

AN EXPERIMENTAL TEST OF MULTI-SPECIES MARKOV MODELS: ARE BARNACLES LONG-TERM FACILITATORS OF MUSSEL BED RECOVERY?

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ABSTRACT

Predicting responses of complex ecosystems to environmental impacts is challenging because of the web of species interactions and their potential to generate indirect effects. Multispecies Markov chain models provide one potential predictive framework for complex ecosystems. A previously parameterized Markov model of a rocky intertidal community predicted little effect of removing acorn barnacles from the system on sessile species composition. In contrast, short-term observations of recovery following disturbance suggest that acorn barnacles play a key facilitation role in mussel-bed recovery. In a 6-yr experiment in which balanoid acorn barnacles [*Balanus glandula* Darwin, 1854 and *Semibalanus cariosus* (Pallas, 1788)] were chronically and selectively removed, final species composition did not differ significantly from that of model predictions (90.3% of mean composition explained, $P > 0.5$), and the mussel *Mytilus californianus* Conrad, 1837 was able to attain its typical dominance. These results demonstrate that multispecies Markov chain models can generate reliable predictions and that acorn-barnacle facilitation does not have a substantial effect on long-term community composition in this system.

Appreciation has been growing for the need to implement ecosystem-based perspectives when ecological management approaches are developed and assessed (Palumbi et al. 2009; other articles in this issue). This approach is challenging, however, because of the complex web of interactions present in complex ecosystems. These interaction networks can generate a myriad of indirect pathways by which ecological impacts can be transmitted through ecosystems, often leading to surprising consequences (Wootton 1994b, Menge 1995). Grappling with these complex ecosystem responses requires mathematical frameworks with which to keep track of many simultaneously changing pathways, but these frameworks require empirical data to constrain their behavior and make useful predictions. A challenge, then, is to identify frameworks with sufficient flexibility to account for multiple pathways of interaction but with parameters that are empirically measurable.

Multispecies Markov chain models (hereafter just termed Markov models) are one approach that offer promise in meeting these challenges (Horn 1975, Caswell 2001). These models are based on transitions describing the probability that a unit of study will change from one ecological state to another over a defined time interval. In the context of communities of sessile species, for example, one can model points in space as study units and characteristics of those points (occupied by an individual or not; species identity or size class of an occupying individual) as the potential ecological states. These transitions can be summarized in a matrix M with elements m_{ij} that represent the probability of a transition from state i (column) to state j (row) over a defined interval such as a year. The consequences of this pattern of transitions can

be projected through time by multiplication by a column vector (P) describing the proportion of study units ($p_{i,t}$) in each ecological state i at time t :

$$P_{t+1} = M \times P_t.$$

This formulation represents a first-order Markov process, where realized states at time t depend only on the state of a point during the previous observation; more complicated formulations are possible. Predictions of average long-term system composition can be determined by iterated multiplication of the equation or by analysis of the proportional steady-state distribution defined by the eigenvector of the dominant eigenvalue of the transition matrix (M ; see Caswell 2001 for details and conditions necessary for this calculation).

Before they can be confidently used, modeling approaches must be rigorously tested, a process often best carried out in experimentally tractable "model" ecosystems. Evidence suggests that Markov chain models can be useful frameworks for predicting ecosystem response to environmental impacts. Many studies have shown that they can recapture observed abundances of species under conditions where transition rates were estimated and are robust to deviations from underlying assumptions (Tanner et al. 1994, Wootton 2001a, Hill et al. 2002). Furthermore, Markov models have shown promise in predicting ecological responses to experimental conditions outside of those in which the model parameters were estimated (Wootton 2001a, 2004, Nelis and Wootton 2010). I further tested the Markov approach using an experiment from the rocky intertidal of the northeast Pacific.

The role of positive interactions has received increasing interest in ecology (Bertness et al. 1999). On rocky shores, several investigators have provided short-term evidence that barnacles facilitate various mussel species. For example, Menge (1976) experimentally removed barnacles [*Semibalanus balanoides* (Linnaeus, 1767)] from plots in Maine and found that *Mytilus edulis* Linnaeus, 1758 colonization was eliminated over a 7-mo period, whereas control plots showed strong increases. Similarly, in Oregon, Berlow (1997) removed acorn barnacles [*Balanus glandula* Darwin, 1854, *Semibalanus cariosus* (Pallas, 1788)] over a 3.5-yr period and found reduced abundance of *Mytilus trossulus* Gould, 1850 and *Mytilus californianus* Conrad, 1837. Menge et al. (2011) also found experimental evidence for barnacle facilitation of *M. trossulus* at two of six sites in a 2-yr experiment. Evidence of barnacle facilitation of *Perumytilus purpuratus* (Lamarck, 1819) has also been found on Chilean (Navarrete and Castilla 1990) and Argentinian (Bertness et al. 2006) shores. Taken together, these results suggest that barnacles exert a strong influence on intertidal community structure by controlling mussel-bed development. In contrast to expectation from these empirical patterns, a Markov model previously parameterized for the rocky intertidal predicted minor effects of barnacle deletion on the composition of sessile species in the community (Wootton 2001a). These strikingly opposing expectations suggested that experimental manipulation of barnacles would offer an additional strong test of the Markov model framework. I therefore implemented a long-term barnacle-removal experiment both to test predictions of Markov models and determine the long-term consequences of facilitation effects by barnacles on mussel-bed development.

METHODS

The study took place on the middle intertidal shoreline of Tatoosh Island, Washington, USA (48.39°N, 124.74°W), a site of long-term experimental study of ecological processes and site of parameterization of my previously published Markov model predictions (Wootton 2001a). The middle intertidal community is dominated by a dense band of the mussel *M. californianus*, with interspersed gaps created by wave disturbance at different points in the past (Paine and Levin 1981). These gaps contain different combinations of species, depending on their age (Paine and Levin 1981); during the middle to late succession, gaps are usually dominated by the acorn barnacles *B. glandula* and *S. cariosus*, which are followed by *M. trossulus* and/or the leaf or goose barnacle, *Pollicipes polymerus* Sowerby, 1933, until the dominance of *M. californianus* is reestablished (Paine and Levin 1981, Wootton 2002).

Beginning in 1993, I established 14 permanent quadrats (60 × 60 cm) on wave-exposed benches around the island. Each quadrat was marked at two corners by permanent stainless steel markers and encompassed 100 points defined by a grid of monofilament crosshairs. Each year in late spring, I determined whether an individual was present under each grid point and, if so, the species to which it belonged. In the case of *M. californianus*, I subdivided individuals into large (>2 cm wide) and small (<2 cm wide) size classes. Censuses continue through the present. Plots initially started in different gaps undergoing different stages of disturbance and were unmanipulated. These data were used to estimate transitions among common classes of species or lumped functional groups and bare space. Rare species, which include the acorn barnacles, *Chthamalus dalli* Pilsbry, 1916 and *Balanus nubilus* Darwin, 1854, were lumped into a single group for the purposes of the analysis. Further details are presented by Wootton (2001a).

In 2005, I chose 11 60- × 60-cm plots placed in 0- to 1.5-yr-old gaps within the mussel bed for experimental manipulations of barnacles. The barnacles *B. glandula* and *S. cariosus* were regularly removed by hand from the plots with a pocket knife, 1-cm-wide scraper, or 1-cm-wide hammer, depending on the abundance of barnacles and the risk of disturbing other species. Removals were carried out opportunistically at each visit to the island (usually bi-weekly from April through late August), and special attention was paid to manipulations in late spring and early summer after the spring recruitment pulse of barnacles at the site. The manipulations were carried out through 2011, at which time a new cycle of disturbance was expected to begin (Paine and Levin 1981, Wootton 1995); that expectation was confirmed in 2011 when several plots entered a new disturbance cycle. The 6-yr span of data therefore reasonably reflects the composition through a typical disturbance and recovery period. In early summer, I censused each plot for the abundance of sessile species (percentage cover, with the aid of the 121 squares subdividing the quadrat) and mobile species (all visible macro-organisms). Because the Markov model predictions are for sessile species, I focused on these but also report responses of the common predators on barnacles and mussels: dogwhelks [*Nucella ostrina* Gould, 1852, and *Nucella canaliculata* (Duclos, 1852)] and the small brooding seastar *Leptasterias hexactis* (Stimpson, 1862).

I generated the predictions from the Markov model by removing any data involving changes to or from *B. glandula* and *S. cariosus* and calculating transition probabilities among the remaining groups. This procedure is the same as setting barnacle transitions to zero in the unmanipulated transition matrix and proportionally renormalizing all other transition probabilities to meet the requirement that all columns sum to 1 (see Wootton 2001a). I used the same ecological state categories as Wootton (2001a) for consistency. These included the two *M. californianus* size classes, five common species [*B. glandula*, the articulated coralline alga *Corallina vancoveriensis* Yendo, the fleshy red alga *Halosaccion glandiforme* (S. G. Gmelin) Ruprecht, *M. trossulus*, *P. polymerus*, and *S. cariosus*], bare or diatom-covered rock, four algal functional groups [filamentous red algae, fleshy red algae, fleshy crustose algae, and ephemeral algae (*Ulva* and *Porphyra* spp.)], and the aggregated rare species.

Data from the barnacle removals were combined into the ecological states used for the Markov model. Running averages were calculated for each plot over the course of the manipulation for generation of an estimated long-term average composition, similar to the predictions generated from the Markov model. Similar statistics were calculated for 16 unmanipulated plots for the subset of censuses concurrent with the barnacle removal manipulations and served as a comparison for treatment effects of barnacle removal. Sessile species generally interact with neighbors, so spatially explicit transition-based models might be relevant. I chose not to explore them in the study reported here because I was interested in testing the limits of first-order Markov models, because of the much larger data requirements of these models, and because a prior study using a spatially explicit model found minimal differences between predictions of species composition from spatial and nonspatial models (Wootton 2001b).

I related model predictions to barnacle-removal data by comparing multivariate (Euclidean) distances between model predictions and empirical results from each plot with average multivariate distances between empirical results from the members of each pair of plots (Wootton 2004). If the model fit poorly, average distances would generally be greater than those observed between pairs of plots, so the two types of distances were compared with a one-tailed t -test. Euclidean distances were chosen because they do not weight rare species disproportionately and because abundance data for all species were on the same scale (percentage cover) and were therefore directly comparable. I also applied MANOVA as an alternative test, using ecological states as dependent variables and plot observations plus the model prediction as the replicates, and compared observed with predicted as the treatment effect. Note that MANOVA lacks the a priori directional information of the former test. I also calculated other metrics of model fit, including similarity between model predictions [$\sum \min(f_{i,pred}, f_{i,obs})$] across all states i (where $f_{i,x}$ is the proportion of points in state i) and the average abundance of each ecological state across all plots, as well as the proportion of variance in average abundance of each taxon explained by the model predictions [$1 - \text{variance of (observed - predicted abundance)}/\text{variance of observed abundance}$].

RESULTS

The dominant species in the system, *M. californianus*, was able to attain dominance when barnacles had been removed (Fig. 1). Barnacle-removal and unmanipulated plots differed significantly in taxon composition (MANOVA: $P = 0.034$), but the differences were subtle (Fig. 1, similarity of mean abundances: 0.738); *C. vancouveriensis* and bare rock tended to be higher in the absence of barnacles, whereas *H. glandiforme* tended to be lower (t -tests: $P < 0.05$). The predators on barnacles declined on average 36%–57% on barnacle-removal plots [MANOVA, $P = 0.015$; *Nucella* spp.: from 39.09 (SD 9.64) to 25.04 (SD 10.57) m^{-2} ; *L. hexactis*: from 2.05 (SD 1.61) to 1.18 (SD 1.00) m^{-2}].

Results of the Markov chain model, updated to include data through 2011, predicted dominance of *M. californianus*, as in past analyses (Wootton 2001b). Removing the barnacles *S. cariosus* and *B. glandula* from the model produced a very similar compositional prediction (similarity = 0.824); *M. californianus* maintained its dominance (Fig. 2). The distribution of multivariate distances between model predictions and results from replicate barnacle-removal plots [0.258 (SD 0.214), $n = 11$] were smaller than average distances between replicate pairs of plots [0.365 (SD 0.224), $n = 55$], so no evidence supported systematic deviations of model predictions from observed results ($P > 0.5$). MANOVA also failed to detect a significant difference between observed and predicted results ($P = 0.357$). The model successfully predicted 90.3% of the variance in average species abundance (Fig. 2).

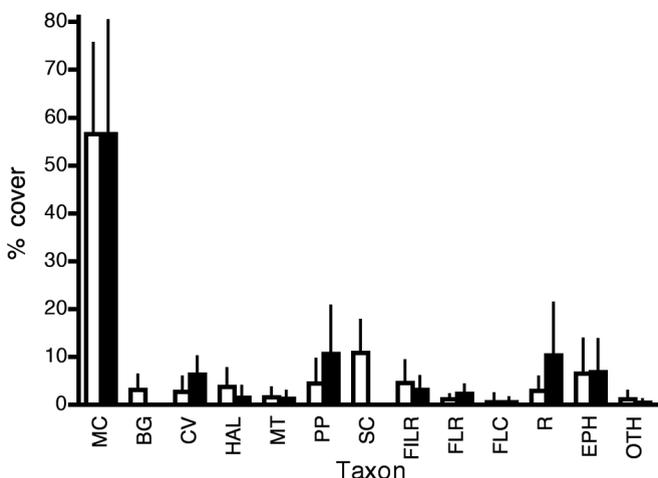


Figure 1. Comparison of average percentage cover (SD) of sessile species or functional groups on unmanipulated plots (open bars, $n = 16$) and plots from which barnacles were removed for 6 yrs (filled bars, $n = 11$). MC = *Mytilus californianus*; BG = *Balanus glandula*; CV = *Corallina vancouveriensis*; HAL = *Halosaccion glandiforme*; MT = *Mytilus trossulus*; PP = *Pollicipes polymerus*; SC = *Semibalanus cariosus*; FILR = filamentous red algae; FLR = fleshy red algae; FLC = fleshy crustose algae, R = bare rock; EPH = ephemeral algae (*Ulva* spp., *Porphyra* spp.); OTH = other rare species.

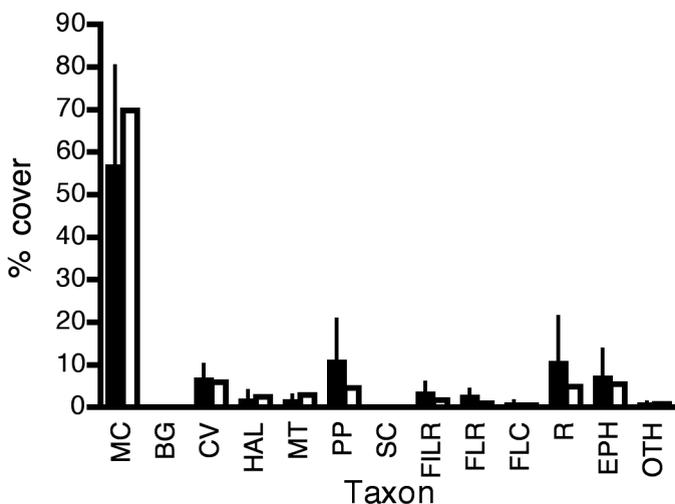


Figure 2. Comparison of average percentage cover (SD) of sessile species observed on barnacle-removal plots (filled bars) with predicted composition (open bars) from a multispecies Markov-chain model parameterized from data from unmanipulated plots with all transitions involving *Balanus glandula* and *Semibalanus cariosus* removed. MC = *Mytilus californianus*; BG = *Balanus glandula*; CV = *Corallina vancouveriensis*; HAL = *Halosaccion glandiforme*; MT = *Mytilus trossulus*; PP = *Pollicipes polymerus*; SC = *Semibalanus cariosus*; FILR = filamentous red algae; FLR = fleshy red algae; FLC = fleshy crustose algae, R = bare rock; EPH = ephemeral algae (*Ulva* spp., *Porphyra* spp.); OTH = other rare species.

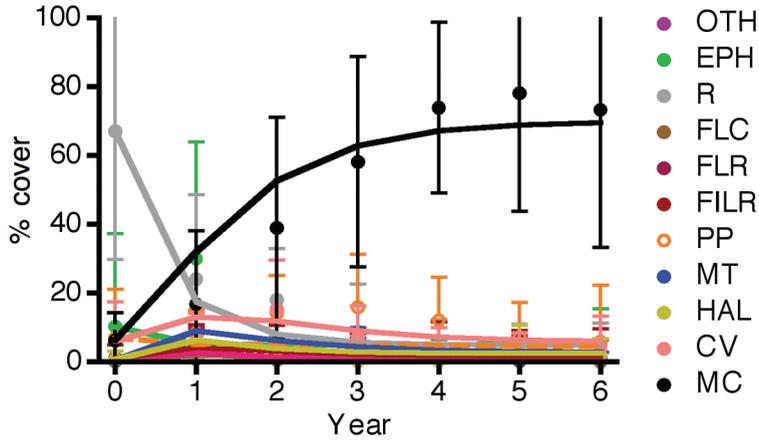


Figure 3. Plot of recovery patterns of each ecological state in experimental plots [mean (SD) in each year] compared to compositions (lines) predicted by the Markov model through time from the same starting conditions. Model predictions generally followed annual means closely, especially for the dominant categories of rock, *Mytilus californianus*, and *Corallina vancouveriensis*, and did not fall outside of standard deviations among plot years. MC = *Mytilus californianus*; CV = *Corallina vancouveriensis*; HAL = *Halosaccion glandiforme*; MT = *Mytilus trossulus*; PP = *Pollicipes polymerus*; FILR = filamentous red algae; FLR = fleshy red algae; FLC = fleshy crustose algae, R = bare rock; EPH = ephemeral algae (*Ulva* spp., *Porphyra* spp.); OTH = other rare species.

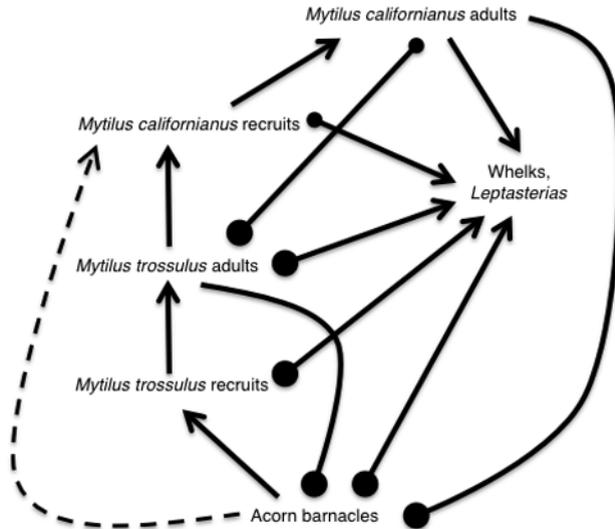


Figure 4. Diagram of known or strongly suspected (dashed line) interactions among barnacles, mussels, and their predators at the study site. Arrows indicate positive effects, circles at the ends of lines indicate negative effects. Note that links between species can have arrows and/or circles at both ends, indicating reciprocal effects. Size-specific interactions are indicated by division of mussels into recruit and adult size classes.

The first-order Markov models I used do not include time-varying parameters and are therefore most likely to provide insight into large-scale average species composition, rather than details of population dynamics within a given plot. Nevertheless, the model generally did a good job of tracking the dynamics of average species abundance from initial, recently disturbed plot conditions (Fig. 3), so it appears to be useful in predicting general successional patterns (see also Wootton 2001a).

DISCUSSION

Despite experimental evidence of their facilitation of mussels (Menge 1976, Berlow 1997, Navarrete and Castilla 1990, Bertness et al. 2006, Menge et al. 2011), chronic removal of barnacles over a 6-yr period had only minor effects on long-term community composition and recovery to a *M. californianus*-dominated bed. The observed subtle shifts in algal composition are consistent with results of prior studies documenting effects of barnacles on these species: barnacle topography benefits *H. glandiforme* by interfering with limpet grazing, whereas *C. vancouveriensis* is grazer resistant (Johnson 1992). Barnacles may also filter out and eat algal spores; their loss may not be offset by grazer protection for *C. vancouveriensis*.

Given prior demonstration of barnacle effects on mussels, why was no long-term effect on community dominance by *M. californianus* evident? The complex linkages among barnacles, mussels, and shared predators (Fig. 4) provide possible explanations, because other compensating biological interactions may arise over a longer time frame. In addition, understanding this result may depend in part on how barnacles facilitate mussels, which has not been carefully explored. One consideration is that *M. californianus* is ecologically very different from the other mussel species that exhibit facilitation by barnacles. A key difference is that *M. californianus* grows large and secretes a thick shell, which makes it invulnerable to predators above the foraging range of the seastar *Pisaster ochraceus* (Brandt, 1835) (Paine 1966). In contrast, *M. trossulus* and most other intertidal mussels have a life history geared toward rapid growth and reproduction, and their thin shells do not provide full protection from drilling predators such as whelks (Suchanek 1981). Because barnacles and *M. trossulus* share many of the same predators (Dayton 1971, Menge 1972, Palmer 1984, West 1986), the presence of barnacles can serve as a reliable cue that a site has low predation risk, which might be far more important to *M. trossulus* than to *M. californianus*. Other mechanisms may cause facilitation that might benefit both species, however, such as reduced desiccation or shear stress for mussel recruits or the swamping of predator feeding. Given the relatively small sizes of barnacles compared to adult mussels in this system, desiccation effects are probably most important for new recruits rather than for adults, so a facilitation effect might be diluted over longer time scales. Similarly, predators are expected to increase numerically in response to higher prey levels, thereby offsetting saturating functional responses over the long run.

Mytilus californianus is also known to recruit to substrates other than barnacles, including rock, filamentous algae, and the byssal threads of other mussels (Petersen 1994). Any loss of recruitment facilitation by barnacles might therefore be counteracted by availability of other substrate. Because recruitment can be facilitated by *M. trossulus*, one might expect indirect facilitation of *M. californianus* recruitment by barnacles through their effects on *M. trossulus*, but *M. trossulus* inhibits larger *M.*

californianus (Wootton 2002), so initial benefits might be counteracted in the long run by size-dependent shifts in the nature of their interaction.

The lack of long-term response in *M. trossulus* was also unexpected given its strong response in other studies. One possible explanation is that negative feedback cancels out facilitation effects over the longer term (Fig. 4). As an important prey resource, barnacles can boost predator populations (Wootton 1994a), which may then increase predation on *M. trossulus*. Consistent with this hypothesis, populations of predators on both barnacles and mussels decreased in barnacle-removal plots. Experimental context may also explain the result in several ways. First, facilitation effects in other studies were most apparent when predators of mussels were excluded (Menge 1974, Berlow 1997, Menge et al. 2011); in the study reported here, predators were not excluded. Second, the physical conditions of the Washington coastline are relatively benign compared to other well-studied sites (Bertness et al. 2006), so facilitation by barnacles that alleviate stressful physical conditions may simply be unimportant there. In any event, more careful manipulations of underlying causal mechanisms seem essential to full elucidation of the role of facilitation of mussel bed recovery under different conditions.

A key motivation underlying implementation of the present study was to challenge predictions of a Markov chain model that seemed contrary to past empirical studies, but the Markov predictions in fact quantitatively matched the results of the experiment well. This result supplements other successful tests in novel situations, including community composition on vertical walls (no bird predation or adult mussel recruitment; Wootton 2001a), in bird exclusion experiments (Wootton 2001a), and in long-term reductions of either *M. californianus* or *M. trossulus* (Wootton 2004). Taken together, these results indicate that Markov chain models have significant predictive ability in the face of ecosystem complexity. In some ways, this result is surprising in light of the abstracted mechanisms underlying species interactions that are contained in transition parameters, but the reduced complexity of these models and relative ease of collecting data for parameterization may limit difficulties imposed by measurement error in other approaches (Novak et al. 2011). The study reported here should lend confidence to predictions of results of environmental impacts in less tractable situations, including probing ecological impacts of global climate change (e.g., ocean acidification; Wootton et al. 2008), the effects of invasive species (Nelis and Wootton 2010), and responses in other less tractable ecosystems.

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