

PREDICTION IN COMPLEX COMMUNITIES: ANALYSIS OF EMPIRICALLY DERIVED MARKOV MODELS

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Abstract. Understanding and predicting the effects of species extinction and other environmental impacts in natural ecosystems is difficult because of their inherent complexity. Successful prediction in complex systems requires empirically accessible theoretical frameworks to limit the range of possible outcomes. I explored the predictions of multi-species Markov models, based on transition probabilities derived from repeated censuses of fixed points in the middle intertidal community of Tatoosh Island, Washington, USA, under natural conditions and after altering the model to reflect species extinction and changes in size-structured processes. The unmanipulated model predicted a mussel-dominated community and quantitatively captured 98.7% of the variation in community composition in independent transects. Although model assumptions that transition probabilities did not vary over time and depended only on the state of a point at the previous census were violated, altering the model to account for these violations provided no improvement in model performance. The manipulated models indicated that most species and transitions had relatively weak effects on community composition, the strongest effects being associated with California mussels (*Mytilus californianus*), articulated coralline algae (*Corallina vancouveriensis*), and predatory birds. The manipulated models also predicted that extinction of several species, particularly predatory birds, affects the resilience of the system, as assessed by return time. The effects of species on composition and resilience were poorly correlated, suggesting that assessing the importance of species depends on the type of ecosystem response being considered. The model successfully predicted quantitative shifts in community composition and ecosystem dynamics under several novel conditions: on vertical walls where bird predation and adult mussel recruitment are absent, and in previously published experiments that excluded birds from horizontal benches. These results suggest that Markov models can provide a useful predictive framework for some types of environmental impacts on complex ecosystems.

Key words: California mussels; community composition; ecosystem dynamics; environmental perturbation; extinction; *Larus glaucescens*; multispecies Markov models; *Mytilus californianus*; resilience; rocky intertidal; sensitivity analysis; transition matrix.

INTRODUCTION

A major challenge for ecologists is to understand and predict the consequences of environmental change in natural ecosystems. Meeting this challenge is difficult in complex natural ecosystems because impacts such as species extinction, changes in disturbance regime, and alterations of system productivity often produce unanticipated results through various indirect effects among interacting species (reviewed in Schoener 1993, Wootton 1994b, Menge 1995, Abrams et al. 1996), and through the interplay between physico-chemical factors and species interactions (e.g., Menge and Sutherland 1976, Connell 1978, Sousa 1979, Wootton and Power 1993, Wootton et al. 1996a, b). Therefore, the tremendous complexity of natural ecosystems requires approaches that can synthesize into a single framework a number of ecological processes, such as

interactions among various component species, size structure, and disturbance regime.

Grappling with complex interactions of simultaneously acting processes often is facilitated by the use of mathematical models. Additionally, by examining changes in the behavior of such models when adding further biological realism, one can use them as the starting point for understanding the potential importance of unaccounted complexity and to focus empirical studies. The natural inclination is to develop a complex model incorporating all of the details of our current understanding of a given system. Complex theoretical approaches, however, present practical limitations for application to real systems. Models of complex systems demonstrate that even the predicted, qualitative consequences of environmental changes depend critically on the parameter values used (e.g., Puccia and Levins 1985, Yodzis 1988). At the same time, actual parameterization becomes more difficult as the number of required parameter estimates increases, and the risk of error propagation can sometimes increase faster than the increase in accuracy as more parameters are esti-

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mated (Ludwig and Walters 1985). The challenge, then, is to develop approaches with sufficient complexity that they capture the dynamics of natural communities, yet permit parameterization with a reasonable degree of accuracy.

Multispecies Markov models of community structure (Waggoner and Stephens 1970, Horn 1975), hereafter called Markov models, probably represent the simplest multispecies models to parametrize with field data, and therefore offer great promise as ecological tools if the approach reasonably characterizes natural communities. Because these models primarily have been applied to systems with large organisms that exhibit slow population dynamics, such as forests, their ability to predict ecosystem structure under novel circumstances remains untested. Utilizing experimentally tractable communities as model ecosystems can provide a unique opportunity to evaluate whether Markov models can make useful predictions of ecosystem response to various environmental perturbations, and can identify portions of the ecosystem that exert the strongest effects on ecosystem structure. In this paper, I present an in-depth analysis of a Markov model for an experimentally tractable rocky intertidal community, examining the consequences of species extinction, size structure, disturbance regime, and temporal variation. I then test the model predictions against independent data from the intertidal community. The predictions also serve to motivate future experimental tests of the model.

Multispecies Markov models

Multispecies Markov models were introduced to community ecology by Waggoner and Stephens (1970) and Horn (1975), who used them to project the successional dynamics and overall composition of forests in eastern North America, and to obtain the first theoretical derivation of the intermediate disturbance hypothesis. Like island biogeography theory (MacArthur and Wilson 1969, Holt 1996), metapopulation/community theory (Gilpin and Hanski 1991, Tilman 1994), spatial competition/disturbance models (Petraitis et al. 1989), and stage-structured population viability analysis (e.g., Leslie 1945, Crouse et al. 1987, Caswell 1989, Getz and Haight 1989, McFadden 1991, Doak 1992, Wootton and Bell 1992, Brault and Caswell 1993, Crowder et al. 1994, Pfister and Bradbury 1996), Markov models are based upon probabilities of moving from one ecological state to another. The relative ease of measuring transition probabilities among ecological states, rather than detailed functions describing specific ecological processes, makes the models relatively accessible to field data. The choice of ecological states to consider can reflect, to some extent, major mechanisms that the investigator believes are important. Ecological states may include different species or species combinations, different size classes of a given species, and open space. Consequently, this approach can synthesize, in an abstract way, the effects of interactions

among species, disturbance rates (leading to empty space), and size classes. Transitions among species do not necessarily reflect specific mechanistic processes, but rather represent the sum of a variety of potential direct and indirect effects among species. Because transitions combine multiple processes, they highlight parts of ecosystems on which to focus more detailed mechanistic studies, rather than provide a direct interpretation of the importance of a particular process such as competition.

The transition matrix is multiplied by a column vector containing the proportion of points characterized by each state at one time interval to project the proportion of points characterized by each state at the next time interval. As a matrix model, the approach shares a number of analytical similarities with stage-structured matrix models of populations of a single species (e.g., Leslie 1945, Crouse et al. 1987, Caswell 1989, Getz and Haight 1989, McFadden 1991, Doak 1992, Wootton and Bell 1992, Brault and Caswell 1993, Crowder et al. 1994, Pfister 1998). For example, the long-term behavior of the model usually converges to a stable-stage distribution that represents a prediction of the large-scale composition of the community. Furthermore, starting the model from 100% bare space provides a prediction of the successional trajectory of the community. Several assumptions of simple Markov models are of particular note: (1) transition probabilities depend only on the state that a particular point exhibited in the previous time step, (2) transition probabilities are constant over time and do not depend on density, and (3) there is no influence of the spatial arrangement of organisms.

To date, the application of empirical data to the Markov approach has been limited. Aside from terrestrial plant communities (Waggoner and Stephens 1970, Horn 1975, Runkle 1981, Barnes and Dibble 1988, McAuliffe 1988, Acevedo et al. 1995), the approach has been applied to arthropod communities (Usher 1979), beaver pond dynamics (Pastor et al. 1993), coral reefs (Tanner et al. 1994, 1996), and oceanic fish and cephalopod communities (Saila and Erzini 1987). For the most part, analysis of these models has been restricted either to predicting stable-stage distributions and successional patterns, or to discussing the degree to which model assumptions are met. Although these analyses provide important information, further insight could potentially be gleaned from more in-depth analyses. In particular, elements of the matrix can be analyzed in much greater detail to determine the sensitivity of model behavior (return times, species composition) to changes in particular transitions in order to investigate the importance of particular species or processes (e.g., disturbance rates). To date, only a study on coral reefs (Tanner et al. 1994) has conducted such an analysis. Furthermore, several critical questions have not been explored in detail. First, it would be beneficial to know how robust the model predictions are to violations in

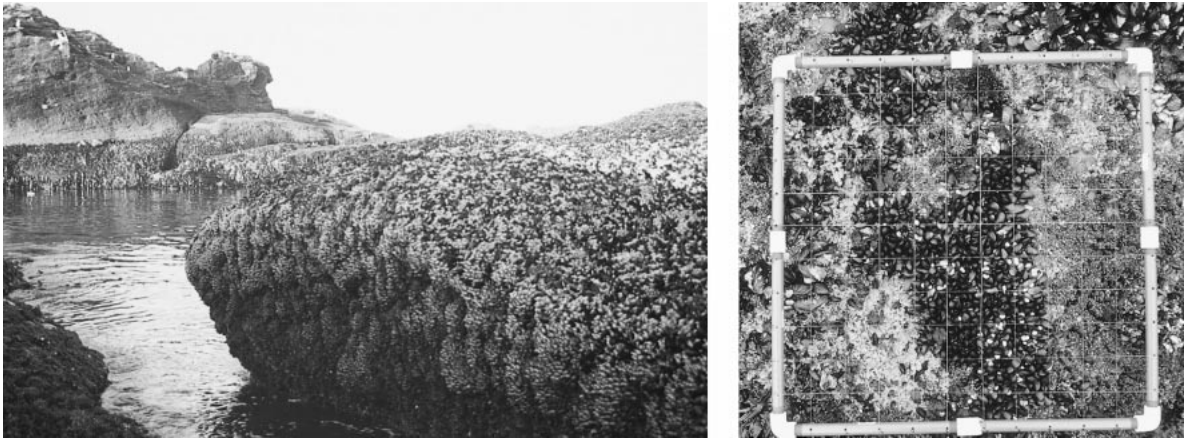


PLATE 1. (Left) Illustration of the shift in dominance from the mussel *Mytilus californianus* on horizontal benches (right side of photo) to the goose barnacle *Pollicipes polymerus* on vertical walls (center of photo) characteristic of wave-exposed shores in the middle intertidal zone of Tatoosh Island, Washington, USA. (Right) Example of a 60 × 60 cm permanent quadrat used to collect transition probabilities. Both photographs by J. T. Wootton.

assumptions (e.g., time-varying matrices) and whether models constructed with more realistic assumptions provide significantly better predictions (Usher 1981, Lippe et al. 1985, Lough et al. 1987, Tanner et al. 1996). Second, the ability of Markov models to predict species responses to novel conditions has never been tested.

METHODS AND STUDY SITE

Study site

The study was conducted in the rocky intertidal community of Tatoosh Island, Washington, USA, and focused on the mussel (*Mytilus californianus*) bed assemblage in the middle-intertidal zone. Mussel beds are typical of many shores throughout the world (Stephenson and Stephenson 1972), particularly along the wave-washed rocky shores of the northeastern Pacific (Shelford et al. 1935, Ricketts et al. 1985). Although they are a predictably identifiable feature of these shores, mussel beds, like many other communities of sessile species, are actually quite dynamic, with wave-induced disturbance creating a mosaic of gaps in which other species temporarily dominate (Dayton 1971, Paine and Levin 1981, Sousa 1984). Mussel beds also contain a diverse assemblage of mobile consumers that utilize mussels and other sessile species for both cover and food (Suchanek 1979). Hard-substrate marine communities have made ideal model systems for studying the interplay of species interactions, productivity, and disturbance in complex natural communities, because of their experimental tractability (e.g., Connell 1961, Paine 1966, 1980, Dayton 1971, Menge 1976, Lubchenco 1979, Sousa 1979, Paine and Levin 1981, Underwood et al. 1983, Bertness 1984, Schmitt 1987, Fairweather 1990, Petraitis 1990, Wootton 1992, 1993a, 1994a), and important insights have arisen from these experiments. These systems also have tremendous under-utilized potential to test general approaches

or theories in ecology that cannot be rigorously evaluated in other settings.

Previous work on rocky intertidal communities along the Pacific coast of North America has shown that competition for space, mediated by disturbance events, consumer–resource interactions, and recruitment differences, is a major organizing force, and experiments have identified the roles of selected species within this system (e.g., Paine 1966, 1980, Paine and Vadas 1969, Connell 1970, Dayton 1971, Sousa 1979, 1984, Paine and Levin 1981, Gaines and Roughgarden 1985, Farrell 1991, Wootton 1992, 1993b, 1994a, Menge 1995, Pfister 1995). Although it is probably one of the best understood communities in the world, we still have an incomplete understanding of the role that different species play within the rocky intertidal system and the strength of their effects on other ecosystem members because we currently have no systematic method to identify a priori these effects (however, for several possibilities, see Seifert and Seifert 1976, Wootton 1994a, 1997, Pfister 1995, Laska and Wootton 1998, Ives et al. 1999). Furthermore, it may be important to understand the roles of other processes that have not been intensively investigated. For example, size structure may play an important role in determining the relative competitive ability of different sessile species, with larger individuals outcompeting smaller individuals (Wootton 1993b). Additionally, mussels are a fairly unique “sessile” organism, because adults detached from one portion of the shore can be deposited in other areas (Paine and Levin 1981), where they can potentially overcome size-dependent competition. This feature, in concert with the elimination of predation on goose barnacles (*Pollicipes polymerus*) by Glaucous-winged Gulls (*Larus glaucescens*), may be critical for understanding a major shift in dominance from mussels on horizontal benches to *Pollicipes* on vertical walls

TABLE 1. Major ecological state categories for each fixed point used in the Markov models, and their codes used in subsequent tables and figures. The two numbers in parentheses indicate sample sizes for summer and winter transitions, respectively, for each ecological state.

Code	Ecological state
B	Large (>2 cm wide) <i>Mytilus californianus</i> (3605, 4095)
BG	<i>Balanus glandula</i> (216, 484)
CV	<i>Corallina vancouveriensis</i> (1027, 821)
HAL	<i>Halosaccion glandeforme</i> (255, 432)
MT	<i>Mytilus trossulus</i> (553, 356)
PP	<i>Pollicipes polymerus</i> (369, 331)
SC	<i>Semibalanus cariosus</i> (505, 432)
SMC	Small (<2 cm wide) <i>Mytilus californianus</i> (751, 739)
FIRD	Filamentous red algae (primarily <i>Endocladia muricata</i> , <i>Microcladia borealis</i> , and <i>Polysiphonia</i> spp.) (81, 133)
FLRD	Fleshy red algae (primarily <i>Iridea cordata</i> , <i>Iridea flaccida</i> , and <i>Mastocarpus papillatus</i>) (53, 64)
FLCR	Fleshy crustose algae (<i>Hildenbrandia</i> , <i>Petrocelis</i> , and <i>Ralfsia</i> spp.) (104, 88)
R&D	Bare rock or rock covered by a diatom coating (880, 325)
UV&PR	Ephemeral algae (primarily <i>Porphyra</i> and <i>Ulva</i> spp.) (239, 241)
Other	Other species of algae and invertebrates including <i>Acrosiphonia coalita</i> , <i>Anthopleura elegantissima</i> , <i>Chthamalus dalli</i> , <i>Entodesma navicula</i> , <i>Fucus distichus</i> , <i>Halichondria bowerbanki</i> , <i>Haliclona</i> spp., <i>Hedophyllum sessile</i> , <i>Leathesia difformis</i> , <i>Postelsia palmaeformis</i> , and <i>Prionitis lanceolata</i> (76, 74)

(Wootton 1993b; see Plate 1, left). Adult mussels are not deposited on vertical walls, so their recruitment cannot upset size-dependent competitive hierarchies. Similarly, gulls cannot stand, and therefore cannot feed, on vertical walls.

Data collection and model parameterization

Beginning in May 1993, I collected data from fixed points on transects and quadrats to derive transition probabilities. I established a total of 1830 fixed points to collect these data. Points were censused using one of two methods. Eleven transects 9.1 m long with 30 randomly placed points were censused in locations scattered around the island. The transect was made of a vinyl-covered wire cable with an adjustable hook on one end to maintain tension. The transect was suspended above the rock using 30 cm high eyescrews attached to permanent end holes with wall anchors. Eyescrews were also placed along the transect in one or two spots, which insured that the transects were suspended above the rock throughout its length, and which permitted changes in transect direction to avoid topographic irregularities of rock benches. When not in use, stainless steel marking screws of lower stature replaced the eyescrews to prevent waves and waterborne objects from bending the latter. Aluminum cable sheaths crimped down around the cable at random intervals permanently marked the transect points, and the end of the transect was marked to insure the same transect orientation at each sample date. The other 1500 points were derived from 15 quadrats placed at scattered locations around the island. The quadrats were initially established in gaps of different ages (0–3 yr old) within the mussel bed, and were marked at two corners with permanent stainless steel screws in holes

drilled into the rock. The quadrats were sampled with a 0.6 × 0.6 m square, constructed of PVC with holes drilled in to accommodate monofilament lines defining 100 points (see Plate 1, right). The points were given a specific set of coordinates for reference and the corners of all quadrats were marked so that they were positioned in the same orientation at every census. I deployed the quadrats in gaps of different ages to intensively sample transitions from rarer sessile taxa in the ecosystem. Transects and quadrats were censused twice annually, in May and in late August–early September, to account for possible seasonal changes in the transitions. To avoid inaccuracies due to parallax, censuses were made with a plumb-bob. At various censuses, the number of data points was somewhat less than the number of sampling points originally established. One quadrat was lost after one year when waves knocked out the corner markers. Additionally, several transect points that crossed crevices or tidepools, or that fell over areas cleared for eyescrews, were discarded because they did not reflect the predominant habitat type being studied (rock benches). Finally, I occasionally could not locate transect ends because animals had overgrown the screws. The analyses used data collected over a 5-yr period (through May 1998).

Tables of transition probabilities were derived for winter and summer periods across all years. Data were collapsed into 14 ecological states, based on the number of observations available to estimate transitions and on the similarity in ecology of less abundant taxa (Table 1). The categories included empty rock (either bare or covered by diatoms) created by disturbance and other sources of mortality, mussel size structure in the form of large (≥ 2 cm wide) and small (<2 cm wide) *Mytilus californianus*, various dominant algal and invertebrate

species, and a lumped category including rare sessile species.

Model analysis

Tests of assumptions.—I explored the assumptions and appropriateness of different model variants by analyzing the data in several ways. I used log-linear analysis to examine the match between several assumptions of Markov models and the data (Caswell 1989, Sokal and Rohlf 1995). The factors in the model included the starting ecological state, the ecological state at the following census, the season between the censuses, and the year of the censuses. Four terms were of particular interest for the analysis. The interaction between the starting and ending ecological state was examined to verify that the transitions were nonrandom, which would indicate that species interaction significantly influenced community structure. Additionally, the three-way interactions between starting state, ending state, and either season or year, and the four-way interaction between all factors were examined to determine whether transitions among ecological states varied temporally. The effects of spatial variation could not be incorporated because not all ecological states were present in each transect or quadrat at each census.

Any observed seasonal effects might have been caused by the different time scales over which summer and winter transitions were collected (four and eight months, respectively). To test this possibility, the winter transitions were compared to the squared summer transition matrix comparing the log-likelihood goodness-of-fit equation to a χ^2 distribution with $s \times (s - 1)$ degrees of freedom as follows:

$$-2 \ln(\lambda) = 2 \sum_{i=1}^s \sum_{j=1}^s n_{w,ij} \ln \left(\frac{p_{w,ij}}{p_{\sigma,ij}} \right)$$

where $n_{w,ij}$ is the number of winter transitions to state i from state j , $p_{w,ij}$ is the proportion of winter transitions to state i from state j , and $p_{\sigma,ij}$ is the proportion of transitions in the summer \times summer matrix to state i from state j .

To examine the assumption that transitions only depended on the ecological state of a point in the previous census, the annual matrix derived from the product of the summer and winter matrices was compared to the observed annual transition matrix from one spring to the next using the following formula:

$$-2 \ln(\lambda) = 2 \sum_{i=1}^s \sum_{j=1}^s \sum_{k=1}^2 n_{ijk} \ln \left(\frac{p_{ijk}}{p_{ij}} \right)$$

where s is the number of states in the matrices, n_{ijk} is the number of transitions from state j to state i in matrix k , p_{ijk} is the proportion of transitions from state j to state i in matrix k , and p_{ij} is the average transition probability from state j to state i across both matrices. The log-likelihood value was compared to a χ^2 distribution with $s \times (s - 1)$ degrees of freedom. If the two

matrices differ, then the results indicate that the transitions depended on composition in the prior spring, beyond its effects on composition in the previous autumn.

Analysis and predictions of the model.—Because it incorporated seasonal variation and was analytically tractable, analysis focused on the pooled annual (spring to spring) transition matrix, which was derived from the product of the winter and summer transition matrices (“seasonal” matrices) pooled across years. I analyzed the basic pooled annual model in detail as follows. The dominant eigenvector, standardized so that its elements summed to 1, was examined to estimate the predicted long-term composition of ecological states in the community (i.e., the stable-stage distribution; Leslie 1945, Caswell 1989). The ratio of the dominant (λ_1) to the subdominant (λ_2) eigenvalue was also examined to estimate return time (Caswell 1989, DeAngelis 1989). Because each column must sum to 1 in a Markov community model, λ_1 always equals 1.

To predict the overall effect of species or ecological categories in the community, the model was then altered by systematically setting to zero each element in both the summer and winter transition matrices involving the target species or ecological state, calculating the product of the matrices to derive the adjusted annual matrix, and conducting eigenvalue and eigenvector analyses on each matrix.

Because multispecies Markov models evaluate the *proportion* of fixed points in ecological states, not the *number* of individuals of a particular stage in a population, all columns in a Markov community model must sum to 1. Thus, for a valid sensitivity analysis of these models, one or more other elements in the matrix must change to compensate for any change in the value of a target matrix element. I proportionally allocated the transition for the state being removed to the remaining states in each column of the summer and winter matrices before multiplying the matrices together, which is equivalent to simply deleting the observed transitions involving the target state in the raw data and recalculating a square matrix of dimension $(s - 1)$. This manipulation implies that any unaccounted differences within an ecological state do not predispose that state both to become the target state under normal circumstances and to change disproportionately to particular alternative states upon elimination of the target state.

Following removal of a species or ecological state from the summer and winter matrices, I then compared the matrix from the resulting modified annual matrix in several ways to evaluate the importance of that species to community structure. I explored the predicted response of the community to deletion of particular ecological classes by comparing the predicted community composition in the unmanipulated annual matrix and the matrices with ecological classes deleted. I derived community similarity following the formula:

$$\begin{aligned} \text{Similarity} &= \sum_{k=1}^s \min(p_{u,k}, p_{m,k}) \\ &= 1 - \left(\sum_{k=1}^s \sqrt{(p_{u,k} - p_{m,k})^2} \right) / 2 \end{aligned}$$

where $p_{u,k}$ is the proportion of the unmanipulated community in ecological state k , $p_{m,k}$ is the proportion of the community with an ecological state deleted in ecological state k , and s is the total number of ecological states in the model. Because the basic similarity comparison included changes in the community arising both from the absence of the target ecological state and from proportional shifts in other ecological states, I also compared the similarity of the manipulated model with the remaining species in the unmanipulated model after proportionally increasing their contribution so that their contributions summed to one. I also derived a similarity value for the predictions of the manipulated and the unmanipulated model, with the contribution of the target ecological state re-allocated to bare space, the expected consequence of species removal in a non-interactive community. Finally, the return time of the unmanipulated matrix and each manipulated matrix was calculated as $1/\lambda_2$, where λ_2 was the subdominant eigenvalue of the matrix, and was compared as an index of the effects of different ecological states on community resilience (Caswell 1989, DeAngelis 1989).

Each element contributing to the pooled seasonal matrices was also analyzed to determine the "sensitivity" and "elasticity" of the model predictions to each transition probability. Again, the procedure was not strictly the same as traditional sensitivity and elasticity analyses applied to stage-structured population models (Crouse et al. 1987, Caswell 1989, Doak 1992, Wootton and Bell 1992, Pfister 1998), and the Tanner et al. (1994) analysis of coral reefs. Again, elements beyond the target transition were proportionally adjusted to meet the constraint that all columns in the matrix must sum to 1. Sensitivity was explored by reducing each transition in the seasonal matrices by a fixed amount, equal to half of the minimum nonzero transition in either matrix, and proportionally adjusting the rest of the elements in the column to maintain a sum of 1. Elasticity was estimated by proportionally reducing each matrix element by 50% and proportionally adjusting the remaining elements in the column so that all elements summed to 1. Both sensitivity and elasticity were then evaluated, as previously described for the analysis of complete removals of particular ecological states, by comparing (1) the community similarity and (2) the return time of the resulting product of the summer and winter matrix to those of the unmanipulated annual matrix.

In addition to the systematic evaluation of the effects of particular ecological states and transitions, I explored the model to probe several potentially interesting processes. First, the model was analyzed after re-

moving both size classes of *Mytilus californianus* to predict the consequences of entirely eliminating the dominant species from the community. Second, the model was altered to estimate the independent and joint effects (1) of direct recruitment of large mussels into an area, rather than through larval recruitment; and (2) of Glaucous-winged Gull (*Larus glaucescens*) predation on goose barnacles (*Pollicipes polymerus*). Exploring the interactive effects of these two processes was of particular interest because they represent two fundamental differences between horizontal and vertical rock surfaces, which might lead to a shift in community composition, and because prior experiments demonstrated that bird predation can strongly affect community dynamics of the mussel bed (Wootton 1993b). To explore the effect of large-mussel recruitment, this process was eliminated by setting all transitions going from non-*Mytilus californianus* states to large *Mytilus californianus* to 0, and proportionally re-adjusting the other transitions so that all columns in the matrix summed to 1. In this model configuration, a site could only contain a large *Mytilus californianus* if it was first colonized by a small *Mytilus californianus*.

Markov models are most easily applied to sessile organisms; using them to estimate the effects of mobile predators is challenging. I applied one possible approach to the models by drawing upon extensive prior observational and experimental information on the rate of gull predation on goose barnacles (Wootton 1993b, 1994a, 1997). On the basis of both feeding rates and short-term experimental exclusions, gull predation triples the probability that a goose barnacle will not be present in a spot after a year. Therefore, to simulate the effect of gull extinction, I reduced all transitions in the annual matrix going from goose barnacles to other ecological states by one-third, and tripled all transitions leading from other ecological states to goose barnacles, adjusting all other transitions proportionally so that the columns of the modified transition matrix summed to 1. To explore the joint effects of large-mussel recruitment and bird predation, I first derived the summer and winter matrices without large-mussel recruitment, and then adjusted the resulting annual matrix for the change in gull predation on goose barnacles.

Consequences of violating model assumptions.—To evaluate the implications of using constant transition probabilities from the pooled data, rather than temporally varying transitions, I compared the predicted composition of the pooled model to two different models incorporating temporal variation in transition probabilities. First, I compared the model predictions to a time-varying stochastic model by running simulations in which a summer and winter transition matrix were randomly drawn for each year from the set of year-specific transition matrices derived from the data. The time-varying stochastic model was simulated 100 times and the results after 100-yr periods were tested against

the deterministic pooled annual model by comparing the distribution of similarities in community composition observed between different stochastic model runs to the similarities in composition between each stochastic run and the deterministic model. I used a *t* test to determine whether the deterministic model was significantly different from the stochastic model. I also compared the pooled annual model to an alternative time-varying model in which variations in transitions were not random, but varied cyclically in the sequence observed over the course of the study. The composition was calculated analytically from each of the five possible annual sequences (sequences ending with each of the five different years), and the average composition across each sequence was calculated to compare with the composition calculated for the pooled annual matrix. For example, the composition for the sequence starting with the matrix from year 5 and cycling through to year 4 (i.e., 5-1-2-3-4), was calculated from the matrix (M_1) arising from the formula:

$$M_1 = W_4 S_4 W_3 S_3 W_2 S_2 W_1 S_1 W_5 S_5$$

where W_x and S_x are the winter and summer transition matrices from year *x*, respectively.

*Tests of predictions under natural
and novel conditions*

To test the model, I first compared predictions of different model forms with independent transect data on species composition collected from Tatoosh Island. Transects were taken by starting at the edge of the mussel bed on a particular rock bench, randomly choosing a compass direction, laying a tape measure over the rock in the designated direction until it reached the end of the mussel bed, and recording the ecological state under each mark at 0.5-m intervals. When the transect reached the edge of the mussel bed, another compass direction was randomly chosen and the procedure was repeated. To insure a representative sample of the island, 20 transects were taken at 11 different wave-exposed sites, and were collected in three different years (1996–1988).

In total, 1128 data points were collected and compared to model predictions in two ways. First, I compared the model predictions to the observed community composition to determine whether they provided a significantly better fit than expected at random. To do this, I generated 200 randomly assembled communities by ordering each ecological state by its observed proportional composition, drawing a random number for each ecological state in a random community, ranking the random numbers, and then replacing the ranks with the proportional composition corresponding to the ranked value observed in the actual community. I then calculated the goodness-of-fit between the model predictions and either the observed community composition or the randomly assembled communities, using the proportion of variance in community composition ex-

plained and the similarity in community composition as indices of fit. The proportion of runs in which a randomly generated community explained more variance in community composition than did a particular model prediction was used as the probability value that a random model fit as well or better than the Markov model being examined. Second, I tested the models to determine whether their predictions differed significantly from the observed community composition, using a *G* test for goodness-of-fit (Sokal and Rohlf 1995). These two approaches provided complementary perspectives on the ability of the Markov models to predict community structure: the former indicates that the models can provide valuable predictive information, whereas the latter indicates that model predictions can be improved either by deriving more accurate estimates of model parameters after collecting more data, or by using a model of different structure.

As one initial test of the annual model to a novel set of circumstances from those used to parameterize the model, I compared model predictions derived from eliminating direct recruitment by large mussels, predation by gulls on goose barnacles, or both, to the composition of points collected from transects on vertical walls in the intertidal zone. Transects were established in 1997 and 1998 by identifying all investigator-accessible vertical walls along exposed shores of Tatoosh at the same tidal range as the mussel bed on horizontal benches, drilling holes into each end of the wall and attaching eyescrews, and suspending a tape measure between the eyescrews. Where necessary, additional eyescrews provided support of the transect to accommodate irregularities and directional changes of the vertical walls. The ecological state was characterized at 10-cm intervals along each transect, and 1146 points were collected. Fits of the modified models to the vertical-wall transect data were carried out following the procedures outlined previously for comparisons of the unmanipulated model and transect data from horizontal benches.

I also tested the model predictions derived from eliminating predation by gulls on goose barnacles to results from a previously published experiment (Wootton 1993b) in which gulls were experimentally excluded. In this experiment, birds were excluded from gaps in the mussel bed dominated by recently settled goose barnacles by using large-mesh (4.0 × 2.5 cm) cages over a period of 3–5 yr (median 4 yr), depending on staggered starting dates. There were 22 replicates of the experiment, each paired with an unmanipulated control area adjacent to the cage. At annual censuses, data were taken on the percentage of area covered by (1) *M. californianus*, (2) *Pollicipes*, and (3) other ecological states. In the present analysis, I used cover data from the last date censused for each cage–control pair. More detailed descriptions of the experiment and its results are presented in Wootton (1993b).

The Markov models were compared with two pre-

dictions of these experiments. First, the predicted and observed composition in the presence and absence of birds was compared by deriving the Euclidean distance in multivariate space (1) between each pair of cage or control plots, and (2) between each cage or control plot and the predictions of community composition from the manipulated (no gull predation on *Pollicipes*) or unmanipulated Markov models, respectively. The Euclidean distances were compared using one-tailed *t* tests to determine whether the distances between model predictions and experimental plots were significantly larger than the distances among pairs of plots. One-tailed tests were used because significant model deviations from the observed points should produce larger Euclidean distances, on average, between predictions and observations than the deviations among the different replicates. Second, the predicted change in community resilience in the presence and absence of gulls was examined, using a one-sample *t* test, by deriving the cage : control plot ratio of the rate of invasion of *M. californianus* for each experimental replicate, and comparing the distribution of ratios to the factor change in return time between the manipulated and unmanipulated Markov models. The latter value was calculated as $\ln(1/\lambda_{2u})/\ln(1/\lambda_{2m})$, following the formulas for return time presented in Caswell (1989: 71), where λ_{2m} and λ_{2u} are the subdominant eigenvalues of the manipulated (no gull predation on *Pollicipes*) and unmanipulated Markov models, respectively.

RESULTS

Unmanipulated model

The majority of transitions in the summer (186/196), winter (183/196), and annual matrix were nonzero (Table 2). In general, the largest terms in the matrices were associated with states remaining the same between samples and with transitions to large *Mytilus californianus* and *Corallina vancouveriensis*. Eigenvalue and eigenvector analysis of the annual matrix predicted a community dominated by large individuals of *M. californianus* (~60%), with small *M. californianus* occupying another 7% of the points (Table 3). Other community components persisted at low levels (<10%). The eigenanalysis of the annual matrix predicted a damping ratio of 2.72, corresponding to a return to within 95% of steady-state conditions from bare rock within four years (Fig. 1). Successional patterns predicted by the model beginning with 100% bare space agree well with patterns reported in Paine and Levin (1981) for this site: bare rock and diatoms are followed by acorn barnacles and ephemeral algae, followed by perennial algae, *Pollicipes polymerus*, and *Mytilus trossulus*, which are then displaced by *M. californianus* (Fig. 1). Transitions in the summer and winter matrices underlying the pooled annual matrix differed significantly from each other, justifying the seasonal structure of the model ($G = 661.7$, $df = 169$, $P < 0.0001$). The

seasonal differences remained when comparing the pooled winter and summer transitions over the same time scale ($G = 2562$, $df = 182$, $P < 0.0001$). Transitions among ecological states differed significantly from random ($G = 12524$, $df = 169$, $P < 0.0001$), indicating that components of the intertidal community were interactive.

Model predictions

Sensitivity of model predictions to a small reduction (-0.00014, half of the smallest nonzero transition in either pooled seasonal matrix) in individual transitions exhibited a skewed distribution, with most transitions having minor effects (Fig. 2). Transitions having relative large sensitivity (> 0.01% composition change) included those moving from large *M. californianus* to *Balanus*, *Halosaccion* and ephemeral algae (*Ulva/Porphyras*) during the summer, and from large *M. californianus* to all states except large and small *M. californianus* in winter. Moderate sensitivities (>0.001% composition change) were associated with other transitions from large *M. californianus*, most transitions from *Corallina* in winter, most transitions from small *M. californianus* in winter, and transitions from small *M. californianus* to *Balanus*, *Halosaccion*, and ephemeral algae in summer. Effects on model predictions of proportional reductions in single transitions (elasticity) exhibited an even more skewed distribution, with most transitions having little effect on model predictions (Fig. 2). Only two transitions (0.5%), summer and winter self-replacement rates of large *M. californianus*, caused >10% change in community composition in response to a 50% drop in transition probability. Altering another seven terms (1.8%), all contained in the winter matrix, caused >1% change in community composition. These terms included transitions from *Corallina* and small *M. californianus* to large *M. californianus*, *Corallina* self-replacement, and transitions from big *M. californianus* to *Pollicipes*, small *M. californianus*, ephemeral algae (*Ulva/Porphyras*), and empty space (rock/diatoms).

Predicted community composition changed substantially with removal of large *Mytilus californianus*, but was relatively insensitive to deletion of most other species or ecological states (Table 4). Removing all *M. californianus* also caused large changes in predicted community composition (Fig. 3). In the absence of California mussels, the model predicted that *Corallina* would become the community dominant, with lesser contributions by *Semibalanus*, *M. trossulus*, and *Pollicipes*. The model predicted that eliminating direct recruitment by large *M. californianus* would produce a modest change in the community (27% change in composition), reducing California mussel cover to 45% and increasing *Corallina* cover (Fig. 3). The model also predicted modest changes in long-term community composition with the removal of gulls (25% change in composition), with *M. californianus* covering 51% of

TABLE 2. Summer and winter transition matrices pooled across years for the middle-intertidal community of Tatoosh Island, Washington, USA. Codes are as in Table 1.

To:	From:								
	B	BG	CV	HAL	MT	PP	SC	SMC	FIRD
Summer transitions (May–September)									
B	0.885	0.023	0.134	0.028	0.152	0.339	0.182	0.477	0.148
BG	0.0003	0.236	0.021	0.031	0.051	0.005	0.065	0.004	0.025
CV	0.014	0.056	0.470	0.165	0.036	0.108	0.115	0.032	0.198
HAL	0.001	0.232	0.080	0.365	0.005	0.014	0.057	0.009	0.049
MT	0.004	0.023	0.012	0.031	0.418	0.033	0.032	0.047	0.037
PP	0.024	0.019	0.031	0.031	0.016	0.379	0.026	0.037	0.012
SC	0.011	0.046	0.031	0.126	0.054	0.024	0.307	0.031	0.124
SMC	0.045	0.014	0.094	0.051	0.154	0.068	0.099	0.336	0.136
FIRD	0.003	0.014	0.067	0.008	0	0.008	0.020	0.007	0.148
FLRD	0.0003	0.014	0.009	0.024	0.005	0.003	0.012	0	0.012
FLCR	0.001	0.009	0.015	0.016	0.009	0.003	0.008	0.001	0.025
R&D	0.004	0.134	0.023	0.051	0.065	0.014	0.022	0.007	0.062
UV&PR	0.002	0.167	0.008	0.059	0.034	0.003	0.042	0.001	0.025
Other	0.005	0.014	0.004	0.016	0	0	0.014	0.012	0
Winter transitions (September–May)									
B	0.799	0.043	0.297	0.060	0.348	0.468	0.313	0.622	0.308
BG	0.009	0.118	0.006	0.049	0.020	0.006	0.023	0.004	0
CV	0.014	0.107	0.437	0.347	0.048	0.070	0.113	0.043	0.301
HAL	0.003	0.089	0.011	0.171	0	0.003	0.005	0.003	0.023
MT	0.005	0.337	0.017	0.035	0.199	0.009	0.076	0.049	0.030
PP	0.034	0.025	0.037	0.035	0.008	0.320	0.039	0.027	0.015
SC	0.018	0.031	0.031	0.069	0.031	0.024	0.220	0.027	0.053
SMC	0.045	0.021	0.113	0.074	0.157	0.054	0.118	0.184	0.113
FIRD	0.002	0.046	0.013	0.014	0.011	0	0.028	0.004	0.083
FLRD	0.003	0.025	0.009	0.007	0.003	0	0.007	0.003	0
FLCR	0.004	0.017	0.002	0.019	0.031	0	0.014	0	0.008
R&D	0.030	0.097	0.016	0.083	0.143	0.042	0.030	0.024	0.038
UV&PR	0.029	0.043	0	0.030	0	0	0.012	0.008	0.008
Other	0.006	0.002	0.011	0.007	0	0.003	0.002	0.004	0.023

the rock and *Pollicipes* covering another 29% (Fig. 3). Simultaneously removing both the gulls and the recruitment of large *M. californianus*, a circumstance found on vertical rock walls, was predicted to have relatively large effects (46% change in composition), with *M. californianus* cover being reduced to 28% and *Pollicipes* cover increasing to 42% (Fig. 3).

The model predicted quite different patterns for effects of different species or ecological states on return times, a measure of stability (Table 4). Large impacts of *M. californianus* on community composition were not necessarily reflected in its effects on return time. Although removing large *M. californianus* caused a modest acceleration of return time (14% faster than in the unmanipulated model), removing small *M. californianus* caused a modest slowing in return time (25% slower). Consequently, removing all *M. californianus* caused little change (8% slower) in return time. In contrast, some ecological states that had minimal effects on community composition had effects comparable to *M. californianus* on return time; removing *Balanus*, *Halosaccion*, fleshy red algae, fleshy crustose algae, and rock/diatoms all accelerated return times by $\geq 5\%$, whereas removing *Corallina*, *Pollicipes*, and ephemeral algae all slowed return times by $\geq 5\%$. The model predicted that removing gulls would increase return time nearly twofold.

Tests of assumptions

Transitions from the annual model derived from the product of the winter and summer matrices differed significantly from the observed pattern of transitions from spring to spring ($G = 732.36$, $df = 182$, $P < 0.0001$), suggesting that transitions from fall to spring depended, in part, on the state of the community in the previous spring, a violation of the assumptions of the simple Markov models. Nevertheless, the long-term composition predicted by the spring-to-spring matrix was nearly identical to that predicted by the annual matrix (Table 3; similarity = 0.9764).

Summer and winter transitions exhibited significant variation between years ($G = 1399.6$, $df = 676$, $P < 0.0001$), a violation of assumptions of the Markov model. Nevertheless, community composition predicted by a stochastic model version incorporating observed interannual variation in transitions did not differ significantly from the pooled Markov model (Table 3). The similarity between community composition among each pair of different stochastic model runs (0.8795 ± 0.0563 , mean ± 1 SD, $n = 4950$) was not larger than the similarities between the prediction of the pooled Markov model and each stochastic run (0.9000 ± 0.0275 , $n = 100$). A deterministic, time-varying version of the model in which the transitions cycled

TABLE 2. Extended.

FLRD	From:			
	FLCR	R&D	UV&PR	Other
0.038	0.096	0.049	0.029	0.381
0.132	0.058	0.305	0.239	0.053
0.264	0.096	0.048	0.042	0.066
0.113	0.144	0.116	0.222	0.066
0.038	0.019	0.009	0.021	0.013
0.038	0.010	0.006	0.008	0
0.019	0.106	0.064	0.071	0.066
0.094	0.029	0.028	0.004	0.105
0	0.039	0.016	0	0.026
0.151	0.029	0.015	0.046	0
0.019	0.183	0.033	0.042	0
0.019	0.144	0.183	0.134	0.105
0.019	0.019	0.113	0.130	0.053
0.057	0.029	0.017	0.013	0.066
0.141	0.193	0.160	0.037	0.378
0.063	0.011	0.025	0.071	0.014
0.281	0.159	0.203	0.187	0.095
0.078	0.034	0.025	0.129	0.081
0.063	0.068	0.071	0.187	0.014
0.031	0.011	0.071	0.025	0.027
0.031	0.057	0.034	0.033	0.054
0.031	0.171	0.077	0.083	0.068
0.063	0.034	0.046	0.046	0.041
0.078	0.011	0.012	0.017	0.027
0.016	0.057	0.065	0.033	0.014
0.047	0.171	0.160	0.091	0.108
0.047	0	0.022	0.062	0.014
0.031	0.023	0.031	0	0.068

through the sequence observed in the data also predicted results similar to the Markov model, with a similarity in average long-term community composition of 0.9025 (Table 3).

Model tests: natural community

Quantitative predictions of the basic Markov model fit the distribution of ecological states observed from points on independent transects very closely (Table 3, Fig. 4). The Markov model successfully predicted 98.7% of the variance in composition among ecological states, and the similarity index between observed and predicted composition was >90%. This degree of fit was significantly better than expected at random ($P < 0.005$), indicating that the model provided useful predictive ability. Nevertheless, the observed composition differed significantly from the predicted composition in a goodness-of-fit test (G test, $G = 115$, $df = 13$, $P < 0.0001$), perhaps because of the large number of sample points on the transects. Other model variants (spring–spring, stochastic time-varying, ordered time-varying) also fit the data well, all predicting >98% of the variance in composition and exhibiting similarities to the observed data of >89%. All model variants also did a significantly better job at predicting the community composition than predicted at random ($P < 0.005$), but despite the high quantitative similarity, predictions of all model variants differed significantly from the observed composition (G tests, all $G > 108$, $df = 13$, $P < 0.0001$). Although violations of the assumptions of the basic annual model were detected in my analysis, the basic model nevertheless provided the best overall fit in terms of the percentage of variation

TABLE 3. Predicted composition of ecological states in different Markov models, and of observed values ($n = 1126$) from independent transects. Indices of model fit and statistical significance are presented at the bottom of table.

Ecological state	Model				Observed
	Annual	Spring–Spring	Time-varying	Ordered time	
Big <i>M. californianus</i> (B)	0.621	0.642	0.644	0.636	0.594
<i>Balanus</i> (BG)	0.015	0.015	0.013	0.013	0.018
<i>Corallina</i> (CV)	0.078	0.072	0.071	0.075	0.040
<i>Halosaccion</i> (HAL)	0.015	0.015	0.012	0.011	0.005
<i>M. trossulus</i> (MT)	0.033	0.028	0.022	0.026	0.017
<i>Pollicipes</i> (PP)	0.044	0.045	0.050	0.044	0.059
<i>Semibalanus</i> (SC)	0.030	0.027	0.032	0.032	0.053
Small <i>M. californianus</i> (SMC)	0.069	0.062	0.074	0.075	0.070
Filamentous red algae (FIRD)	0.009	0.008	0.010	0.010	0.017
Fleshy red algae (FLRD)	0.005	0.005	0.004	0.004	0.018
Fleshy crustose algae (FLCR)	0.008	0.008	0.006	0.007	0.006
Rock and diatoms (R&D)	0.042	0.041	0.034	0.040	0.053
Ephemeral algae (UV&PR)	0.023	0.025	0.022	0.019	0.032
Other	0.007	0.007	0.007	0.008	0.018
Similarity to observed	0.907	0.898	0.903	0.903	
P (random as good)	<0.005	<0.005	<0.005	<0.005	
Variance of observed explained	0.987	0.983	0.983	0.985	
P (random as good)	<0.005	<0.005	<0.005	<0.005	
Goodness-of-fit	115.0	114.4	108.1	109.6	
P (different from observed)	<0.0001	<0.0001	<0.0001	<0.0001	

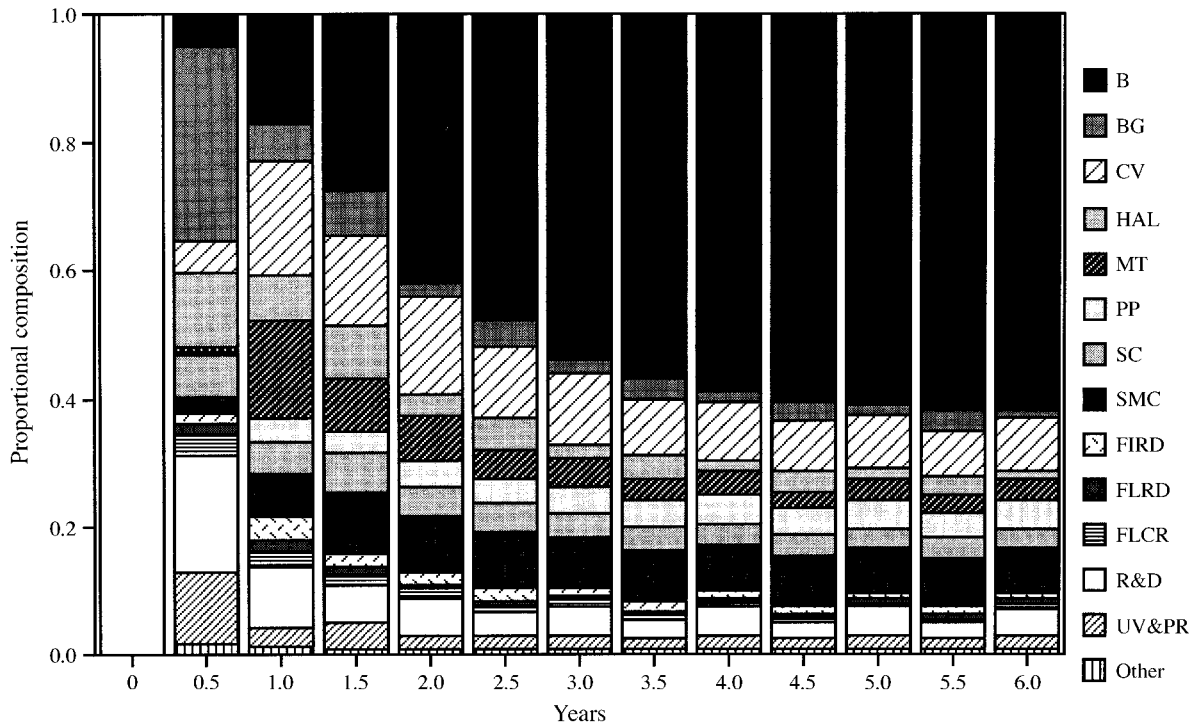


FIG. 1. Successional pattern predicted by the Markov community model over time, starting from 100% bare space. Ecological state codes are: B, large *Mytilus californianus*; BG, *Balanus glandula*; CV, *Corallina vancouveriensis*; HAL, *Halosaccion glandiforme*; MT, *Mytilus trossulus*; PP, *Pollicipes polymerus*; SC, *Semibalanus cariosus*; SMC, small *Mytilus californianus*; FIRD, filamentous red algae; FLRD, fleshy red algae; FLCR, fleshy crustose algae; R&D, rock and diatoms; UV&PR, ephemeral algae; Other, other sessile taxa.

in community composition predicted, and the percent similarity to the observed data from the independent transects.

Tests of model predictions in novel situations

The basic annual model also quantitatively predicted the community composition in a novel situation: on vertical walls in the absence of bird predators and big mussel recruitment (Fig. 5). The observed composition on horizontal benches and vertical walls differed significantly (G test, $G = 550.8$, $df = 13$, $P < 0.0001$), and had a similarity of only 0.557, indicating that vertical walls provided a novel challenge to the model predictions. The basic model successfully predicted 90.2% of the observed variation among ecological states in composition on vertical walls, and had a similarity value of 0.819, significantly better than expected at random ($P < 0.005$). Again, despite the relatively high amount of variation predicted by the model, the observed distribution of ecological states differed significantly from that predicted by the model (G test, $G = 341.6$, $df = 13$, $P < 0.0001$). Models that only incorporated the effect of eliminating either big-mussel recruitment (23.6% variance in community composition explained, similarity to observed = 0.627, G test, $G = 1076.6$) or gull predation on *Pollicipes* (61.8% variance in community composition explained, simi-

ilarity to observed = 0.745, G test, $G = 541.8$) did not fit the observed data as well as did the model with both processes eliminated.

The Markov model predictions also matched previous results from experiments excluding gull predation on *Pollicipes* (Wootton 1993b). The composition of *M. californianus*, *Pollicipes*, and other ecological states in control plots did not differ significantly from model predictions (Fig. 6a; Euclidean distance = 0.287 ± 0.202 (mean ± 1 SD) among replicates [$n = 231$ pairs of points], 0.239 ± 0.098 between predictions and replicates [$n = 22$ points]; one-tailed t test, $P > 0.5$). Similarly, the composition in bird exclusion plots did not differ significantly from model predictions (Fig. 6a; Euclidean distance = 0.213 ± 0.139 among replicates, 0.210 ± 0.085 between replicates and predictions; one-tailed t test, $P > 0.5$). Finally, the change in dynamics predicted by the model did not differ significantly from the observed change in the rates of *M. californianus* invasion between control and bird exclusion plots (Fig. 6b; one-sample t test, $P = 0.91$).

DISCUSSION

Markov community models did a good job of characterizing the sessile species occupying the middle-intertidal zone of Tatoosh Island. The basic model accounting for seasonality successfully projected almost

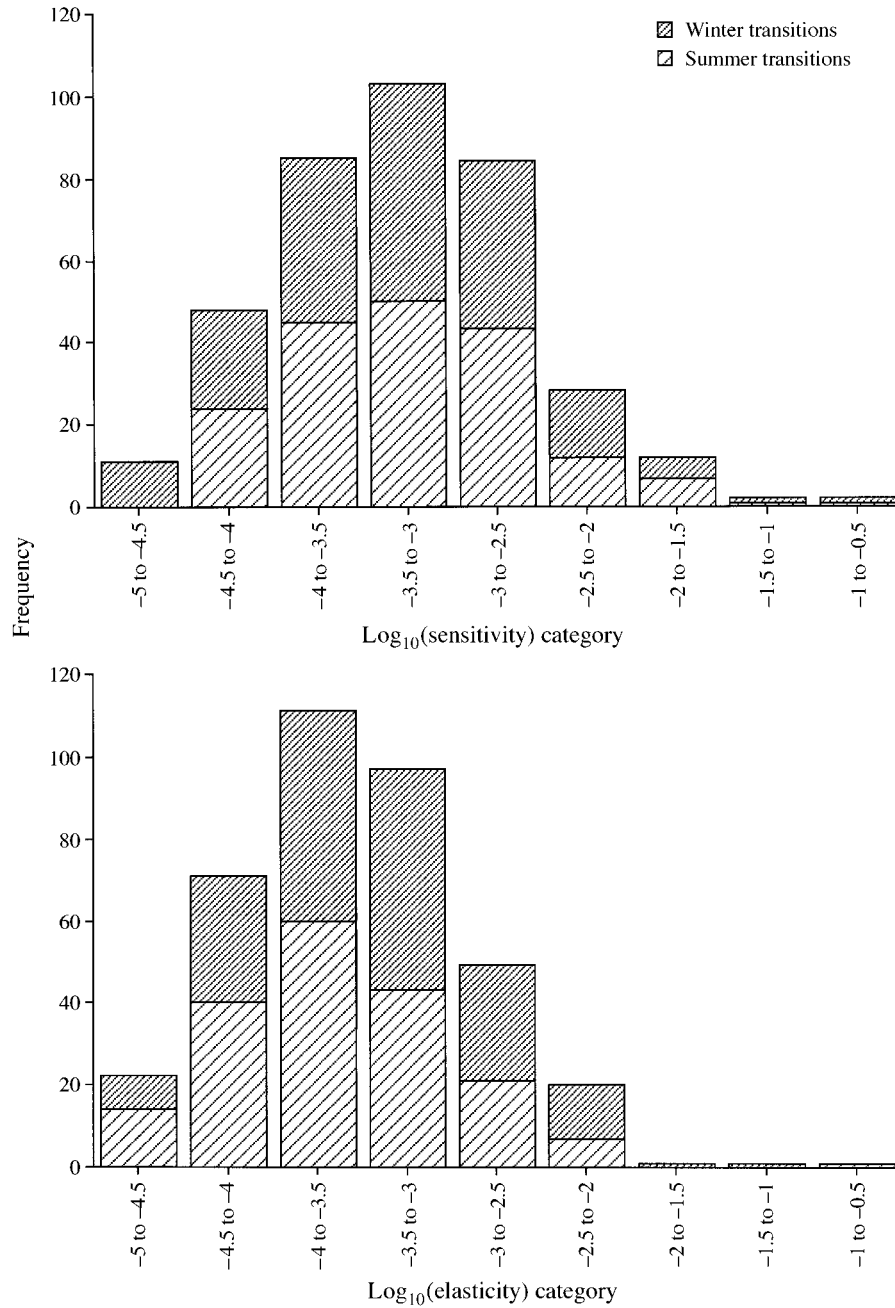


FIG. 2. Frequency distribution of \log_{10} sensitivity (top graph) and \log_{10} elasticity (bottom graph) for transitions in the winter (heavily hatched bars) and summer (lightly hatched bars).

99% of the variation in species abundance observed in independent transects, an extremely encouraging quantitative match between model predictions and observations. Studies of Markov models of forests (Horn 1975), herbaceous plant communities (Lippe et al. 1985, Lough et al. 1987), and arthropod communities (Usher 1981) have also found good matches to Markov model predictions, suggesting that these models gen-

erally may be effective at recapturing the basic structure of complex communities.

The high quantitative agreement between predictions and observations is surprising, given some of the potentially important processes that are not explicitly included in the model. First, the model predictions are for the equilibrium state, and intertidal communities are probably never exactly at equilibrium, even over large

TABLE 4. Similarity of long-term community composition of manipulated and unmanipulated annual matrices.

Ecological state removed	Sim†	Psim‡	Rsim§	Δ damping ratio	Time factor¶
Big <i>M. californianus</i> (B)	0.3718	0.7856	0.4145	0.480	0.860
<i>Balanus</i> (BG)	0.9707	0.9822	0.9707	0.205	0.932
<i>Corallina</i> (CV)	0.9217	0.9796	0.9296	-0.226	1.095
<i>Halosaccion</i> (HAL)	0.9763	0.9881	0.9765	0.362	0.889
<i>M. trossulus</i> (MT)	0.9668	0.9872	0.9668	0.0003	0.9999
<i>Pollicipes</i> (PP)	0.9558	0.9967	0.9573	-0.152	1.061
<i>Semibalanus</i> (SC)	0.9681	0.9924	0.9698	-0.066	1.025
Small <i>M. californianus</i> (SMC)	0.9309	0.9702	0.9367	-0.487	1.245
Filamentous red algae (FIRD)	0.9899	0.9973	0.9907	-0.0004	1.000
Fleshy red algae (FLRD)	0.9933	0.9977	0.9936	0.036	0.987
Fleshy crustose algae (FLCR)	0.9913	0.9970	0.9913	0.041	0.985
Rock and diatoms (R&D)	0.9386	0.9694	0.9595	0.143	0.951
Ephemeral algae (UV&PR)	0.9555	0.9714	0.9555	-0.143	1.057
Other	0.9913	0.9968	0.9913	-0.027	1.010
All <i>M. californianus</i> (B&SMC)	0.3026	0.7386	0.3598	-0.193	1.079
Big <i>M. californianus</i> recruitment	0.7339	NA	NA	-1.031	1.910
Bird predation on <i>Pollicipes</i>	0.7502	NA	NA	-1.040	1.929
Big <i>M. c.</i> recruitment and bird predation	0.5540	NA	NA	-1.177	2.308

Note: NA, not applicable.
 † Similarity in composition across all ecological states.
 ‡ Similarity in proportional composition of all remaining ecological states.
 § Similarity in composition to the long-term community composition where all sites that would have been occupied by the removed ecological state are instead occupied by bare rock.
 || The change in the damping ratio (from 2.723 in the unmanipulated model) for each change in the model structure.
 ¶ The corresponding factor by which predicted return time changed.

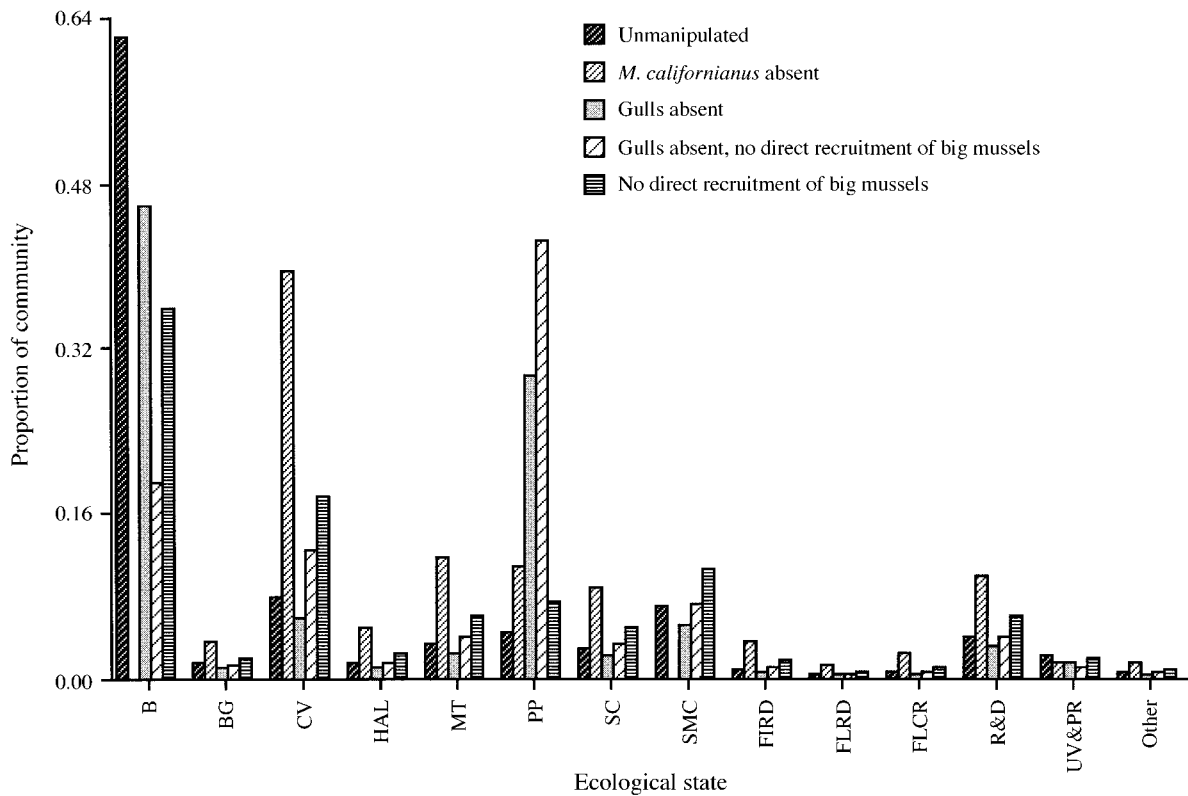


FIG. 3. Predicted community composition for selected model manipulations, compared with predictions from the unmanipulated model. Ecological state codes are as in Fig. 1.

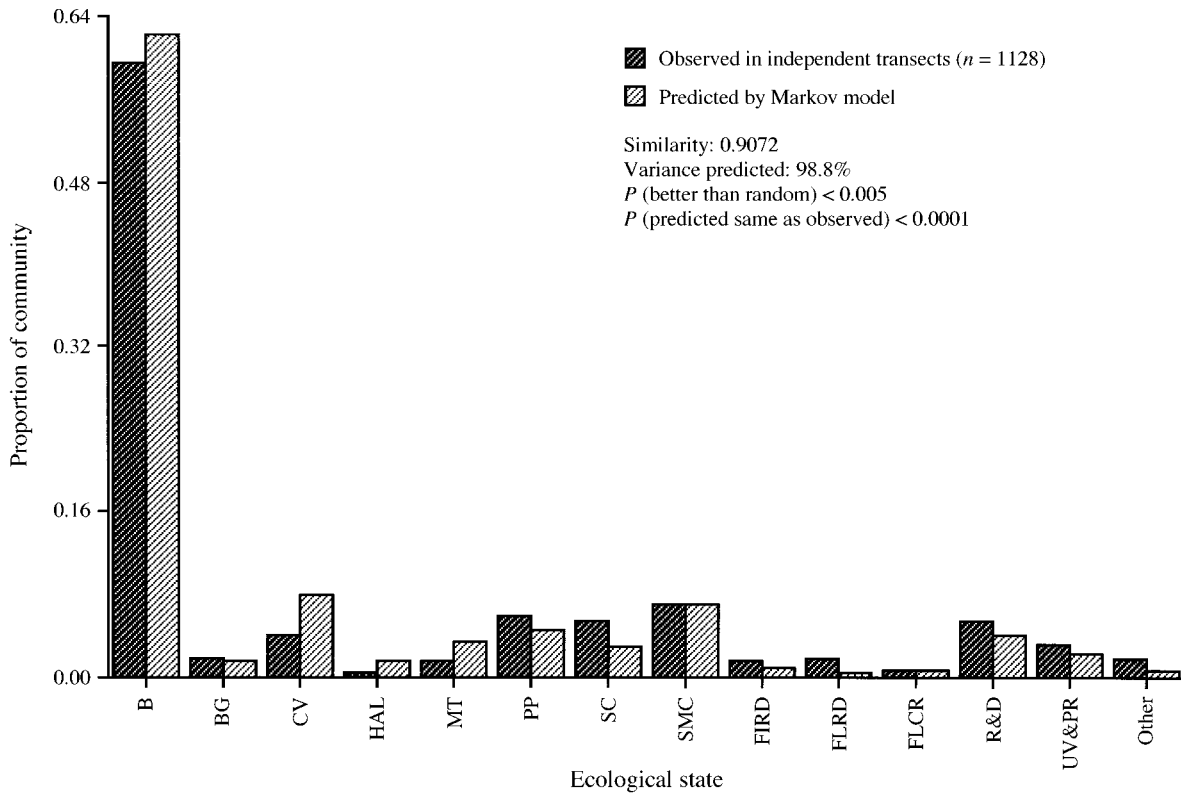


FIG. 4. Comparison of species composition observed in independent transects (dark bars) and predicted by the Markov community model (light bars). Ecological state codes are as in Fig. 1.

scales. Second, the models are spatially unstructured, yet transitions are likely to vary spatially because of differences in physical conditions such as tidal height, wave exposure, water runoff, proximity to bird colonies, and exposure to sun (e.g., Connell 1961, Lewis 1964, Paine 1974, Menge and Sutherland 1976, Underwood 1978, Leigh et al. 1987, Wootton 1991, Menge et al. 1994, Wootton 1994a, Bertness and Leonard 1997), and because of localized disturbances and interactions among sessile species thought to be important in producing the observed strong spatial patterning in this system (Paine and Levin 1981). Third, the transitions do not vary with species abundance, despite experimental documentation that species modify interactions between other species pairs within this community (Wootton 1992, 1993a).

Several interpretations might be drawn from this result. First, complexities introduced by spatial heterogeneity, local interactions, and interaction modifications may play minor roles in shaping the overall community composition in this system. Second, the complexities might be important, but are adequately imbedded in the transition probabilities (i.e., they do not introduce strong nonlinearities). Third, accounting for the complexities in future modeling extensions might be important: despite the large amount of variation in species composition predicted by the model,

the deviations of the observed composition were still statistically significant, indicating that more refined models or models using alternative structures could potentially improve predictive ability. Development of models incorporating some of these complexities is currently underway. Notwithstanding these and other potential complications, the high degree of fit by simple Markov models represents a high standard to be met by alternative approaches. Furthermore, increasing accuracy by 1.3% at most may not be worth the effort in some circumstances.

Model analyses of sensitivity, elasticity, and species deletion all suggest a skewed distribution of importance in specific transitions and overall effects of a species. The observed pattern of many weak interactions and few strong interactions is quite similar to patterns reported for more direct estimates of interaction strength in other studies of this intertidal system (Paine 1992, Wootton 1997) and in other systems (Fagan and Hurd 1994, DeRuiter et al. 1996, Raffaelli and Hall 1996). Predictions and sensitivity analyses of the model indicate that *Mytilus californianus* is the dominant interactor in this community, a fact previously reflected by a number of studies focusing on this species, its dynamics, and its interactions with other species (e.g., Dayton 1971, Harger 1972, Paine 1974, Suchanek 1979, Paine and Levin 1981, Sousa 1984, Wootton

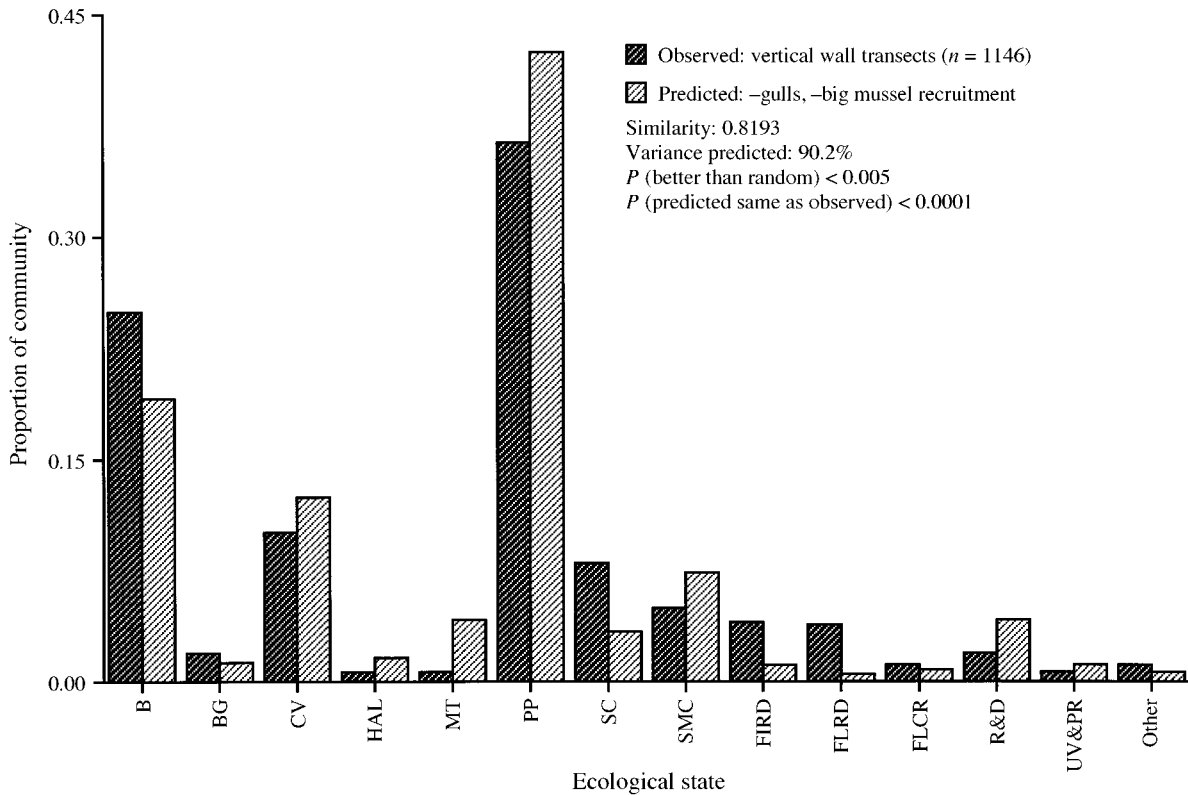


FIG. 5. Comparison of species composition observed in transects from vertical walls (dark bars) and predicted by the Markov community model, modified by removing adult mussel recruitment and gull predation on *Pollicipes* (light bars). Ecological state codes are as in Fig. 1.

1993b). Other model predictions were less obvious. The model also identified the importance of size structure, recruitment of adult mussels, and predation on goose barnacles by birds, as suggested by previous studies (Wootton 1993b, 1994a). Finally, the analyses identified relatively important effects of transitions involving *Corallina vancouveriensis*, and predicted its

dominance of the community with the removal of *M. californianus*. This species, which has received little study to date (Palumbi 1985), appears to be an unappreciated, but important, player in the community. Consequently, the model predictions have highlighted new directions for future experimental and mechanistic studies to better understand this intertidal system.

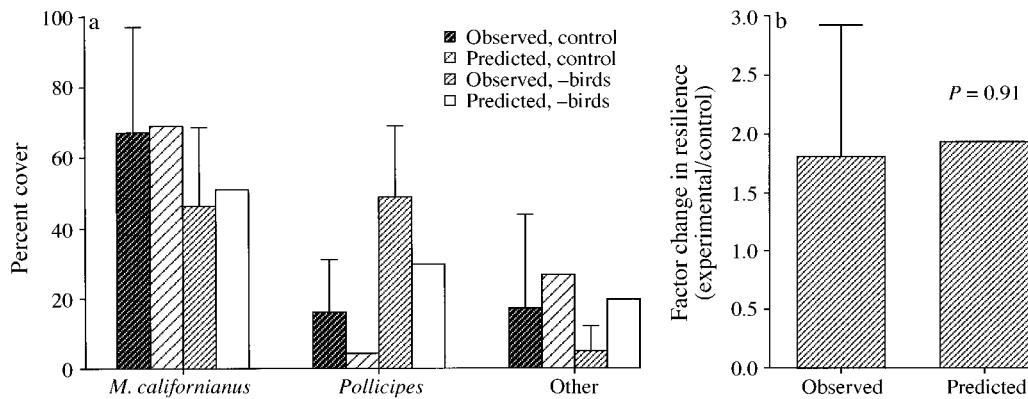


FIG. 6. Comparison of (a) species composition and (b) change in resilience (estimated by the ratio of the rates of *Mytilus californianus* invasion into experimental and control plots) observed in bird exclusion experiments reported in Wootton (1993b) and predicted by the Markov community model, modified by removing gull predation on *Pollicipes*. Error bars represent 1 SD ($n = 22$).

Model analysis also predicted important effects of removing species on the resilience of the system, as assessed by return times from a perturbation. Removing gulls had particularly strong effects, causing a near doubling in return time. Surprisingly, the strengths of effects of species on resilience and community composition were not well correlated. Therefore, focusing on only one aspect of the consequences of species extinction may underestimate the impacts that species loss may have (Berlow 1999). Reasons for the low correlation between effects on resilience and on composition are presently unclear, and the generality of this result is unknown. These results point to an intriguing area of investigation for future studies.

Data and model analysis indicated that the middle-intertidal zone of Tatoosh Island violated some of the assumptions of simple Markov models. In particular, transitions varied significantly over time and depended, to some extent, on the ecological state exhibited by a point more than one census period prior. Surprisingly, the basic Markov model performed better than models that accounted for these violations in predicting actual community composition. Several studies in other systems have also found that violations of these assumptions have minimal effects on model predictions (Usher 1981, Lippe et al. 1985, Lough et al. 1987, Tanner et al. 1996). Taken together, these results indicate that predictions of Markov models may be quite robust to some violations of their assumptions. In this study, the more accurate predictions of species composition by the simple Markov models could have resulted because expected increases in accuracy after accounting for assumption violations were offset by the increased error rates introduced when estimating more model parameters, a problem common to complex models in general (Ludwig and Walters 1985). Although the types of assumption violations identified here had little effect on the model, other unexplored violations might still cause substantial deviation. For example, if interannual variation in transitions reflects persistent directional trends, rather than stochastic or cyclical fluctuations, Markov models, like most other models, will probably make inaccurate predictions of the community composition. Identifying and characterizing directional changes in parameters over time will be challenging because of the long-term time series required.

Models are most useful when they can successfully predict new situations, rather than simply recapture observations of current conditions, yet quantitative ecological models are rarely subject to rigorous tests under novel circumstances. In this study, Markov models did a good job at quantitatively predicting community structure under several novel situations. First, the models parameterized with data from horizontal rock benches predicted well the change in community structure on vertical walls, after I modified them to eliminate gull predation on goose barnacles and direct recruitment by adult *M. californianus*. The good fit of this

modified model relative to model versions that retained one of these two processes supports previous suggestions (Wootton 1993b) that both processes are important in causing the observed dominance shifts in vertical-wall habitats. Other studies have found similar shifts in important ecological processes with changes in substrate slope (e.g., Witman and Cooper 1983, Sebens 1985, Larson et al. 1999).

The model also predicted the results of a prior experiment excluding birds from horizontal benches (Wootton 1993b). Beyond recapturing the change in species composition between treatments, the model also accurately predicted the average change in temporal dynamics observed in this experiment. The comparison with the compositional results of the prior bird manipulation experiment should be viewed with some caution, however, for several reasons. The duration of individual replicates varied and had not necessarily converged to a single attractor. Additionally, the starting conditions within the experiments were focused on gaps with recently colonized *Pollicipes*, which might have caused overrepresentation of this species in the plots. These two factors should have resulted in significant deviations from the model predictions if they were important. Finally, the data were not collected at the same taxonomic resolution as the model predictions, so the lumping of most categories may have masked important deviations from model predictions. Ideally, repeating the bird exclusion treatment and sampling it specifically to test the model predictions would be desirable. Furthermore, none of these issues is likely to strongly affect the test for resiliency. In any event, the match between model predictions and novel circumstances is encouraging, particularly in light of the indirect methods required to estimate effects of bird predation under the Markov model structure.

The model predictions also motivate other rigorous, independent experimental tests for the future. In particular, selective local extinction of *M. californianus* should produce large changes in community structure, permitting a severe test of the model. Although the qualitative prediction that removing mussels should produce large changes should not be surprising, in light of its numerical dominance and the results of previous work at this and nearby sites (e.g., Paine 1966, 1974, Dayton 1971, Paine and Levin 1981, Wootton 1993b), quantitative predictions about the new community composition have never been made, and long-term experiments selectively removing *M. californianus* have never been carried out. Additionally, experimental manipulations of other sessile species that produce substantial long-term changes in community composition would raise serious questions about the predictive ability of Markov models in the face of novel conditions.

Despite the initial success of Markov models in predicting features of this rocky intertidal system, several factors may limit their successful application in some settings. In particular, some types of environmental im-

pacts, such as changes in limiting nutrients or in physical conditions that affect physiological performance rather than mortality, are not readily incorporated into this modeling framework. Additionally, these models are most easily applied to sessile species. Markov models might incorporate mobile organisms in two ways. One method is to use ancillary information on the effects of mobile species on sessile species, as this study demonstrates. The detailed information necessary in this approach may not be readily available in many circumstances. Furthermore, strong effects of mobile species on multiple sessile species, or on other mobile species, which, in turn, affect sessile species would probably compromise the accuracy of Markov model predictions. For example, aside from eating goose barnacles, birds also strongly reduce limpet grazers in this system (Wootton 1992, 1993a). Limpets, in turn, strongly affect densities of algae and barnacles (Dayton 1971, Johnson 1992, Wootton et al. 1996b). My failure to account for these interactions when estimating the effects of birds probably did not seriously compromise model predictions in this study, only because of the predicted weak effects that barnacles and algae have on community composition over the long term. A second method is to collect abundance data for both sessile and mobile species in defined areas such as quadrats or individual lakes or ponds, rather than on fixed points, and to characterize ecological states of each area at each census by dividing abundances of each species into several discrete categories (such as absent, "low", and "high"). A study of oceanic fish and cephalopod assemblages (Saila and Erzini 1987) illustrates this approach. Incorporating the abundances of multiple species may be more difficult than focusing on sessile individuals, both because the required size of the study area may be large, and because formation of a limited number of categories may require fairly arbitrary division of abundance for each species.

Despite these limitations, the ability of Markov models to quantitatively predict aspects of the composition and dynamics of the rocky intertidal zone under current and novel conditions is very encouraging. These models are some of the most empirically accessible models available for characterizing complex ecosystems, making them potentially useful for identifying important interactions and processes in natural communities, for detecting changes in ecosystem function, and for permitting insight into the consequences of species extinction, size-structured interactions, and disturbance regime. Given their performance in this study, Markov models may merit exploration in other communities.

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