Detection of alternative stable states in marine communities

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Abstract

During the last 20 years there have been several attempts to test the theory of alternative stable states using marine systems. The results have been mixed, and there have been conflicting interpretations of the outcomes. In an attempt to resolve some of the problems, the theory and evidence for alternative stable states are reviewed. There are several different views of what is meant by alternative stable states, and so the key elements of the theory of alternative stable states are set in the context of marine systems. Appropriate experimental designs for detecting alternative states are discussed, and recent experimental studies in coral reefs, rocky intertidal systems, soft-sediment beds, and subtidal systems are briefly reviewed. Suggestions for improving experimental designs are proposed and unresolved issues are highlighted.
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1. Introduction

There has been a renewed interest in the theory of alternative stable states because marine communities may provide tractable systems for experimental tests (Petraitis and Latham, 1999). In theory, alternative stable states occur in dynamical systems with more than one equilibrium point, and Lewontin (1969) is often cited by ecologists as the first one to pose and answer the question, "Can there be more than one stable community composition in a given habitat?" His answer was "yes," and as with most ideas in

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ecology, it is easy to find earlier references to multiple stable points. For example, Lotka (1956) noted the possibility of multiple stable points and referred the reader to literature going back to 1891.

It would seem a good test of the theory would simply require showing that a given habitat would support two or more different assemblages of species and that these assemblages were stable (Peterson, 1984). Moving from theory to practice is, however, not straightforward. While the meaning of stability and equilibrium points are very clear-cut in theory, it is not so in nature. Problems of time scales and spatial extent blur what stability, equilibrium, and habitat might mean in nature (Grimm and Wissel, 1997; Petraitis and Latham, 1999).

At the very minimum, experimental tests of the existence of alternative stable states in natural communities must fulfill three conditions (Connell and Sousa, 1983). First, alternative states must be shown to occur in the same environment or habitat. Second, the experimental manipulation must be a "pulse" perturbation (Bender et al., 1984) that actually changes the species composition or environmental conditions that initiates the switch from one state to the other. Knowlton (1992) suggested the switch between alternative stable states should occur at a critical environmental threshold. The critical threshold may be correlated with the scale of the perturbation because large events are more likely to cause dramatic shifts in species composition which are needed to tip an ecosystem from one alternative state to another (Knowlton, 1992; Petraitis and Latham, 1999). Third, the experiment and observations must be carried out over a sufficient time period and over a large enough area to ensure that the alternative states are self-sustaining (however, see Law and Morton, 1993, for a different viewpoint). Moreover, the ecological processes responsible for initiation of alternative states may be quite different from the processes needed to maintain those alternative states (Drake, 1991; Petraitis and Latham, 1999).

Peterson (1984) believed that Connell and Sousa's (1983) first and third criteria were too rigorous, and has suggested proof of an alternative community required showing by experiment that the same site could be occupied by different self-replacing communities. Sousa and Connell (1985) agreed that this is the minimal condition, which has been called Peterson's criterion (Petraitis and Latham, 1999).

Connell and Sousa (1983) concluded that there was very little direct experimental evidence for alternative stable states in natural systems. Since their review, there have been several attempts to test for alternative stable states using different systems and different experimental approaches, and not surprisingly with different outcomes and conclusions. Some of the diversity in approaches is the result of the constraints of different marine systems, but we think the diversity also reflects a misunderstanding of the theory and a lack of consensus of how theory can be translated into experiment.

Given the confusion about the theory itself, we will first attempt to clarify what theory can and cannot tell us about constructing good experimental tests. Moving from theory to experiment is difficult in many areas of ecology, and this is certainly the case for the study of alternative stable states. Such difficulties arise from differing viewpoints of what constitutes a valid experimental test of theory, and we will point out areas of disagreement and lack of consensus. Differing viewpoints are often caused by different definitions, and in fact, theorists have provided two different definitions of alternative stable states.

We will then review the recent work that has been done in temperate intertidal systems, seaweed beds, and coral reefs, and will offer suggestions about what needs to be done to move the field forward. There have been only a few experimental tests in marine systems since Connell and Sousa's review. All of the published studies have weaknesses, and we will provide some suggestions of how experimental tests could be improved. We will conclude with a summary of what progress has been made and what issues remained to be resolved.

2. Theory

One of the simplest linear systems with two stable points that could be considered to have alternative states is the Lotka-Volterra competition model for two species with a saddle point (Knowlton, 1992). The saddle point is an unstable equilibrium for the two species coexistence and the single species equilibrium point for each species is stable. The stabilities of the three equilibrium points are set by the parameter values (i.e. the values of the r's, the K's and the competition coefficients). Initial conditions of the state variables (i.e. the initial densities of the two species) determine which species wins. Park's (1948, 1954) work with *Tribolium* is one of earliest experimental demonstrations of how initial conditions determine the outcome of competition between two species.

From this viewpoint, alternative states occur in dynamical systems when multiple equilibria can exist for the same set of parameter values. We suggest Lewontin's (1969) condition of multiple equilibria in "a given habitat," in fact, implies the same set of parameter values. For example, suppose mussels and seaweeds are competitors for space and the adult replacement rate per unit area for seaweed (A) and mussels (M) are:

$$\frac{\mathrm{d}A}{\mathrm{d}t} = a - bA - uM \tag{1}$$

$$\frac{\mathrm{d}M}{\mathrm{d}t} = r - \mathrm{d}M - vA \tag{2}$$

where for seaweeds, a is the recruitment rate, b is the mortality rate from recruitment to adulthood due to the presence of adult plants, and u is the mortality rate due to the presence of mussels, and for mussels, r is the recruitment rate, d is the mortality rate due to mussels, and v is the mortality rate due to seaweeds. If $r/d > a/u$ and $a/b > r/v$, the system has two stable equilibria at which each species can resist the invasion of the other (Fig. 1). The two species equilibrium is not stable.

The two stable equilibrium points, one for each species, are alternative states. Patches of mussels cannot be invaded by seaweeds and vice versa. Replacement of one species by the other can only occur if a disturbance removes the current dominant, which in turn could allow invasion by the other species.

The equations themselves provide the structure of the model, and the structure is not defined by changes in parameter values. Parameters (e.g., per capita rates or mass rates) define how various state variables (e.g., species densities or biomass) interact. The different species assemblages found at the different equilibria are governed by the same
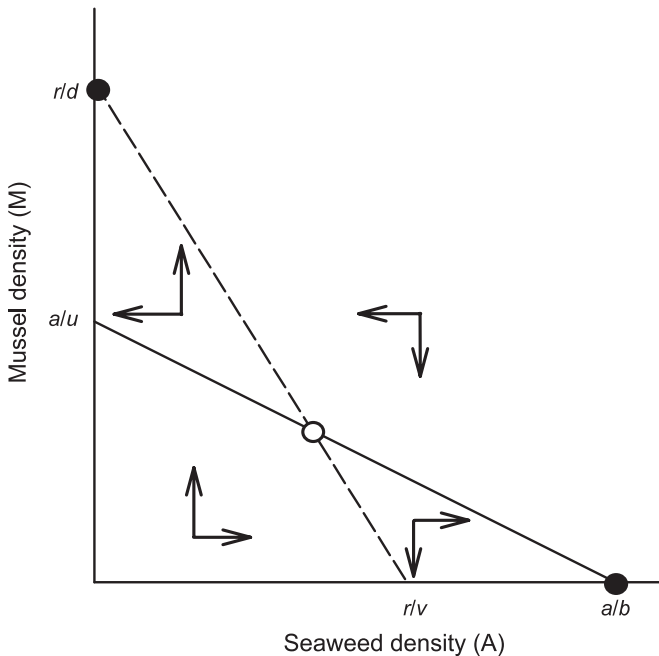
Fig. 1. Unstable equilibrium between mussels and seaweeds. Mussels and seaweeds are alternative stable states in a model system with a single set of parameter values. Parameters are defined by the environment. Dotted line is mussel isocline; solid line is seaweed iscoline. Open dot is the unstable point; closed dots are stable points.

set of rates for resource delivery, probabilities of mortality due to natural enemies, and all other processes that control densities. This does not mean that resource levels or densities of natural enemies, which are state variables, must be the same at each of the equilibria, rather only that the same set of rates of these processes (i.e. the parameter values) are in effect at each equilibrium point. Whether a system has multiple stable equilibria is simply determined by the parameter values. Moreover the presence or absence of a species at equilibrium point does not define a different model structure, just a different equilibrium point. Thus a system with a fixed value for each parameter seems to be what is assumed in the phrase "in a given habitat" (Lewontin, 1969). Each unique set of parameter values are defined by a single environment or habitat. Lewontin (1969) noted that there may be small scale variation of parameter values such that individuals will experience both spatial and temporal variation (also see Chapter 5 in Tilman, 1982 for a more comprehensive discussion).

There is an alternative view of habitat. Ecologists often think of habitats in terms of species that occupy them or as a range of environmental conditions found at a particular place and time. There are, for example, grassland habitats, marine rocky intertidal habitats, and soft-sediment habitats, and in each of these habitats, the rates of consumption and resource renewal may vary. If parameter values, such as consumption rates and rates of resource renewal, vary within what is recognized as a distinct habitat, then it seems logical that different alternative stable states may arise from small changes in parameters.

This is the system of alternative stable states envisioned by May (1977) in which small changes in parameter values cause a catastrophic shift in state variables. These sudden shifts occur in dynamical systems that have a bifurcation fold and show hysteresis (Scheffer et al., 2001). Hysteresis has been suggested as the underlying cause of dramatic shifts seen in lakes, coral reefs, grasslands, and fisheries (May, 1977; Scheffer et al., 1993, 2001; Chase, 2003). Lewontin (1969) also recognized that small changes in parameter values in certain models could cause large discontinuous shifts in state variables, which he called structural instabilities. Unlike May (1977), Lewontin emphasized the problems caused by such model systems and suggested structural instabilities would make a predictive theory difficult.

Hysteresis can arise in any system in which at least one process shows a steep threshold over a range of parameter values. For example, suppose the adult replacement rate of a seaweed per unit area dA/dt is changed to include a term for enhancement of recruitment due to the presence of adult plants, and so

$$\frac{dA}{dt} = a + g(A) - bA - uM \tag{3}$$

This system will show bifurcation and hysteresis if $g(A)$ has a steep threshold. Let $g(A)$ follow a Hill function (Scheffer et al., 2001):

$$g(A) = \frac{cA^p}{A^p + h^p}$$

in which the parameter p adjusts the steepness of the environmental threshold and h sets the midpoint of the threshold. A larger p value will make the curve steeper and a larger h value will shift the curve to the right.

Now suppose that recruitment shows a critical threshold depending on the number of adult plants. Adult plants may increase recruitment by preventing zygotes from being washed out of the adult bed or by limiting desiccation stress. This benefit, however, may be an all or nothing effect, and there may need to be a critical minimum number of adult plants for there to be any improvement in recruitment.

This critical number of adult plants itself, depends on environmental conditions. For example, only a few adult plants may be needed to prevent loss of recruits at protected sites with low wave surge. In this case, h would be small. In contrast, the needed number of adults at exposed sites may be quite a bit larger to confer the same amount of improvement in recruitment.

If the threshold is steep enough, this system will show a bifurcation fold and hysteresis (Fig. 2). With hysteresis, state variables (e.g., species composition and densities) change smoothly as parameter values (e.g., environmental conditions) are altered but only up to the bifurcation fold. The variables then show a discontinuous shift at the fold to an alternative stable point with a very small change in parameter values. Moreover, the state of the system before the fold cannot be recovered by a small reversal in parameter values. Parameters must be pushed back to the other edge of the fold. Thus alternative stable states occur over the range of parameter values between the two threshold points.

This can be seen in the mussel and seaweed model in which there are two alternative stable states over a range of intermediate values for h (Fig. 2). Seaweeds are common, and
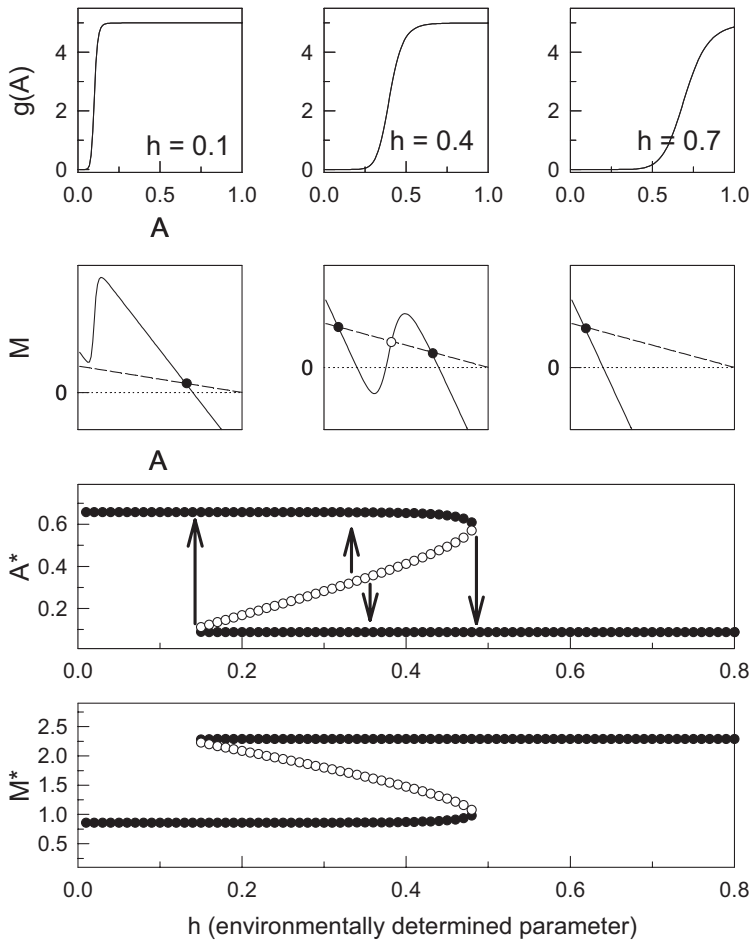
Fig. 2. Mussels and seaweeds as alternative states in a model with a bifurcation fold. Model based on Eqs. (2) and (3). Top row gives plots of $g(A)$ vs. A at three values of h. Middle row shows phase diagrams and zero isoclines for mussels (dashed lines) and seaweeds (solid lines) for three values of h. Bottom two rows give plots of equilibrium values for seaweeds (A^*) and mussels (M^*) vs. h. Parameters: $a = 2$, $b = 10$, $c = 5$, $p = 10$, $u = 0.5$, $r = 5$, $d = 2$, $v = 5$, and h is allowed to vary from 0 to 1. Solid dots are stable equilibrium points; open dots are unstable equilibrium points.

mussels are rare on protected shores where the threshold effect of adult plants on recruitment occurs in the presence of a few adults (i.e. small h). Small increases in h, which occur with increased wave surge, gradually push the threshold to the right as more adult plants are required to induce the threshold. At the fold, the equilibrium tips to a new point, and mussels are common and seaweeds are rare. The system cannot be returned to the old equilibrium by small reversals in parameter values and thus the system shows hysteresis. Note that in this model, smooth and continuous changes in parameters produce discontinuous shifts in the equilibrium value of the state variables. Moreover, models with

bifurcation folds always contain a range of parameter values over which more than one alternative stable state can exist (Fig. 2).

We would suggest that the hallmark of alternative stable states is the presence of multiple basins of attraction across a range of parameter values. Lewontin's (1969) view posits multiple stable points for a single set of parameter values while May's (1977) view suggests systems with bifurcation folds have multiple stable points over a range of parameter values. Both require multiple basins of attractions at least one set of parameter values.

The presence of an environmental threshold does not guarantee that a system has alternative states. Gradual changes in parameters may result in steep shifts in equilibrium densities but without multiple stable points at the same parameter values (Fig. 3). Such
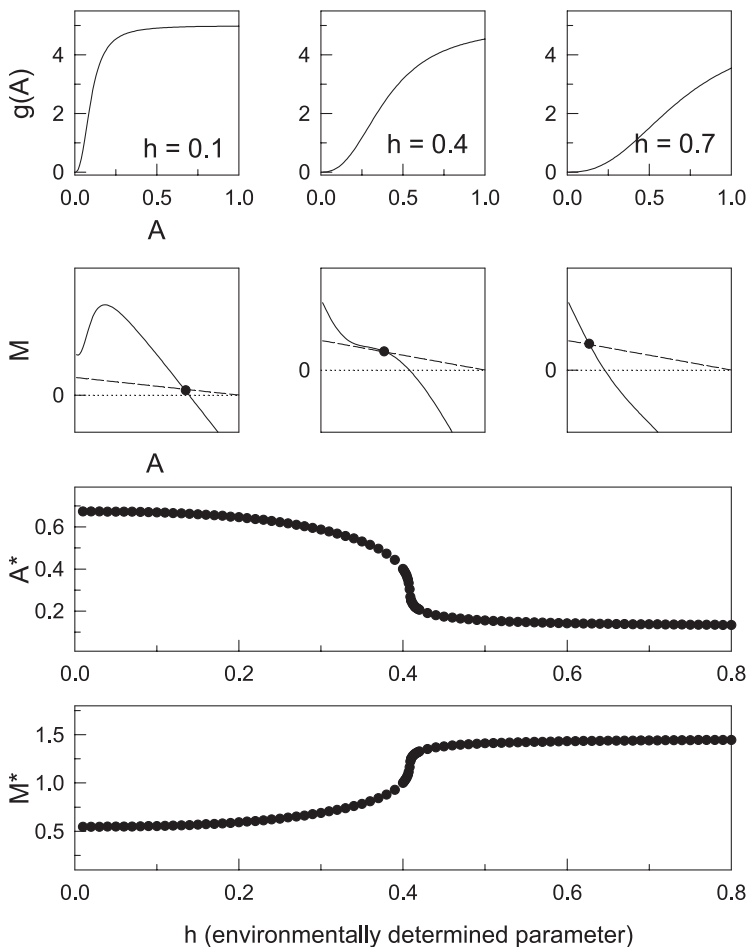

Fig. 3. Mussels and seaweeds as different states that occur in different habitats and maintained by site-specific differences. Model shows only a threshold. Parameters: $a = 2$, $b = 10$, $c = 5$, $p = 12.5$, $u = 0.5$, $r = 5$, $d = 3$, $v = 5$, and h is allowed to vary from 0 to 1. Solid dots are stable equilibrium points. See Fig. 2 for further details.

systems have thresholds but only contain a single basin of attraction. The basin of attraction may shift in shape and location in state space with changes in parameters, but different equilibrium states under different parameter conditions cannot be considered alternative stable states. Thus demonstrations that an ecosystem can show abrupt shifts in either equilibrium conditions or ecological processes such as recruitment with small changes in environmental parameters are not sufficient tests of alternative stable states.

We would also argue that state and transition models (Westoby, 1980; Westoby et al., 1989) may also not be of much help. State and transition models are descriptive models that are at least one level of abstraction above the types of models we have examined here. In fact, Westoby et al. (1989) stated, ''We are proposing the state-and-transition formulation because it is a practical way to organize information for management, not because it follows form theoretical models about dynamics.'' Westoby et al.'s representation of the relationship between range condition and stocking levels for the range succession model also lacks a bifurcation fold although it could easily be transformed into such a model.

At the bare minimum, the presence of multiple non-contiguous basins of attraction is the single property that distinguishes a system with alternative states (Fig. 2) from a system with a single basin of attraction (Fig. 3). The system must contain at least two separate basins of attraction at least one point in the parameter space. Experiments must then be designed that can separate the two alternatives—quite simply, does a system have one or more than one basin of attraction?

3. Critique of published experiments

There have been few attempts to test explicit hypotheses about alternative stable states since Connell and Sousa's (1983) review. Perhaps Connell and Sousa provided a sense that the issue was experimentally intractable, and the relevant experiments would take a long time relative to the duration of research grants (Sutherland, 1990). However, Petraitis and Latham (1999) suggested short-term experiments testing the initiation of alternative states were possible but require carefully designed experiments. With this in mind, we review both the evidence and the methods from a number of studies done since Sousa and Connell's (1985) review. We would stress that a critique of methods is crucial because tests of alternative stable states must at a minimum, meet Peterson's criterion. We focus on four marine ecosystems where alternative states have been postulated to exist: coral reefs, soft sediments, subtidal hard substrate communities and rocky shores.

3.1. Coral reefs

The most well-known and best documented cases of large scale changes in marine ecosystems are those on coral reefs. The switch between coral and macroalgal-dominated communities have been variously termed alternative stable states, first by Knowlton (1992) and recently by Scheffer et al. (2001), or phase shifts (Done, 1992; Hughes, 1994; McCook, 1999). We emphasize that these terms reflect very different characterizations of the dynamics of reef ecosystems, though the distinction is often blurred. Both alternative

states and phase shifts show large-scale changes in species composition in response to, perhaps small, changes in environmental conditions. However, alternative states implies at least two different assemblages (states or stable equilibria) can occur at the same parameter values (i.e., environment) over at least some of the range, whereas a phase shift has but a single state (albeit changing at the threshold) under all parameter values (cf. Figs. 2 and 3).

It is possible that coral and macroalgal-dominated assemblages represent alternative states, but we know of no experimental evidence to support this hypothesis. The relevant experiments simply have not been done and, given the degraded state of many reefs, ethical considerations may preclude them being done at the appropriate scale with sufficient replication. On the other hand, there is solid evidence showing that the phase shift from coral to algal assemblages resulted from a change between environments favoring corals to environments favoring macroalgae (Done, 1992; Hughes, 1994; McCook, 1999; Jackson et al., 2001). Principal sources underlying the change in reef environments include overfishing, disease, habitat destruction and eutrophication. In instances where these environmental stressors have been reduced, corals have increased in abundance. For example, in Jamaica, the return of the sea urchin *Diadema antillarum* in some areas is associated with a concomitant reduction in macroalgal cover and an increase in juvenile coral cover, providing evidence of a reversal in community structure (Edmunds and Carpenter, 2001).

Cases of persistent shifts from coral to algal assemblages tend to be isolated in specific regions (Ninio et al., 2000), whereas other areas show no such shift over relatively long ecological time scales (Connell et al., 1997). The Long-Term Monitoring Project (LTMP) in Australia is addressing the spatial and temporal extent of coral decline and shifts to macroalgae across the Great Barrier Reef (GBR). Fifty meter transect surveys over 5 years spanning three sites in a reef region and three shelf regions (corresponding to distance offshore) along the length of the GBR found no evidence of large scale shifts between assemblages. Hard coral cover, on average, increased during the study and instances of high algal cover were transient features of succession back to the coral state. Although the study by Ninio et al. (2000) suggests phase shifts are restricted spatially and temporally, there is cause for concern over the expanding scale of environmental change, the associated loss of resilience of coral communities, and species turnover events (Aronson et al., 2002; Hughes et al., 2003; Pandolfi et al., 2003).

The changes in reef environments do not exclude the possibility of alternative stable states, but it makes detection difficult because the ''alternative state'' and ''phase shift'' interpretations are confounded. Indeed, the changes in reef environments may have either eliminated previously existing potential alternative states, created new potential ones, or made no difference to their existence in this ecosystem. Without direct experimental tests, the only recourse may be evidence derived from large-scale experimental attempts to restore previous reef environments. If tropical reef ecosystems can support alternative states, then restoration of environmental conditions (i.e., parameter values) more suitable for corals will not guarantee a switch from algal back to coral communities; the environment may still be suitable for macroalgae. Reversion to coral reefs requires either of two events prevailing: (1) under the 'rehabilitated' environment, a large scale pulse perturbation that moves the system from the algal to the coral basin of attraction, or (2) a press of conditions further into the ''suitable environmental space'' for corals to some

unknown threshold value that is unsuitable for macroalgae causing a switch. Either scenario seems unlikely. On the other hand, if the coral to algal transition is a simple phase shift, then the state change from algal to coral assemblages, as the data of Edmunds and Carpenter (2001) suggest, is reversible to the extent that environmental conditions reverse. Assuming tropical reefs have a single equilibrium state in each environment one prediction seems clear: phase shifts to macroalgal states will remain and corals will not recover without environmental conditions being reversed.

3.2. Soft sediments

Peterson (1984) first identified soft sediment systems as likely candidates for supporting alternative states because of the biotic feedback with the sediment environment. Sousa and Connell (1985) agreed that evidence existed showing that resident organisms alter the environment they occupy (Woodin, 1976; Highsmith, 1982). However, neither Woodin (1976) nor Highsmith (1982) provided evidence supporting Sousa and Connell's criterion that the process of habitat modification contributed to self-replacement of the resident population. For this reason, Connell and Sousa discounted these studies as candidates for alternative states. However, direct interactions between species, particularly between resident adults and arriving larvae, could maintain the alternate states in soft sediment systems. We suggest that the important issue is not whether the modified habitat serves as the factor maintaining an assemblage, but whether these different assemblages at different times can occupy the same site and show some stability property such as resilience or self-replacement (sensu Grimm and Wissel, 1997), In this context, modification of soft sediments could easily be categorized into the four classes of positive feedback switches that Wilson and Agnew (1992) proposed for plant communities. We think that it would be worth revisiting soft sediment ecosystems to conduct explicit experimental tests of habitat modification as part of a test for the existence of alternative stable states.

A recent study in soft sediments has sought evidence for positive feedbacks that lead to self-replacement via habitat modification by primary producers. Van De Koppel et al. (2001) provide laboratory experimental and field observational evidence consistent with a model of alternative states based on positive feedback between diatom growth and silt content. The two alternative states are high diatom, high silt content versus low diatom, low silt content (i.e., sandy). The model predicted a threshold transition between the two states at intermediate levels of bottom shear stress. At low levels of bottom shear stress, diatoms and silt accumulate while at high levels, erosion removes diatoms and silt. Field observations sampled from 92 plots across ∼ 4 km^2 area of tidal flat in the Westerschelde estuary, Netherlands were consistent with model predictions. Silt content of samples from areas with intermediate to high levels of bottom shear stress showed a bimodal distribution suggestive of alternative states, whereas samples from low shear stress areas were unimodal.

Data supported all model assumptions except one—that diatom growth rate increased with sediment silt content. Two laboratory experiments comparing diatom growth rates in sand- versus silt-dominated sediments ($n=2-5$ per sediment treatment depending on experiment) provided evidence for higher diatom growth rates in silt. This coupled with earlier evidence that benthic diatoms decrease sediment erosion (see numerous references

in Van De Koppel et al., 2001) supports the premise that diatom–silt interactions are governed by positive feedbacks.

High diatom–silt versus low diatom–sandy states may represent alternative stable states of tidal flats, but, as in most cases, further evidence is required. Specifically, field experiments are necessary to demonstrate a mechanism of switching between the alternative states in areas with intermediate levels of bottom shear stress. Furthermore, a field experimental test of a stability property is necessary to explain the maintenance of each state.

3.3. Subtidal systems

Like coral reefs, kelp forest ecosystems are well-known ecosystems that are often cited as examples of alternative stable states. These rocky subtidal ecosystems occur in either of two states, a kelp forest or a coralline algal crust pavement. Simenstad et al. (1978) suggested that the subtidal kelp forests and coralline barrens of Alaska were alternative states mediated by predation of sea urchins (that control kelp abundance) by the sea otter, *Enhydra lutris*. Connell and Sousa (1983) dismissed this as an example of alternative states because the states could only be maintained with human intervention continually pressing the system. Moreover, they supported Paine's (1977) suggestion that communities with and without consumers should not be regarded as stable entities, since if consumers can return and consume prey again, they will.

It is worth reconsidering kelp forests and coralline barrens as candidates for alternative stable states in light of new evidence bearing on the question. First, it is now widely recognized that the dynamics of kelp forest systems are far more complex than previously imagined and include predation on sea otters by killer whales that can mediate the two states (Estes et al., 1998). Ultimately, the food web cascade effects reach all the way up to humans because the recent killer whale mediated switch between kelp forests and coralline barrens may stem from previous commercial whaling (Springer et al., 2003). The fact that humans intervene in these systems no longer seems to be a simple argument for artificial maintenance between alternative stable states. Hindsight provided by evidence from several recent publications emphasizes that humans are a natural part of all ecosystems and we can strongly affect their dynamics (Jackson et al., 2001; Pandolfi et al., 2003). Whether kelp forests and coralline algal barrens are viewed as alternative stable states may simply hinge on whether the decisions made by humans to modify ecosystem states are seen as artificial press events that are imposed from outside the natural system or as positive feedback to maintain an alternative state by a species (humans) within the system.

The above argument does not mean that kelp forests and coralline barrens are alternative stable states, just that they should not be excluded from consideration. On the contrary, they seem to be prime candidates for continued testing of the hypothesis. For example, Konar and Estes (2003) recently examined if kelps altered urchin behavior and thus enabled kelp bed persistence in the face of sea urchins. They manipulated both urchin and algal abundances as a pulse perturbation via additions and removals. They used only two levels of treatment (i.e. presence or absence treatments) and had low replication (usually only four replicates). However, the results showed that the presence of kelps

prevents invasion by urchins. Konar and Estes (2003) proposed that variation in the interaction of urchin behavior and initial abundance of kelp may be a mechanism of maintaining alternate stable states. Interestingly, two other examples of variation in predator–prey interactions are associated with hypothesized cases of alternative stable states. The persistence of mussel beds may persist via positive feedbacks because established mussels can kill predatory dogwhelks by trapping them with byssal threads and prevent invasion (Petraitis, 1987). In much the same way, high densities of whelks (the usual prey) can overwhelm and consume rock lobsters (Barkai and McQuaid, 1988).

Kelp forests and coralline algal barrens of the northeast Pacific differ from similar switches between these states elsewhere because of the effect of sea otters on sea urchins, which in turn controls the abundance of upright foliose macroalgae. Chapman and Johnson (1990) hypothesized the switch from coralline barrens to kelp in the northwest Atlantic occurs when urchin grazing is drastically reduced by mass mortality events caused by water-borne pathogens (also see Mann, 1977; Scheibling et al., 1999). The reverse switch from kelps to coralline barrens is thought to be the result of high-density aggregations of roving sea urchins that decimate kelp forests. Food is thought to a trigger that switches urchin behavior from low-density sedentary feeding to dense roving aggregations but there may not be a single key factor (Mann, 1977; Bernstein et al., 1983; Hagen and Mann, 1994; Scheibling and Hatcher, 2001). Early claims that predators of urchins in the northwest Atlantic (e.g., lobsters, crabs and fish) were functionally analogous to sea otters in the Pacific have not held up to scrutiny (Elner and Vadas, 1990).

There is accumulating experimental evidence concordant with abundant observational evidence that kelp forests and coralline barrens represent alternative stable states. The experimental evidence is derived from small-scale experiments and for the most part has focused on the positive feedbacks that maintain alternative assemblages. What is still needed are experiments that test for the occurrence of thresholds associated with factors underlying switches between states and address the stability of each state. However, like coral reefs, ethics and logistics of doing the appropriate large-scale experiment with sufficient replication in kelp forests may be impossible. We may have to accept observational evidence, modeling, and small-scale experiments that test portions of the model rather than a definitive series of replicated experiments demonstrating Peterson's criterion.

A broader scale pattern that is suspected to be alternative states is the occurrence of algal turfs and algal crusts in relation to kelps. These two habitat types occur in the shallow subtidal zone in many parts of the world (Witman and Dayton, 2001). In Australia, these benthic communities are associated with the presence or absence of a kelp canopy. Crusts tend to dominate underneath kelp canopies, and turfs and invertebrates tend to dominate outside of canopies (Connell, in review). The kelps are hypothesized to play a central role modifying light intensity and sedimentation in the understory environment and thus affect which subset of the regional species pool that can become established (Connell, in review). In a series of studies, Connell et al. have experimentally manipulated light intensity and sedimentation rates in factorial combinations and followed the effects on crustose coralline, articulated coralline macroalgae, turf macroalgae, and invertebrates (Fowler-Walker and Connell, 2002; Irving and Connell, 2002a,b; Connell, 2003a,b, in review). Connell tested for the existence of positive feedback mechanisms, which may control the

assembly and maintenance of subtidal communities. The number of treatment combinations associated with the factorial designs precluded including enough treatments levels that would allow detection of thresholds. The evidence suggests that light intensity and sedimentation rates interact to strongly influence community development. Moreover, the presence of kelps (e.g., *Ecklonia radiata*) affects light intensity and sedimentation, hence the composition of the underlying community. These experiments provide evidence for mechanisms that facilitate maintenance of community states. However, they were not designed as explicit tests of alternative stable states, so the studies did not directly test whether a switch between states can occur at a single site. Also not addressed were the scales and type of naturally occurring perturbations that may cause a switch between community states, and the evidence needed to demonstrate stability of the alternative assemblages.

Finally, the study by Barkai and McQuaid (1988) of the subtidal hard substrate communities of two islands in South Africa is a commonly cited example of alternative stable states (e.g., Menge and Branch, 2001). On Malgas Island, predation by the rock lobster, *Jasus lalandii*, on whelks of the genus *Burnupena* maintains an assemblage of abundant lobsters and few whelks. In contrast, on Marcus Island, where rock lobsters were removed in the 1960s, the benthos is dominated by mussels, holothurians, sea urchins and large numbers of whelks. Laboratory experiments showed that a bryozoan living commensally on the shell of the whelk, *Burnupena papyracea*, made the whelk unpalatable to lobsters. Field experiments demonstrated that although rock lobsters can physiologically tolerate conditions at Marcus Island, they cannot re-invade because whelks, which are normally prey of lobsters, attack and consume the introduced lobsters.

The community at Marcus Island has persisted for about 20 years suggesting that these two assemblages represent alternative stable states. Although a reversal in the predator–prey interaction maintains the community on Marcus Island, what would cause a natural switch between community states is not known. While a natural event could decimate lobsters, the removal of lobsters from Marcus Island was due to overfishing. One would need to show that a naturally occurring event could reduce or eliminate lobsters and that the reduction in predation would be sufficient to allow a numerical response by whelks. Similarly, it is not known if a switch from a whelk-dominated to lobster-dominated state could occur naturally.

3.4. Rocky intertidal shores

Marine rocky intertidal shores have been among the most intensively studied natural ecosystems, but we are unaware of experimental tests of alternative stable states prior to that of Paine et al. (1985) and later those of Petraitis and colleagues and Bertness and colleagues in the late 1990s. The lack of attention to alternative stable states on rocky shores probably reflects the notion that intertidal assemblages are unstable systems because of strong environmental gradients, variability in recruitment and frequent disturbances. Moreover, the paradigm of intertidal community structure is that site-specific factors, particularly water motion, strongly influence rates of recruitment, production, competition, predation and abiotic disturbance, all of which contribute to patterns of

distribution, abundance and diversity of species in the community (Dayton, 1971; Menge, 1976; Lubchenco and Menge, 1978; Underwood and Denley, 1984; Gaines and Rough-garden, 1985; Petraitis, 1990; Hatcher, 1997; Dye, 1998; Leonard et al., 1998; Foster et al., 2003).

Experimental data that explain the association between the type of rocky shore habitat and species composition of an assemblage are evidence that site-specific rates of processes can underlie community structure. However, the existing paradigm does not completely explain the distribution of mussels. For instance, Lewis (1964) and others since have noted that mussels (*Mytilus*) in the North Atlantic may dominate sheltered shores usually occupied by the fucoid, *Ascophyllum nodosum*, and not just exposed rocky shores predicted by the classic paradigm. Assemblages dominated by either mussels or rockweeds are capable of persisting in very similar environments and may represent alternative stable states (Petraitis and Latham, 1999). The assemblage that develops at a particular site may be the outcome of an historical event (Ricklefs, 1987). Petraitis and Latham (1999) pointed out that if Knowlton's (1992) assertion that large-scale perturbations are more likely to tip an assemblage to an alternative state, then traditional small-scale experiments (<3 m^2) performed by ecologists are unlikely to detect such thresholds. Consequently, typical experimental designs are not suitable to test hypotheses about the occurrence of alternative stable states and the role of history in shaping community dynamics may go unrecognized. However, recent and relatively long-term studies show that historical events can leave strong signatures on community dynamics for years afterwards (e.g., Paine et al., 1985; Knowlton, 1992; Dye, 1998; Underwood, 1998a, 1999; Foster et al., 2003; Witman et al., 2003).

Paine et al. (1985) evaluated the potential for alternative stable states in mussel bed communities in Chile, Washington and New Zealand. At each location, the experiment involved removal of seastars for varying lengths of time after which seastars were allowed to return and community dynamics were monitored for several years afterwards. The experiment consisted of unreplicated removal and control plots at each site. The presence/absence style experimental manipulation precluded detecting any evidence of critical community thresholds, which require several treatment levels (Petraitis and Latham, 1999). Nevertheless, the results are instructive in the context of alternative states and they highlight some of the difficulties in interpreting outcomes.

Outcomes of the experiment differed in each location in accord with relative sizes of predator and prey in each location and the positive feedback of established mussels on subsequent recruitment (Paine et al., 1985). In Chile, the seastar *Heliaster* was removed for 22 months, and community dynamics were monitored another 44 months following the end of *Heliaster* removal. At the end of the 44 months, the control and manipulated communities were identical. In contrast, both in New Zealand (removal of seastar, *Stichaster*, for 10 months and a single removal of the fucoid, *Durvillea antarctica*) and Washington, USA (removal of seastar, *Pisaster* for 5 years), the mussel bed communities that developed in the absence of seastars persisted long after seastars returned (14 and 16 years, respectively).

Paine et al. (1985) recognized two different interpretations of their data depending on the definition of stability applied. Using Connell and Sousa's (1983) criterion of one turnover of all individuals, the persistent mussel assemblages are not alternative states.

Using Slobodkin's (1961) approach for stability in ecological time of intervals of the order of ten times the length of one generation these assemblages are considered alternative stable states.

There are several additional difficulties with this study that make it difficult to conclude that it demonstrates the existence of alternative stable states. First and foremost is the issue of whether the seastar removal mimics a natural event. In other words, is predation by seastars ever reduced naturally over such a long time span (10 months in New Zealand, 5 years in Washington)? The persistence of mussels following the return of seastars may have depended on the mussels attaining an invulnerable size, which in turn, may have depended upon an unnaturally long removal of predators. Under shorter, and possibly more natural pulse perturbations, removal plots in Washington and New Zealand may have converged with the control plots soon after the return of seastars, as occurred in Chile.

Second, tests of maintenance using Slobodkin's stability criterion, or any observational approach, are conceptually problematic because they assume an inhibition model of succession (sensu Connell and Slatyer, 1977). For instance, in New Zealand, the persistence of the mussel, *Perna*, over 14 years suggested it had resisted invasion by seven cohorts of the fucoid *Durvillea antarctica*, but there are no experimental data testing that hypothesis. An important component of testing the maintenance of an alternative stable state is demonstrating an inhibition mechanism of succession and showing that it is resilient to small-scale perturbations (Grimm and Wissel, 1997). In contrast, a tolerance model of succession would suggest that an assemblage is a successional feature of a single basin of attraction. In both New Zealand and Washington, Paine et al. (1985) note a persistent decline in mussel abundance over the years and the eventual return of the original assemblage suggesting that the system may exhibit slow rates of succession via either a mechanism of tolerance or inhibition, but without resilience of the established state.

In the North Atlantic, observations that mussel beds and stands of rockweeds (*Fucus* and *Ascophyllum*) represent distinct species assemblages, either of which can dominate sheltered rocky shores and often occupy adjacent areas of the shore prompted Petraitis and Latham (1999) to hypothesize that these assemblages may represent alternative stable states, in which the transition between states becomes possible following rare (i.e., ~ 4 events per century), large-scale ice scour events in the Gulf of Maine. An experiment testing whether an alternative state could be initiated at a threshold clearing size (intended to mimic ice scour) was executed in stands of *A. nodosum* at 12 sites distributed evenly across 4 bays in Maine, USA. Clearing sizes of 1, 2, 4 and 8 m in diameter and an uncleared control were performed as a pulse perturbation during winter. We know of three events in the northeast region of the Gulf of Maine in which ice scoured areas larger than the largest clearing. They occurred in the winters of 1978–1979 and 2002–2003 on Swan's Island, Maine (L. Ranquist, personal communication, P.S. Petraitis, unpublished data for 2003) and in 1987 in the Bay of Fundy (A.R.O. Chapman, personal communication). Chapman reports that ice removed all of the *Ascophyllum* and 16 years later the site continues to be occupied by *Chondrus crispus*.

Following the clearing, recruitment, mortality and abundance of common species were monitored. The design of experiments enabled detection of, both, any existing threshold

clearing size above which species composition in the developing assemblage changed as well as positive feedbacks that affect rates of ecological processes that maintain either the resident assemblage in small clearings, or the alternative state in large clearings.

A series of papers (Petraitis and Dudgeon, 1999; Dudgeon et al., 2001; Dudgeon and Petraitis, 2001; Petraitis et al., 2003) provide experimental evidence for scale-dependent rates of ecological processes that support the hypothesis that these assemblages represent alternative states. Rates of recruitment and survivorship of taxa representing putative alternate states are greater in large clearings than in small ones with a minimum threshold clearing size of 4 m in diameter. In contrast, the resident, *A. nodosum*, can disperse zygotes tens of meters, but recruitment declines exponentially with distance from the edge of a stand because post-settlement mortality in clearings is high.

Associated with changes in rates of recruitment and survivorship with clearing size are differences in succession between large and small clearings during the first 6 years (P. Petraitis, unpublished data). In small clearings, succession has been slow, but appears to be converging with the surrounding *A. nodosum* community. As predicted by theory, successional outcomes in large clearings have been more variable. Many large clearings have been dominated by *Fucus* spp. and *Semibalanus balanoides* for the past 6 years, a few have only *S. balanoides*, and a few have slowly established small, but persistent patches of *Mytilus*.

Despite evidence from replicated experiments for critical perturbation thresholds and positive feedbacks that facilitate persistence of assemblages, there is insufficient evidence at present to conclude the assemblages invading large clearings represent alternative stable states. Succession continues to reduce the available space in all clearings except those dominated by *Fucus* in which succession stalled following complete cover of the substrate by the canopy. The persistence of *Fucus* in these clearings suggests it may be an alternative state to that of *Ascophyllum* in the mid intertidal zone of sheltered shores, but such an inference suffers from the same criticism as that of Paine et al. (1985). Although *Fucus* that established in clearings became reproductive within 1 year and have persisted for six years, it is ambiguous whether the assemblage represents a stable alternative basin of attraction, or a successional stage in the trajectory towards the *Ascophyllum* state. The longevity of individuals of *Fucus vesiculosus* averages about four years, but probably does not exceed seven years (Fritsch, 1945). Thus, these clearings are nearing the complete turnover of all individuals and in that context may soon satisfy the Connell and Sousa (1983) criterion for stability. However, the prevailing view is that *Fucus* is a successional stage, albeit a protracted one, in the trajectory towards the *A. nodosum* community state (Lubchenco, 1983; S. Hawkins, personal communication). Long-term monitoring of large clearings of *A. nodosum* in Britain has shown that *Fucus* colonized soon after and has persisted 12 years (S. Jenkins, personal communication). *A. nodosum* has recently appeared in these clearings (S. Jenkins, personal communication), but it is uncertain if tolerance (i.e., *A. nodosum* colonizes in the presence of *Fucus*) or inhibition (i.e., colonization only following *Fucus* mortality) is the mode of succession. In this context, an experimental demonstration of resilience by *Fucus* in these clearings to a small perturbation (non-significant perturbation sensu Sutherland, 1990) seems preferable evidence of stability of an alternative state to that of observational approaches such as generation time or population turnover that do not necessarily distinguish the

tolerance and inhibition models of succession and hence, single or multiple basins of attraction.

In addition, Bertness et al. (2002) suggest that alternative rockweed and mussel states do not exist in the rocky intertidal ecosystem in the Gulf of Maine. They used a very different design which consisted of an uncleared control, and 1×1 and 3×3 m clearings in a tidal estuary. They also included a caging treatment within clearings and established the experiment in both *Ascophyllum* stands and mussel beds (see Petraitis and Dudgeon, in press, for a more detailed comparison of designs). Their results after three years showed that succession was unresolved in control plots within clearings, but that plots from which consumers were excluded quickly converged to the state of the surrounding community in both types of habitat, implying strong determinism in the system.

The results of Bertness et al. (2002) are consistent with the classic paradigm of communities being controlled by the interaction between water motion and consumer pressure but do not reject a model of alternative states. Petraitis and Dudgeon (in press) have suggested that the experiments of Bertness et al. (2002) violate the requirements for valid tests of alternative states (Connell and Sousa, 1983; Peterson, 1984; Sousa and Connell, 1985), do not use clearings that were large enough, and were not properly analyzed. Given the differences in experimental design between Petraitis and his colleagues, and Bertness et al. (2002), differences in interpretation may reflect different approaches rather than different ecologies (Underwood and Fairweather, 1989). If this is true, then implementation of identical experiments that are valid tests of alternative stable states should resolve the question.

4. Designing better experiments

A good experimental test of alternative stable states must show that different communities can occur in the same environment and that the communities are self-replicating over time (Peterson, 1984; Petraitis and Latham, 1999). The alternative states cannot be externally maintained (Connell and Sousa, 1983; Peterson, 1984; Sousa and Connell, 1985). Theory provides no insight as to how alternative communities might be initiated, although it seems plausible that the larger a perturbation or disturbance, the more likely a switch could occur (Knowlton, 1992; Petraitis and Latham, 1999). Theory does suggest that bifurcation folds require at least one population process, such as birth rate, death rate or recruitment rate, has a threshold response with a change in an environmental parameter (May, 1977; Scheffer et al., 1993, 2001; Chase, 2003).

A good test of the theory should insure that the above conditions are met by the experimental design. Replication and randomization provide some protection of the same environmental criterion. Appropriate choice of treatments and treatment levels can assure that the states are not externally maintained and allow the ability to detect scale-dependence and threshold responses (Petraitis and Latham, 1999). Inclusion of not only observations over time, but also perturbations over time may provide insight into stability of the system.

Randomization and replication are crucial. All experiments should include a large number of replicate sites that are spread at random and over an appropriate spatial scale

(Underwood, 1998b), but appropriate replication and randomization are critical for testing alternative stable states because of the same environment requirement (Connell and Sousa, 1983; Peterson, 1984). It is impossible to prove different communities occur in the same environment especially since organisms can transform the environment itself (Peterson, 1984), and so the only protections against unknowingly including several different environments within a single test are replication and randomization.

The appropriate spatial scale for randomization depends on how the "same environment" criterion is operationalized. One could imagine using either a physical condition such as the mid-intertidal shores over a defined range of wave forces or a community type such as seaweed beds. Regardless of the approach, replicate plots need to be randomly spaced and treatments need to be randomly assigned within the same environment. This protects against the possibility that different community states within what is thought to be the same environment are, in fact, maintained by unknown site-specific effects, and thus do not represent alternative states. We would advise against combining different community types, which are suspected to be alternative states, within a single experiment (e.g., Bertness et al., 2002). Inclusion of two or more different community types runs the risk of confounding treatment effects with site-specific effects (Underwood, 1998b).

Choice of appropriate treatments is also important because different states cannot be maintained by extrinsic factors (Connell and Sousa, 1983). This has been interpreted to imply that all experimental manipulations must be pulse, not press, perturbations because press perturbations could simply maintain different outcomes (Petraitis and Latham, 1999). We think Petraitis and Latham's interpretation is too narrow because Connell and Sousa stressed the maintenance of alternative states by extrinsic factors but not the initiation of alternative states. This suggests to us that press perturbations could be used to move species composition of a community to a point where the community will tip to an alternative state. Once at the tipping point, the press could be removed and the successional changes could be followed in a free-running system. This is, in fact, what Paine et al. (1985) did by removing seastars for extended periods, which allowed mussels to become established. Within the context of alternative stable states, it seems reasonable that any experimental perturbation, pulse or press, should mimic a natural event that is suspected to be a promoter of the switch between states. Connell and Sousa (1983) made a similar suggestion and noted that disasters caused by novel events (e.g., Hatcher, 1984) should be excluded. If a proposed pulse perturbation is defined in terms of natural events, then there is a benchmark by which we can judge if an experimental manipulation is appropriate both in duration and scale.

The experimental design should also vary the scale of the suspected environmental perturbation (Knowlton 1992; Petraitis and Latham, 1999). Small perturbations are expected to have little effect because they are not sufficient to tip the system from one alternative state to another state. Large perturbations would be more likely to do so. However, it is also likely that the tipping point is not known with certainty and may vary from one replicate site to the next. Thus a range of perturbations should be used so that the tipping point is completely bracketed.

The basic experimental design that incorporates these elements would be a two-factor layout with perturbations at several scales crossed with the time of successive samples.

The design should include unmanipulated controls and sufficient replication. Time is a fixed factor since we are interested in how the system changes over time rather than in controlling for temporal variation. Effects of perturbation and time and their interaction can be tested for each species or process singly in a univariate analysis or as a group of dependent variables in a MANOVA or in an MDS analysis. If responses at a single time point are considered, then the basic design reduces to a one-way layout.

We think there are six distinct experimental outcomes if alternative communities exist, and if a large perturbation was successful in moving the system into another basin of attraction. First, the scale of the perturbation should have a significant effect, and in replicates exposed to large perturbations, the species patterns and the processes of recruitment, mortality and individual growth should be, on average, significantly different from the surrounding community. In contrast, patterns and processes in replicates exposed to a small perturbation should be, on average, similar to those patterns and processes found in the surrounding community.

Second, there should be an interaction between time and perturbation because the response over time should depend on the scale of the perturbation. Small perturbations should converge to the unmanipulated control while large perturbations may cause the system to diverge. How replicates are sampled over time will affect the analysis. Ideally, a new replicate would be taken at each time. In practice, logistical constraints of time and cost prevent such ambitious designs, and so often the same replicate plot is sampled at each time point (Bertness et al., 2002). Time can be considered a repeated measure, either in a univariate or a multivariate design although use of these designs requires restrictive assumptions (Quinn and Keough, 2002).

Third, the outcome in replicates exposed to larger perturbations should be more variable than those treated with small perturbations because not all large perturbations will cause a switch between alternative states. This presents a problem for undertaking parametric analyses because it is likely that variances across levels of perturbation will be heterogeneous. MDS plots could be used to examine the spread of replicates from each level of perturbation, and we would expect those from larger perturbations to show more spread. Another approach, which is not well-known among ecologists, is Flury's (1988) hierarchy of similarities among variance–covariance matrices. Matrices can be identical, be proportional (i.e. same eigenvectors but different eigenvalues), share some but not all eigenvectors in common, or be unrelated. Flury (1988) has developed a log-likelihood statistic for comparing similarities among matrices, and Phillips and Arnold (1999) provide a good introduction to its application to genetic variance–covariance matrices. This approach could be used to compare the variance–covariance matrices based on perturbation levels.

Fourth, there may be location-specific effects, but they should be smaller than effects of the perturbation treatment. The basic design layout of perturbation by time does not allow a direct test of location-specific effects but replicate locations could be included as part of the design. We have used this approach by nesting replicate sites within different locations (Petraitis and Dudgeon, 1999; Dudgeon and Petraitis, 2001; Petraitis et al., 2003). If a community state is simply maintained by location-specific differences (Fig. 3), then analysis should show significant effects of location and the interaction of location x time. If a community is one of several alternative states then analysis may

show a significant interaction between the scale of the perturbation treatment and location. However, a design of perturbation treatment crossed with locations and replicate sites nested within locations, which is a partly nested design, has the same problems as univariate repeated measure designs (Quinn and Keough, 2002; Petraitis and Dudgeon, in press).

An alternative approach would be to test for spatial autocorrelation using a Mantel test (Petraitis and Latham, 1999). The Mantel test compares the correlation between two matrices. If location-specific effects are less important to than perturbation effects, then the correlation between a dissimilarity matrix for a variable (e.g., recruitment) and the distance matrix should be less than the correlation between the variable matrix and a matrix based on the perturbation levels.

Fifth, if the alternative state is to be considered "stable" then at least one of the species in the alternative community must become common enough in biomass, individual size, and/or density in order to establish the positive feedbacks needed to maintain the assemblage. The presence of positive feedbacks could be tested directly by doing small perturbations inside replicate plots that originally received large perturbations. For example, doing 1 or 2 m clearings within the 8 m clearings that Petraitis and Dudgeon (1999) established in 1997. If the state is self-replicating, then these small perturbations should return to the species composition of the rest of the clearing.

Finally, we would expect that we would not see the same result if we re-ran the experiment. Central to the issues of stability and detecting alternative states is the problem of distinguishing the early trajectories of alternative states from successional events that may initially diverge but eventually converge to the same mature assemblage (Samuels and Drake, 1997). If community types are alternative states and not the result of undetected site-specific differences, then re-setting replicates to initial conditions should produce different outcomes than previously observed. This is a direct test of Peterson's criterion that the same site should give rise to different communities and would be the strongest and most compelling test of the hypothesis that two communities were alternative states.

We think a BACI type of design in which half of the replicates are re-set to initial conditions would be the best approach. The choice of which half should be done in a stratified randomized fashion so that each level of perturbation is balanced. There are four possible groups: Before-Control, Before-Impact, After-Control, and After-Impact (Fig. 4). The Before-Control is the original run of data in half of the experiment that is left unmanipulated. The Before-Impact is the original run of data in half of the experiment that is re-set to initial conditions. The After-Control and the After-Impact are the second runs of data from the replicates that were either unmanipulated or manipulated.

The successional trajectories will depend on the scale of the perturbation and whether there are alternative states (Fig. 5). The successional changes in replicate plots re-set using small perturbations should be quite predictable from the Before data. This would also be true for plots that were re-set using large perturbations if only site-specific effects are important. In contrast, if there are alternative states, then the successional changes in plots re-set using large perturbations should not be predictable from the Before data.
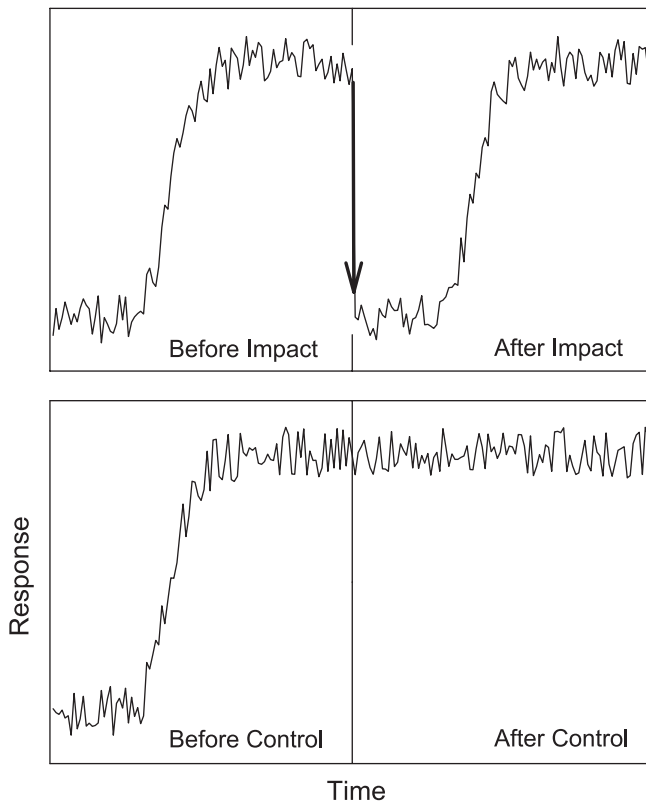
Fig. 4. Successional trajectories after pulse manipulations in a Before-After-Impact-Contol design. Before panels show succession after initial pulse manipulations were done in all replicates. After panels show succession after half the replicates received a second perturbation (After-Impact) and half were left untouched (After-Control). Arrow shows second perturbation in the impact replicates.

Examination of spatial autocorrelations between the Before and After data may also provide some insight. If undetected site-specific effects are important then the spatial pattern in the After-Impact data should be correlated to the pattern in the Before-Impact data. If site-specific effects are not important, then the spatial pattern in the original data should not explain the patterns in the same plots after being re-set by large perturbations. We would expect there to be some level of spatial correlation and so there needs to be a benchmark in order to test if site-specific effects are "important" (Petraitis, 1998).

We think the spatial autocorrelation in nearby Before-Control plots could be used as a benchmark. We would predict that if alternative states occur, then the correlation between the Before-Impact and After-Impact data should be significantly less than the correlation between the two closest Before-Control plots with the same level of perturbation. Moreover, if site-specific differences are important then nearby plots should predict the patterns and processes seen in the re-perturbed plots. Thus pairing each After-Impact (i.e.
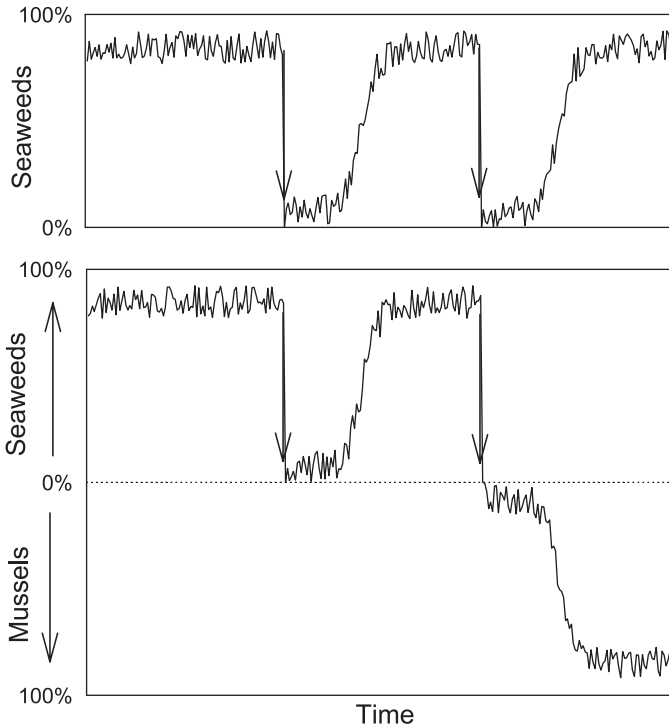
Fig. 5. Expected outcomes in a BACI design if mussel beds and seaweed stands exist as alternative states. All plots are dominated initially by seaweeds. Panels show the initial perturbations result in return to seaweeds (other outcomes are possible but not shown). If seaweed stands always occur in site-specific locations then re-setting no replicate plot should convert to a mussel bed (upper panel). If seaweeds and mussels are alternative states, then some replicate plots should show a different outcome when re-setting the plot (lower panel).

re-perturbed) plot with the nearest After-Control plot that initially received the same level of perturbation should be informative.

5. What has been achieved and what needs to be done

There has been progress in the past 20 years of research in marine systems in defining the criteria to identify alternative states as well as the experimental designs that satisfy those criteria. In each ecosystem we surveyed, there is some evidence in support of, but insufficient evidence to conclude, the existence of alternative stable states. In some cases, there is evidence both for and against alternative states in a single system. Clearly, much more research is needed.

There are also several unresolved issues and we will briefly mention four. All involve the difficulty of translating the metaphor of theory (May, 1977) into experimental tests. First, what constitutes a good experimental manipulation? Second, are threshold responses a hallmark of alternative states? Third, do there need to be stochastic events

in order to have alternative states? And fourth, what is meant by stability and how do we measure it?

While it is clear that a manipulation should match the spatial and temporal scale of natural events, it is not at all clear how this should be done. For example, suppose a pulse perturbation is used to eliminate a predator from the system. This could be done by using a temporary cage. However, what is being changed by the cage-a parameter or a state variable? The cage could be seen as changing a parameter (i.e. a cage alters the rate of predation because the predator is viewed as still in the system) or as reducing predator density to zero (which is true if the system is defined only by the space inside of the cage). The problem becomes increasingly complex as other species are considered. Paine et al. (1985) altered mussel densities by removing predators, but did they alter a state variable (mussels) by manipulating a parameter (the rate of predation) or another state variable (the presence of predators)? We believe this depends on how one defines the system.

It could also be argued that the change in species composition could occur directly or indirectly but we think this is an artificial distinction based on which species are considered members of a species assemblage. For example, the loss of most of the individuals of a sessile species in a fouling community might occur via a storm event or via a brief visit of a highly mobile predator. Most would agree that the effect of the storm is direct, but whether the effect of a predator is direct or not depends on if the predator is included as a member of the species assemblage under consideration.

Parameter space could also be perturbed so that members of an alternative state can invade. Changes in parameters will change the landscape between basins of attraction and thus species composition may be altered as individual species respond to the parameter changes. When the parameter space returns to initial conditions, the species assemblage may be in a different basin and unable to revert to the species composition imposed by the original basin of attraction. Once this happens, any introduction could be successful if the shift in parameters is held long enough to move the species composition to one that is contained within the basin of attraction of an alternative state. Once this occurs, releasing the press perturbation and returning parameters to their original values will have no effect on the outcome. The invaders will continue to displace the established species.

For example, intertidal herbivores can be very effective in controlling macroalgae by consuming small plants but large plants can escape control if they get large enough. If a short perturbation, such as a period of unusually cold or warm weather, limits the per capita foraging rate of herbivores, then macroalgae may escape control. The community may then switch from one dominated by sessile animals to one dominated by algae. Moreover algae may continue to dominate even when per capita rates of foraging (i.e. part of the parameter space) return to initial conditions.

We think much of the ambiguity about parameters and state variables arises from using models such as the Lotka-Volterra equations to guide our intuition. These models are not mechanistic (Dunham and Beaupre, 1998), and so it is not clear if a manipulation should be viewed as changing a state variable or a parameter. Explicit mechanistic models of alternative stable states would help guide the design of experimental manipulations.

Second, it has been suggested that systems with alternative stable states should show dramatic or catastrophic shifts from one to another community assemblage, and thus a test

of alternative states should provide evidence of a threshold response by at least one member of an alternative community (Knowlton, 1992). Petraitis and Latham (1999) concurred with this view, but we are not so certain. Thresholds can occur in models with smooth continuous shifts in state variables (e.g., Fig. 3). Tuning parameters may not provide a strong test because systems with continuous but abrupt thresholds may not be distinguished from systems with bifurcation folds.

In addition, different basins of attraction may be very shallow and so perturbing the system so that state variables (species composition) move from one basin to the next may not cause a rapid change in species composition. If the basin is shallow, the changes in densities may proceed at a very slow rate. Moreover, systems with a single contiguous basin of attraction over a broad range of parameter space may show rapid shifts with small changes in parameters (Fig. 3).

Perturbing state variables is also not a fool-proof test since it will not distinguish systems with very tight folds from systems with gradual shifts in equilibrium states. It is possible to have a continuous model with a bifurcation fold that is so tightly curved that the jump across the fold from one equilibrium point to the other is small. Such a model has alternative stable states but these states would be impossible to detect.

Third, there have also been suggestions that alternative stable states somehow involve "stochastic events" or are non-equilibrium systems (Bertness et al., 2002), but this was never part of the original theory. Development of the theory of alternative stable states was done initially within the context of closed dynamical systems (Lewontin, 1969; May, 1977), and the switch from one basin of attraction to another was envisioned as the result of a perturbation that shifted the state variables. While many versions of alternative stable states imply that the models are stochastic or non-equilbrial, the original formulation of these models did not contain these aspects. While stochastic changes in parameters and state variables play a role, we are uncertain if they are central to the development of clear testable hypotheses concerning alternative states.

Finally, the above discussion does not address the question of stability in natural ecosystems and the problem of moving from theory to practice is well-known (Law and Morton, 1993; Grimm and Wissel, 1997; Gunderson, 2000; Dambacher et al., 2003; Hansson and Helgesson, 2003). Even relatively simple models can produce extraordinary dynamics and include long transient times, fractal basins of attraction, and strange attractors (Grebogi et al., 1987; Savage et al., 2000; Huisman and Weissing, 2001a,b). Grimm and Wissel (1997) provide a very comprehensive summary of 163 definitions of stability and found six distinct features—constancy, resilience, persistence, resistance, elasticity, and domain of attraction. Most were anticipated by Lotka (1956) and Lewontin (1969), who discuss various definitions of equilibria and stability that go beyond the mathematical definition of stability within linear dynamical systems. Both Lotka and Lewontin note that constancy does not imply stability and that stability is a dynamical property. Both note that one conception of stability is energetic with stable points being associated with local minima of some measure. The landscape of stability was described to be like a topographic map with "pits" (Lotka, 1956, Fig. 29; Lewontin, 1969, p. 18). Both acknowledge that stable points are rare in nature and biologists should be more concerned with the forces maintaining a system near a stable point.

Lewontin (1969) suggested that the properties of relative stability included the size and shape of the basin of attraction, as well as the steepness of the sides of the basin. He also noted that presence of oscillatory behavior was also important because weaker oscillations during the return to an equilibrium point could be viewed as "more stable." In some systems, external forces or "a constant expenditure" (Lotka, 1956) is required to maintain a system at constancy or what Lotka called quasi-equilibrium, and what today is called press perturbations (Bender et al., 1984). We would also note that Lotka's quasi-equilibrium embodies the dynamic between successional change and grazing found in the range succession model (see Fig. 1 in Westoby et al., 1989).

It is also possible for alternative states to be just persistent rather than stable by the virtue of species-specific longevity of individuals rather than the self-replication of individuals. This has been rejected by some as not part of the theory (Connell and Sousa, 1983; Peterson, 1984; Sousa and Connell, 1985) and defended by others (Sutherland, 1990). We, however, think that theory does provide for such a scenario. For example, a system may have two equilibrium points in which one point is stable and the other is not. The system, by definition, has two alternative states. Within a persistent state there may be some species that can self-replace. The existence of the self-replacing assemblage then depends on single species that provides habitat even though that single species is not self-sustaining—for example, the endemic insect fauna in a relic forest that unable to re-seed. The insect fauna itself may be self-sustaining but long-term persistence or resilience is not possible because the trees are relics. This example highlights the difficulty of defining stability for systems in which we often focus on a subset of the interactions and species over arbitrarily determined time periods and spatial scales.

In closing we would like to emphasize that detection of alternative states is not a purely academic pursuit. The existence of alternative stable states means that history can play a profound role on structuring present-day assemblages (Lewontin, 1969; Ricklefs, 1987; Knowlton, 1992; Petraitis and Latham, 1999). Small changes can tip a system from one state to another, and more importantly, the initial state cannot be recovered by small reversals. In contrast, if the switch between different communities is merely a phase shift, then reversal is possible. Here, there may be a historical context to how a phase shift occurred, but the initial community state can be recovered by small reversals. In a sense, the community carries no memory. We have witnessed in the last 20 years large-scale changes, and in some cases collapses, of ecosystems, and the need to distinguish between alternative states and phase shifts is clear. Each implies very different strategies for management, conservation and restoration.

Acknowledgements

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