Mechanisms of successional dynamics: Consumers and the rise and fall of species dominance

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Insight into potential mechanisms of succession following disturbance to an ecological community can be gained by considering processes that contribute to the rise (colonization, interactions with established species) and demise (differential mortality) of specific stages within the successional sequence. Most successional theories focus on the rise to dominance, assuming demise is the result of competition, but other factors can cause differential mortality among species, including physical disturbance, senescence, and consumers. In rocky intertidal communities on the coast of Washington state, USA, gaps in mussel beds exhibit a succession from predator-susceptible to predator-resistant species following disturbance, suggesting that differential consumption by mobile species may play an important role in the demise of early succession species and the eventual dominance of the mussel *Mytilus californianus*. Experimental manipulation of a dominant species earlier in succession, the blue mussel *Mytilus trossulus,* demonstrated that this species inhibits the invasion of *M. californianus* in the absence of predators. Experimental manipulation of predatory snails (*Nucella emarginata* and *Nucella canaliculata*), which feed heavily on *M. trossulus* but not *M. californianus*, greatly increased the rate at which *M. californianus* invaded gaps. These results and those of other studies indicate that consumers frequently have important effects on the dynamics of succession in benthic marine systems, and might also play a role in other settings.

Key words: competition; indirect effects; inhibition succession; intertidal communities; *Mytilus*; *Nucella*.

INTRODUCTION

Although succession has been studied by ecologists for nearly a century (Warming 1883; Cowles 1899; 1901), critical experimental tests of theories of succession are scarce. Such tests are difficult because of the long time scales required. Like terrestrial communities, intertidal communities are often dominated by sessile organisms that provide physical structure and undergo periodic disturbance, followed by succession. Hypotheses of successional mechanisms can be tested rigorously in rocky intertidal communities because they exhibit relatively rapid dynamics, and are amenable to experimentation (e.g. Connell 1961; Paine 1966,

1977; Dayton 1971; Lubchenco & Menge 1978; Sousa 1979a, 1979b, 1984; Lubchenco 1983; Turner 1983; Farrell 1991; Wootton 1993). The present paper presents a general framework in which hypotheses of succession mechanisms can be placed. It then elaborates on one conclusion that falls out of this framework: that associated mobile species, particularly consumers, may be important to many successional situations. Finally, it reports results from a series of experiments in a Washington state intertidal community testing this hypothesis.

Mechanisms of succession

Succession is usually described as a series of distinct (the choice being somewhat arbitrary) assemblages of dominant species over time (often termed stages or seres), where dominance is generally related to the relative amount of biomass present. When
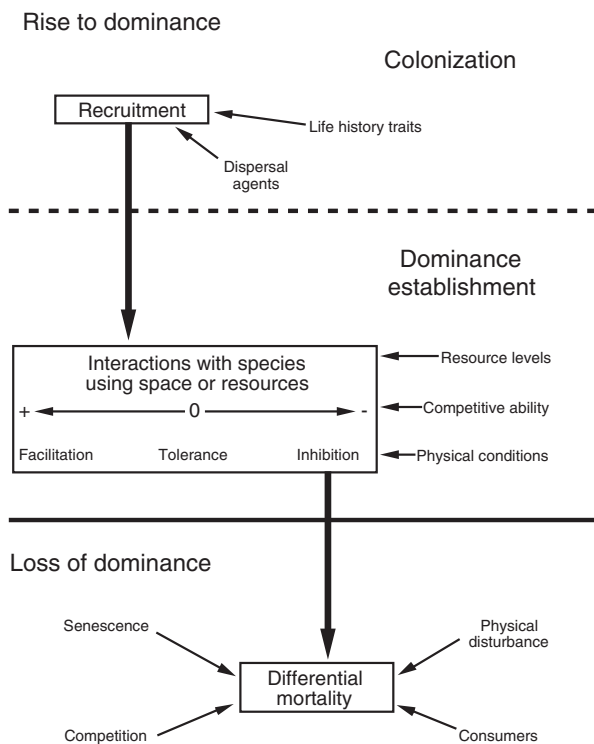
Rise to dominance

Colonization

Fig. 1. Potential mechanisms in the rise to, and fall from, dominance in a given stage of ecological succession.

examining possible causes of succession it is helpful to investigate what mechanisms might be important in determining the existence of any given stage (Fig. 1, Wootton 1990; Farrell 1991). Each stage in a successional sequence can be divided into two fundamental processes: the rise to dominance, and the demise of dominance. The rise of dominance can again be divided into two subprocesses, which parallel the two fundamental processes identified in the invasion of exotic species to new habitats (Elton 1958). First, colonization of the area by members of a stage must occur, which is influenced by dispersal ability and the relative density of a species in surrounding areas. Second, once present, members of a stage must interact with any previously established species and the abiotic environment to become established. Mechanisms of succession, then, should relate to the rise and fall in dominance of a stage, and may vary both among different successional stages within a given community, as well as among different communities.

Within this 'rise and fall' scheme, most succession hypotheses have tended to focus primarily on the rise to dominance. The first hypothesis of successional mechanisms to gain prominence (Clements 1916) suggested that early species altered the environment, making it more favorable for later species but less favorable for established species. This view was countered by Gleason (1917, 1927) who maintained that species dynamics were independent of each other. Succession would occur as differences in longevity among species manifested themselves. Later workers noted that differences in the time that species invaded an area could also play a role in the temporal pattern of species replacement (Keever 1950; Egler 1954; Drury & Nisbet 1973), thus life history differences (both dispersal and longevity) could partly determine the observed patterns. Additionally, Keever (1950) and Egler (1954) noted that early species might inhibit the invasion of later-arriving species. Connell and Slatyer (1977) synthesized these views, grouping successional mechanisms into three basic models contrasted by the manner in which species in early stages of succession interact with species of later stages. Early species can promote the establishment of later species (facilitation model), have no effect on the establishment of later species (tolerance model), or reduce the establishment of later species (inhibition model). In the recent models of Tilman (1985), species alter the nutrient environment sufficiently that other species become favored in competition. Huston and Smith (1987) provide a different approach to modeling succession, concentrating on successional patterns produced by differences in competitive ability and life history at the level of the individual, rather than the species.

In the context of the two-step process described above (Fig. 1), these hypotheses of successional mechanisms address the rise to dominance. In contrast, alternative mechanisms causing the demise from dominance of a given stage have been largely ignored (but see Connell & Slatyer 1977); competition (either interspecific or intraspecific) has been assumed to be the cause of the decline of early stage species, perhaps because succession has been viewed primarily with an eye towards plants or sessile invertebrates, the structurally important, space-occupying organisms (Connell & Slatyer 1977). Recently, attention has been paid to the importance of a variety of factors that inflict mortality on the members of early stages of succession

(Connell & Slatyer 1977; Lubchenco & Menge 1978; Sousa 1979b; Lubchenco 1983; Bryant & Chapin 1986; Pickett *et al*. 1987; Wootton 1990, 1993; Farrell 1991). The demise of dominance is fundamentally related to mortality processes, and many factors in addition to competition can cause mortality (Fig. 1), including senescence, physical disturbance (e.g. fire, wind, drought, waves, extreme temperature), and consumers (i.e. disease, parasites, predators and herbivores). Any source of mortality that acts differentially on species can play an important role in succession by promoting the decline of early stage species while permitting later stage species to thrive.

Consumers are an extrinsic mortality factor likely to affect succession by causing the differential demise of species. Consumers have long been considered important in successional habitats as agents that stop succession (Tansley & Adamson 1925; reviewed in Edwards & Gillman 1987; Davidson 1993), but only recently have been suggested as agents of successional change (Connell & Slatyer 1977; Sousa 1979b; Lubchenco 1983; Bryant & Chapin 1986; Pickett *et al*. 1987; Farrell 1991; Wootton 1993). Although certain consumers may generalize to some extent, no consumer species can feed on all possible prey types with equal effectiveness, thus consumers will differentially affect species within the community. Furthermore, consumer pressure is often not temporally or spatially uniform, and its effects are frequently not independent of successional stage. Whereas prey species can exist without their consumers, consumers cannot exist in a gap for long if their prey are absent. Thus, the establishment of consumers in a gap undergoing succession will often lag behind prey species (cf. Huffaker 1958; Kareiva 1987; Holt 1996). Additionally, foraging theory predicts, and empiric studies generally find, that consumers prefer patches of high prey density (MacArthur & Pianka 1966; Charnov 1976; reviewed in Krebs *et al*. 1983; Stephens & Krebs 1986; Schoener 1987), so gaps may be ignored by consumers until some degree of dominance by their prey is attained. Because consumers will generally lag behind the rise of prey populations, a key feature of successional sequences may be an initial period of escape from consumers followed by more intense consumer pressure that leads to the demise of the prey.

Study system: Succession in intertidal mussel beds

The pattern of intertidal succession on the rocky shores of the Olympic Peninsula has been well described (Suchanek 1979; Paine & Levin 1981; Johnson 1989; J. T. Wootton, unpubl. data, 1984–2001). Above the effective feeding range of the sea star *Pisaster ochraceus*, the middle intertidal community of wave-exposed, rocky shores in Washington state is generally characterized by a band of the California mussel (*Mytilus californianus*), as are many other sites along the west coast of North America (Shelford *et al*. 1935; Paine 1974; Sousa 1984; Ricketts *et al*. 1985). Winter waves and occasional floating logs clear gaps in the mussel bed, providing bare space for other organisms to colonize and persist within the community (Dayton 1971; Paine & Levin 1981). Gaps are generally colonized by diatoms, and then undergo a succession from ephemeral algae such as *Ulva* and *Porphyra*, to perennial algae (particularly *Halosaccion glandiforme*, *Mastocarpus papillata*, and *Endocladia muricata*), to acorn barnacles (*Balanus glandula* and *Semibalanus cariosus*), to blue mussels (*Mytilus trossulus*, formerly considered *Mytilus edulis*, McDonald & Koehn 1988) and goose barnacles (*Pollicipes polymerus*), until the dominance of California mussels is restored (Fig. 2, Paine & Levin 1981). The successional sequence generally takes about 5 years at wave-exposed sites, longer in more sheltered sites (Paine & Levin 1981; J. T. Wootton, pers. obs., 1984–2001).

The mechanism behind succession in this system has been assumed to be competition for space, leading to more competitively dominant species as succession proceeds (Paine & Levin 1981). In competition for space, large size has been considered to confer a competitive advantage (the 'might is right' hypothesis; Paine 1977; Wootton 1993), in part because of asymmetry in the ease of overgrowth, and because large individuals capture resources such as light or plankton first as it impinges from above. Thus, large acorn barnacles species are superior to smaller acorn barnacle species, and adult *M. californianus* are superior to smaller adult *M. trossulus* in competition for space (Connell 1961; Dayton 1971; Harger 1972); likewise, taller plants shade out shorter plants (Harper 1977; Grace 1987). The successional sequence in
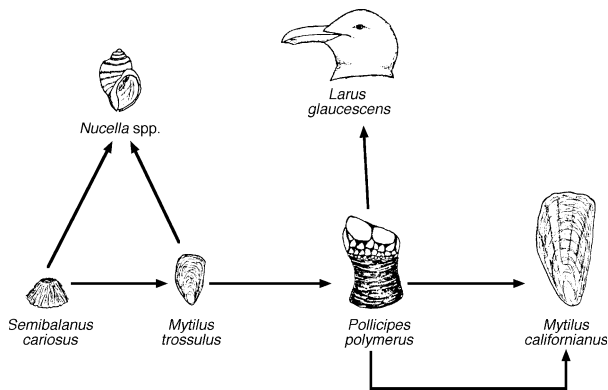
Fig. 2. General pattern of dominance (horizontal arrows) during late succession in gaps within the mussel (*Mytilus californianus*) beds of Washington state intertidal communities (after Paine & Levin 1981). Important predator species (vertical arrows) are also included. As succession proceeds, species with smaller adult body size are replaced by larger species, and predator-susceptible species are replaced by predator-resistant species.

the mussel bed appears at first glance to follow this pattern, as succession proceeds from species with small to large adult body size. Upon further inspection of the system dynamics, however, one uncovers some problems with the idea of a purely competition-driven process. In particular, species which eventually dominate later stages of succession, notably *M. californianus*, often recruit to gaps later in the successional sequence than do earlier stage species such as *M. trossulus* and *Pollicipes* (Paine 1974; Petraitis 1977; Suchanek 1978, 1979; Paine & Levin 1981; Petersen 1984). Therefore, earlier stage species have the opportunity to become established and reach adult size. Consequently, small *M. californianus* spat must compete with individuals of other species larger by an order of magnitude or more (Petraitis 1977; Wootton 1993). If size determines competitive success (Wootton 1993), then succession should not proceed to *M. californianus*.

Considering the pattern of predation during succession suggests an alternative mechanism. Early species in the successional sequence are all consumed by associated mobile members of the community. Limpets (*Lottia* spp.) and chitons (*Katharina tunicata*, *Mopalia* spp.) consume diatoms and macroalgae (Dayton 1971; Nicotri 1974; Suchanek 1979; Johnson 1989; Wootton et

al. 1996; Kim 1997); three species of dogwhelks (*Nucella canaliculata*, *Nucella emarginata*, and *Nucella lamellosa*) consume acorn barnacles and *M. trossulus* (Dayton 1971; Palmer 1980; Navarrete 1996; Navarrete & Menge 1996; Noda 1999); and glaucous-winged gulls (*Larus glaucescens*) consume *Pollicipes* (Wootton 1992, 1993, 1997; Meese 1993). In contrast, *M. californianus* appears largely resistant to predation from all predators but the sea star *Pisaster ochraceus* (Dayton 1971; Paine & Levin 1981; Palmer 1983; Wootton 1997). Thus, in the middle intertidal zone above the effective feeding range of *Pisaster*, *M. californianus* is relatively free from predation. Therefore, mussel bed succession proceeds from predator-susceptible to predator-resistant species. If late-stage species are inhibited by earlier stage species, as the temporal size patterns might suggest, then predators and herbivores may push succession to its conclusion.

To gain a clearer understanding of the role of predators in mussel bed succession, I conducted experiments testing possible mechanisms during the transition from *M. trossulus*- to *M. californianus*-dominated gaps in this intertidal successional sequence. Elsewhere, I have considered the effects of body size and predation on *Pollicipes* on the successional sequence (Wootton 1992, 1993, 1994).

METHODS

Experiments were conducted on Tatoosh Island, located 0.5 km off the north-west tip of the Olympic Peninsula in Washington state, USA. Tatoosh receives extremely heavy wave wash because of the deep surrounding waters and its exposure to large expanses of open water in all directions but the south-east. More detailed descriptions of the island can be found in Dayton (1971, 1975), Paine (1974, 1988), Paine and Levin (1981), and Leigh *et al.* (1987). The experiments were carried out on the more wave-exposed areas of the island where the mussel bed was best developed and where previous studies describing the pattern of mussel bed succession had been carried out. Specific sites included Simon's Landing and the south side of Strawberry Island (see Paine & Levin 1981; Paine 1988 for locations). *Nucella* density on Tatoosh averages 147 ± 100 snails m^{-2} ($n = 9$) in gaps dominated by *M. trossulus*.

To determine the effect of *M. trossulus* on *M. californianus*, experimental manipulations of *M. trossulus* were carried out in the absence of predators. Pairs of 29 × 34 cm plots were established in each of seven gaps dominated by *M. trossulus*. One plot of each pair was randomly assigned as a control, while the other plot was designated the *M. trossulus* removal treatment. Individual *M. trossulus* in the manipulated treatment were carefully removed by hand with a pocket knife to insure that all other species were left undisturbed. Over the duration of the experiment, new *M. trossulus* that appeared in the experimental plots were removed. Because *M. californianus* and *M. trossulus* are indistinguishable in the field at small sizes (< 5 mm), any mussels that could not be definitively identified as *M. trossulus* were allowed to remain in the plots until they grew large enough to be identified. Because the goal of the experiment was to determine the effects of *M. trossulus* on *M. californianus* in the absence of predators, all individuals of *Nucella* were removed from both the experimental and control plots by hand at 2-week intervals throughout the experiment. The experiment ran from 28 May 1998 to 24 August 1998, and the percent area covered by *M. californianus* and *M. trossulus* was censused with a quadrat divided into 100 squares at the beginning and end of the experiment. I analyzed percent cover rather than population size because this measure more accurately reflects community dominance for species with indeterminate growth. Data were log-transformed prior to analysis to meet statistical assumptions, and were analyzed using a paired *t*-test comparing control plots with *M. trossulus* removal plots at each site.

To assess the effects of *Nucella* and bird predation on succession, a second experiment was carried out manipulating snails in portions of five large (> 1 m²) gaps in the mussel bed dominated by *M. trossulus*. Adjacent areas in the same gap served as controls. All *Nucella* were removed by hand or with tweezers from the removal plots at 2-week intervals throughout the experiment. To reduce snail immigration, each *Nucella* removal plot was encircled by a fence of 4 mm plastic mesh (6 cm high) cemented to the rock. Because gulls and American black oystercatchers (*Haematopus bachmani*) will feed on *M. trossulus* (Hartwick 1976; Hartwick & Blaylock 1979; Irons *et al.* 1986;

Marsh 1986; Wootton 1997), *Nucella* removal treatments were crossed with treatments excluding birds using large-mesh, vinyl-coated wire cages (29 × 34 × 7.5 cm in dimension, 4 × 2.5 cm mesh tops, 7.5 × 2.5 cm mesh on the sides) constructed from office letter baskets which were strapped to the rocks with vinyl-coated copper wire attached by eyescrews (see Wootton 1992, 1993, 1994 for details of the method). Consequently, the experiment had four treatment combinations: (i) unmanipulated controls (birds and *Nucella* present); (ii) birds present with *Nucella* removed; (iii) *Nucella* present with birds removed; and (iv) birds and *Nucella* absent. The *Nucella* removal experiment was initiated in June 1986 and terminated 4 months later when heavy winter surf prevented maintenance of *Nucella*-free treatments. Plots in the experiments were censused for percent cover with a quadrat divided into 100 squares at the beginning and end of the experiment. *Mytilus* cover data were log-transformed to meet linearity, homoscedasticity, and normality assumptions prior to analyses. The experiment was analyzed with a blocked two-way ANOVA to test for overall treatment effects for each sampling date. I also applied ANCOVA with *M. trossulus* cover as a covariate to the *M. californianus* data to further examine the possible indirect effects of *M. trossulus* on *M. californianus*, relative to the possible direct effects on *M. californianus* of *Nucella* and birds.

RESULTS

With reduced predation, *Mytilus trossulus* inhibited the rise of dominance by *M. californianus*. *Mytilus trossulus* averaged 56.0 ± 31.2% (mean ± 1 SD) in controls and was absent from the removal areas. As a consequence, although the percent cover of *M. californianus* did not differ between treatments at the start of the *M. trossulus* manipulation (Fig. 3, paired *t*-test, $t_6 = 1.443$, $P = 0.28$), it was twice as high in areas where *M. trossulus* was experimentally removed compared to controls after 3 months (Fig. 3, paired *t*-test, $t_6 = 4.144$, $P = 0.0025$).

Nucella, but not birds, pushed succession towards a *M. californianus*-dominated community. Neither *M. trossulus* nor *M. californianus* differed between treatments at the start of the experiment (Fig. 4, blocked two-way ANOVA, all $F_{112} < 1.20$,
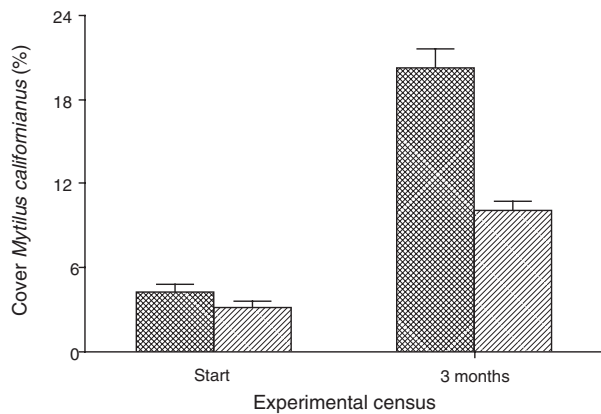
Fig. 3. Effect on *Mytilus californianus* cover of experimentally manipulating *Mytilus trossulus* cover in the absence of dogwhelk (*Nucella* spp.) predation. Mean percentage of space covered ± 1 SE shown for each treatment after removing variance due to block effects, *n* = 7. Data back-transformed from log-transformed values. (▨), No. *Mytilus trossulus*; (▧), Control.

P > 0.25). At the end of the experiment, however, *Nucella* predators promoted the demise from dominance of *M. trossulus*, reducing the cover it held by nearly one-half when compared to removal areas (Fig. 4a; Table 1, ANOVA, *P* < 0.003). Moreover, within plots where *Nucella* was not removed, *M. trossulus* correlated negatively with average *Nucella* density (*r* = −0.755, *n* = 10, *P* = 0.012). Estimates from multiple regression of each *Nucella* species on *M. trossulus* (Table 2) indicated that both species were significantly negatively associated with *M. trossulus*, with *N. canaliculata* having a per-capita effect approximately twice that of *Nucella emarginata*. In contrast, birds had no effect on *M. trossulus* (Fig. 4a; Table 1, ANOVA, *P* = 0.62). Noda (1999) reported similar effects of snail and bird predation on *M. trossulus* in Oregon, suggesting that this result may be general.

At the end of the experiment, *M. californianus* cover was negatively correlated with *M. trossulus* cover across all plots (Fig. 5; *r* = − 0.635, *n* = 20, *P* = 0.003). By consuming *M. trossulus*, *Nucella* enhanced the rise to dominance of *M. californianus*. *Mytilus californianus* cover in the presence of *Nucella* increased 1.6 times that in areas without *Nucella* (Fig. 4b; Table 1, ANOVA, *P* = 0.031). However, when *M. trossulus* was included as a covariate, the effect of *Nucella* on *M. californianus*
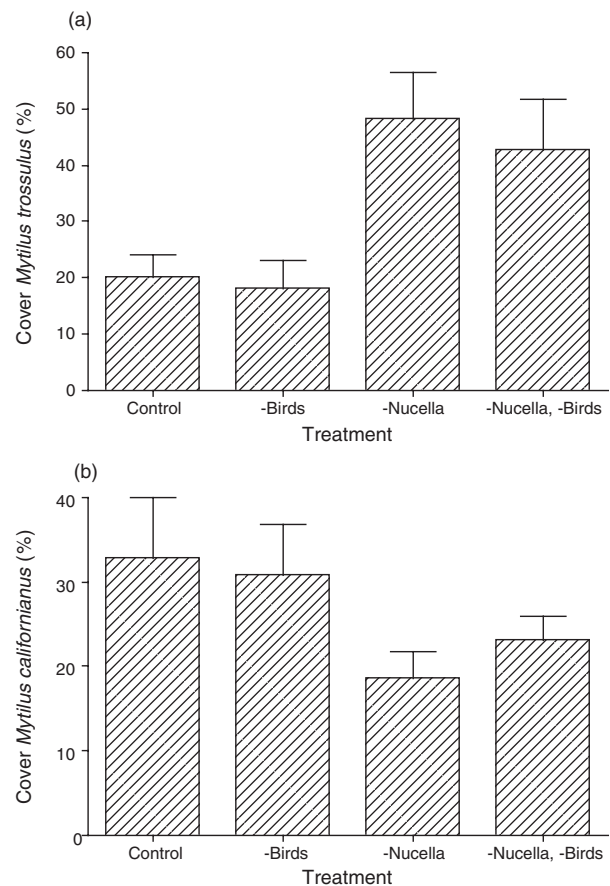

Fig. 4. Effects of dogwhelk (*Nucella* spp.) and bird predation on mussel bed succession. Mean percentage of space ± 1 SE shown for each treatment following removal of variance due to block effects, *n* = 5. (a) The direct effect of *Nucella* and bird predation on the blue mussel *Mytilus trossulus*, *n* = 5. (b) The indirect effect on *Mytilus californianus* of *Nucella* and bird predation on *M. trossulus*, *n* = 5. Data back-transformed from log-transformed values. Start: *P* = 0.28; 3 months: *P* = 0.0025.

disappeared (Table 1, ANCOVA, *P* = 0.74), whereas the relationship between *M. californianus* and *M. trossulus* was significant (Table 1, ANCOVA, *P* = 0.004), indicating that the differences in *M. californianus* between *Nucella* manipulations arose indirectly through changes in *M. trossulus* abundance rather than as a direct effect of *Nucella*. *Mytilus californianus* did not differ between bird manipulation treatments in these experiments whether or not the effects of *M. trossulus* were accounted for statistically (Table 1, ANOVA and ANCOVA, both *P* > 0.65).

Table 1 Results of ANOVA and ANCOVA from the end of the predator manipulation experiment

Independent variable Source	SS	d.f.	F	P
ln(*Mytilus trossulus*)				
Nucella	3.732	1	14.220	0.003
Birds	0.069	1	0.264	0.62
Nucella × Birds	0.0001	1	0.0005	0.98
Block	3.972	4		
Error	3.149	12		
ln(*Mytilus californianus*)				
Nucella	0.931	1	6.007	0.03
Birds	0.030	1	0.193	0.67
Nucella × Birds	0.099	1	0.642	0.44
Block	1.053	4		
Error	1.859	12		
Nucella	0.009	1	0.120	0.74
Birds	0.0005	1	0.007	0.94
Nucella × Birds	0.095	1	1.265	0.28
ln(*Mytilus trossulus*)	1.031	1	13.694	0.004
Block	1.362	4		
Error	0.828	11		

Table 2 Results of multiple regression of the average density of different *Nucella* species on log(final *M. trossulus* cover) in plots where *Nucella* was not removed in the predator manipulation experiment*

Term	Coefficient	Standard error	P
Constant	−0.591	0.317	0.1
Nucella emarginata	−0.122	0.036	0.01
Nucella canaliculata	−0.240	0.076	0.016

*($r^2 = 0.692$, $n = 10$). *Nucella lamellosa* did not occur in the experimental plots.

DISCUSSION

By feeding differentially among potential prey items, predation provides a mechanism sufficient to cause the differential demise of earlier stages of the mussel succession. Early arriving species such as *Mytilus trossulus* and *Pollicipes polymerus* (see Wootton 1993) can inhibit the invasion of the
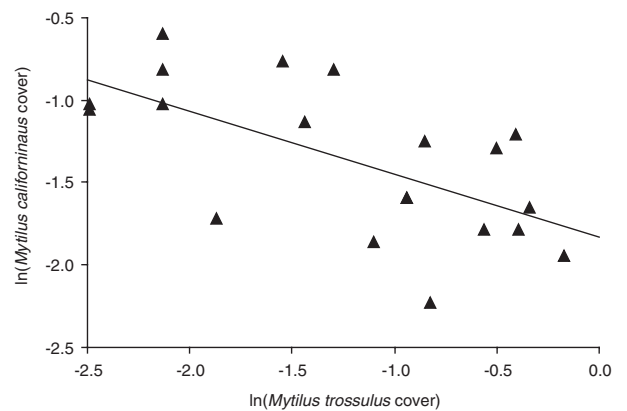

Fig. 5. Relationship between the log proportion of space covered by *Mytilus californianus* and by *Mytilus trossulus* across all plots in dogwhelk manipulation experiments, $n = 20$.

eventual competitive dominant member of the community, *M. californianus*, by usurping attachment space. This inhibition is diminished, however, because predators such as snails or gulls differentially reduce the populations of these early succession species. On the surface, the inhibition of *M. californianus* by previously established species is surprising given the preference that larval *M. californianus* exhibit when selecting habitats in which to settle (Paine 1974; Suchanek 1978, 1979; Petersen 1984; J. T. Wootton, pers. obs., 1984–2001; but see Petraitis 1977). *Mytilus californianus* may settle late into gaps because established species may reduce juvenile mortality arising from desiccation, and because predation on earlier species predictably occurs when the interaction between sessile species shifts from facilitation to competition. Recent experimental studies of *Nucella* predation on *M. trossulus* by Navarrete (1996) are consist with this hypothesis. In these experiments, *M. trossulus* only became established in snail exclusion plots, and this apparently resulted in increased recruitment and juvenile survival by *M. californianus*.

Other experiments in intertidal communities have also found that consumers promote succession. For example, Lubchenco and Menge (1978) and Lubchenco (1983) reported that grazing snails in a New England intertidal community removed the inhibitory effects of fast-settling ephemeral algae, accelerating the invasion of predator-resistant perennial algae. Likewise, Sousa (1979b)

removed crabs from an intertidal boulder-field in southern California and found that crab grazing also promoted the succession to perennial herbivore-resistant algae by selectively removing quickly recruiting and fast-growing ephemeral algae. Day and Osman (1981) found that predation by the sea star *Patiria* on cyclostome bryozoans promoted succession to cheilostome bryozoans on subtidal fouling plates. Kim (1997) removed limpets from intertidal benches on Vancouver Island, Canada, thereby arresting succession from ephemeral to perennial algae. Taken together, these experimental manipulations suggest that food web interactions may often be important in determining the dynamics and trajectory of succession, and that their roles may be worth considering in other systems.

Some evidence exists that might point to an important role in succession for consumers in terrestrial systems as well. To date, however, few experiments have directly tested whether herbivores can promote the demise of one dominant species, allowing a more resistant species to take over (reviewed in Edwards & Gillman 1987). An experimental exclusion of ungulates in a coniferous forest showed that succession from shrubs to conifers was enhanced by browsing (Hanley & Taber 1980). Similarly, removal of foliar-feeding insects inhibited succession from forbs and early successional grasses to perennial grasses in British fields (Brown & Gange 1992; Fraser & Grime 1998). Patterns of plant defense also provide some indirect support for an effect of consumers. Plants exhibit reduced herbivore damage and increased defenses against herbivores with successional stage (Cates & Orians 1975; Coley 1983; Godfray 1985; Bryant & Chapin 1986). This pattern has been interpreted as the result of evolution in response to selection pressures stemming from the status of the plant as a late (or early) successional species, thus successional status determines plant defensive characteristics. Equally valid is the opposite view, that plant defensive characteristics determine successional status, thus late succession species tend to be more heavily defended as consumers eliminate less defended plants.

Studies of seed predators also provide hints of the possible importance of consumers in terrestrial succession. Seed predators can cause enormous mortality, particularly where seed density is high (Janzen 1970). Furthermore, competition is often implicated among seed predators (e.g. Davis 1973; Brown & Davidson 1977; Cameron 1977; Chappell 1978; Brown & Munger 1985; Schluter *et al.* 1985; Grant 1986; Wootton 1987), suggesting a large negative effect on the seeds available to establish or maintain a successional stage. More importantly, seed predators forage selectively (Krebs *et al.* 1983; Stephens & Krebs 1986; Reader 1997), potentially causing different mortality and altered plant species composition. While the effects of seed abundance on seed predator behavior and the effects of seed predators on each other have been well studied, the effects of seed predators on the composition and population dynamics of their resource plants have not.

In conclusion, if we view succession as a sequence of 'rises and demises' of dominance stages, then consumers that hasten the demise can obviously play a major role. If each stage in succession is considered a two-step process of the establishment and demise of dominance, factors that cause differential mortality among species become important as mechanisms. Competition has been assumed to be the cause of differential mortality in most successional schemes, but is not the only possible cause. Many characteristics of consumers make them good candidates as agents of successional change and experiments demonstrate the important role that consumers can play in the successional dynamics of several intertidal communities. These experiments, and several lines of indirect evidence from terrestrial communities suggest that the role of consumers should be investigated in other systems undergoing succession. However, focusing on the causes of the rise and demise of each stage in succession indicates that the operation of different mechanisms within a single successional trajectory may be not only possible, but likely, a prediction borne out by experiments in intertidal (Turner 1983; Farrell 1991), freshwater (Dudley & D'Antonio 1991; Tuchman & Stevenson 1991; Sarnelle 1993), and terrestrial (Morris & Wood 1989; Brown & Gange 1992) settings.

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