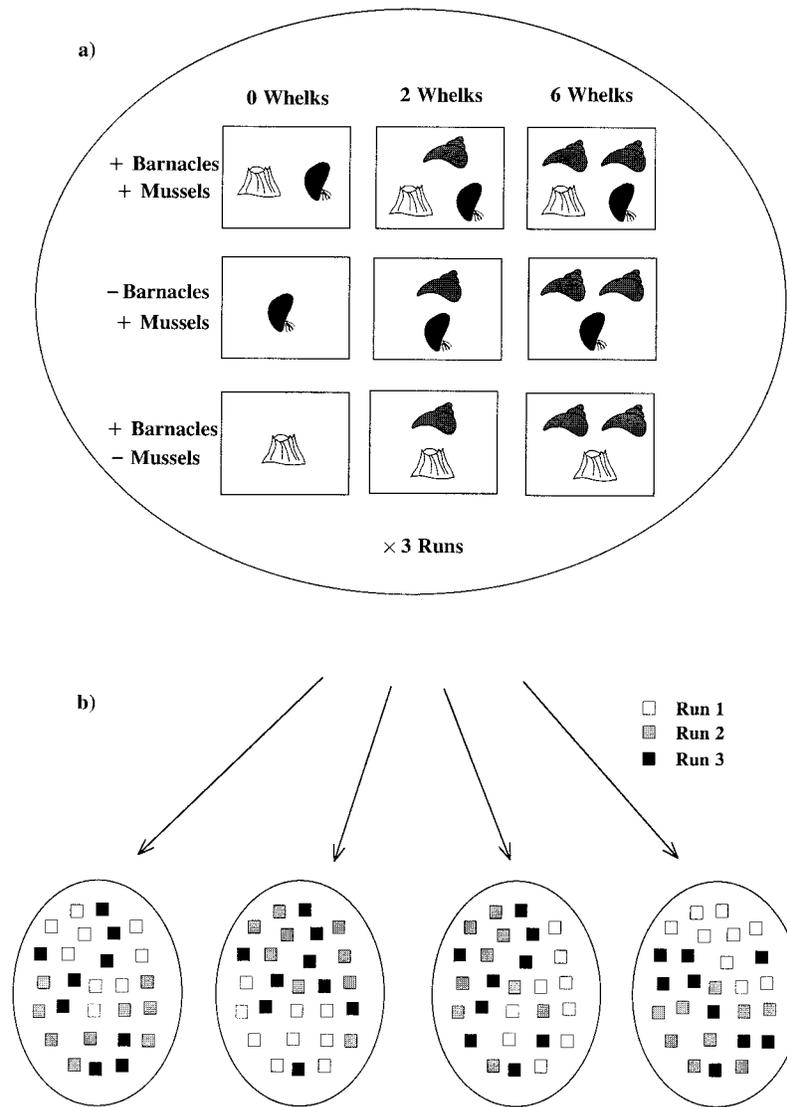
FIG. 3. Part (a) shows the experimental design for each run, or starting date. Each box indicates a separate stainless steel mesh cage, which contained one of nine combinations of whelk, barnacle, and mussel treatments. Treatments for each run were assigned at random within a block, or large patch in the bed of *M. californianus.* Part (b) is a schematic representation of the layout of the three runs within four blocks, which were spaced ~25 m apart. Runs 1, 2, and 3 were initiated in April of 1991, 1992, and 1993, respectively. See *Methods* for details.

1995), and these results are consistent with a concurrent study at this site by Navarrete (1996). However, the cages may have introduced artifacts after this time, when later successional invertebrates and algae increased in abundance. These potential effects include: (1) Shading by the cages may have resulted in low cover of macroalgae in plots with cages or roofs (see *Results*); (2) Exclusion of birds may have been more important after the first year (e.g., Wootton 1993*b*); (3) Grazing by small limpets may have been more intense in plots with cages or roofs (e.g., Wootton 1992); and (4) *Nereis* polychaetes and small sea stars appeared to be attracted to the area under the cage rims, which

served to secure the cages to the rock. Any individuals present were removed during monthly monitoring.

Because of these possible artifacts of the cages, I restricted the analysis to comparisons among treatments with cages, assuming that the effects of cages were the same across treatments. Thus, the treatment effects in this study should be interpreted in the context of low algal cover, exclusion/removal of birds and small sea stars, and other potential cage effects. Data from the control plots are presented to illustrate the natural patterns of succession at this site.

Run 1 was initiated in April 1991 and maintained through March 1994. Run 2 was initiated in April 1992

and maintained through September 1994. Run 3 was initiated in April 1993 and maintained through October 1994. All runs were terminated because some cages were eventually damaged during severe storms, leaving less than three replicates for several treatments. In addition, by the beginning of the third year of succession, many of the species present that are consumed by *Nucella* had grown large enough to escape predation.

Data analysis

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

Separate ANOVAs for each species are not always desirable since correlations among species might affect the Type I error rate (Tabachnick and Fidell 1989, Scheiner 1993). However, since mussels and barnacles were simultaneously both manipulated factors and response variables, separate univariate ANOVAs were preferable to a multivariate ANOVA because they allowed me to analyze orthogonal groups of treatments in which the response variable was not manipulated (i.e., +mussel or +barnacle). Thus, I used only +barnacle treatments to analyze effects on the three barnacle species (*B. glandula, C. dalli,* and *S. cariosus*) and +mussel treatments to analyze the two mussel species (*M. trossulus* and *M. californianus*). For the two other species (*Pollicipes* and *Anthopleura*), I first included all treatments in the ANOVAs, but since mussels had no significant effects on either species in any year or for either starting date ($P > 0.05$ in all cases), I pooled across mussel treatments. This had the advantage of making the resulting design completely orthogonal (because there were no −barnacle, −mussel treatments) and increasing the power to detect interactions among the remaining factors. To facilitate interpretation of the univariate results and of correlations among species, I also present figures illustrating the patterns of change of all species together. To correct the experiment-wise significant levels for performing multiple tests (two ANOVAs and/or multiple species), I used a conservative form of the sequential Bonferroni method proposed by Rice (1989). The correction for each factor was determined by the number of times that particular

factor was tested. For example, the factor *Nucella* (three levels) was tested for each of the two ANOVAs (Fig. 2) for each of seven species, so the initial adjusted significance level for this factor was α/14, or 0.0036. In all the tables I also present unadjusted P values.

Assumptions of normality and variance heterogeneity were checked by normal probability plots, stem and leaf diagrams of residuals, and visual inspection of residual vs. predicted plots. In all cases, arcsine square-root transformed cover data exhibited more normal distributions and homogeneity of variances than the raw data. However, in many cases, variances remained heterogeneous because some treatments exhibited extreme variance. This usually occurred when most of the replicates of a treatment group had zero values. One consequence of this was that, in an ANOVA, some treatments differed significantly (statistically) when the cover of a species was extremely low in one and almost absent in the other. Thus, the ecological difference may have been trivial. These cases are clear in the figures, and were taken into consideration when interpreting the results. One solution could have been to remove groups with extreme variance from the analysis or to perform separate *t* tests on individual treatment pairs of interest (see Farrell 1991, Wootton 1993*a*, 1994*a*). However, a primary objective of the present study was to explore the interactions among manipulated factors; thus, the results of the factorial ANOVAs are presented. Data were also analyzed by performing ANOVAs on ranked data as recommended by Conover (1980) for complex designs, which preclude the use of simple nonparametric tests. Rank transformations did not always reduce heteroscedasticity, and the results of the ANOVAs were generally similar to those for arcsine square-root transformed data. Results from the latter analyses are presented (Conover 1980).

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

RESULTS

General successional patterns in caged plots

Here I describe some qualitative trends of species replacement in the caged plots where all sessile species
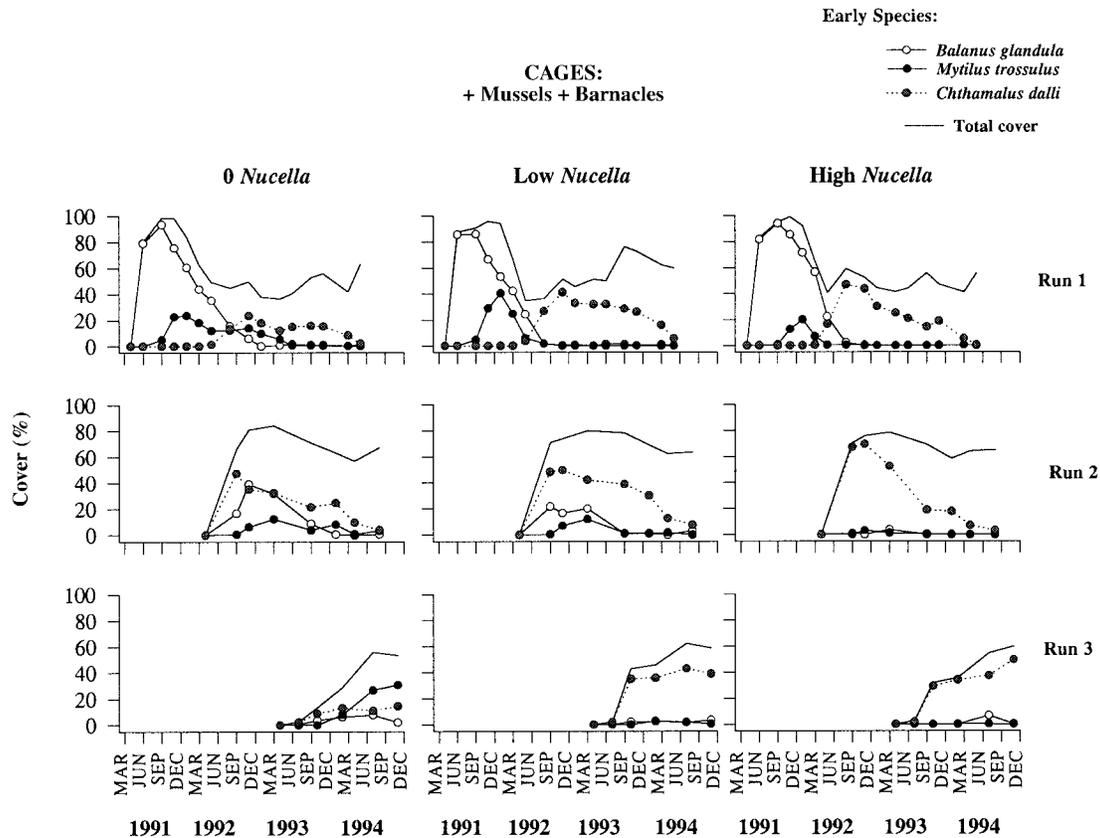
FIG. 4. Mean percent cover ($n = 4$) of *B. glandula, M. trossulus, C. dalli,* and all macroscopic sessile species (total cover) in cages where both mussels and barnacles were allowed to settle naturally (+mussels, +barnacles). Error bars were omitted for clarity and to show general trends for each species. Each row of panels represents a run that was initiated at a given starting date (April of 1991, 1992, and 1993; 0 *Nucella,* predator exclusion; low *Nucella,* two *Nucella* enclosed; high *Nucella,* six *Nucella* enclosed).

were allowed to settle naturally to (1) illustrate the general similarities and differences in successional patterns between starting dates and (2) facilitate interpretation of subsequent analyses of individual species.

Early species: B. glandula, C. dalli, *and* M. trossulus.—Plots cleared in the spring of 1991 (Run 1; Fig. 4, top row) were rapidly colonized by *B. glandula.* Within the first few months *B. glandula* reached ~80% cover in most plots, regardless of the presence of whelks. In the fall of the first year, *M. trossulus* colonized the tests of *B. glandula* and reached a peak in cover during the first winter. Both *B. glandula* and *M. trossulus* declined by the end of the second year in all plots, regardless of the presence of *Nucella,* although they reached their lowest cover sooner in the presence of *Nucella* (Berlow 1995). Space made available by the decline of *B. glandula* and *M. trossulus* was occupied by *C. dalli* during the second year, and the colonization by *C. dalli* was facilitated by the presence of *Nucella* (see *Results: Consumer-mediated contingent succession*). The total cover of sessile species peaked early and then stabilized at ~45–60% during the second year regardless of the presence of *Nucella,* as *C. dalli* col-

onized newly available space. By the end of the third year the primary cover of all three species (*B. glandula, M. trossulus,* and *C. dalli*) was scarce, apparently due to a combination of factors. In some cases they appeared to be overgrown by later successional species. In other cases, they appeared to be more susceptible to dislodgment by waves than later species. In particular, when individual *B. glandula* died or were smothered by *M. trossulus,* the matrix of barnacles was weakened and clumps of both barnacles and the small mussels living on top of them were dislodged.

In plots cleared in the spring of 1992 (Run 2; Fig. 4, middle row), the initial rapid pulse of *B. glandula* was notably absent. Instead, *C. dalli* colonized first, but more slowly than did *B. glandula* in Run 1. In this experiment, *B. glandula* gradually increased in cover in the absence of predators during the late summer and fall of the first year and peaked during the first winter. *M. trossulus* also reached peak abundance during the first winter, as it had in Run 1. Both *B. glandula* and *M. trossulus* were generally less abundant than in Run 1, and both were scarce or absent in plots with high densities of *Nucella. C. dalli* achieved higher cover for
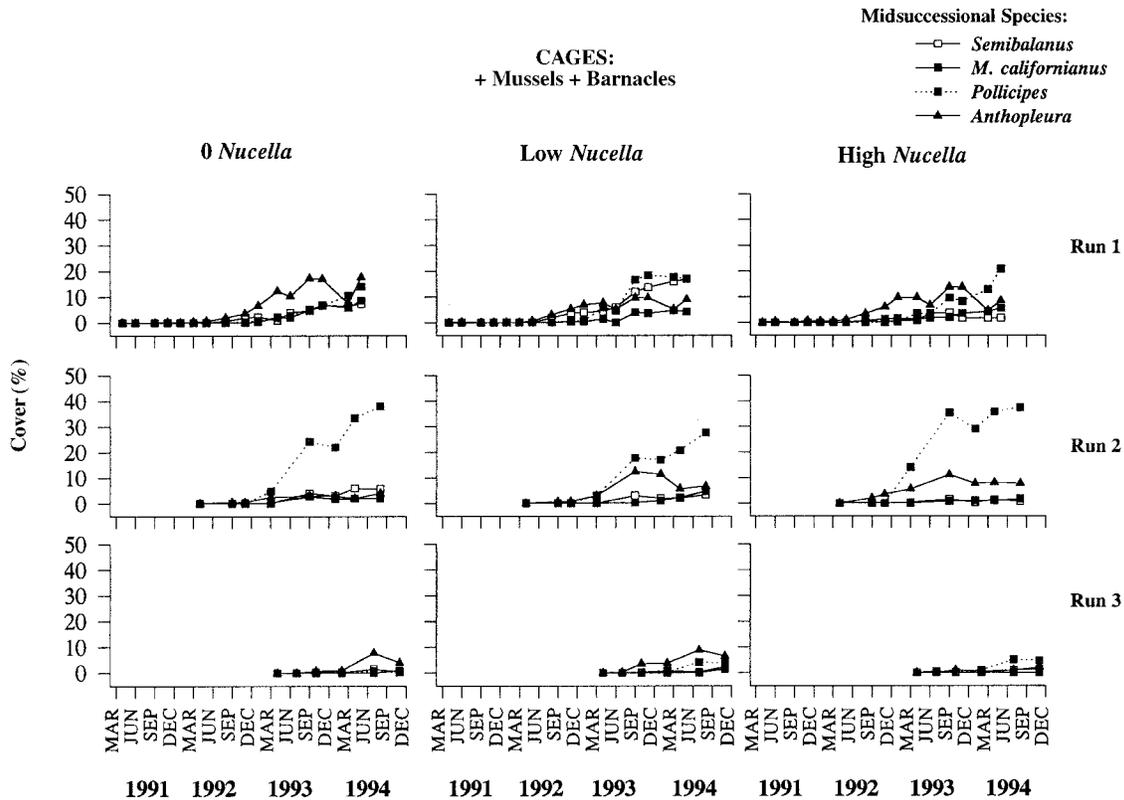
FIG. 5. Mean percent cover of *S. cariosus, M. californianus, Pollicipes,* and *Anthopleura* in cages where both mussels and barnacles were allowed to settle naturally. See caption for Fig. 4.

a longer amount of time when predators were present vs. where they were excluded. Thus, as in Run 1, the total cover of sessile species stabilized at ~60–80% by the second year, regardless of the negative effects of *Nucella* on *B. glandula* and *M. trossulus.* Also, as in Run 1, all three species declined after the second year of succession.

In plots cleared in the spring of 1993 (Run 3; Fig. 4, bottom row), like those in Run 2, *C. dalli* was the first to colonize, and there was no initial rapid colonization of *B. glandula.* In plots with predators, *B. glandula* and *M. trossulus* were scarce or absent, and *C. dalli* was the dominant space occupier. In contrast to Run 1, in predator-exclusion plots, *B. glandula* colonized more slowly and never exceeded 15%. *M. trossulus* also colonized more slowly than in the previous two experiments, but by the fall of the second year was the most abundant sessile species in plots where predators were excluded. As in the previous two runs, the early negative effects of *Nucella* on *M. trossulus* and *B. glandula* did not dramatically affect the total cover of sessile species, as *C. dalli* compensated by increasing in abundance.

To summarize, Run 1 had an intense, early pulse of *B. glandula,* while in Runs 2 and 3, *C. dalli* was the more abundant early colonizer. The effects of *Nucella*

were most dramatic in Runs 2 and 3, when *B. glandula* was generally less abundant than in Run 1. *M. trossulus* generally peaked in cover during the first winter, except in the third experiment, where it did not increase markedly until the following fall. In both experiments that ran longer than two years, all three species eventually declined in cover, regardless of the presence of *Nucella.* In all cases, the total cover generally remained >50% regardless of the presence of *Nucella.*

Midsuccessional species: S. cariosus, M. californianus, Pollicipes, *and* Anthopleura.—By the middle of the second year after plots were cleared, *S. cariosus, M. californianus, Pollicipes,* and *Anthopleura* gradually increased in abundance (Fig. 5). Three of these (*S. cariosus, M. californianus,* and *Pollicipes*) are capable of reaching a size refuge from predation by *Nucella.* The other (*Anthopleura*), is not eaten by *Nucella.* Run 3 was terminated after ~1.5 yr, so the cover of all four species generally remained < 5% (Fig. 5, bottom row). In Run 1, all four species slowly increased in cover, but no single species clearly dominated this stage of succession (Fig. 5, top row). In contrast, *Pollicipes* was conspicuously more abundant in Run 2, while *S. cariosus* and *M. californianus* were rare or absent (Fig. 5, middle row). After three years of succession in Run 1, the mean cover of *M. cali-*
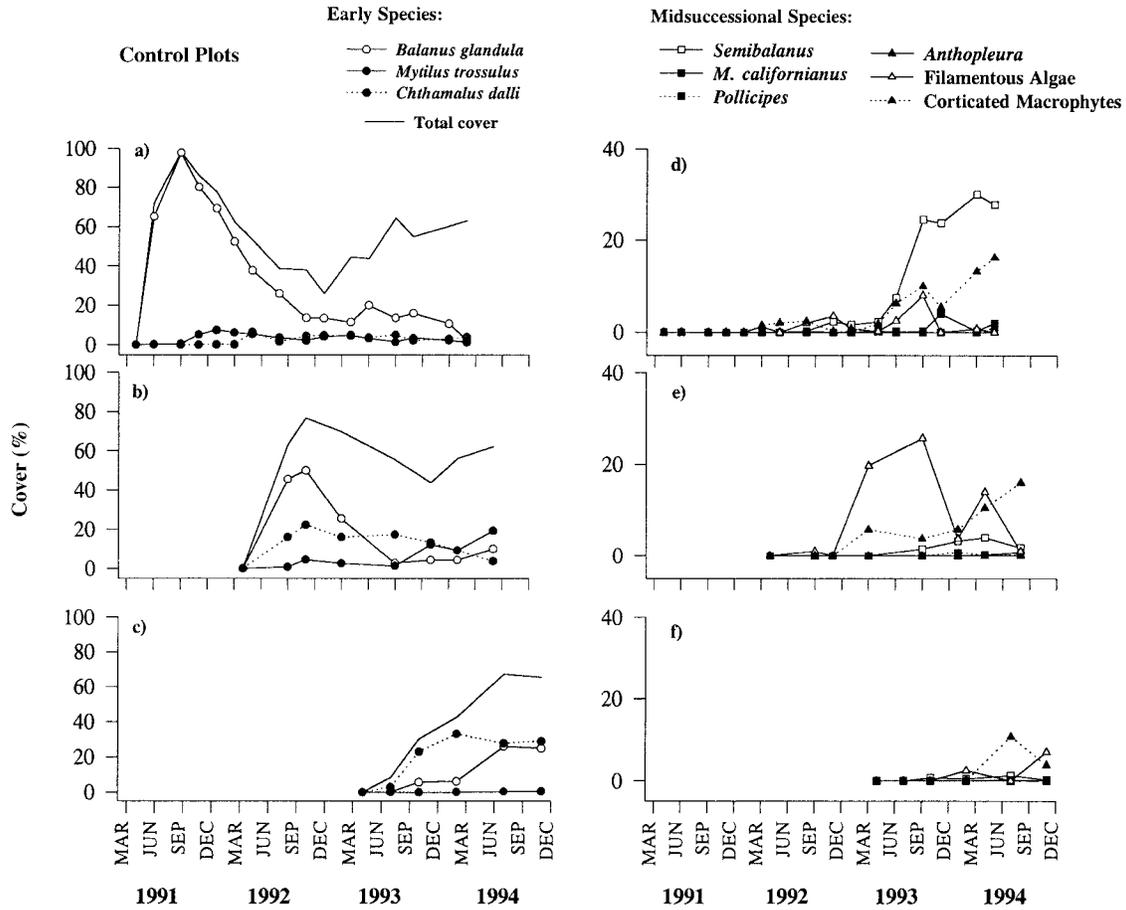
FIG. 6. Parts a–c show mean percent cover of *B. glandula, M. trossulus, C. dalli,* and all macroscopic sessile species (total cover) in control plots cleared at the same time as the caged plots. Parts d–f show mean percent cover of *S. cariosus, M. californianus, Pollicipes, Anthopleura,* filamentous algae, and corticated macrophytes (sensu Steneck and Dethier 1994) in control plots. The top, middle, and bottom rows of panels represent Runs 1, 2, and 3, respectively. See caption for Fig. 4, and see *Results: General successional patterns in control plots* for the definition of algal functional groups.

fornianus remained < 10%, regardless of the presence of *Nucella* (Fig. 5, top row).

General successional patterns in control plots

The control plots (which were scraped but not caged) exhibited some general trends and differences between starting dates that resembled those in the cages (Fig. 6). Run 1 was characterized by an immediate pulse of *B. glandula,* while in Runs 2 and 3 the recruitment of *B. glandula* to newly cleared plots was slower and less intense (Fig. 6a–c). As in the caged plots with *Nucella, C. dalli* was more abundant in Runs 2 and 3 than Run 1 (Figs. 4 and 6a–c). In Run 3, *C. dalli* was the dominant space occupier for the first year of succession, after which *B. glandula* slowly increased in abundance (Fig. 6e). As in the caged plots, both *B. glandula* and *C. dalli* were consistently scarce by the middle of the third year of succession, regardless of their initial abundance (Fig. 6a, b). Similar to caged plots with high densities of *Nucella, M. trossulus* was generally rare

in all control plots (where birds also had access to them) regardless of starting date (Fig. 6a–c). However, in Run 2, *M. trossulus* started to increase in cover at the end of the experiment (Fig. 6b).

In Run 1 controls, like the low-density *Nucella* caged plots initiated at the same time, the decline of *B. glandula* was followed by an increase in the cover of large *S. cariosus* (which are not eaten by birds) during the third year of succession (Figs. 4 and 5: top row, Figs. 6d and 10c). This increase in *S. cariosus* was not observed in Run 2 controls of the same age or at the same point in time (Fig. 6e). *M. californianus* was consistently rare in all control plots during the first 2.5 yr of succession (Fig. 6d–f), and only started to increase slightly in abundance at the end of the third year of Run 1 (Fig. 6d). In contrast to the caged plots, *Pollicipes* and *Anthopleura* rarely colonized any of the control plots (Fig. 6d–f). Also, several macroalgae, mostly filamentous algae (sensu Steneck and Dethier 1994: e.g., *Pterysiphonia* spp., *Plocamium* spp., *Microcladia* spp., *Polysiphonia* spp.), corticated macrophytes (e.g.,
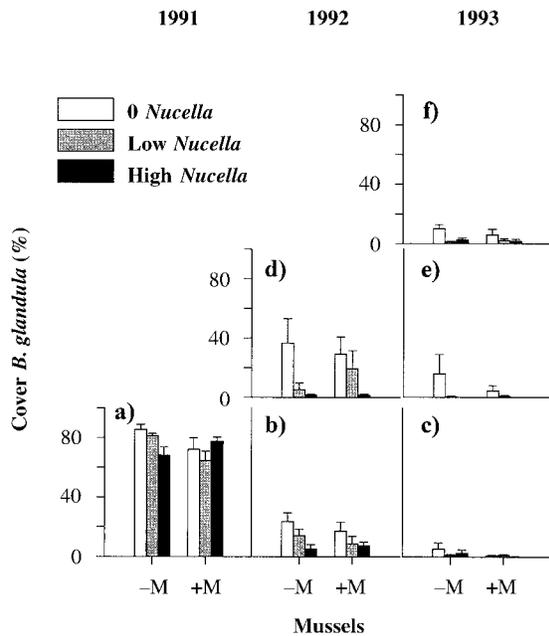
FIG. 7. Cover (mean + 1 SE) of *B. glandula* in the cages averaged over each year for each starting date, or run. The bottom, middle, and top rows of panels represent Runs 1, 2, and 3, respectively. Since all plots were initiated in the spring, 1991, 1992, and 1993 represent the mean from 1991–1992, 1992–1993, and 1993–1994, respectively. −M = mussel recruits removed monthly; +M = mussels allowed to settle naturally. Other codes are the same as in Fig. 4.

FIG. 8. Cover (mean + 1 SE) of *Anthopleura* in the cages averaged over each year for each starting date. −B = barnacle recruits removed monthly; +B = barnacles allowed to settle naturally. Data were pooled across ± mussel treatments. Other codes are the same as in Fig. 7.

Mastocarpus papillatus, Iridea spp. *Endocladia muricata, Cryptosiphonia* spp., and *Odonthalia* spp.), and articulated calcareous algae (e.g., *Corallina vancouveriensis, Bossiella plumosa*), became abundant in controls in the second and third year of succession (Fig. 6d and e), while they were rare in most of the caged plots.

To summarize, succession in the controls was characterized by an initial colonization of *B. glandula* and/or *C. dalli,* with their relative abundances and rates of colonization varying markedly between starting dates. By the end of the second year of succession, both species declined, regardless of the starting date. Subsequent species composition varied with starting date. In Run 1 *B. glandula* was replaced primarily by *S. cariosus* and secondarily by corticated macrophytes (Fig. 6d). In Run 2, *B. glandula* and *C. dalli* were replaced by a pulse of filamentous algae and then a slow increase in corticated macrophytes (Fig. 6e). In most cases, control plots of the same successional age, but different starting dates, varied considerably in species composition (Fig. 6). As observed in mid-intertidal patches in Washington State, high spatial and temporal variability in the specific algal species contributed greatly to the complexity of succession in control plots relative to that in caged plots (Paine and Levin 1981). Thus, the patterns of historic effects for caged plots described below should be interpreted in the context
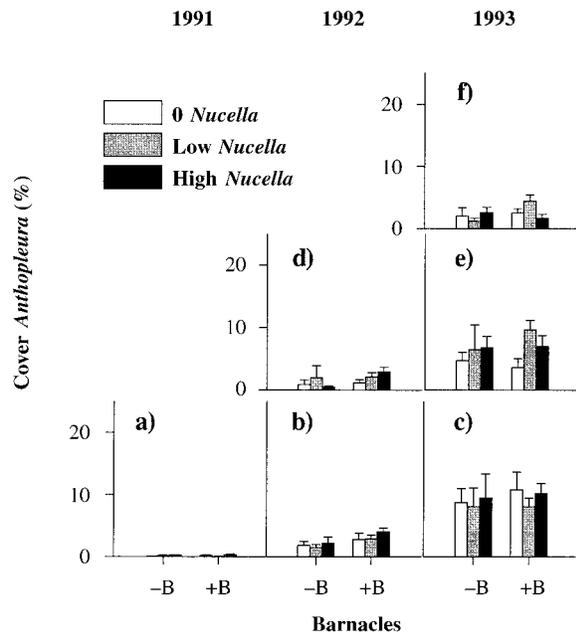
of a "simplified" successional assemblage with very little macroalgae.

Patterns of historical effects

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

Canalized noise: B. glandula *and* Anthopleura.— Both *B. glandula* and *Anthopleura* abundances appeared partially driven by stochastic yearly variation and partially canalized into a repeatable pattern of change with successional age (Figs. 7 and 8). In neither case were stochastic differences between starting dates or years magnified into fundamentally different successional trajectories.

B. glandula consistently colonized early, and consistently declined by the end of the second year (Fig. 7). However, the intensity of initial recruitment varied dramatically between starting dates (Table 1: START is significant; Fig. 7: a vs. d). In Run 1 *B. glandula* rapidly reached close to 100% cover in many plots,

TABLE 1. Randomized block analysis of variance of the first two years of the first two runs (starting dates) (ANOVA 1, Fig. 2) to test for the effects of AGE (experimental duration in years), START (experiment starting date), NUC (*Nucella*), and MUS (mussels) on the cover of *Balanus glandula, Chthamalus dalli,* and *Semibalanus cariosus.*

Source	df	Statistic	*B. glandula*	*C. dalli*	*S. cariosus*
BLOCK	3	MS	0.11	0.12	0.007
		F	3.87	7.41	1.18
		P	**0.01***	**0.0002***	0.33
AGE	1	MS	5.11	0.11	0.40
		F	180.73	6.49	64.25
		P	**0.0001***	**0.01***	**0.0001***
START	1	MS	5.35	3.35	0.07
		F	189.01	202.45	10.85
		P	**0.0001***	**0.0001***	**0.002***
NUC	2	MS	0.5	0.17	0.015
		F	17.74	10.48	2.41
		P	**0.0001***	**0.0001***	0.10
MUS	1	MS	0.02	0.004	0.01
		F	0.68	0.24	1.73
		P	0.41	0.63	0.19
AGE × START	1	MS	1.40	3.30	0.04
		F	49.67	199.58	5.90
		P	**0.0001***	**0.0001***	**0.02**
AGE × NUC	2	MS	0.002	0.01	0.02
		F	0.08	0.89	3.52
		P	0.92	0.41	**0.04**
AGE × MUS	1	MS	0.003	0.005	0.009
		F	0.11	0.33	1.41
		P	0.74	0.57	0.24
START × NUC	2	MS	0.74	0.05	0.003
		F	2.60	2.27	0.56
		P	0.08	0.07	0.57
START × MUS	1	MS	0.02	0.0001	0.005
		F	0.82	0.01	0.82
		P	0.37	0.94	0.37
AGE × START × NUC	2	MS	0.06	0.1	0.06
		F	2.29	6.22	0.95
		P	0.11	**0.003***	0.39
AGE × START × MUS	1	MS	0.24	0.003	0.005
		F	0.83	0.16	0.85
		P	0.36	0.69	0.36
NUC × MUS	2	MS	0.05	0.01	0.002
		F	1.65	0.64	0.27
		P	0.20	0.53	0.76
AGE × NUC × MUS	2	MS	0.001	0.006	0.001
		F	0.03	0.40	0.14
		P	0.97	0.67	0.87
START × NUC × MUS	2	MS	0.6	0.05	0.004
		F	2.21	3.04	0.71
		P	0.12	**0.05**	0.50
AGE × START × NUC × MUS	2	MS	0.01	0.01	0.002
		F	0.43	0.59	0.39
		P	0.65	0.55	0.68
Model	26	MS	0.55	0.32	0.03
		F	19.33	19.28	4.20
		P	**0.0001***	**0.0001***	**0.0001***
Error	66	MS	0.03	0.02	0.006
R^2			0.88	0.88	0.62

Notes: Data are arcsine square-root transformed covers averaged over each year for each experiment. df: degrees of freedom; MS: Type III mean squares; *F*: standard *F* values. Boldface *P* values indicate that the factor is significant at $\alpha = 0.05$. Asterisks indicate that the factor is significant when α is adjusted using a conservative sequential Bonferroni correction (see *Methods: Data analysis*).

TABLE 2. Randomized block analysis of variance of the second two years of Run 1 and the first two years of the Run 2 (ANOVA 2, Fig. 2) to test for the effects of YEAR (census year), START (run starting date), NUC (*Nucella*), and MUS (mussels) on the cover of *Balanus glandula, Chthamalus dalli,* and *Semibalanus cariosus.*

Source	df	Statistic	B. glandula	C. dalli	S. cariosus
BLOCK	3	MS	0.14	0.26	0.02
		F	5.10	14.51	1.26
		P	**0.003***	**0.0001***	0.30
YEAR	1	MS	1.21	0.82	0.71
		F	44.72	46.20	54.46
		P	**0.0001***	**0.0001***	**0.0001***
START	1	MS	0.00001	0.82	0.15
		F	<0.0001	46.11	11.40
		P	0.98	**0.0001***	**0.001***
NUC	2	MS	0.46	0.18	0.09
		F	17.15	9.94	7.26
		P	**0.0001***	**0.0002***	**0.001***
MUS	1	MS	0.015	0.00002	0.06
		F	0.57	<0.001	4.50
		P	0.45	0.97	**0.04**
YEAR × START	1	MS	0.002	0.32	0.0005
		F	0.06	18.09	0.04
		P	0.81	**0.0001***	0.83
YEAR × NUC	2	MS	0.07	0.10	0.04
		F	2.64	5.82	3.28
		P	0.08	**0.005***	**0.04**
YEAR × MUS	1	MS	0.02	0.00003	0.04
		F	0.64	<0.001	3.31
		P	0.43	0.97	0.07
START × NUC	2	MS	0.08	0.03	0.05
		F	3.02	1.84	3.73
		P	**0.05**	0.17	**0.03**
START × MUS	1	MS	0.02	0.006	0.006
		F	0.74	0.34	0.45
		P	0.39	0.56	0.50
YEAR × START × NUC	2	MS	0.001	0.01	0.02
		F	0.04	0.65	1.58
		P	0.97	0.53	0.21
YEAR × START × MUS	1	MS	0.005	0.02	0.003
		F	0.18	1.11	0.20
		P	0.67	0.30	0.66
NUC × MUS	2	MS	0.03	0.006	0.02
		F	1.07	0.36	1.38
		P	0.35	0.70	0.26
YEAR × NUC × MUS	2	MS	0.0001	0.01	0.01
		F	<0.001	0.82	0.75
		P	0.99	0.45	0.47
START × NUC × MUS	2	MS	0.03	0.06	0.01
		F	0.95	3.60	0.76
		P	0.40	**0.03**	0.47
YEAR × START × NUC × MUS	2	MS	0.02	0.001	0.01
		F	0.66	0.06	0.79
		P	0.52	0.94	0.46
Model	26	MS	0.12	0.14	0.06
		F	4.48	8.03	4.76
		P	**0.0001***	**0.0001***	**0.0001***
Error	64	MS	0.03	0.02	0.01
R^2			0.65	0.77	0.66

Note: See Table 1 for details.

while in Run 2, it trickled in more slowly and peaked at ~50% cover (Fig. 7: a vs. d, Fig. 4). Consequently, the decline in cover between Age 1 and Age 2 was more dramatic in Run 1 than Run 2 (Table 1: AGE × START is significant). The initial difference between

starting dates was rapidly dampened so that, by 1992 and 1993, there were no overall differences in *B. glandula* cover between the two experiments in a given year (Table 2: START not significant; Fig. 7: b and c vs. d and e). *B. glandula* in both experiments continued to

decline in 1993 at similar rates, regardless of starting date (Table 2: YEAR is significant, YEAR × START not significant). The patterns of change with age or year were not affected by mussels or by the presence of *Nucella* (Table 1: AGE × NUC, and AGE × MUS not significant). Removing mussels had no overall effect on *B. glandula* in either experiment (Tables 1 and 2: MUS not significant; Fig. 7). Predation by *Nucella* consistently had a negative effect on *B. glandula* cover, but it did not dampen or magnify initial differences between starting dates (Tables 1 and 2: NUC is significant, AGE × START × NUC and YEAR × START × NUC not significant). While the effects of *Nucella* on *B. glandula* were relatively weak in the first year of Run 1 relative to Run 2 (Berlow 1995; Fig. 7: a vs. d), by 1993 the only surviving *B. glandula* were primarily in plots without predators, regardless of starting date (Fig. 7c and e, open bars).

Thus the successional patterns of *B. glandula* were characterized by stochastic differences in initial colonization/recruitment, which were dampened by a relatively canalized decline regardless of the presence of mussels or whelks. The decline of *B. glandula* appeared to be due to a combination of factors: (1) Dense barnacles grew thin and were easily dislodged by waves. (2) Any mortality of individual barnacles either due to predation, overgrowth by other species, or natural mortality appeared to weaken the matrix and make the rest more susceptible to dislodgment. (3) In each successive year, the recruitment of *B. glandula* appeared to be less intense (Fig. 7 a, d, and f).

Anthopleura consistently colonized slowly, but its subsequent abundance at a given age varied consistently between starting dates (Fig. 8: a vs. d, b vs. e; Table 3: AGE and START are significant). The cover of *Anthopleura* showed similar patterns of change with time for both Runs 1 and 2 (Table 3: AGE × START not significant), but the overall cover differed consistently between runs (Table 4: YEAR and START are significant, YEAR × START not significant). Thus, initial differences between starting dates were consistently maintained through time. However, because the cover of *Anthopleura* in the first year of succession was always relatively low, regardless of the starting date, this suggests that variation in *Anthopleura* cover was not entirely driven by stochastic differences between years. For example, the cover of *Anthopleura* was low in the first year of Run 3 relative to Runs 1 and 2 in the same year (Fig. 8c, e, and f). While the effects of *Nucella* on *Anthopleura* were marginally significant in the first two years of succession (Table 3: NUC effect $P = .05$), the cover of *Anthopleura* was generally low, and the differences detected do not appear to be ecologically significant (Fig. 8c and d). This is reflected in the fact that in 1992 and 1993, *Nucella* did not have any significant effects on *Anthopleura* (Table 4: NUC not significant). Similarly, removing barnacles appeared to have a significant effect overall on *Antho-*

pleura (Tables 3 and 4: BAR is significant), but a visual inspection of ± barnacle treatments in Fig. 8 suggests that the effects of barnacles were small in magnitude and probably not ecologically significant. In any case, the temporal patterns of change in *Anthopleura* cover with successional age or year were not influenced by *Nucella* or barnacles (Table 3: AGE × NUC and AGE × BAR not significant; Table 4: YEAR × NUC and YEAR × BAR not significant). Similarly, neither the presence of *Nucella* nor the removal of barnacles played a role in dampening or magnifying stochastic variation between starting dates (Tables 3 and 4: AGE × START × NUC, AGE × START × BAR, YEAR × START × NUC, YEAR × START × BAR not significant). Thus, *Anthopleura* was characterized by a relatively canalized pattern of slow initial colonization with stochastic variation between years influencing its later abundance at a given age regardless of the presence of whelks or barnacles.

Consumer-mediated contingent succession: C. dalli and S. cariosus.—Both *C. dalli* and *S. cariosus* exhibited contingent patterns of succession which were, in turn, influenced by the presence of *Nucella* (Figs. 9 and 10). For *C. dalli,* differences between starting dates resulted in different patterns of change with time (Fig. 9; a–c vs. d–e; Tables 1 and 2: both AGE × START and YEAR × START significant). For example, in 1992, the pulse of *C. dalli* that recruited to newly cleared plots in Run 2 did not equally colonize plots of Run 1 that had been cleared one year earlier (Fig. 9b and d). Thus plots with different starting dates responded differently to the same externally driven event in 1992.

The degree to which the successional trajectory of *C. dalli* was contingent on the starting date appeared to depend on the presence of *Nucella* (Fig. 9b and d; Table 1: AGE × START × NUC is significant). In addition, the effect of *Nucella* varied with the presence of mussels (Table 2: START × NUC × MUS is significant). Thus, in plots without mussels (and where *Nucella* focused its foraging on *B. glandula*), the presence of *Nucella* appeared to magnify differences between starting dates and/or years. For example, in a given census year (1992 or 1993), differences between runs in the cover of *C. dalli* were more pronounced in cages with *Nucella* and without mussels than in cages where *Nucella* were excluded (Fig. 9: b and d, c and e [−M, open bars vs. gray and/or black bars]). This general pattern is corroborated by the results of Run 3: *C. dalli* was more abundant overall in newly cleared plots than in older plots in the same year and the differences were greatest in cages with *Nucella* (Fig. 9: f vs. e, c). Thus, in the presence of *Nucella, C. dalli* was characterized by patterns of succession that were contingent on the starting date (Fig. 9, gray and black bars). Differences between plots at a given point in time could not easily be attributed to age or to simple stochastic variation in recruitment between years. In the absence

TABLE 3.   Randomized block analysis of variance of the first two years of the first two runs (ANOVA 1, Fig. 2) to test for the effects of AGE (experimental duration in years), START (run starting date), NUC (*Nucella*), and BAR (barnacles) on the cover of *Mytilus trossulus, M. californianus, Pollicipes,* and *Anthopleura.*

Source	df	Statistic	*M. trossulus*	*M. californianus*	*Pollicipes*	*Antho-pleura*
BLOCK	3	MS	0.05	0.004	0.08	0.03
		F	3.99	3.67	6.78	7.40
		P	**0.01***	**0.02**	**0.0003***	**0.0001***
AGE	1	MS	0.14	0.04	0.56	0.53
		F	11.16	37.21	44.56	114.01
		P	**0.001***	**0.0001***	**0.0001***	**0.0001***
START	1	MS	0.34	0.006	1.05	0.21
		F	27.51	5.11	83.51	45.03
		P	**0.0001***	**0.03**	**0.0001***	**0.0001***
NUC	2	MS	0.17	0.002	0.01	0.01
		F	14.09	1.54	0.87	3.12
		P	**0.0001***	0.22	0.42	**0.05**
BAR	1	MS	0.45	0.01	0.25	0.03
		F	36.00	11.96	20.35	5.99
		P	**0.0001***	**0.001***	**0.0001***	**0.01***
AGE × START	1	MS	0.03	0.004	3.71	0.001
		F	2.80	3.71	0.41	0.23
		P	0.10	0.06	33.17	0.63
AGE × NUC	2	MS	0.01	0.002	0.001	0.001
		F	0.95	1.62	0.07	0.25
		P	0.39	0.21	0.93	0.78
AGE × BAR	1	MS	0.15	0.011	0.09	0.0001
		F	12.66	9.76	7.26	0.03
		P	**0.0007***	**0.003***	**0.008***	0.87
START × NUC	2	MS	0.03	0.004	0.01	0.007
		F	2.39	3.56	0.86	1.51
		P	0.10	**0.03**	0.43	0.22
START × BAR	1	MS	0.002	0.01	0.23	0.001
		F	0.19	7.66	18.02	0.23
		P	0.67	**0.007***	**0.0001***	0.63
AGE × START × NUC	2	MS	0.01	0.003	0.001	0.0005
		F	1.16	2.71	0.05	0.12
		P	0.32	0.07	0.95	0.89
AGE × START × BAR	1	MS	0.05	0.007	0.07	0.01
		F	3.94	5.92	5.90	2.42
		P	**0.05**	**0.02**	**0.02**	0.12
NUC × BAR	2	MS	0.03	0.006	0.01	0.005
		F	2.28	0.54	0.93	1.19
		P	0.11	0.58	0.40	0.31
AGE × NUC × BAR	2	MS	0.01	0.0005	0.009	0.006
		F	0.84	0.41	0.72	1.36
		P	0.43	0.67	0.49	0.26
START × NUC × BAR	2	MS	0.02	<0.0001	0.02	0.004
		F	1.69	0.01	1.29	0.92
		P	0.19	0.99	0.28	0.40
AGE × START × NUC × BAR	2	MS	0.002	0.0002	0.007	0.005
		F	0.13	0.15	0.61	1.04
		P	0.88	0.86	0.55	0.36
Model	26	MS	0.07	0.005	0.15	0.04
		F	6.05	4.29	12.33	9.07
		P	**0.0001***	**0.0001***	**0.0001***	**0.0001***
Error	66,† 114‡	MS	0.01	0.001	0.01	0.005
R^2			0.70	0.63	0.74	0.67

Note: Data for *Pollicipes* and *Anthopleura* were pooled across ± mussel treatments. See Table 1 for details.

†*Mytilus trossulus* and *M. californianus.*

‡*Pollicipes* and *Anthopleura.*

TABLE 4. Randomized block analysis of variance of the second two years of Run 1 and the first two years of the Run 2 (ANOVA 2, Fig. 2) to test for the effects of YEAR, census year; START, fun starting date; NUC, *Nucella*; and BAR, barnacles on the cover of *Mytilus trossulus, M. californianus, Pollicipes,* and *Anthopleura.*

Source	df	Statistic	M. trossulus	M. cali- fornianus	Pollicipes	Antho- pleura
BLOCK	3	MS	0.06	0.02	0.16	0.03
		F	6.69	5.71	8.15	4.64
		P	**0.0005***	**0.002***	**0.0001***	**0.004***
YEAR	1	MS	0.14	0.16	1.16	0.63
		F	15.22	40.23	60.60	86.32
		P	**0.0002***	**0.0001***	**0.0001***	**0.0001***
START	1	MS	0.0003	0.06	0.35	0.09
		F	0.04	14.54	18.53	12.54
		P	0.85	**0.0003***	**0.0001***	**0.0006***
NUC	2	MS	0.11	0.008	0.005	0.01
		F	12.46	2.10	0.27	1.56
		P	**0.0001***	0.13	0.76	0.21
BAR	1	MS	0.12	0.02	0.60	0.03
		F	13.90	6.00	31.23	4.90
		P	**0.0004***	**0.02***	**0.0001***	**0.03**
YEAR × START	1	MS	0.04	0.01	0.10	0.001
		F	4.09	3.59	5.18	0.16
		P	**0.05**	0.06	**0.02**	0.69
YEAR × NUC	2	MS	0.03	0.004	0.003	0.0001
		F	3.75	0.92	0.14	0.01
		P	**0.03**	0.40	0.87	0.99
YEAR × BAR	1	MS	0.007	0.02	0.30	0.007
		F	0.79	4.15	15.61	0.91
		P	0.38	**0.05**	**0.0001***	0.34
START × NUC	2	MS	0.01	0.01	0.02	0.01
		F	1.53	2.45	0.94	1.38
		P	0.22	0.09	0.39	0.26
START × BAR	1	MS	0.07	0.004	0.04	0.0001
		F	7.06	1.05	2.26	0.02
		P	**0.01**	0.31	0.13	0.90
YEAR × START × NUC	2	MS	0.02	0.001	0.001	0.002
		F	1.91	0.35	0.06	0.34
		P	0.16	0.70	0.95	0.71
YEAR × START × BAR	1	MS	0.007	0.005	0.001	0.0001
		F	0.78	1.18	0.04	0.02
		P	0.38	0.28	0.83	0.89
NUC × BAR	2	MS	0.009	0.005	0.02	0.008
		F	0.98	1.31	1.29	1.10
		P	0.38	0.28	0.28	0.34
YEAR × NUC × BAR	2	MS	0.005	0.002	0.02	0.005
		F	0.50	0.50	0.92	0.66
		P	0.61	0.61	0.40	0.52
START × NUC × BAR	2	MS	0.01	0.003	0.009	0.003
		F	1.19	0.63	0.48	0.40
		P	0.31	0.61	0.62	0.67
YEAR × START × NUC × BAR	2	MS	<0.0001	0.002	0.002	0.005
		F	0.01	0.57	0.10	0.65
		P	0.99	0.57	0.90	0.53
Model	26	MS	0.04	0.02	0.15	0.04
		F	4.11	4.02	7.94	5.37
		P	**0.0001***	**0.0001***	**0.0001***	**0.0001***
Error	64,† 112‡	MS	0.009	0.004	0.02	0.007
R^2			0.63	0.62	0.65	0.55

Note: See Table 3 for details.

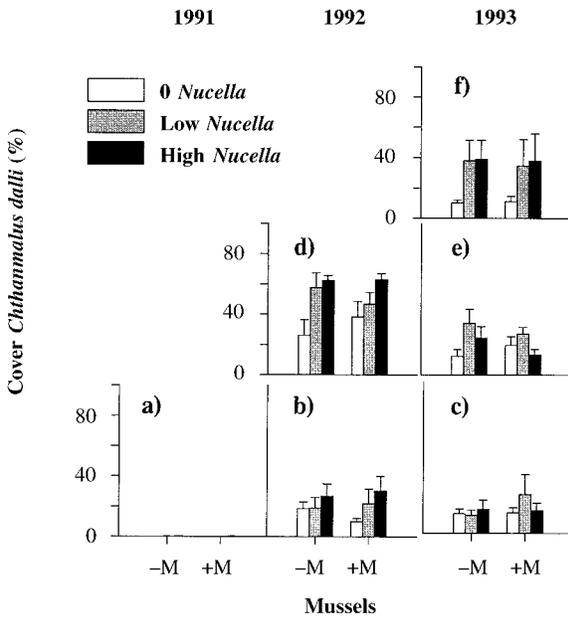†*Mytilus trossulus* and *M. californianus.*

‡*Pollicipes* and *Anthopleura.*

FIG. 9. Cover (mean + 1 SE) of *C. dalli* in the cages averaged over each year for each starting date. Codes are the same as in Fig. 7.

FIG. 10. Cover (mean + 1 SE) of *Semibalanus* in the cages averaged over each year for each starting date. Codes are the same as in Fig. 7.

of *Nucella* (Fig. 9, open bars), *C. dalli* cover was more similar between runs in a given year, and differences between years appeared externally driven (i.e., independent of successional age or the starting date).

S. cariosus exhibited similarly contingent patterns of succession (Fig. 10). Overall, changes during the first two years of succession varied with the starting date (Fig. 10: a and b vs. d and e; Table 1: AGE × START is marginally significant). In Run 2 *S. cariosus* was more abundant by the second year than in Run 1 plots of the same age (Fig. 10: b vs. e). Some of these differences appeared to be driven by natural variation in recruitment between years, independent of starting date or successional age (Fig. 10 e and c; Table 2: YEAR is significant, YEAR × START not significant). For example, 1993 was a relatively "good" year for *S. cariosus* in both Runs 1 and 2 regardless of starting date. However, the degree to which *S. cariosus* cover tracked yearly variation depended on the density of *Nucella* enclosed (Table 2: YEAR × NUC and START × NUC are significant). In particular, low densities of *Nucella* appeared to magnify differences between runs in a given year (Fig. 10c and e: gray bars). Mussels had a significant negative effect on *S. cariosus* by 1993 (Table 2: MUS is significant; Fig. 10 c and e); however, neither the patterns of change with time, nor the way in which they were contingent on *Nucella,* were affected by mussels (Tables 1 and 2: none of the higher order interactions, which include mussels, were significant). Despite the contingent nature of *S. cariosus'* successional trajectory, it consistently was not abundant during the first year of succession (Fig. 10a, d, and f). Thus, despite the fact that *S. cariosus* was abun-
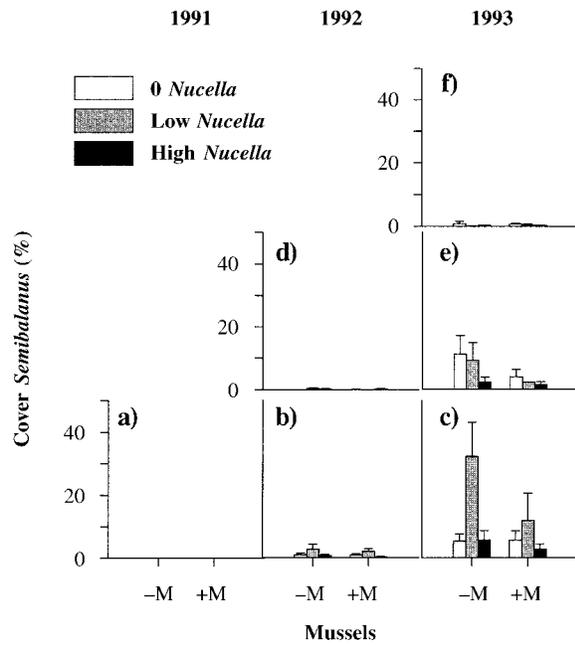
dant in both Runs 1 and 2, it was rare in the recently cleared plots of Run 3. Thus, *S. cariosus* was characterized by a relatively canalized pattern of slow initial colonization, while its later abundance at a given age was influenced by random variation in recruitment between years. The degree to which different starting dates responded differently to the same yearly variation in recruitment depended on the density of *Nucella.*

Facilitation-mediated contingent succession: Pollicipes.—*Pollicipes* exhibited a contingent pattern of succession, which depended on the presence or absence of acorn barnacles (Fig. 11). The cover of *Pollicipes* was consistently low in the absence of acorn barnacles (Fig. 11: −B). Any statistically significant variation in the facilitation effect of barnacles (Tables 3 and 4: AGE × START × BAR is marginally significant, and YEAR × BAR is significant) was probably not ecologically significant and was primarily because, in Run 1, *Pollicipes* was rare in all plots (regardless of barnacles) until 1993 (Fig. 11a and b). When *Pollicipes* did colonize Run 1, they were more abundant in plots with barnacles (Fig. 11c). When *Pollicipes* was present (i.e., in plots with barnacles) changes in the cover of *Pollicipes* with time varied with starting date (Tables 3 and 4: AGE × START and YEAR × START are significant). For example, *Pollicipes* was abundant in Run 2 by the end of the second year of succession (1993), while in Run 1 *Pollicipes* remained rare or less abundant regardless of the age of the plot or the census year (Fig. 11 b and c vs. e). Thus differences in the cover of *Pollicipes* between Runs 1 and 2 could not be attributed simply to age or yearly variation. Different
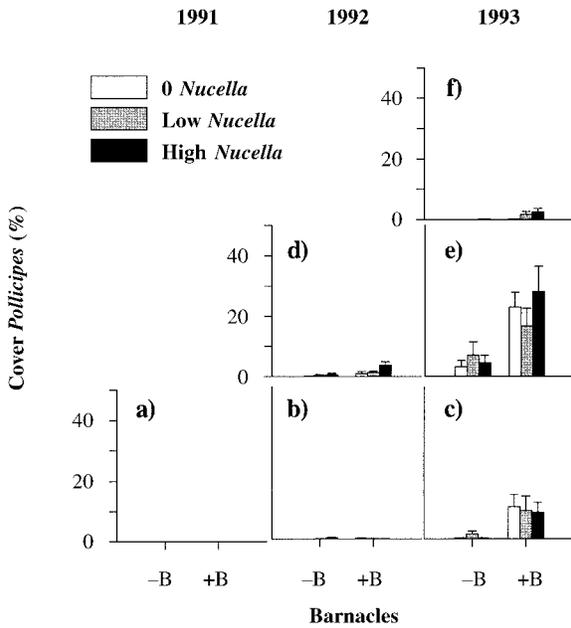
FIG. 11. Cover (mean + 1 SE) of *Pollicipes* in the cages averaged over each year for each starting date. Data were pooled across ± mussel treatments. Codes are the same as in Fig. 7.
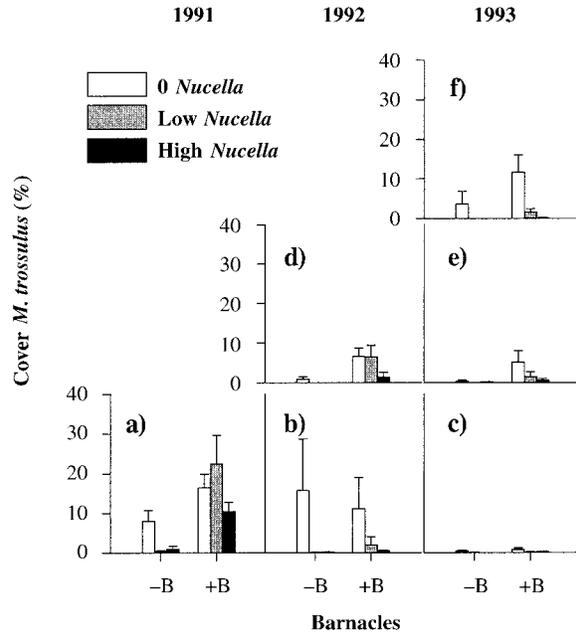

FIG. 12. Cover (mean + 1 SE) of *M. trossulus* in the cages averaged over each year for each starting date. Codes are the same as in Fig. 7.

starting dates respondent differently to the same natural variation between years in *Pollicipes* recruitment. Despite the contingent nature of *Pollicipes'* successional trajectory, it consistently was not abundant during the first year of succession (Fig. 11a, d, and f). While *Pollicipes* was present in both Runs 1 and 2 in 1993, it was rare in the recently cleared plots of Run 3. Thus, *Pollicipes* was characterized by a relatively canalized pattern of slow initial colonization, which was consistently facilitated by barnacles; however, its later abundance at a given age was contingent on the way starting date interacted with stochastic differences between years.

Facilitation-mediated canalized succession: M. trossulus *and* M. californianus.—In contrast to *Pollicipes,* *M. trossulus* and *M. californianus* both exhibited relatively canalized succession in the presence of barnacles. However, where barnacles were removed, their patterns of change with time were both more variable and contingent on the starting date (Figs. 12 and 13).

Barnacles consistently facilitated *M. trossulus* in the first year of succession regardless of starting date (Berlow 1995; Fig. 11a, d, and f). In the presence of barnacles, *M. trossulus* exhibited a relatively canalized pattern of colonization in the first year of succession and subsequent decline in years 2 and 3 (Figs. 4 and 12: a and b [+B] are similar to c and e [+B]; Table 3: AGE × BAR and AGE × START × BAR are significant, Table 4: YEAR × BAR is significant). In the presence of barnacles, initial differences between starting dates in the abundance of *M. trossulus* (Fig. 12a,

d, and f: [+B]) were dampened in the second year by the canalized decline (Fig. 12b and e [+B]) For example, differences between +barnacle treatments in the first year of Runs 1 and 2 (Fig. 12a and d [+B]) were smaller by the second year of succession in both runs (Fig. 12b and e [+B]). In contrast, in the absence of
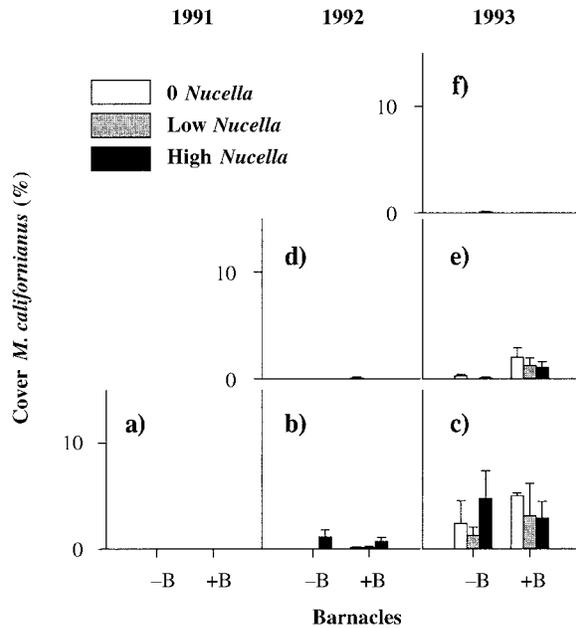

FIG. 13. Cover (mean + 1 SE) of *M. californianus* in the cages averaged over each year for each starting date. Codes are the same as in Fig. 7.

barnacles, differences between starting dates led to different patterns of change with time (Fig. 12: −B; Tables 3 and 4: AGE × START × BAR and YEAR × START are significant; START × BAR is marginally significant). In Run 1, *M. trossulus* successfully colonized plots without barnacles in the first year and increased slightly in mean cover during the second year (Fig. 12a and b [−B]). However, in −barnacle plots that were cleared in 1992, *M. trossulus* remained scarce throughout the experiment (Fig. 12d and e).

While *Nucella* had variable effects on *M. trossulus* in the first year of succession (Berlow 1995, Fig. 12a, d, and f), they consistently hastened the decline of *M. trossulus* in year two regardless of starting date (Table 3: START × NUC, AGE × START × NUC not significant; Fig. 12b and e). Thus, by the second year of succession, *M. trossulus* were rare in any plots with *Nucella,* regardless of starting date (Fig. 12b and e). *Nucella* also consistently eliminated most *M. trossulus* in any plots where barnacles were removed (Fig. 12: all −B treatments). The fact that *M. trossulus* was more abundant in +barnacle plots of Run 3 than in older +barnacle plots during the same year (Fig. 12: e and c vs. f) further suggests that, in the presence of barnacles, variation in *M. trossulus* at a given point in time is at least partly attributable to successional age rather than to random yearly variation in recruitment. Thus, in the presence of barnacles, stochastic differences between starting dates in initial abundances were dampened by a relatively consistent and repeatable pattern of early colonization and subsequent decline. In the absence of barnacles, differences between starting dates were associated with more variable and contingent successional change.

M. californianus cover remained <10% in all experiments (Fig. 13). Therefore, many of the statistically significant effects of different treatments were the result of very small changes in *M. californianus* cover (e.g., from scarce or absent to rare; Fig. 13: especially a, b, d, and e). However, since *M. californianus* is such an important dominant species in this community, some general trends are noteworthy. In the presence of barnacles, *M. californianus* exhibited a relatively canalized pattern of succession, which was characterized by a slow increase, regardless of starting date (Fig. 13a–c, and d–e [+B]). However, in the absence of barnacles, different starting dates were associated with different patterns of change with time. *M. californianus* managed to slowly colonize plots without barnacles that had been initiated in 1991 (Run 1); however, it remained rare or absent in −barnacle plots initiated one year later (Fig. 13b and c vs. e). *Nucella* had no significant effects on the later abundance of *M. californianus,* regardless of the presence of barnacles (Table 4: no NUC effects are significant; Fig. 13c and e). Thus, in the presence of barnacles, variation in *M. californianus* appeared largely attributable to differences in age alone. In the absence of barnacles, differences

between starting dates were associated with more variable and contingent successional change.

DISCUSSION

Despite the fact that this experimental assemblage was simplified by the relative absence of macroalgae, it exhibited complex patterns of historic effects, which varied among species and among different attributes (e.g., timing of colonization, peak abundance, timing of decline) within a given species. As observed in similar systems on the Oregon coast, different mechanisms of succession appeared to be operating at different times with different species (Turner 1983*a, b,* Farrell 1991). The combination of these processes operating simultaneously in the same system suggests that, overall, the entire successional process in this community should be chaotic, magnifying even the smallest stochastic variation in recruitment, disturbance events, environmental conditions, and other variables (Wilson 1992, Ellner and Turchin 1995). However, despite its potential complexity, this system also exhibited some consistent and repeatable patterns of succession. While the results are relatively restricted in spatial and temporal scale, the patterns of contingency and consistency in this assemblage may provide some heuristic insights into some of the factors that act to dampen or magnify stochastic variation during succession:

Noise-dampening forces

Constraints and trade-offs.—Many organismal traits are ultimately based on the allocation of finite resources (Mooney 1972, Tilman 1990). Trade-offs in allocation imply that it is usually difficult for an organism to be a "master of all trades." In the rocky intertidal, where body size often influences competitive ability and susceptibility to predation (Connell 1961*a, b,* Dayton 1971, Paine 1976, 1977, 1981, Wootton 1993*b*), trade-offs between dispersal ability and competitive ability may be important (e.g., Suchanek 1981). Consequently, despite the complexity and variety of successional trends exhibited in this study, the general progression from small-bodied species to large-bodied species was highly consistent with the observations of Wootton (1993*b*) in Washington State. In the present study, this general pattern of species replacement also appeared to be independent of the starting date and independent of variation in exact timing or absolute abundances. These consistencies corroborate the idea that physiological and life history trade-offs may canalize succession by making the range of probable trajectories a small subset of what would otherwise be possible (Connell and Slatyer 1977: tolerance model, Noble and Slatyer 1980, Walker et al. 1986, Huston and Smith 1987, Halpern 1989, Tilman 1990, reviewed in McCook 1994). Consequently, some have suggested that, where trade-offs between dispersal and competition are important, anthropogenic disturbances will cause widespread and predictable extinctions of good competitors,
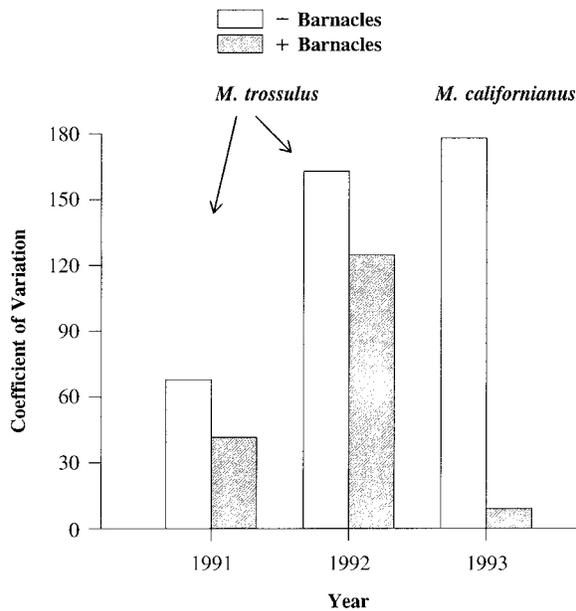
FIG. 14. Coefficient of variation for the cover of *M. trossulus* in years 1 and 2 (1991 and 1992) and *M. californianus* in year 3 (1993) of Run 1 (starting date: April 1991) in predator-exclusion cages. *M. californianus* was not abundant in 1991 or 1992. *M. trossulus* was not abundant in 1993 (see Figs. 12 and 13). −Barnacles, barnacle recruits removed monthly; +Barnacles, barnacles allowed to settle naturally.

regardless of the specific species or system involved (Tilman et al. 1994).

Direct species interactions, which dampen environmental variation.—

1. *Facilitation.—*In the absence of predation, barnacles consistently facilitated the recruitment of *M. trossulus* and *M. californianus* (Figs. 11 and 12: white bars). The presence of barnacles appeared to dampen variation between years and starting dates by possibly providing a more reliable settlement substrate (Fig. 12 a vs. d, b vs. e, b vs. d; Fig. 13 c vs. e; Suchanek 1986). In Run 1 (the only one where mussels successfully colonized −barnacle plots), the presence of barnacles reduced the spatial variation in mussel cover between individual replicates (Fig. 14). Within individual +barnacle plots, mussel recruits were also relatively homogeneously scattered among the barnacles within a given plot. Where barnacles were removed, however, mussel recruitment was more patchy and depended on the local substrate. In some plots a few mussels successfully recruited to small crevices in the rock surface, and once established, more new mussels recruited among their byssal threads (Paine and Levin 1981, Suchanek 1986). In other replicates of the same treatment where the substrate was smoother, no mussels ever colonized bare rock (Fig. 12b, −B, open bar: note large error bar). Thus, in the absence of barnacles, mussel colonization appeared to be an "all or none" phenomenon, depending on the local patterns of substrate rugosity. This pattern of variability between −barnacle replicates is consistent with the idea that pos-

itive-feedback switches (sensu Wilson and Agnew 1992) can make succession variable and contingent. In the presence of barnacles, however, detailed information about small-scale variation in microhabitats and how it interacts with mussel settlement preference was not important to understand or predict patterns of mussel colonization.

2. *Competition.—*While not explored in the present study, it has been demonstrated elsewhere that *M. californianus* is a strong competitive dominant in this system (Harger 1972, Paine 1974, Paine and Levin 1981, Suchanek 1986). This strong effect ultimately canalizes the endpoint of succession, regardless of the complex and conditional dynamics of the early and midsuccessional stages. Stochastic variation among patches in early events (e.g., predation by whelks or birds, variable pulses of recruitment, physical disturbances, and other events) may alter the transient dynamics of succession, but not the endpoint (e.g., Wootton 1993*b*). The eventual dominance of *M. californianus* is consistent enough that the general dynamics of patch creation and disappearance have been successfully modeled independent of within-patch composition (Paine and Levin 1981).

3. *Predation.—*In this study, high densities of *Nucella* tended to dampen the effects of starting date or census year on the abundance of both *M. trossulus* and large *S. cariosus*. In the first year of succession, high whelk densities also consistently dampened spatial variation between individual replicates *within* a given run in the abundance of *M. trossulus* and *B. glandula* (Berlow 1995). Predation should be more likely to dampen stochastic spatial or temporal variation in a prey species if their effects remain strong across a wide range of prey densities (see *Discussion*: *Predator saturation*). For example, predation by the sea star, *Pisaster,* at wave-exposed headlands can consistently exclude adult mussels from the low intertidal zone for long periods of time and across many wave-exposed headlands regardless of environmental factors, which generate temporal and/or geographic variation in mussel recruitment (Paine 1974, Menge et al. 1994, Robles et al. 1995). Similar effects have been observed in freshwater communities, where strong predation by fish and salamanders eliminated the importance of initial conditions (Morin 1984, 1995). In these situations, information about factors that regulate the timing and intensity of recruitment events may not be essential for predicting spatial or temporal patterns of prey abundance.

*Diversity.—*While I did not explicitly manipulate individual barnacle species or the diversity of barnacle species, the results of the present study are consistent with other evidence that species diversity within a functional group can be a noise-dampening factor (Walker 1991, 1995, Tilman and Downing 1994, Chapin et al. 1995*a*, Holling et al. 1995). For example, while *Nucella* had a negative effect on *B. glandula* (Fig. 7), it had no

significant effects on midsuccessional species that were facilitated by the presence of barnacles (e.g., *M. californianus* and *Pollicipes*) (Figs. 11 and 13). This pattern may have been because reductions in *B. glandula* were associated with concomitant increases in *C. dalli* (Fig. 4). Consequently, early in succession, when barnacles were the most abundant sessile species, total cover generally remained >40–50% regardless of predator density (Fig. 4). Thus, variability in barnacle cover induced by whelks could have been dampened by the compensatory response of *C. dalli*. Similar dampening effects due to compensatory responses appear to be common in some freshwater (Frost et al. 1995) and arctic (Chapin et al. 1995*a*) ecosystems. In mid-intertidal patches, this meant that the general patterns of recruitment of midsuccessional species could be understood without a detailed knowledge of variability in the timing and intensity of predation by whelks on individual barnacle species.

Noise-amplifying forces

Variable indirect effects.—Indirect interactions between species occur when the effect of one species on another depends on the presence of a third species. Consequently, they can make both the magnitude and sign (or direction) of a biotic interaction highly sensitive to the context in which it occurs (Levine 1976, Holt, 1977, 1984, Wootton 1994*a, b*, Menge 1995). In this study, the facilitation of *C. dalli* by whelks was probably an indirect effect of whelks consuming *B. glandula* (Dayton 1971, Paine 1981, Farrell 1991). Variation in the magnitude of indirect facilitation by whelks magnified differences between starting dates in the abundance of *C. dalli* (Fig. 9b and d). Consequently, at a given point in time, predicting *C. dalli* abundance in a particular patch required information about prior interactions between *Nucella* and *B. glandula* that influenced the amount and timing of available space (See *Discussion: Predator saturation*).

Predator saturation, or prey swamp escapes.—If a predator is not capable of eliminating a prey species throughout the natural range of variation in prey densities encountered, random variation in the supply of prey can drive variation in the effects of predation (e.g., Fairweather 1988, Underwood and Fairweather 1989). In the present study, the intensity of initial colonization of *B. glandula* varied dramatically between starting dates (Figs. 4 and 7a, d, and f). While *Nucella* consistently had a negative effect in all three experiments, *B. glandula* was so abundant in the first year of Run 1 that the proportional effect of predation was relatively weak (e.g., *B. glandula* maintained >70% cover in cages with *Nucella*; Fig. 7a). Variation between starting dates in the proportional reduction of *B. glandula* cover may have been responsible for the observed variation between starting dates in the indirect positive effect of *Nucella* on *C. dalli* (Fig. 9a and d; Dayton 1971, Paine 1981, Farrell 1991). Recruitment data from a neigh-

boring site (Boiler Bay), and observations at Fogarty Creek, suggest that *C. dalli* could have potentially colonized plots in the summer of 1991 if space had been available (B. A. Menge, *unpublished data*). If predation by *Nucella* were strong enough to rapidly eliminate *B. glandula* even in years where they formed a dense monoculture, the patterns of *C. dalli* colonization probably would have been more consistent between starting dates and/or years. Thus, predicting variation in the effect of *Nucella* on *C. dalli* would require an additional understanding of the functional response of *Nucella* and its relation to the expected range of variation in *B. glandula* recruitment.

Size escapes.—When prey species are capable of attaining a size refuge from predation, spatial and/or temporal variation in predation intensity can have relatively long-lasting effects on community structure (Connell 1971, Paine 1976, 1977, Lubchenco 1983, Sebens and Lewis 1985, Farrell 1988, Navarrete 1996). For example, on San Juan Island, some beds of large, adult *S. cariosus*, which characterize the mid-intertidal landscape, have been attributed to a single winter freezing event that reduced the density of *Nucella* 10 years earlier (Sebens and Lewis 1985). In the present study, low densities of *Nucella* appeared to magnify differences between starting dates in the cover of *S. cariosus* (Fig. 10c and e, gray bars). High densities of *Nucella* apparently were more consistently successful at preventing *S. cariosus* from reaching a size refuge from predation, regardless of the year or starting date. Thus, predicting the current abundance of adult *S. cariosus* in a given locality would require an understanding, not only of local *S. cariosus* recruitment intensity, but also of past patterns of spatial variation in *Nucella* density.

Conclusions

The results of this and other studies point to some important gaps in our knowledge about factors that determine the patterns and prevalence of noise-amplifying and noise-dampening forces in natural communities: (1) Although physiological constraints and trade-offs have the *potential* to canalize some successional trends, key questions remain about the general patterns of trade-offs among different systems and about the conditions that regulate their relative importance. (2) As seen in this study, biotic interactions have the potential to *both* simplify and complicate community responses to a disturbance; thus, a critical challenge for ecologists is to develop a reliable framework for anticipating the types of systems, conditions, or species traits that make biotic interactions more likely to be ''robust'' or ''chaos-prone.'' (3) Similarly, species diversity can both simplify successional patterns (e.g., due to buffering responses of functionally similar species; Chapin et al. 1995*b*) and complicate them (e.g., by increasing the number of nonlinearities and feedback loops; May 1973). Thus, it is increasingly important to understand not *if* diversity can dampen en-

vironmental variation, but *when* it is most likely to do so (e.g., Tilman 1996). Understanding the causes of consistency or contingency in succession will be critical for our ability to manage variability in landscapes that are increasingly dominated by anthropogenic disturbance regimes.

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