Succession on Marine Hard Substrata: A Fixed Lottery

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Summary. Community development is described for a temperate fouling community near Bremerton, Washington. Multivariate and functional group analyses are undertaken which reveal certain underlying patterns in the observed succession. These patterns include a steady increase in the dominance of solitary animals over their colonial counterparts, as well as a gradual convergence upon a few relatively persistent species assemblages. In our discussion of these results, a Markov model for succession on marine hard substrata is introduced. Implications of the model and its limitations are explored in terms of community development and stability. Finally, an attempt is made to reconcile the model's results with our field observations.

Introduction

Natural communities are characterized by structural changes in response to various biotic and abiotic forces. These changes through time, referred to as community development, are often continuous, reflecting the processes associated with each species' recruitment, survival and mortality. In the analysis of community development, ecologists are faced with the task of relating community structure at one instant in time with that at some other instant. If the development is orderly and directional, some type of predictive capability can be achieved from the analysis. In many natural communities, however, the stochastic nature of the developmental process can often mask any underlying order and directionality. To reveal underlying patterns in the face of such stochastic noise is a difficult undertaking, and largely dependent on the spatial and temporal scales chosen for the analysis. Structural changes over "moderate" time intervals are typically referred to as succession (MacMahon 1979). The concept of succession is somewhat elusive, certainly controversial (Connell and Slatyer 1977; MacMahon 1979) and quite often conotes different processes to different ecologists. We will retain the term in our discussion, however, its usage is not intended to imply anything more than the directional changes observed in community composition through time.

Successional studies had their origin and greatest proliferation in terrestrial communities (see review in MacMahon 1979). Nevertheless, the rapidity of community development in certain marine environments has endeared the "en-

crusting beasties of rocky seashores" (Horn 1976, p. 188) to many of the recent workers addressing the topic of succession (Osman 1977; Sutherland and Karlson 1977; Dean and Hurd 1980; Sousa 1979, 1980). The subtidal, epibenthic communities associated with the fouling of man-made structures (i.e., fouling communities) appear to be nearly ideal experimental testing grounds for investigating the processes associated with succession. In addition to rapid development, fouling communities offer the practical advantages of working with organisms which are relatively well-known, predominantly sessile and which can be induced to settle on easily replicated artificial substrates (Sutherland and Karlson 1973). Recognition of these assets has led to a considerable number of studies describing the community development on artificial substrates in marine environments (WHOI 1952; Schoener, in press). Despite their numerical abundance, however, there is little agreement among these studies about whether or not succession really occurs in fouling communities (Sutherland and Karlson 1977). The purposes of the present study are twofold: first, to describe the succession observed in the fouling community at Bremerton, Washington and second, to fit these observations into a more general, theoretical framework.

Study Site and Methods

Fouling community development was monitored for 81 weeks in Phinney Bay, a small bay adjacent to Bremerton, Washington. In mid-June 1978, 16 textured, white formica panels (412 cm² each) were submerged at 1–1.3 m beneath the Bremerton Yacht Club's floating docks. Percent cover for sessile species growing on the "primary space" (Dayton 1971) of a given panel's undersurface was estimated by a point sampling technique (Sutherland and Karlson 1973), using 100 points randomly positioned over the panel's area. This sampling technique is nondestructive with panels being resubmerged for further development after censusing. More details on the sampling methodology are given in Schoener and Greene (1980; 1981).

Relative to our other study sites in Puget Sound and the San Juan Archipelago, the Bremerton fouling community is rich in terms of the number of attached, epibenthic organisms. Fifty-two sessile, macrofaunal species were recorded over the 81 weeks of the study. Five macroalgal species were recorded as well, however, these algae were generally rare throughout the study and never became an important component in the community. In this diverse community, multivariate and functional group analyses have greatly facilitated the investigation of community de-

Table 1. Classification of the Bremerton species into their appropriate functional groups

I. Solitary animals
  A. Sessile animals
      Metazoa: Annelida: Polychaeta
                     Eudistylia vancouveri   Serpulid sp. 1
                     Nereid sp. 1   Spionid sp. 1
                     Pseudopotamilla occelata   Syllid sp. 1
                     Sabellid sp. 1   Syllid sp. 2
                     Schizobranchia insignis
             Arthropoda: Crustacea
                     Amphiphod sp. 1   Balanus crenatus
             Chordata: Tunicata
                     Ascidia sp.   Corella willmeriana
                     Boltenia villosa   Styela gibbsii
                     Chelysoma productum   Tunicate sp. 1
             Cnidaria: Anthozoa
                     Metridium senile
                 Scyphozoa
                     Unknown scyphistomae
             Mollusca: Gastropoda
                     Coryphella sp. eggs   Hermissenda crassicornis eggs
                     Crepidula sp.
                 Bivalvia
                     Chlamys sp.   Mytilus edulis
                     Hiatella sp.
           Unknown egg mass
      Protozoa: Ciliophora: Ciliatea
                     Folliculina sp.
  B. Sedentary animals N.A.
  C. Excavators N.A.

II. Colonial animals
  A. Runners
      Metazoa: Cnidaria: Hydroida
                     Clytia sp.   Hydroid sp. 1
                     Tubularia sp.
  B. Sheets
      Metazoa: Chordata: Tunicata
                     Diplosoma macdonaldi
             Ectoprocta: Gymnolaemata
                     Electra crustulenta arctica   Rhamphostomella sp.
                     Hippothoa hyalina   Tubulipora sp.
                     Membranipora membranacea Bryozoan sp. 1
                     Reginella sp.   Bryozoan sp. 2
             Porifera: Demospongiae
                     Halichondria panicea   Sponge sp. 1
                     Haliclona permolis
  C. Mounds
      Metazoa: Chordata: Tunicata
                     Aplidium sp.
  D. Plates N.A.
  E. Vines
      Metazoa: Cnidaria: Hydroida
                     Obelia sp.
             Ectoprocta: Gymnolaemata
                     Bowerbankia sp.   Bryozoan sp. 3
  F. Trees
      Metazoa: Chordata: Tunicata
                     Distaplia occidentalis   Tunicate sp. 2
             Ectoprocta: Gymnolaemata
                     Bugula sp.   Bryozoan sp. 4
                     Crisia sp.
             Porifera: Calcarea
                     Scypha raphanus

velopment. A multivariate clustering technique was employed in this study to reveal possible underlying patterns in the observed community development. The clustering method we adopted is agglomerative and hierarchical, being based on the Bray-Curtis Similarity Index (Clifford and Stevenson 1975) and utilizing a flexible combinatorial strategy (Lance and Williams 1967). Data were entered into the Clustan© statistical program as a data matrix consisting
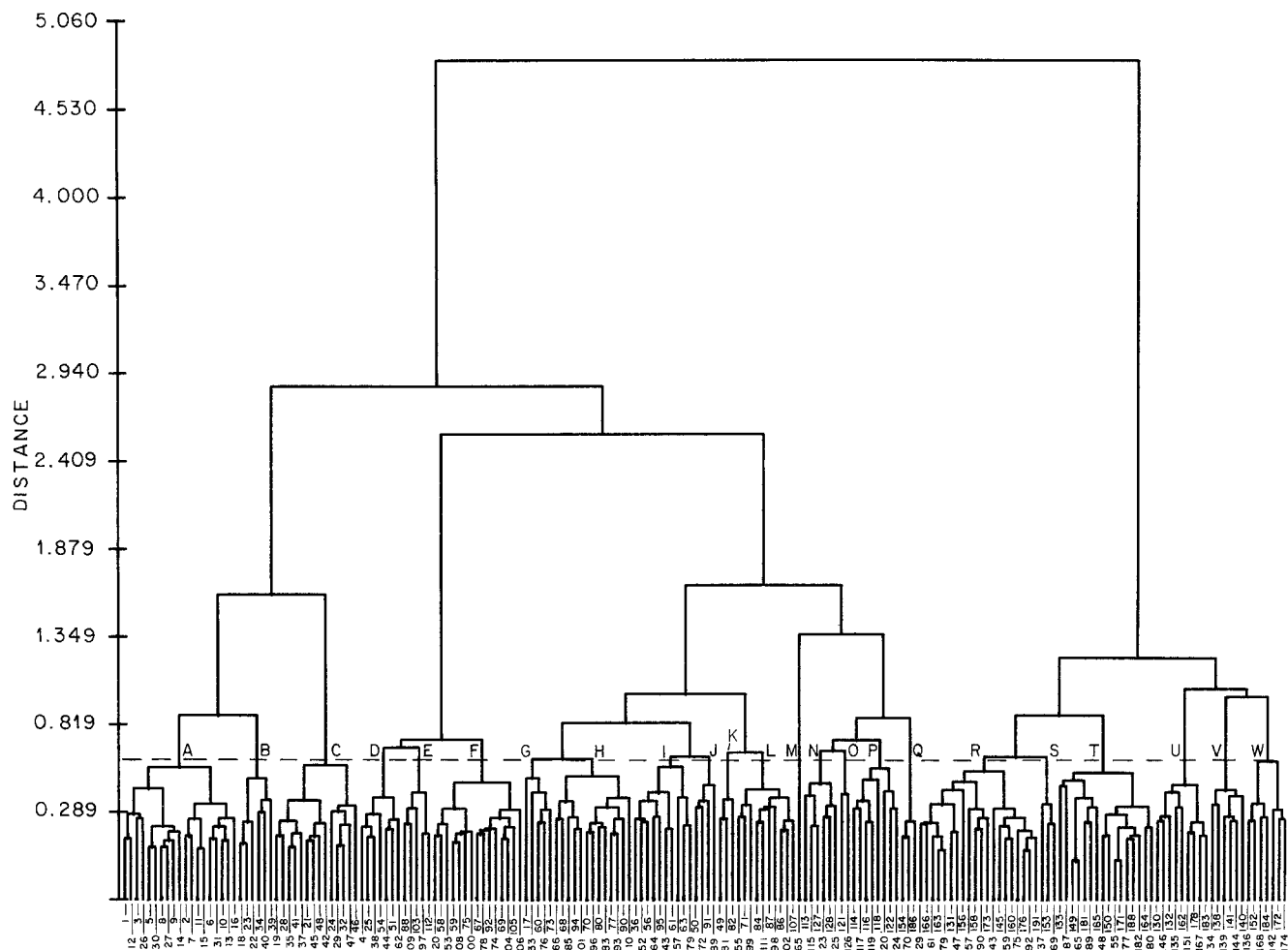
Fig. 1. The dendrogram corresponding to the 16 panels censused on 12 sampling dates ($16 \times 12 = 192$ entries). An agglomerative, hierarchical clustering technique was utilized with a flexible combinatorial strategy (clustering intensity coefficient $\beta = -0.25$). Groups A through W were designated at a distance level $D = 0.60$

of 192 separate individuals (representing the 16 panels for each of 12 sampling dates) and their 58 corresponding attributes (representing the relative abundance of each species). Empty space was treated as another species in the analysis since, as does Quinn (1979), we view it as an essential and interacting element in space-limited systems.

Functional group analysis provides an additional analytical tool in describing community development, perhaps more clearly extracting the relationship between form and function in the hard substratum epibenthos (Greene and Schoener, in preparation). This method involves, first, assigning epibenthic organisms to functional groups on the basis of how they use and alter their environments (Woodin and Jackson 1979), and then following the development of these species aggregates through time. Using the definitions of Jackson (1979) and Woodin and Jackson (1979), all macrofaunal species in the Bremerton fouling community were classified and placed into their appropriate functional groups (Table 1). Since data were only collected for sessile species, sedentary animals were not included in the analysis.

Results

The dendrogram in Fig. 1 corresponds to the output of the clustering program described previously. From this dendrogram, 23 characteristic species assemblages were assigned at a distance level equal to 0.60 and then given a letter designation from A through W. The 0.60 level was
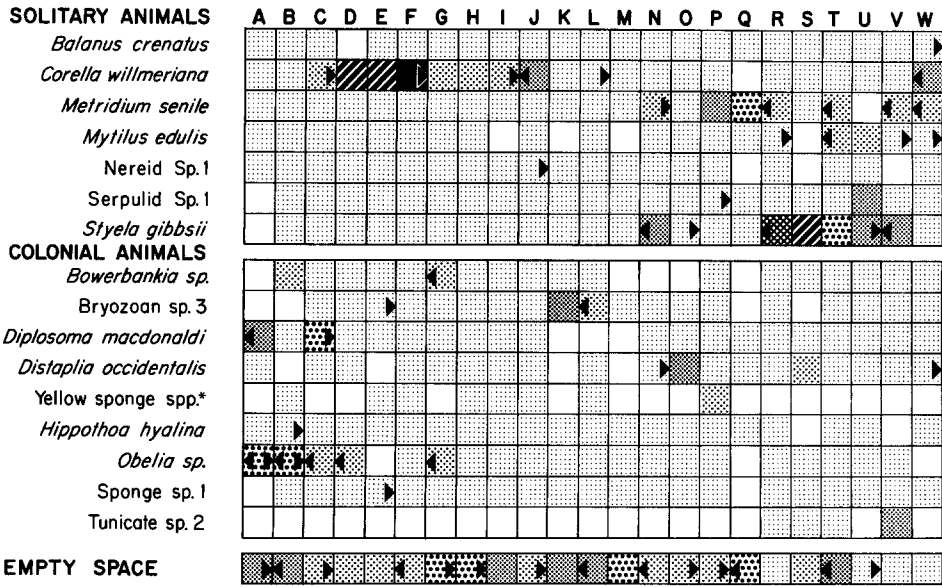
Table 2. The species assemblage designation corresponding to each of the 12 sampling dates during the Bremerton study

Panel	Week											
	7	11	16	20	24	30	39	48	58	67	74	81
1	A	G	G	K	M	K	E	N	R	R	R	T
2	A	B	B	J	H	K	L	P	U	U	U	U
3	A	C	C	D	F	H	L	N	R	R	R	R
4	D	F	I	I	H	L	F	P	U	T	T	T
5	A	C	C	F	F	H	H	P	T	T	T	T
6	A	B	D	D	H	L	L	P	V	T	R	T
7	A	B	B	L	L	L	E	P	U	U	U	U
8	A	C	B	I	J	E	F	P	W	W	W	W
9	A	D	C	I	G	J	F	O	S	S	S	T
10	A	A	C	F	F	H	F	P	V	Q	Q	Q
11	A	A	I	F	F	J	L	N	V	T	T	T
12	A	C	D	G	G	F	F	P	V	R	W	T
13	A	C	C	I	H	H	E	N	V	R	R	T
14	A	A	C	D	F	H	H	O	W	R	W	R
15	A	A	C	I	I	I	L	N	R	R	R	R
16	A	C	C	I	H	H	E	N	V	R	R	R

SOLITARY ANIMALS

Balanus crenatus
Corella willmeriana
Metridium senile
Mytilus edulis
Nereid Sp.1
Serpulid Sp.1
Styela gibbsii

COLONIAL ANIMALS

Bowerbankia sp.
Bryozoan sp. 3
Diplosoma macdonaldi
Distaplia occidentalis
Yellow sponge spp.*
Hippothoa hyalina
Obelia sp.
Sponge sp. 1
Tunicate sp. 2

EMPTY SPACE

A B C D E F G H I J K L M N O P Q R S T U V W

*Halichondria panicea
Haliclona permolis

☐0 ⊞1-10 ▨11-20 ▦21-30 ⊡31-40 ▨41-50 ▩51-60 ■61-70

Fig. 2. Compositions, in terms of the relative abundances of solitary and colonial species, for species assemblages A through W. The coded key corresponds to 8 relative abundance categories based on mean percent cover; the mean percent cover for a given species being determined from all of the panels represented in each species group. *Arrows to the left* indicate that the 95% confidence interval for the observed mean overlaps with the next lowest category, *arrows to the right* indicate an overlap with the next highest category

TIME (WEEKS)

TIME (WEEKS)

TIME (WEEKS)
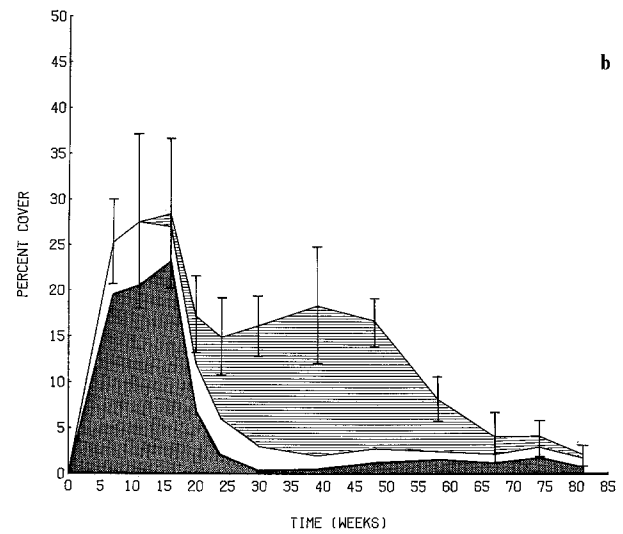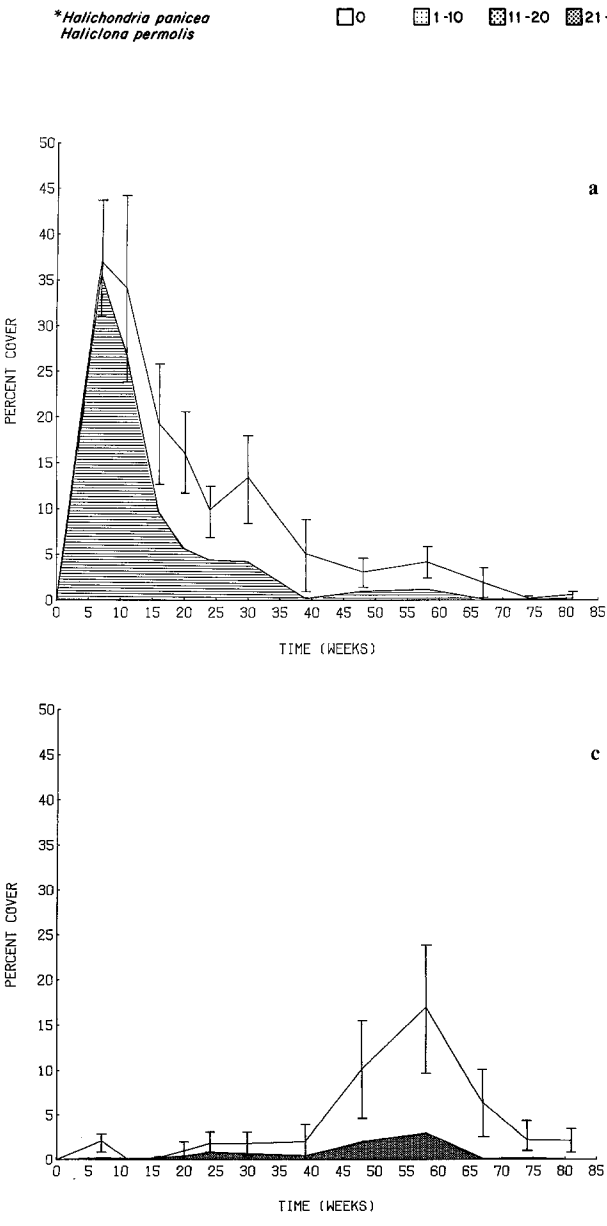
Fig. 3. The trends in relative abundances through time of the various morphological subdivisions of colonial animals. Relative abundances are measured in terms of percent cover; each point representing the mean value of 16 panels and enclosed by its corresponding 95% confidence interval. Figure 3a corresponds to the vine-like morphological types; the hatched area representing the hydroid *Obelia* sp., the *open area* representing a pair of vine-like bryozoans. Figure 3b corresponds to the sheet-like morphological types; the *hatched area* representing three sheet-like sponges, the *stipled area* representing the tunicate *Diplosoma macdonaldi*, and the *open area* representing a variety of sheet-like bryozoans. Figure 3c corresponds to the tree-like morphological types; the *stipled area* representing three tree-like bryozoans, the *open area* representing a pair of tree-like tunicates
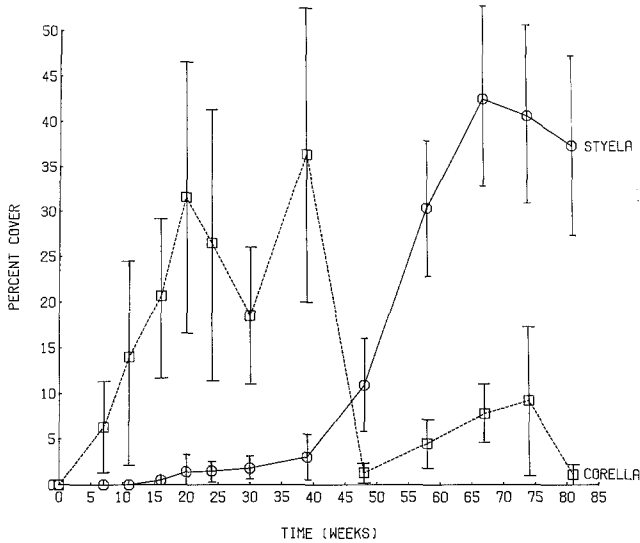
Fig. 4. The trends in relative abundances through time of the solitary tunicate species *Corella willmeriana* and *Styela gibbsii* at Bremerton, Washington. Relative abundances are measured in terms of percent cover; each point representing the mean value of 16 panels and enclosed by its corresponding 95% confidence interval
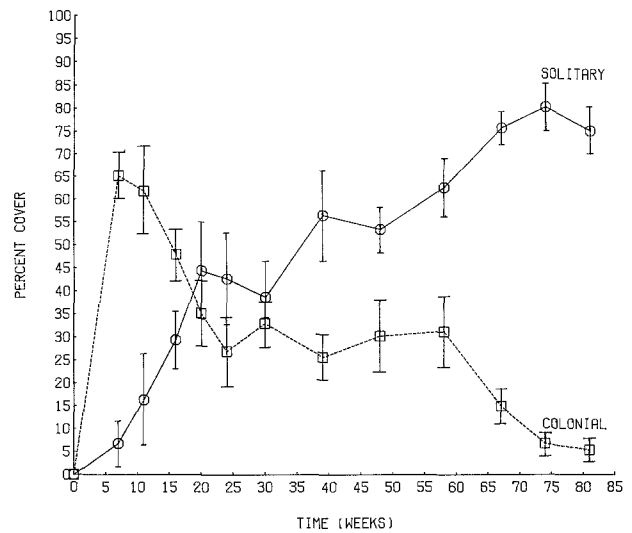

Fig. 5. The trends in relative abundances through time of the solitary and colonial animals at Bremerton, Washington. Relative abundances are measured in terms of percent cover; each point representing the mean value of 16 panels and enclosed by its corresponding 95% confidence interval

chosen somewhat subjectively after the analysis was attempted at a number of different distance levels. The choice of an appropriate "stopping rule" is typically subjective (Boesch 1977), and this level seemed to yield the most consistent results (further details on this choice are available, upon request, from the authors).

Table 2 lists the species assemblage corresponding with each panel on a given sampling date. The species compositions of these assemblages are portrayed in Fig. 2, each assemblage being broken down into its solitary and colonial components. Only species which on the average occupied greater then 10% of the space in a given assemblage were included in the figure. Less abundant species have little effect on the results with the clustering method employed (Boesch 1977), and this relatively arbitrary lower limit is consistent with Sutherland and Karlson's (1977, p. 427) criteria for defining the community's foundation species.

By following the transitional sequences of species assemblages observed for each panel through time (Table 2), and then inspecting the composition of these assemblages (Fig. 2), a fairly detailed picture of the community's development can be described. Initially, most of the bare panels underwent a similar development, being rapidly exploited by the colonial tunicate *Diplosoma macdonaldi* and the hydroid *Obelia* sp. As the first season progressed, however, the development on many of the individual panels began to diverge from one another. A variety of colonial species (Fig. 2) and morphological types (Fig. 3) were important space occupiers on different panels and at different times during the first year. During the same period of time, only one solitary species, the tunicate *Corella willmeriana*, ever made a large contribution to the percent cover (Fig. 4). Its high abundance, however, is responsible for the early conversion in week 20 from a colonial- to solitary-dominated community (Fig. 5). This feature, as well as *Corella*'s high relative abundance at some point in every panel's development during the first year, serves to emphasize the tunicate's early importance in the community.
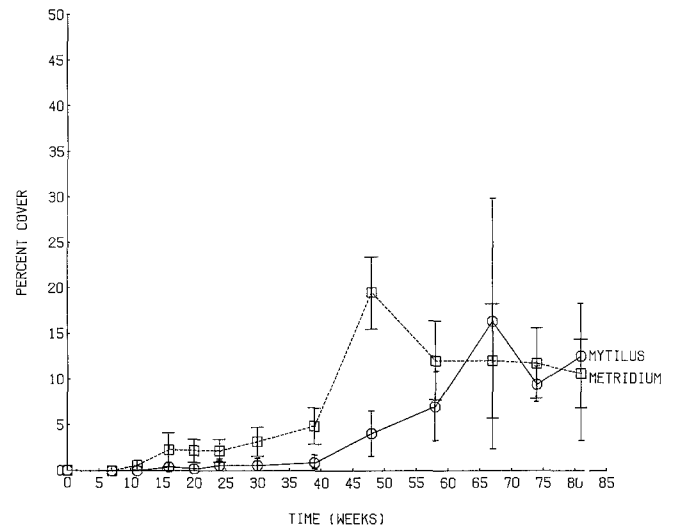

Fig. 6. The trends in relative abundances through time of the solitary species *Metridium senile* and *Mytilus edulis* at Bremerton, Washington. Relative abundances are measured in terms of percent cover; each point representing the mean value of 16 panels and enclosed by its corresponding 95% confidence interval

By week 48, *Corella*'s abundance had declined, and this was followed by a rapid but brief increase by the tree-like bryozoans and tunicates on the newly available, primary space (Fig. 3). More striking than this brief resurgence of colonial animals, however, was the relatively steady increase in percent cover by solitary animals beginning with week 48 (Fig. 5). Another solitary tunicate, *Styela gibbsii*, took over *Corella*'s position as the community's dominant species (Fig. 4). In addition, two other solitary species, the anemone *Metridium senile* and the mussel *Mytilus edulis*, became important space occupiers during the second year (Fig. 6). Each of these species contributed, to a greater or lesser extent, in the dominance by solitary animals in each of the species assemblages from weeks 58 through 81 (Ta-

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ble 2, Fig. 2). A particularly noteworthy feature of the community's development during this period is its convergence upon a few, relatively persistent species assemblages. Unfortunately, before the stability of these assemblages could be fully evaluated, the floating docks which supported our panels were repositioned, thus terminating the study after week 81.

Discussion

Upon first inspection, the transitional sequences in Table 2 appear quite variable, with perhaps little apparent pattern. This variability, especially in the early stages of panel development, is highly reminiscent of the stochastic effects observed in the recovery of small patches in the rocky intertidal (Paine and Levin 1981). As Paine and Levin (1981) suggest:

"when attention is focused on a single site (or panel), the dynamics appear highly stochastic... (thus each panel) may go through any of a number of possible transitional sequences in a pattern which can only be described probabilistically."

This line of reasoning suggests to us the necessity of developing a stochastic model for succession on marine hard substrata. Here we introduce such a model, and then attempt to reconcile its results with the field observations described previously.

The "Fixed Lottery" Model

If we take Gleason's (1927) reductionist approach and assume that changes in community structure can be viewed as the result of each component species' patterns of recruitment, survival and mortality, then community development in space-limited systems can be analyzed as a species by species replacement process (Horn 1975, 1976; Connell and Slatyer 1977). For illustrative purposes, a hypothetical, space-limited community of three species will be examined. We can begin by dividing the community's primary space into identical and contiguous subunits. Each subunit in the community can be in any of four possible states, either occupied by one of the three species A, B or C, or empty, as represented by the null state $\emptyset$. Whenever a change in state occurs within a subunit, there is an associated transitional probability of going from one state to another (Fig. 7). In matrix form the transitional probability matrix, P, looks like:

		To (j)			
		$\emptyset$	A	B	C
From (i)	$\emptyset$	$P_{\emptyset\emptyset}$	$P_{\emptyset A}$	$P_{\emptyset B}$	$P_{\emptyset C}$
	A	$P_{A\emptyset}$	P_{AA}	P_{AB}	P_{AC}
	B	$P_{B\emptyset}$	P_{BA}	P_{BB}	P_{BC}
	C	$P_{C\emptyset}$	P_{CA}	P_{CB}	P_{CC}

where P_{ij} represents the probability of going from state i to state j over some set time interval, t, and the probabilities in each row of the matrix must sum to one (i.e., $\Sigma P_{ij} =$ 1.0). t should be chosen short enough such that any subunit can only undergo one transition during the time interval.
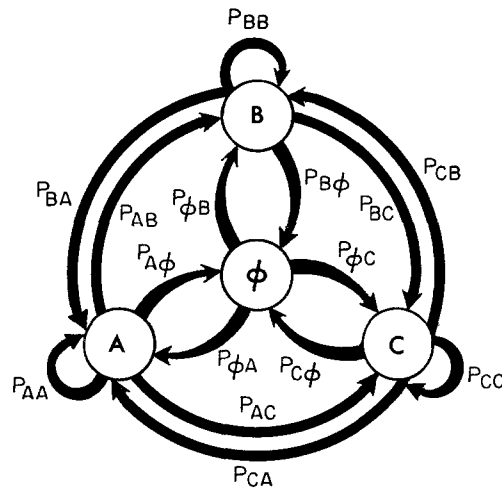

Fig. 7. Graphical representation of the possible states and transitions in a hypothetical, space-limited community of three species. Matrix representation and symbols are described in text

Along the main diagonal of the matrix (i.e., where i=j), each entry can be interpreted as the probability that no change in state occurs during time t. When j is equal to A, B or C, then P_{ij} can be interpreted as the probabilities of: (1) recruitment onto empty space by species j when i=$\emptyset$, or (2) one resident species, i, being directly outcompeted (i.e., overgrown) by another resident, j, when i=A, B or C and i≠j. Finally, when i=A, B or C and j=$\emptyset$, then P_{ij} can be interpreted as the probability that the resident species is disturbed and replaced by empty space after time t.

When the next state of any subunit is only dependent on its current state, and if P remains constant through time, the community development is a stationary Markovian process (Usher 1979). Horn (1975, 1976) has developed a simple, stationary Markovian treatment of forest succession as well as explored some of the interesting nonlinearities of succession, such as when community composition affects the transitional probability matrix. In analyzing the validity of the stationarity assumption, Usher (1979) concluded, both on empirical and theoretical grounds, that most ecological successions are non-stationary processes. Despite this conclusion, we feel that the approach is a valuable one in quantifying certain conceptual models of community development in the ecological literature, and in relating these ideas to our field observations.

Sale (1977, 1978) has likened reef fish community development to a lottery for living space. In a legitimate and purely noninteractive lottery [i.e., the community is structured by the dynamics of larval recruitment and resident mortality, species interactions, especially competition, are presumed insignificant (Anderson et al. 1981)], all entries in P with the exception of $P_{\emptyset\emptyset}$ must be equal in the first row, equal in the first column and equal along the main diagonal. All other entries in the matrix are zero. If these conditions are not met, then the lottery is "fixed", and species will not have an equal chance to reside in the community (Connell 1978). A "fixed lottery" model surely seems the most ecologically realistic. Sources of mortality usually exhibit some type of species selectivity and the pool of available larvae would rarely be expected to give all species the same likelihood of recruitment. In fact, in its
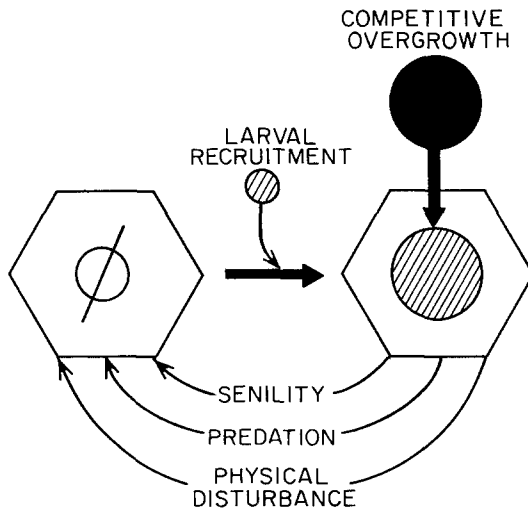
COMPETITIVE
OVERGROWTH

LARVAL
RECRUITMENT

SENILITY

PREDATION

PHYSICAL
DISTURBANCE

Fig. 8. Processes associated with the "fixed lottery" model of succession. For completeness, competitive overgrowth is included in the figure as well

basic form our "fixed lottery" model is largely analogous to the inhibition model of succession proposed by Connell and Slatyer (1977). In this type of succession, community residents inhibit the invasion of subsequent colonist, and space can only become available through the damage or death of resident species. With succession proceeding in the manner of a species by species replacement process, the community composition gradually shifts toward species which live longer (i.e., species with higher probabilities along the main diagonal of the matrix). Hence, succession can be characterized largely as a statistical phenomenon rather than a uniquely biological one (Horn 1976), reflecting the probability of each species' recruitment into the community (entries in the first row of the matrix) and the probability of its subsequent removal from the community (entries in the first column of the matrix). Figure 8 portrays the processes associated with this type of succession.

The basic "fixed lottery" model can be generalized further by adding terms accounting for direct, interspecific competition. Inclusion of nonzero values for P_{AB}, P_{AC}, P_{BA}, P_{BC}, P_{CA} and P_{CB} fills out the remainder of the matrix and relates the probabilistic nature of direct confrontations and their outcomes between species A, B and C. The probability of species j outcompeting i is equal to the product of their encounter probability times the proportion of confrontations j wins. In determining encounter probabilities, obviously position effects (Karlson and Jackson 1981) as well as the relative abundances of both species are important, and thus community composition affects P_{ij}. The theoretical implications of such nonlinearities need further investigation, but could have important consequences on community development and stability (see Limitations of the Model). In comparison, the proportion of successful encounters for species j with species i is less likely to be composition-dependent, and thus may be treated as a constant. In a simple competitive hierarchy of C > B > A, the competition terms below the main diagonal of P (i.e., P_{BA}, P_{CA} and P_{CB}) vanish. Only disturbance and recruitment rates that can keep pace with the rate of competitive overgrowth will maintain the diversity in such an assemblage. As an alternative, competitive networks (Jackson and Buss 1975;

Buss and Jackson 1979; Karlson and Jackson 1981) can be accommodated by the model as well, but we will not elaborate upon the complexities involved at present.

If we ignore nonlinearities and violations of the stationarity assumption for the moment, then our "fixed lottery" model yields several important predictions. As a regular Markovian process, our model of succession exhibits the ergodic property, a fundamental feature of all regular Markov chains (Kemeny and Snell 1976). The ergodic property results in convergence, after sufficient time, upon a stationary community composition irrespective of the community's previous or initial conditions (Horn 1975). This feature is consistent with the concept of "global stability", a situation in which all possible configurations in n-dimensional phase space (where n is the community's species richness) eventually converge upon a single, stable equilibrium point (Lewontin 1969). The final community composition achieved, and in this case appropriately referred to as the "climax community" composition, is determined only by the transitional probability matrix, P, and derived independently of the historical peculiarities associated with each individual succession. As mentioned previously, in situations where species' turnover times in the community are dominated by recruitment and disturbance processes, succession possesses the important features of Connell and Slatyer's (1977) inhibition model. At the other extreme, when competitive terms dominate P, then succession proceeds in a manner more closely resembling that described by Connell and Slatyer's (1977) tolerance model. In the former case, succession leads to a community composed of species that are longer lived; in the latter case, succession leads to a community dominated by species most efficient in utilizing space, i.e., better competitors. Thus, rather than portraying succession as two alternative processes with their consequent alternative conclusions, we prefer to view Connell and Slayter's (1977) models as two extremes of a more generalized successional process.

Limitations of the Model

"The best model is the one that works best. The perfect model, working infinitely well, is not for men now living."

Reginald Aldworth Daly

In nature, succession on marine hard substrata is considerably more complex than our simple model can portray. Throughout the development of the model thus far, we have neglected possible nonlinearities in the system and violations of the stationarity assumption. These omissions can have far-reaching consequences in terms of community development and stability. Nonlinearities arise when community composition can affect the processes of recruitment, competition and disturbance. Nonlinearities in recruitment are exemplified by the phenomena of gregarious and associative settlement (Crisp 1979) common in many sessile, marine invertebrates. The nonlinearities and position effects associated with competition were commented upon before, and the reader is referred to Karlson and Jackson (1981) for further details. Lastly, nonlinearities can develop when community composition affects the survivorship of certain species by altering their susceptibility to both physical and biological disturbances. Examples can be found in the rocky intertidal, where the more dense assemblages of *Mytilus californianus* are less prone to wave damage through byssal reinforcement (Paine and Levin 1981), and in fouling com-

munities, where some residents provide refuges from predators for other species (Sutherland 1974; Russ 1980; Dean 1981). In each of these examples, the observed nonlinearities have the potential to drastically affect development within the community. Horn (1976) recognized this potential and explored some of the theoretical implications in his Markov models for forest succession. Perhaps his most profound finding is that nonlinearities can increase the importance of historical events in the succession and thereby lead to the coexistence of multiple stable points (Lewontin 1969). Sutherland (1974) came to the same conclusion based on empirical evidence from the fouling community at Beaufort, North Carolina, however, he has subsequently modified this interpretation (Sutherland 1981, in preparation).

Although we can speculate with some theoretical assurances on the possible consequences of nonlinearities in community development, the effects of violations of the stationarity assumption are largely unknown. The most common and obvious violations of the stationarity assumption are observed periodicities in recruitment and disturbance processes. In recent papers, Sutherland (1981, in preparation) has operationally defined perturbations as processes potentially capable of changing community structure through the addition or subtraction of species from the resident adult assemblage. Perhaps visualizing violations of the stationarity assumption as perturbations in the system is a reasonable approach to the problem. In this view, perturbations of small magnitude may temporarily impede the succession's convergence toward a given stable point. At the other end of the spectrum, large perturbations may jar the system into another "basin of attraction" (Lewontin 1969; Holling 1973), and thus convergence toward a different endpoint. In addition to their intensity, the frequency of perturbations can significantly alter the speed and course of succession as well (Sutherland and Karlson 1977; Connell 1978; Sousa 1979, 1980). Although we find this perturbation approach conceptually straightforward and intuitively pleasing, we hope to see further theoretical development along these lines in the future.

Finally, before we attempt to reconcile the model's results with our field observations, we wish to point out two additional simplifications. First, the effects of spatial heterogeneity are completely ignored in the model. This may or may not be an important consideration depending on the community being studied. For purposes of keeping the model general, however, we find it useful to separate the successional processes described previously from the complicating effects of spatial heterogeneity. The second simplification involves the lack of any age or size structure in the populations of each resident species. Perhaps greater realism and precision could be achieved by adding more states to the model which would correspond to the different age or size classes in each species' population. For introductory purposes, however, we again prefer to present the model in its more general form.

The Model Versus Reality

In the context of our observations from the fouling community at Bremerton, the "fixed lottery" model yields several important insights and working hypotheses. In this paper, we only stress the deterministic consequences of the model, although part of our original intent was to account

for stochastic variability. Monte Carlo simulations with even the simple, three species system can yield considerable variability (Greene, personal observation). Therefore, when we attempt to interpret the succession of a 57 species system in which both nonstationary and nonlinear processes are at work, the task of revealing underlying patterns would indeed seem formidable. Nevertheless, the emergence of some patterns has both intrigued us and laid the groundwork for further investigations.

In another paper (Greene and Schoener, in preparation), we elaborate extensively upon our functional group analysis of the fouling community at Bremerton. The observed trend in dominance, shifting from colonial to solitary animals (Fig. 5), presents us with a situation in conflict with Jackson's (1977) predicted trend of eventual colonial dominance. In an attempt to explain this trend and reconcile the conflict, we propose a working hypothesis that successional processes other than competition can alter "the adaptive significance of solitary and colonial strategies" (Jackson 1977, p. 743). Relying on some of our own observations, but primarily on the results of other investigations of temperate fouling communities (Sutherland and Karlson 1977; Dean and Hurd 1980), we suggest that succession at Bremerton may possess many features in common with Connell and Slatyer's (1977) inhibition model. In such a succession, as our "fixed lottery" model confirms, the longer-lived species will eventually dominate. At Bremerton, most of the important solitary species do seem to outlive their colonial counterparts (Greene and Schoener, in preparation) and this is proposed to account for their eventual dominance. In addition, one of the solitary species, *Styela gibbsii*, may be able to perpetuate itself in dense assemblages by gregarious settlement and the ability to filter out other species' larvae while sparing its own (C. Young, personal communication). Gregarious settlement and other processes which favor self-replacement may thus represent examples of nonlinear effects which can also "increase the odds" for solitary animals (Jackson 1977; Scheltema et al. 1981). Each of these hypotheses needs to be tested with well-designed, carefully controlled field experiments. The rewards, however, in terms of resolving several broad evolutionary and biogeographical questions (Jackson 1977; Greene and Schoener, in preparation) could be well worth the effort.

One other emergent pattern in the Bremerton data, which we will address finally, involves both successional convergence and community stability. Inspection of Table 2 reveals a high degree of between panel variability during the earlier stages of succession. As the succession proceeded, however, this variability declined and the panels began to converge upon a few, relatively persistent species assemblages. This suggests, as one might expect, that the stochastic effects of succession are reduced with the passage of time. Whether the observed pattern represents convergence toward a globally stable point or multiple stable points cannot be distinguished from our time series. In fact, it is possible that perturbations, as we described them before, may not allow convergence to continue any further. Community stability must be assessed on time scales consistent with the life histories of all the resident species (Connell and Sousa, in preparation) and, unfortunately, we were forced to terminate our study far short of this goal. It is our hope that future studies of community succession and stability will be of sufficient duration to adequately approach these questions of such broad ecological concern.

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