THEME SECTION

Threshold dynamics in marine coastal systems

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Ecological thresholds in marine communities: theory, experiments and management

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ABSTRACT: There is increasing interest in the resilience of marine and estuarine populations, communities and ecosystems, and their rapid change when stresses reach some threshold or tipping point. Current research on thresholds is altering our understanding of these systems, the processes by which they change, and our approach to their management and restoration. In this Theme Section conceptual, modeling, and empirical studies explore threshold dynamics in marine coastal systems in a variety of habitats and across different scales. The contributions provide a window on present research, highlight some of the issues being debated, and point to some of the potential applications of threshold dynamics to resource management issues.

KEY WORDS: Thresholds · Resilience · Multiple stable states · Tipping points · Management

Thresholds within ecological systems are the tipping- or break-points beyond which rapid state or regime shifts occur (Scheffer et al. 2001, Scheffer & Carpenter 2003, May et al. 2008). Threshold dynamics are closely tied to the concepts of system resilience or resistance to change resulting from environmental perturbations (e.g. Pimm 1984, O'Neill et al. 1986, Tilman & Downing 1994, Thrush et al. 2009) and the existence of alternate system states (e.g. Holling 1973, Sutherland 1974, 1990, Folke et al. 2004). All systems are resilient to stress, but at some point stressors will be of sufficient magnitude or persistence to cause dramatic change. If a threshold is crossed, then the original configuration of the system will be displaced by a new configuration with its own resilience and resistance to change. A reduction in stress or a return to the previous environmental conditions may be insufficient to overcome the resilience of the new state and return the system to its previous state. Systems that experience threshold dynamics differ from systems which change incrementally with increases or decreases in stress; management and restoration of ecosystems depend on recognizing and incorporating this difference (Suding et al. 2004, Suding & Hobbs 2009, Thrush & Dayton 2010). The present Theme Section (TS) illustrates the variety of theoretical, experimental and applied research into the threshold ecology of marine and estuarine systems.

The concept of a community existing in alternate states with potential thresholds between them has a rich history (e.g. Holling 1973, Sutherland 1974, Pimm 1984, O'Neill et al. 1986). Dramatic, rapid, and unexplained shifts in populations, communities and ecosystems observed in recent years have resulted in an increased interest in both the theory and its application. The existence of distinct multiple states has been documented in marine and estuarine habitats such as coral reefs (e.g. Knowlton 1992, Mumby et al. 2007), fouling communities (Sutherland 1974, 1990), pelagic ecosystems (Litzow & Ciannelli 2007, Casini et al. 2009), the rocky intertidal (Petraitis & Latham 1999, Petraitis & Dudgeon 2004, Petraitis et al. 2009), benthic communities (Peterson 1984, Thrush & Dayton 2002), kelp forests (Steneck et al. 2002, Konar & Estes 2003), seagrasses (Worm et al. 1999), and coastal wetlands (Lindig-Cisneros et al. 2003). Coupled with this increasing interest is a debate about the stability of these multiple states (Connell & Sousa 1983) and the evidence needed to document their existence (Peterson 1984, Petraitis & Dudgeon 2004). This debate highlights the difficulties in identifying different states, determining their stability and whether they are truly

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alternates of the same system, identifying the environmental conditions that link them and whether transition points are thresholds, and how the temporal aspects of threshold transitions interact with the spatial aspects of multiple states (e.g. metapopulations, metacommunities, landscapes). Given that the existence of multiple states, thresholds, regime shifts, tipping- and break-points are considered in ecosystem management (e.g. Gunderson 1999, Thrush & Dayton 2002, Lindig-Cisneros et al. 2003, Folke et al. 2004, Suding et al. 2004, Marten 2005, Fischer et al. 2009, Suding & Hobbs 2009), it is timely to explore the diverse views on thresholds in marine systems.

This TS presents a broad spectrum of research focusing on thresholds within marine and estuarine systems. We identified and contacted many marine ecologists researching into thresholds and solicited from them additional colleagues who might be able to contribute to this TS. Our search likely missed potential contributors and many of those contacted were unable to contribute. The contributions received include both theoretical approaches and empirical examinations of specific systems. A secondary goal was to examine applications to resource management and how threshold systems affect management approaches. We specifically asked the contributors to address this issue.

Several sub-themes emerged from the papers within this TS.

Habitat diversity: The studies represented a diversity of habitats, ranging from the pelagic (Casini et al. 2010) to subtidal sedimentary (Norkko et al. 2010), coral (Dudgeon et al. 2010) and biogenic (Lundquist et al. 2010) reef, and fouling communities (Osman et al. 2010, Munguia et al. 2010), to intertidal populations and communities (Hewitt & Thrush 2010), and large estuarine ecosystems (Fairweather & Lester 2010).

Conceptual issues: Petraitis & Hoffman (2010) examined the concept of thresholds in multiple stable states and some of the confusion that results from different interpretations of 'threshold'. Dudgeon et al. (2010) explored the differences between multiple states and phase shifts as applied to coral reef communities.

Modeling approaches: Several studies used modeling to examine the contributions of various processes to thresholds in marine and estuarine systems. Simple Lotka-Volterra models were used to demonstrate how thresholds and different states can occur in linear systems (Petraitis & Hoffman 2010) and how the dominance of species with different life histories in a system can be affected by local and regional scales of disturbance (Munguia et al. 2010). Lundquist et al. (2010) used a spatially-explicit patch-dynamics model to explore the effects of temporal and spatial rates of disturbance on a benthic community. They associated disturbance effects with inter-patch connectivity, and showed that as dispersal limitation increases, the tolerance threshold for dominant species shifts. Fairweather & Lester (2010) used a state-and-transition model with states defined by biota and transitions by a classification and regression tree (CART) of environmental data to understand the thresholds within an estuarine ecosystem and predict future ecological outcomes of management decisions.

Long-term data sets: These are highlighted in 3 studies. Casini et al. (2010) used a 30 yr data set to examine threshold dynamics in population processes. For Baltic herring they show that a shift in sprat abundance above a threshold level decouples herring growth from salinity, contributing to declines in spawning stock. Hewitt & Thrush (2010) analyzed a 20 yr data set for an intertidal sand flat to test 2 indicators of regime shifts, changes in abundance of key species and increased temporal variability, both of which were found to precede a shift to an alternate community type with changes in functional and trophic characteristics. Osman et al. (2010) used the results of studies on fouling communities conducted over 20 yr to examine transitions among 4 different community states.

Experimental approaches: Experimental tests of threshold processes are also represented. Norkko et al. (2010) present results from a set of experimental manipulations that assessed the effects of increasing spatial scale of disturbance and differences in environmental context on the recolonization and recovery of benthic fauna, how these may indicate threshold responses, and the implications for understanding regime shifts in species-poor and in more diverse systems. Experimental studies on the effects of predators, temperature, and recruitment were critical to defining the threshold dynamics in the fouling communities examined by Osman et al. (2010).

Management implications: Several studies focused on management concerns. Fairweather & Lester (2010) examined water management in an estuary to provide better predictions and a foundation from which to evaluate management decisions. Casini et al. (2010) looked at the herring fishery and its management. Hewitt & Thrush (2010) examined intertidal stressors within a harbor, many of which are linked to human impacts that can be managed. For example, a system shift may have been produced by a relatively small change in sewage disposal interacting with climate dynamics, and their effects on a habitat-forming key species in the system.

These and preceding studies show that threshold dynamics can be complicated and difficult to define. The differences in thinking over what constitutes thresholds, their relationship to multiple stable states, how they are measured, and the implications for management will continue to be debated. This TS provides a focus for future research and discussion.

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Multiple stable states and relationship between thresholds in processes and states

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ABSTRACT: The concept of thresholds is applied broadly in ecology to both processes and states that exhibit step-like behavior. Thresholds are observed in parameters, equilibrium states, and in states over time, but presence or absence of thresholds at any of these levels does not provide information about the occurrence of thresholds at the other levels. Here we explore the relationship between thresholds and theory of multiple stable states. We present a 2-species Lotka-Volterra model of competition to illustrate that thresholds and hysteresis-like behavior are possible in linear systems. A grazing model is presented to show that multiple stable states are possible without thresholds in the underlying processes. The concept of thresholds within the context of multiple stable states is reviewed in an attempt to resolve some of the confusion that stems from the different meanings of thresholds.

KEY WORDS: Alternative stable states · Coral reefs · Fisheries · Intertidal · Multiple stable states · Rocky shores · Subtidal · Seagrasses · Thresholds

INTRODUCTION

Sudden changes have been observed in many marine ecosystems, e.g. abrupt regime shifts from corals to macroalgae in tropical systems, and from macroalgae to barrens or mussel beds in temperate systems, which result in changes in abundance of exploited fish stocks (Done 1992, Hare & Mantua 2000, Konar & Estes 2003, deYoung et al. 2004, Paine & Trimble 2004, Mumby 2009, Petraitis et al. 2009). Ecologists are especially interested in these sudden shifts because they are common in a variety of situations, often occur unexpectedly, and are difficult to reverse. The unpredictability and irreversibility of the shifts can cause serious management problems and are seen as indicators of an ecosystem with multiple stable states (e.g. deYoung et al. 2004, Huggett 2005, Bestelmeyer 2006, Groffman et al. 2006, Suding & Hobbs 2009, Thrush et al. 2009).

The term 'threshold' is used to describe sharp changes in either a process (e.g. recruitment rate or mortality rate) or a state (e.g. species composition or amount of biomass), and ecologists often use the former in attempts to predict the latter. While thresholds are among those concepts in ecology that are commonly used and intuitively understood, little progress has been made on how to operationalize the concept. Thresholds are perceived as dramatic changes in some aspect of a population, community, or ecosystem, but this very general conceptualization of thresholds involves defining not only what ecologists mean by terms such as 'dramatic', but also the context of the question — how ecologists define a population, community, or ecosystem. We will not fully explore the issue of terminology, but we note that ecologists rarely define what a sudden shift is in terms of background conditions, and more often than not, 'sudden' seems to mean 'unexpected' (Doak et al. 2008).

Here we examine the relationship between sudden changes, or thresholds, in marine ecosystems and the theory of multiple stable states, with 3 specific goals in mind. (1) We discuss how thresholds can occur in parameters, processes, and ecosystem states, but the occurrence of a threshold in, for example, a parameter does not mean there must be a corresponding threshold in the ecosystem state. There need not be a 1:1

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correspondence, even though this is often assumed when multiple stable states are modeled or tested. (2) It is usually assumed that systems with multiple stable states and hysteresis must involve non-linear responses. This is not true, and we show how a well-known linear model — the Lotka-Volterra model of competition — can give rise to thresholds and even appear to exhibit hysteresis. (3) We show that systems with multiple stable states can exist even when the underlying processes do not have thresholds. We use a well-known non-linear model of grazing (Noy-Meir 1975, May 1977) to show that it is very easy to construct a system with multiple stable states without sharp transitions or thresholds in the underlying processes of recruitment and mortality.

All 3 points are important because it is often stated that multiple stable states arise from strong positive feedbacks, non-linearities, and/or thresholds (e.g. Scheffer et al. 2001, Schröder et al. 2005, Mumby et al. 2007). While positive feedbacks, non-linearities, or thresholds are sufficient to produce multiple stable states, what is overlooked is that none is necessary. In the 'Discussion' we explore how insights from the models might enlighten our understanding of thresholds in marine ecosystems.

THRESHOLDS IN STATE VARIABLES AND PARAMETERS

Thresholds in state variables and parameters are not 1:1, but state variables and parameters must be clearly defined before this concept can be appreciated. In ecology, the term threshold has been applied to sharp transitions in both the ecological processes that control the system (i.e. parameters of a model) and the descriptors of the system itself (i.e. state variables of a model), and many of the better known models in ecology are of the form:

$$\frac{dN}{dt} = f(N) \qquad (1)$$

where the rate of change (t = time) is a function of density (i.e N) or some other ecosystem state such as biomass or resource abundance. The rate of change is a function of density, and density is the state variable. The function itself can involve either parameters that cannot be directly measured such as r and K in the logistic model, or parameters such as births and deaths, which can be measured directly. Alternatively, many ecological models are of the form:

$$\frac{dN}{dt} = f(R) \qquad (2)$$

in which the rate of change is a function of a resource or something else (i.e. R) rather than the state variable of interest. These sorts of models are often called 'mechanistic' because it is assumed that the underlying mechanism for conversion of resources into population growth is understood and captured in the function $f(R)$. In ecological systems, any sudden changes in state variables (e.g. densities, biomass, resource levels) or in parameters (e.g. r, K, births, deaths, per capita rate of prey capture) are identified as thresholds. The relationship between state variables and parameters can be generalized to other sorts of ecosystem descriptors.

However, the relationship between a threshold in a parameter and a threshold in a state variable is not 1:1 (Fig. 1, see also deYoung et al. 2004, Andersen et al. 2009, Suding & Hobbs 2009). For example, the change in a parameter such as birth rate could show a linear, curvilinear, or threshold-like change as environmental conditions change (see Fig. 1a). Changes in environmental conditions and parameters could occur over time and/or space, and both can be persistent or brief (e.g. 'press' versus 'pulse' perturbations, Bender et al. 1984), continuous or jump-like (e.g. state threshold versus driver threshold, Andersen et al. 2009), and linear or step-like (e.g. ramp disturbance versus press disturbance, Lake 2000). It is often not clear if the usage of a term such as perturbation, disturbance, or threshold applies to a change in environmental conditions or a change in a parameter.

Moving up 1 level and with the same line of reasoning, a threshold in a parameter does not assure that there will be a corresponding threshold shift in a state variable (compare Fig. 1a versus 1b and 1c). Conversely, a threshold in a state variable does not imply that there must be a threshold in a parameter. Thresholds within the context of models are sharp shifts in parameters or equilibrium values of state variables (i.e. Fig. 1a–c), but experimental ecologists often track transient changes in a state variable such as density over time. Transient behavior of a state variable may or may not exhibit threshold-like changes or even oscillate over time (Fig. 1e) and provides few insights unless there is additional information about the biology of the system. Changes in parameters can easily shift the equilibrium state of the system across a threshold (e.g. effects of Δp in Fig. 1c), but the change in state of the system may occur quite gradually because of demographic inertia or other life history characteristics of the species involved. This point has been made early and often by both experimentalists and theoreticians (Frank 1968, Connell & Sousa 1983, Hastings 2004).

The issue becomes more complex when systems with multiple stable states are considered. First, it is often assumed that the existence of a sudden and unexpected shift in either a parameter or state variable is prima facie evidence of multiple stable states (Knowlton 1992, Petraitis & Latham 1999, Beisner et al.

2003, deYoung et al. 2004, Paine & Trimble 2004). This need not be true (Fig. 1), and we develop this more fully in the grazing model given below. Second, in his discussion of multiple stable states, May (1977) used the term threshold in a much narrower sense than is used in current discussions. In May's terminology, thresholds are bifurcations or discontinuous changes in state variables in response to small, continuous (i.e. smooth) changes in a parameter. Moreover, a system with multiple stable states must have 2 thresholds – 2 discontinuous shifts in a state variable, each at a unique value of a continuous parameter (i.e. T_1 and T_2 in Fig. 1d). It is the existence of these 2 thresholds that gives rise to the familiar S-shaped curve that is used to

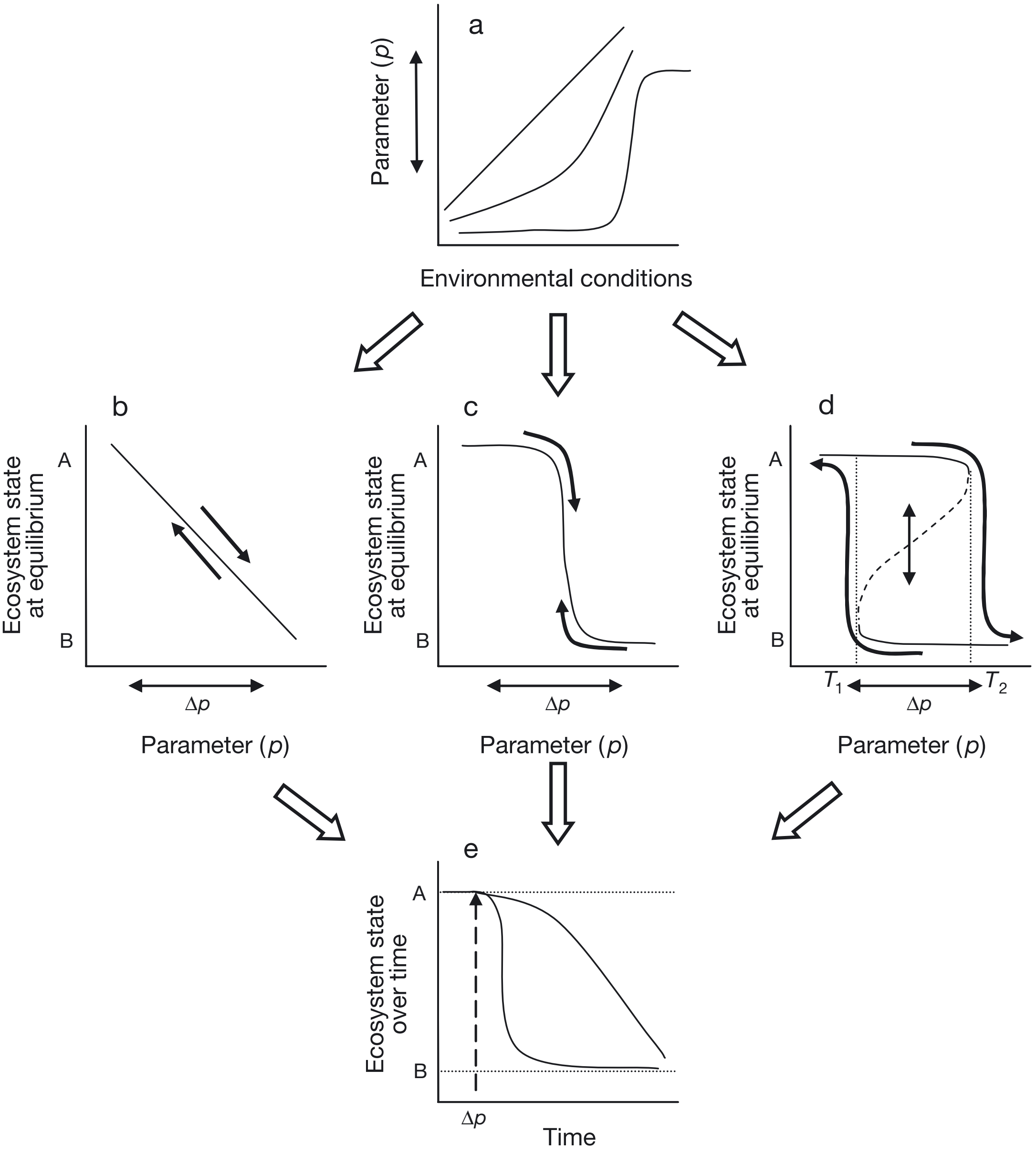

Fig. 1. Thresholds in processes, in equilibrium states, and over time. Open block arrows show the possible pathways from changes in parameters, in equilibrium states, and over time. Solid arrows show shifts in equilibrium values with changes in parameter values. (a) Parameters can show linear, gradual non-linear, and steep non-linear (threshold) responses to changes in environmental conditions. (b) Linear shifts in equilibrium states (e.g. A and B) with changes in parameter values. (c) Steep but continuous shifts in equilibrium states with changes in parameter values. This is a phase shift and does not represent multiple stable states. (d) Steep and discontinuous shifts in equilibrium states from B to A at T_1 and from A to B at T_2 with changes in parameter values. Dashed line is the breakpoint curve; double-headed arrow shows a change in state variable without a change in parameter value. (e) Gradual versus rapid changes in ecosystem state over time. Dashed line gives the point at which the system receives a press perturbation in a parameter value. Dotted lines are the equilibrium states (i.e. A and B)

illustrate multiple stable states and hysteresis. Finally, ecologists often identify the ridgeline that separates 2 basins of attraction as a threshold (i.e. the dashed curve in Fig. 1d). While this is an acceptable and common use of the term, May (1977) used the phrase 'breakpoint curve' to distinguish the shift among basins of attraction from the discontinuous thresholds at specific parameter values.

The breakpoint curve and different basins of attraction are often portrayed as a ridge separated by 2 valleys (Beisner et al. 2003) or a 3-dimensional landscape (Scheffer et al. 2001), although Lotka (1956, p. 147) warned that these representations were 'purely qualitative'. A perturbation of species densities that forces the system past this ridge will cause the system to move downhill towards the new equilibrium point without further intervention. This threshold between basins of attraction is not the same as the threshold in a parameter (Fig. 1a), the smooth threshold in a state variable with changes in a parameter (Fig. 1c), or May's thresholds as found in systems with multiple stable states (Fig. 1d). The ridgeline is often thought to show the position of the unstable equilibrium point that always lies between 2 stable points (e.g. Schröder et al. 2005), but this is not always true. This misconception is explored in the next section as part of the discussion of linear models that exhibit thresholds.

THRESHOLDS AND HYSTERESIS-LIKE BEHAVIOR IN LINEAR MODELS

The simplest linear model in community ecology that has multiple stable points is the 2-species Lotka-Volterra model of competition with a saddle node (Lotka 1956, Knowlton 1992). There are 2 stable points, and at each stable equilibrium point, 1 species excludes the other. Species 1 at equilibrium cannot be invaded by Species 2 and vice versa. At the saddle node, both species are at equilibrium, but the equilibrium point is unstable. Any perturbation of the system, which shifts densities away from the saddle node, will cause the system to move to 1 of the stable points. Lokta (1956, p. 147) noted that 2 stable points in models of this sort must always be separated by a saddle node 'just as it is physically impossible for two mountains to rise from a landscape without some kind of a valley between'.

The existence of the saddle node requires the relationships between carrying capacities of Species 1 and 2 (K_1 and K_2) and the competition coefficients (α, the per capita effect of Species 2 on Species 1, and β, the per capita effect of Species 1 on Species 2) to satisfy the inequalities $\frac{1}{\alpha} < \frac{K_2}{K_1} < \beta$. This requires the interactions between species to be very asymmetrical and either α or β must be greater than 1, which implies that interspecific effects must be greater than intraspecific effects for 1 of the species. It is commonly assumed that this should be rare in nature since intraspecific competition — particularly for resources — is usually much greater than interspecific competition. However, either α or β can easily be >1 under interference competition or in situations where a competitor is also a predator but is not explicitly modeled as such.

Replacement of 1 species by the other can only occur if a disturbance either reduces the density of the current dominant or allows invasion by the other species so that the species composition shifts past the separatrix, which is the line that defines the boundary between the 2 basins of attraction (Slobodkin 1961). Initial conditions of the state variables (i.e. the initial densities of the 2 species) not only determine which species wins but also give rise to priority effects in which the order and timing of the arrival of species determines the final outcome. This simple model also clearly illustrates Lewontin's (1969) comment that while multiple stable points are possible for linear models, 1 or more species must be missing at each stable point. While the relationship between the 1 unstable point and the 2 stable points is often portrayed as a cross-section of a ridge separating 2 valleys, the relative position of the ridge depends on how the combined densities of the 2 species are perturbed relative to the separatrix. The simple representation of a single ridge hides the many alternative paths across the separatrix from 1 basin of attraction to another. Any single representation is only 1 of many possible snapshots of the positions of the stable points and the separatrix.

This can be easily seen by examining 2 different paths across the separatrix. For the first case, imagine the perturbation of the density of Species 2 is large relative to the perturbation of Species 1 (Fig. 2a), and for the second case, imagine the perturbation of both species is similar (Fig. 2b). The position of the ridge that separates the 2 basins of attraction depends on where the separatrix is crossed, so the position of the ridge shifts from 1 example to the other (Fig. 2c versus 2d). Two additional points are worth noting. First, the units on the axis showing the state of the ecosystem (e.g. the *x*-axis in Fig. 2c) depend on how the cross-section through the phase diagram (e.g. Fig. 2a) is drawn. Here we arbitrarily set the density of Species 1 as the ecosystem state of interest, but the cross-section could have just as easily been drawn as a diagonal line connecting K_1 and K_2. If this were the case, the units of the ecosystem state would be a combination of the densities of Species 1 and 2. Second, the contour of the hill and valleys does not indicate changes in ecosystem

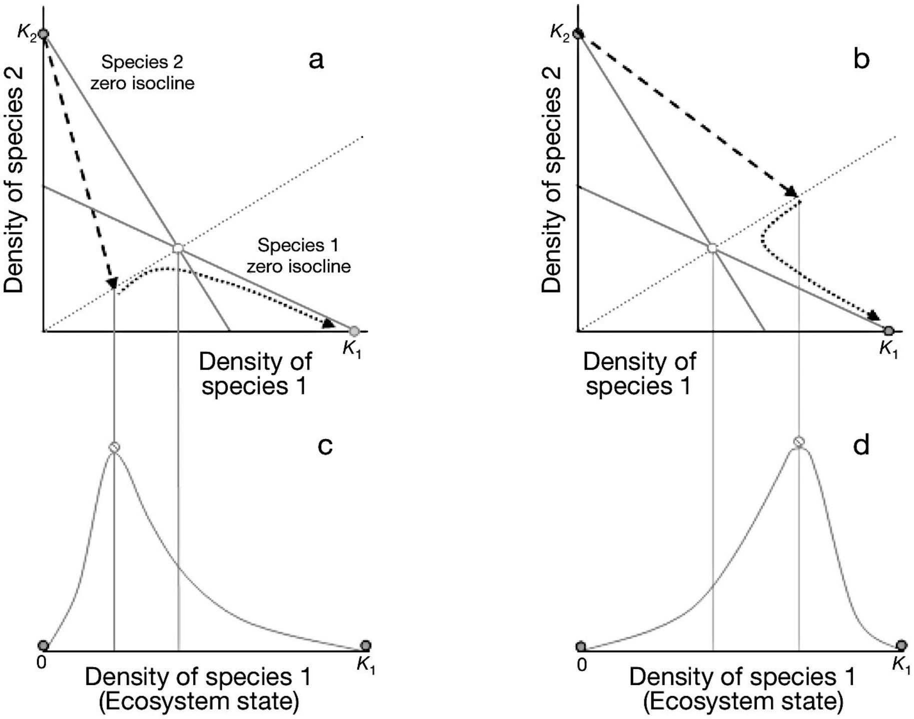

Fig. 2. Comparisons between phase diagrams and the hill and valley representations of stability. (a) Phase diagram of a saddle node in the standard Lotka-Volterra model for 2-species competition. Solid grey lines are 0 net isoclines, and the grey dotted line is the separatrix. The black dashed line with arrowhead is a pulse perturbation of species density across the separatrix, and the black dotted line with arrowhead is the path towards the new equilibrium point after the perturbation. Open (closed) circles are unstable (stable) equilibrium points. (b) Same as in (a), but with a different perturbation. (c) The perturbation and separatrix from the phase diagram mapped onto the hill and valley representation of stability. (d) Mapping of (b)

state. For example in Fig. 2b, the density of Species 1 first declines after the perturbation before increasing to K_1, so the slope in Fig. 2d provides no information about changes in density of Species 1 once the separatrix is crossed.

The relative heights and depths of the hills and valleys are metaphors for the system's stability. In physical systems, a stable point can be represented in a meaningful way as a point of 'minimum potental energy' (Lewontin 1969), and heights and depths are related to the Lyapunov function of the system. Lewontin was the first to make the connections for ecologists among Lyapunov functions, stability, and minimum potential energy. However, Lewontin (1969, p. 18) also stated

> …[f]or ecology the problem of Lyapunov functions is to what extent they represent interesting biological statements...Will it be a useful and illuminating quantity or simply a mathematical formalism with no intuitive content?

Fig. 2 suggests that the representation of stability as a ball on a surface, which is no more than a cartoon of the system's Lyapunov function, may not always provide us with the correct intuition.

It is also not commonly appreciated that linear models can show hysteresis-like behavior, and this can be easily shown in the Lotka-Volterra model (Fig. 3). Suppose changes in environmental conditions can increase the carrying capacity of Species 2 (K_2) but have no effect on Species 1. This could be simply an additional resource that can be utilized by Species 2 but is unavailable or cannot be used by Species 1. In a relatively poor environment for Species 2, the isocline for Species 2 is completely inside the isocline for Species 1 (Fig. 3a), and Species 1 is the competitive dominant and can resist any colonization attempt by Species 2. As conditions improve for Species 2, its equilibrium density (K_2) increases, and its isocline shifts outwards. Eventually the isocline for Species 2 touches and crosses the isocline for Species 1 at the point (0, K_1). Once this occurs, the system has 3 equilibrium points: 2 stable and 1 unstable (Fig. 3b). Further improvements in conditions will then push the isocline for Species 2 until it is completely outside the isocline for Species 1 (Fig. 3c). At this point, Species 2 is the competitive dominant and can resist all attempts by Species 1 to invade the system. Plotting the equilibrium points for Species 2 against changes in environmental conditions produces a Z-shaped curve that is reminiscent of the S-shaped curve in non-linear systems with hysteresis. However, this is not hysteresis in the strict sense because it does not fall within the class of non-linear mathematical models that define hysteresis, even though the ability of Species 1 to invade and resist invasion by Species 2 lags behind changes in environmental conditions.

MULTIPLE STABLE STATES ARE POSSIBLE WITHOUT THRESHOLDS

One of the easiest ways to model multiple stable states is to have a steep non-linear response or threshold in one of the underlying processes (e.g. May 1977, Knowlton 1992, Scheffer et al. 1993, 2001, Mumby et al. 2007), so not surprisingly, it is commonly assumed that multiple stable states require a threshold response. This is not true, and here we show how it is possible to have multiple stable states without thresholds.

We start with a conventional model for grazing in which recruitment and mortality of the exploited species are modeled explicitly. This is a well-known model of grazing that has been often used as an example of a system with multiple stable states (Noy-Meir 1975, May 1977). Let the rate of change of individuals in the exploited species, dN/dt, be:

$$\frac{dN}{dt} = s + Nf(N) - Nv(N) - pN \tag{3}$$

where s is the input supply of recruits that is unrelated to density, $f(N)$ is the per capita effect of facilitation of recruitment by individuals in the population (e.g. enhancement of barnacle recruitment by the presence of adults), $v(N)$ is the per capita mortality rate, and p is the rate of removal of adults by grazing. Per capita recruitment is then the combined effect of facilitation and the mass supply rate. Note that grazing is included in the model as a parameter and not as a state variable, which is how multiple stable states in grazing systems have usually been modeled since May (1977). Now assume the per capita effects of facilitation and mortality are nonlinear but do not have thresholds:

$$\begin{aligned} f(N) &= aN + bN^2 \\ v(N) &= c + dN^2 \end{aligned} \tag{4}$$

The combined effects of recruitment and mortality without grazing (i.e. grazing pressure $p = 0$) is a cubic equation, and the rate of change in the population initially declines before giving rise to the familiar hump-shaped curve usually associated with logistic growth (Fig. 4). The initial decline in recruitment is an Allee effect and is due to the low numbers of adults (Fig. 4a). There is no enhancement of recruitment without adults present, so the per capita rate of mortality at first outpaces the mass supply rate of recruits. The enhancement is a per capita effect, i.e. the more adults are present, the larger is the effect on the per individual recruitment rate, although the additional benefit declines with density and the curve saturates. The individual contributions of mortality, mass supply, and facilitation are non-linear, but none shows a threshold.

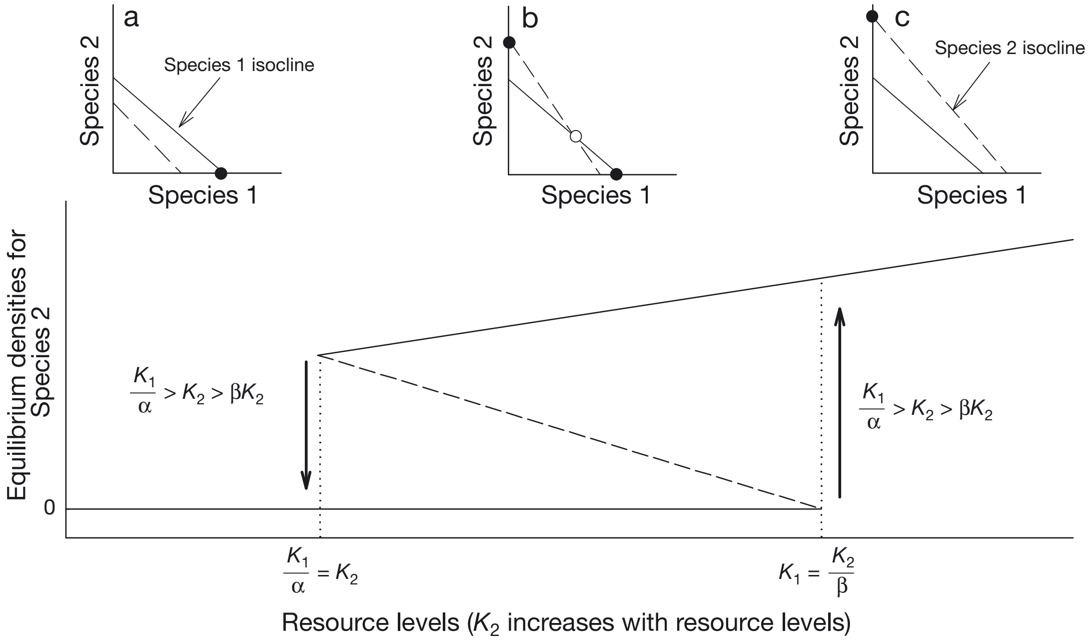

Fig. 3. Standard Lotka-Volterra model for 2-species competition showing hysteresis-like behavior with changes in resource levels expressed as changes in equilibrium density, K_2. The 3 phase diagrams (a–c) show 0 isoclines for Species 1 and 2 at 3 points along the resource gradient. Below, the Z-shaped curve shows the equilibrium points for Species 2 (stable as solid line; breakpoint curve as dashed line). Solid lines give the stable equilibrium points (i.e. 0 and K_2)

When grazing is added, the equilibrium density of the exploited species is a balance between the population's rate of growth and the rate of grazing (Fig. 4b). As grazing pressure (p) increases, the system moves from 1 stable equilibrium point to 2 stable and 1 unstable points, and finally to back to 1 stable point. The transition from 1 stable point to 3 points is discontinuous and occurs over a very small change in p. The system has multiple stable states in the classic sense as defined by May (1977), even though none of the per capita rates shows step-like changes with changes in density.

The range and relative impact of grazing are surprisingly small given the dramatic effect of grazing on the equilibrium density (Fig. 4c). Multiple stable states in this model occur only if p is between 0.0194 and 0.0467, which is between one-twelfth and one-fifth the per capita rate of mortality (i.e. $v[N]$). The range is extraordinarily narrow considering that p can lie between 0 and 1, although for $p > 0.06$, the equilibrium density drops below 10% of the density of an unexploited population.

DISCUSSION

Our critique suggests a single important lesson for ecologists, viz. demonstrations or observations of thresholds at 1 level provide little or no insight into thresholds at another. A threshold in a parameter does not necessarily mean there will be an abrupt shift between equilibrium states. We have shown in both linear and non-linear models how threshold behavior in state variables can occur without a threshold in parameters. The presence or lack of a threshold in one does not imply the presence or lack of a threshold in the other. The same is true for the relationship or lack thereof between transient behavior and parameters.

Obviously there are many possibilities moving from observations of parameters to observations of equilibrium states and from equilibrium states to changes over time. The 8 curves in the 5 panels given in Fig. 1 alone provide 18 possible combinations, although not all are plausible. Yet, it is very difficult to use the plausible combinations to categorize the various studies reported in the literature, even though there have been numerous and well known efforts to catalogue examples of thresholds (May 1977, Scheffer et al. 2001, Folke et al. 2004, Knowlton 2004, Orth et al. 2006, Mumby 2009). The major obstacles to classification are inconsistent terminology, the potential for interactive effects between parameters and state variables, the use of models to confirm rather than to refute patterns, and the limits of inferences that can be drawn from

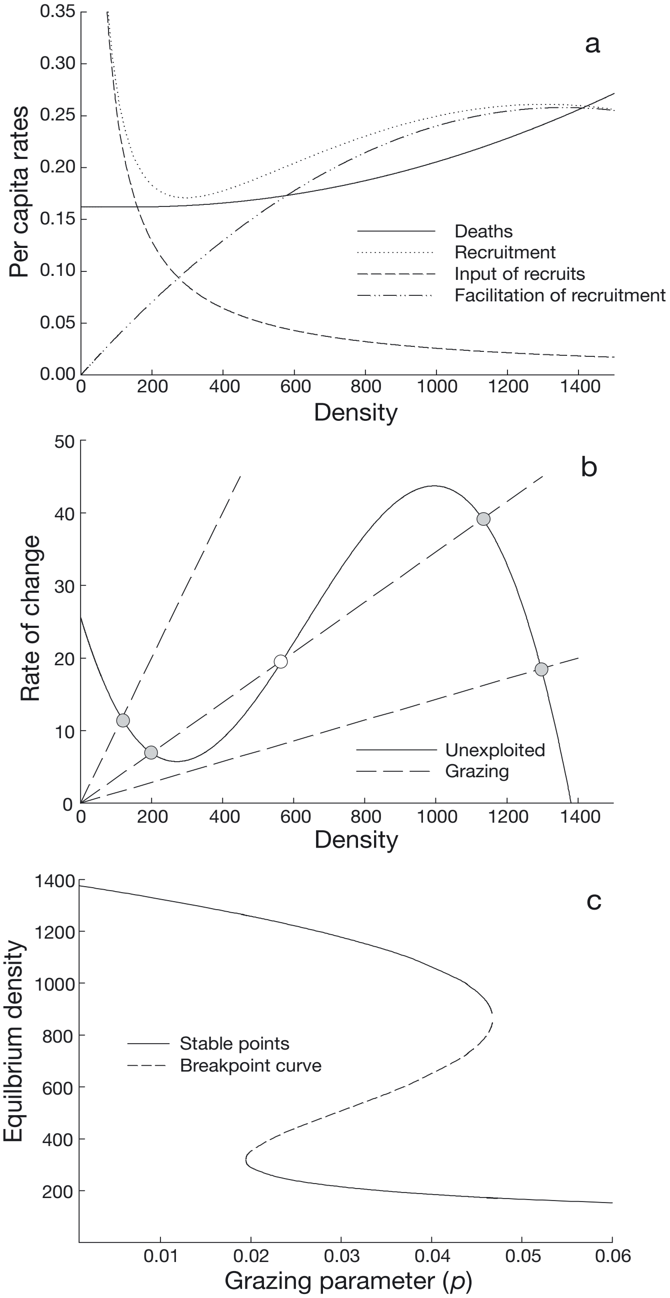

Fig. 4. Grazing model with multiple stable states. (a) Per capita rates for the supply of recruits, facilitation, and mortality as functions of density (N, where N = no. of adults per unit area). Per capita input of recruits equals s/N, where s = 25.7 recruits and is the max. no. of recruits. Per capita rates of facilitation and mortality are $f(N) = aN + bN^2$ and $v(N) = c + dN^2$,where $a = 3.8 \times 10^{-4}$, $b = -1.4 \times 10^{-7}$, $c = 0.162$, and $d = 6.0 \times 10^{-8}$. Parameters a, b, c and d are arbitrary and chosen to produce the shapes of the curves shown. (b) Population growth rate in the absence of grazing (solid line, unexploited) and the harvest rates under 3 levels of grazing (dashed lines). Solid (open) circles show stable (unstable) equilibrium points. (c) Equilibrium densities as a function of the rate of grazing. p is the intensity of grazing (i.e. the slope of the dashed line showing the level of grazing in panel b)

experiments. We briefly discuss several modeling efforts and experimental studies of multiple stable states to illustrate these difficulties.

Terminology is inconsistent

Different terms are used to describe the same concept and the same term is used for different concepts. The term 'threshold' itself has been applied not only to continuous step-like changes in parameters (Fig. 1a), equilibrium states (Fig. 1c), and transient states (Fig. 1e), but also to discontinuous changes in equilibrium states in response to small, continuous, and smooth changes in a parameter (Fig. 1d). The distinctions and relationships between parameters, equilibrium states, and transient behaviors are often unclear. Typically changes in parameters are conceptualized as changes over time and then linked to either changes in ecosystem status over time or in equilibrium state (Lake 2000, Andersen et al. 2009). For example, Lake (2000) noted that environmental conditions can change linearly over time ('ramp disturbances'), and yet give rise to steep but smooth changes in the equilibrium state ('press responses'). Andersen et al. (2009, their Fig. 1) covered much of the same ground as Lake (2000) but listed 3 classes of thresholds — driver thresholds, state thresholds, and driver–state hysteresis — that differ from Lake (2000) in meaning and confound the cause and effect relationship between parameters and state variables.

Interactive effects often blur the distinction between parameters and state variables

In the perfect world of modeling, a perturbation of a state variable occurs without any effect on parameters. For example, in Fig. 1d the perturbation of the ecosystem state across the breakpoint curve is assumed to occur without changing the parameter space. The path of the perturbation does not affect the parameter space (i.e. the double-headed arrow in Fig. 1d, which is the perturbation of the state variable, runs parallel to the *y*-axis). In nature, a perturbation of an ecosystem engineer is likely to affect parameters such as recruitment, the per capita rate of predation, or the strength of competition, so it is very likely that a perturbation changes both the state variables and the parameters.

This seems to be the case with seagrasses, which are well-known ecosystem engineers. Dramatic collapses of seagrass-dominated communities have been observed worldwide, owing to a suite of stressors including eutrophication, coastal loading of sediment and contaminants, rises in sea level and water temperature, increased frequency and intensity of storms, expansion of aquaculture, and spread of non-native species (Orth et al. 2006). Recovery efforts are often unsuccessful (approximately 30% success rate, Orth et al. 2006), and models of multiple stable states have been developed to explain the apparent hysteresis between seagrass meadows and turbid algal states (van der Heide et al. 2007, Viaroli et al. 2008).

In a similar model for *Zostera marina*, van der Heide et al. (2007) suggested that once *Z. marina* falls below a critical density threshold (i.e. crosses the breakpoint curve), turbidity prevents enough stems from recovering to restore ecosystem function. *Z. marina* reduces water movement and as a consequence, reduces turbidity. It is, thus, assumed that this ecosystem function controls light availability, which in turn has a positive feedback loop by promoting plant growth (Scheffer et al. 2001, van der Heide et al. 2007). The model includes a steep threshold, and not surprisingly, the equilibrium densities of *Zmarina* as a function of current velocity show a bifurcation and bistability. Yet there is a bit of circularity, since it is assumed that *Z. marina* density both affects and is a function of water movement.

Viaroli et al. (2008) proposed a similar model to explain the occurrence of seagrass beds (*Ruppia* and *Zostera* spp.) and algal communities (*Cladophora*, *Gracilaria*, and *Ulva* spp.) in Mediterranean lagoons. Here the bifurcation is a function of nutrient loading. The system also has feedback loops, which increases the likelihood of thresholds in parameters. For example, high densities of seagrasses may be able to buffer moderate nitrogen loading through uptake and storage, which is followed by slow decomposition of seagrass detritus (Buchsbaum et al. 1991). This in turn controls algal growth and prevents high densities of macrophytes and phytoplankton that would otherwise reduce light penetration and inhibit seagrass growth. Viaroli et al. (2008) referred to the thresholds encompassing the parameter space where stable states are possible as 'thresholds of reversibility', beyond which any perturbation in state variables cannot flip the system to the alternative state (e.g. below T_1 and above T_2 in Fig. 1d).

As in the case with seagrasses, it has been repeatedly suggested that thresholds and, thus, multiple stable states are associated with ecosystem engineers, environmental switches, and stressful abiotic conditions (Knowlton 1992, 2004, Wilson & Agnew 1992, Petraitis & Dudgeon 1999, Didham et al. 2005). However, all of these ecological features can be found in systems that contain neither thresholds nor multiple stable states, and thus the presence of ecosystem engineers and other environmental conditions does not guarantee the existence of thresholds or multiple stable states.

Use of models to infer mechanism

Observations of sudden shifts over time are commonly cited as examples of multiple stable states (e.g. Scheffer et al. 2001). The observation of a threshold over time is then modeled as a threshold in a parameter to produce a system with multiple stable states. It has even been suggested that the observation of rapid shifts between states is '[t]he key characteristic of a regime shift' in systems with multiple stable states (deYoung et al. 2004, p. 145). In marine systems, the approach of moving from observation to confirmatory models has been commonly used in pelagic fisheries or oceanographic studies where the spatial scale precludes the possibility of undertaking manipulative experiments (Hare & Mantua 2000, Collie et al. 2004, deYoung et al. 2004, Mantua 2004, Andersen et al. 2009). This approach has also been used in studies of seagrass meadows, coral reefs, and pelagic fisheries, and the models almost always include a threshold in a parameter. The notion that there must be a link between thresholds at one level to thresholds in another is deeply embedded in all of these approaches.

For example, Collie et al. (2004) used a model of multiple stable states to explain the collapse of George's Bank haddock *Melanogrammus aeglefinus*. From the 1930s to 1950s, haddock stocks were consistently high (estimated to be 100 000 to 180 000 t, 'haddock-rich' state) despite a harvesting rate between 20 and 45 % of estimated biomass. Haddock biomass spiked sharply to over 400 000 t in the early 1960s, followed by a rapid crash that is believed to be triggered by high rates of harvesting (Fogarty & Murawski 1998). Biomass wavered below 50 000 t for most of the remainder of the century ('haddock-poor' state), with a brief moderate recovery peaking at 100 000 t in 1980 and another recovery of similar magnitude leading up to the year 2000. With the exception of 3 years, harvesting rate during the haddock-poor period was less than or equal to mortality during the haddock-rich period (9 to 45 %). Collie et al. (2004) developed a predator–prey model that exhibited hysteresis in equilibrium stock levels with 2 thresholds in harvesting rate. They found a rapid drop to the haddock-poor state at a harvesting rate of 36 %, and a sharp transition to the haddock-rich state at a rate of 21 %. This hysteresis is consistent with the notion that haddock dynamics contains a discontinuous regime shift between alternative stable states.

Along the same lines, van Leeuwen et al. (2008) modeled the collapse of Baltic Sea cod *Gadus morhua* and also referred to 2 specific harvesting rates as thresholds. In the Baltic Sea, cod stocks and fishing pressure were high from 1974 to 1987. It is assumed that climate forcing from 1988 to 1993 led to decreases in salinity and oxygen, with concurrent increases in temperature and nutrients. During this period, cod biomass plummeted despite no obvious change in harvesting rates. Abiotic conditions reversed to previous levels between 1994 and 2005, but cod biomass remained low (Möllmann et al. 2009). Van Leeuwen et al. (2008) proposed that high and low cod biomasses are alternative stable states that were controlled by adult cod predation on juvenile sprat *Sprattus sprattus*. They suggested that when present in sufficient numbers, adult cod exhibit top-down control of juvenile sprat, releasing the juveniles from intraspecific competition and promoting rapid maturation and reproduction. At low cod densities, juvenile sprat face strong intraspecific competition and remain in a young adult phase for a long period, where they are too large to be eaten by adult cod but not large enough to reproduce and promote recovery. The authors termed this scenario an 'emergent Allee effect' because it based on scarcity of adult cod.

Similarly, Mumby et al. (2007) constructed a model of reef coral cover that exhibits a bifurcation as grazing intensity varies. Under strong grazing pressure, as in the Caribbean prior to mass mortality of the urchin *Diadema antillarum*, the system shows a single stable equilibrium of coral dominance. At low grazing pressure, the only stable equilibrium is macroalgae dominance. At intermediate grazing densities, there are 2 potential stable states – either coral or macroalgae dominance. Mumby et al. (2007) used the term 'threshold' in several ways. They referred to 'critical thresholds of grazing and coral cover beyond which resilience is lost' (Mumby et al. 2007, p. 98), and in a single phrase apply the term to both equilibrium states (i.e. coral cover) and parameter values (i.e. the rate of grazing) at which the bifurcations occur. Mumby (2009) also referred to specific values for the grazing parameter and the unstable equilibria (i.e. the breakpoint curve) as thresholds.

Even so, development and use of models with multiple stable states and thresholds has strengths. Models can provide some of the most compelling examples of plausibility of multiple stable states. However, they are often difficult to confirm independently, and we suggest that modeling should include alternative scenarios that provide clear-cut and testable predictions. This is rarely the case.

Experimental studies

Misunderstanding about the lack of linkage between thresholds at one level versus another has also affected how ecologists have approached the detection of thresholds and multiple stable states experimentally. For example, in the western Pacific, abrupt temporal changes in mussel and macroalgal cover have been reported in response to experimental removal of seastars *Pisaster ochraceus* and to El Niño effects (Paine 1974, Paine et al. 1985, Paine & Trimble 2004). The changes are well documented and matched against control conditions. Paine & Trimble (2004) stated that the shift is evidence for multiple stable states, but it appears that the existence of hysteresis is inferred from the sudden shifts over time.

Konar & Estes (2003) addressed abrupt spatial shifts in the boundary between kelps and barrens. They manipulated both kelps and urchins and provided good evidence that the presence of kelps keeps out urchins and thus sets the boundary. They suggested that the sharp boundary is the edge between 2 alternative stable states and implicitly assumed that the system was being pushed across the breakpoint curve through their manipulation of kelps and urchins, which are state variables.

In the western Atlantic, Petraitis and colleagues have tested whether mussel beds and seaweed stands are alternative states and have explicitly examined the links from parameters to state variables to changes over time. They have experimentally shown sharp thresholds in barnacle and mussel recruitment and rates of predation on mussels and non-linear changes in fucoid recruitment with clearing size, which mimics the damage due to ice scour (Petraitis & Dudgeon 1999, Dudgeon & Petraitis 2001, Petraitis et al. 2003). They demonstrated that these effects translated into changes in adult densities and divergent successional patterns (Petraitis & Dudgeon 2005, Methratta & Petraitis 2008) and that some areas that were seaweed stands are now becoming mussel beds (Petraitis et al. 2009). There has been some discussion whether the thresholds in the mussel–seaweed system are an example of multiple states or 2 states under different levels of top-down control (Bertness et al. 2002, 2004, Petraitis & Dudgeon 2004a), although Petraitis et al. (2009) suggested how these 2 seemingly different views can be reconciled.

These experimental studies document abrupt changes or thresholds in parameters or state variables and place those observations in the context of multiple stable states. Yet again, thresholds at one level are not proof of either thresholds at another level or the existence of multiple stable states. Indeed, multiple stable states can arise in systems in which parameters change in a linear fashion with changes in environmental conditions. Thus, demonstrations that ecosystems show abrupt shifts in parameters, species composition, or other state variables with small changes in environmental conditions are not sufficient tests for multiple stable states. There are ways to test for multiple states that do not depend on linking thresholds in parameters to thresholds in state variables, and Petraitis & Dudgeon (2004b) discussed how experiments using Before-After, Control-Impact (BACI) designs could be used to test for multiple states.

Our brief summary does not cover all that has been published on thresholds and multiple stable states in marine ecosystems and does not include the many studies that have been done in other systems. Many of the issues we have raised are well known and widely discussed in other areas of ecology (e.g. see Lake 2000, Huggett 2005, Bestelmeyer 2006, Groffman et al. 2006), and it is surprising to us how little cross-citation occurs among different disciplines. There is also the unsettling possibility that thresholds, while widely reported, are not the norm in ecological systems because negative results are rarely reported (Rosenthal 1979, Csada et al. 1996).

What is a threshold?

Finally, it is useful to understand how the 2 conventional definitions of thresholds may color the observations made by ecologists. In the most conventional sense, a threshold is nothing more than the sill of a door or window. This functional architectural feature is used to delimit the inside and outside of a house and as an allusion for important milestones in life. The other definition comes from early developers of physiological psychology who viewed a threshold as the level of stimulus required to elicit a response. Fechner, who did pioneering work in experimental psychology in the mid 1800s and who introduced the concept of the median, strictly defined a threshold as the level of stimulus perceived by half of the subjects (e.g. Bi & Ennis 1998). For example, the auditory threshold for hearing for humans – the level of sound that 50% of humans can hear – is about 2×10^{-5} Pa at 1000 Hz (approximately B5, which is the B in the second octave above middle C). Both definitions imply that small incremental changes in some condition or input have no or little effect until a defined limit is reached. At that point, the system enters a new state.

These conventional definitions encompass the ecological notion of passing over the breakpoint curve or ridge separating 2 basins of attraction, but neither definition captures what ecologists usually mean when the term threshold is used to explain sudden shifts. The more important point is that both definitions rely on a limit that is set independently – the sill of the door or the median value. To the extent that ecologists fail to define thresholds independently of the processes under study, the current conceptualizations of thresholds in ecological systems may not be good metaphors for what happens in nature.

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Phase shifts and stable states on coral reefs

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ABSTRACT: Recent transitions from coral to macroalgal dominance on some tropical reefs have engendered debate about their causes and effects. A widely accepted view is that reef environments support stable, alternative coral or non-coral assemblages, despite the lack of evidence to support this hypothesis. Confusion in the literature stems from (1) misunderstanding theory; and (2) conflating a switch between alternative stable states with a shift in the phase portrait of a single equilibrial system caused by a persistent change, or trend, in the environment. In the present paper we outline the conceptual derivation of the hypothesis of alternative stable states, distinguish it from the phase-shift hypothesis, and discuss the evidence required to support each one. For cases in which firm conclusions can be drawn, data from fossil and modern reefs overwhelmingly support the phase-shift hypothesis rather than the hypothesis of alternative stable states. On tropical reefs, a given environment evidently supports at most a single stable community. Corals dominate environments that are disturbed primarily by natural events and have small anthropogenic impacts. In such environments, macroalgae dominate a stage during some successional trajectories to the stable, coral-dominated community. In anthropogenically perturbed environments, the resilience of the coral-dominated community is lost, precipitating phase shifts to communities dominated by macroalgae or other non-coral taxa. The implication for reef management and restoration is both substantial and optimistic. To the extent that the environments of degraded reefs are restored, either passively or actively, the communities should return to coral dominance.

KEY WORDS: Alternative stable states · Community state · Coral · Coral reef · Macroalgae · Multiple stable states · Phase shift

INTRODUCTION

The idea that coral reefs switch between stable, alternative community states of coral and macroalgal dominance is one of the most widely accepted concepts in the coral reef literature (Knowlton 1992, 2004, Nyström et al. 2000, Scheffer et al. 2001, Elmqvist et al. 2003, Scheffer & Carpenter 2003, Bellwood et al. 2004, Mumby et al. 2007a, Elmhirst et al. 2009, Mumby 2009, Norström et al. 2009, Riegl et al. 2009, but see Knowlton 2006). This model of the behavior of reef assemblages has attained the status of a paradigm (sensu lato) among coral reef ecologists (see Graham & Dayton 2002). Despite its ubiquity, attractiveness, and nearly universal acceptance, there is little to no empirical evidence supporting the argument that reefs in general are dominated at a given time by 1 of 2 or more alternative stable states.

Much of the confusion stems from a misunderstanding of the conceptual underpinnings of the stable-states hypothesis and the evidence needed to demonstrate that a state, which is a particular configuration or composition of a reef community, is in fact stable. Reef scientists regularly conflate movement between stable states with phase shifts, although the 2 concepts are very different. A phase shift or regime shift is a change in the equilibrial community in response to a persistent change in environmental conditions. Phase shifts are

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often characterized by dominant populations of an ecological community responding smoothly and continuously along an environmental gradient until a threshold is reached, shifting the community to a new dominant or suite of dominants (Done 1992). In any given environment, there is at most one stable state. 'Alternative stable states,' in contrast, means that >1 configuration of the biological community, i.e. more than one state, can occur in the same place and under the same environmental conditions at different times. If any such configuration can persist under a wide range of environmental conditions, then it will appear to be ecologically locked, i.e. it will resist conversion to a different state.

Confusion in the coral reef literature about phase shifts and alternative stable states is not surprising, because scientists have been confusing and redefining stable states since the idea was formally introduced by Lewontin (1969). With very few exceptions (e.g. Fong et al. 2006), studies of coral reefs either fail to recognize the intellectual precedent established by the early works that shaped the theory or do not persuasively justify their redefinition of key concepts. Rigorous and fixed definitions of stable states, phase shifts, and related concepts are essential if they are to have any utility for describing nature.

In a recent review, Petraitis & Dudgeon (2004) discussed the criteria for rigorous experimental tests of alternative stable states. In this paper, we focus on how and why theory dictates those criteria by outlining the derivation of the concept of alternative stable states. We define and discuss related phenomena such as phase shifts, hysteresis, and resilience. We then evaluate the evidence for stable states and phase shifts in the coral reef literature. Finally, we consider the broad implications for reef management and restoration of incorrectly assuming that alternative stable states are common or ubiquitous.

A PRIMER OF PHASE SHIFTS AND ALTERNATIVE STABLE STATES

Characterizing community dynamics

Graphical abstractions that describe the dynamics of multispecies assemblages are called phase portraits (e.g. Lotka-Volterra predator–prey or competition models [Lotka 1956]; Emlen 1977, Ricklefs 1979). Phase portraits depict the collection of all possible successional trajectories leading to one or more equilibria for a given environment. The phase portraits are derived from curves in the plane that are observed by viewing a time series straight down the time axis from a height corresponding to a large value of time, *t* (Abraham & Shaw 1992). The state of an *n*-species community can be represented at any time *t* by the point in *n*-dimensional space corresponding to the abundance of each taxon (Levins 1968, Lewontin 1969), which ecologists collapse into an aggregate metric of 1 to 3 dimensions using multivariate analysis to visualize changes of state (Petraitis & Dudgeon 2005, Petraitis et al. 2009). Fig. 1A shows one possible time series of community states described in 2 dimensions, and Fig. 1B is a phase plot of the corresponding successional trajectory. Fig. 1C depicts the complete phase portrait of the community for a given environment. (Note that Fig. 1C depicts a plane and a stable point only for heuristic simplicity. The surface may exhibit great complexity. Likewise, the equilibrial state of the system need not show such simple behavior as remaining constant through time; rather, our arguments apply whether the successional end-states are represented in phase space by points, limit cycles, or other behaviors.)

It is worthwhile to delineate what a phase portrait implies in terms that are meaningful to community ecologists, in order to define and distinguish phase shifts and multiple stable states. First, the phase space

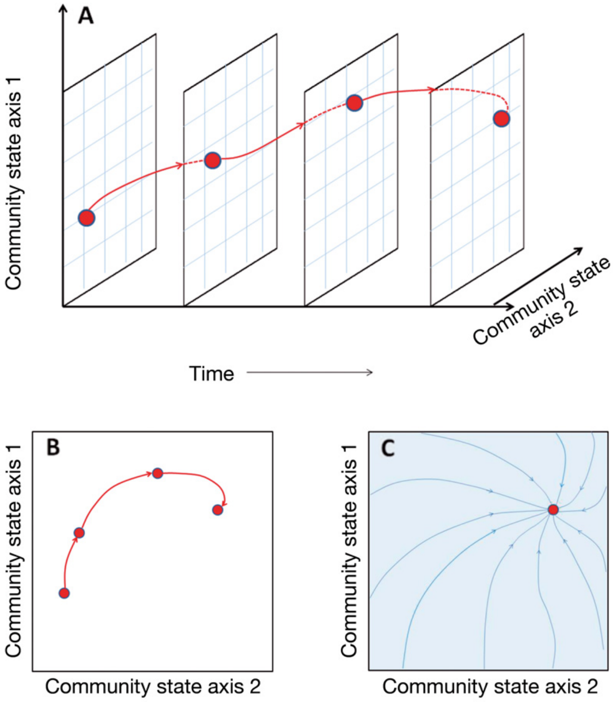


Fig. 1. Community development of a system with a single equilibrial state. (A) Time series of changes in community state plotted in 2 dimensions. (B) Phase plot of successional trajectory of the community shown in the time series in panel (A). (C) Phase portrait showing successional trajectories from any point in the state space towards the attractor. Red symbols: community state sampled at points in time in panels (A) and (B), and the point of equilibrium in panel (C); arrows: trajectories of succession. Modified from Abraham & Shaw (1992)

(the 2-dimensional plane in Fig. 1B,C) represents a specific set of physico-chemical environmental conditions in which the *n* species interact. We define the environment based on Schröder et al. (2005), who followed Peterson (1984). The environment is the set of extrinsic parameters that influence community dynamics but are not in turn affected by these community dynamics. Factors that are dynamically coupled to the community are part of that system and are by definition not part of the extrinsic environment. As Peterson (1984) recognized, there are potential difficulties in distinguishing historical, biotically driven environmental conditions from extrinsic ones, and in some instances they may seem inextricably linked. Essentially, parameters that are either only weakly or not at all affected by the system are considered part of the environment (Schröder et al. 2005).

We offer some examples to clarify this difficult but critical distinction. State variables, such as species abundances, the interactions between them, and their impacts on the local environment (e.g. biotic oxygenation of soft sediments), are dynamically coupled to the system, and are not part of the extrinsic environment. Climatic factors are part of the extrinsic environment. Some large-scale characteristics of the water masses delivered by currents to a community, including volume flux, temperature, and salinity, are likewise extrinsic factors. Other aspects of these water masses, including small-scale variations in flow speed and turbulence, are influenced by the resident biota and are part of the coupled system. Anthropogenic factors, including eutrophication, trends in alteration of climate, and pollution, are part of the extrinsic environment because their rates of action are not affected by community dynamics. How local-scale human interference is construed depends on whether or not one considers humans as part of the resident biota (Petraitis & Dudgeon 2004). To summarize, we use the term 'environment' in this paper to denote parameters that are largely unaffected by community dynamics. Ecologists typically estimate environmental conditions with averages and variances, focusing on those extrinsic parameters that exert significant effects on density or population growth rate (Connell & Sousa 1983, Sousa & Connell 1985).

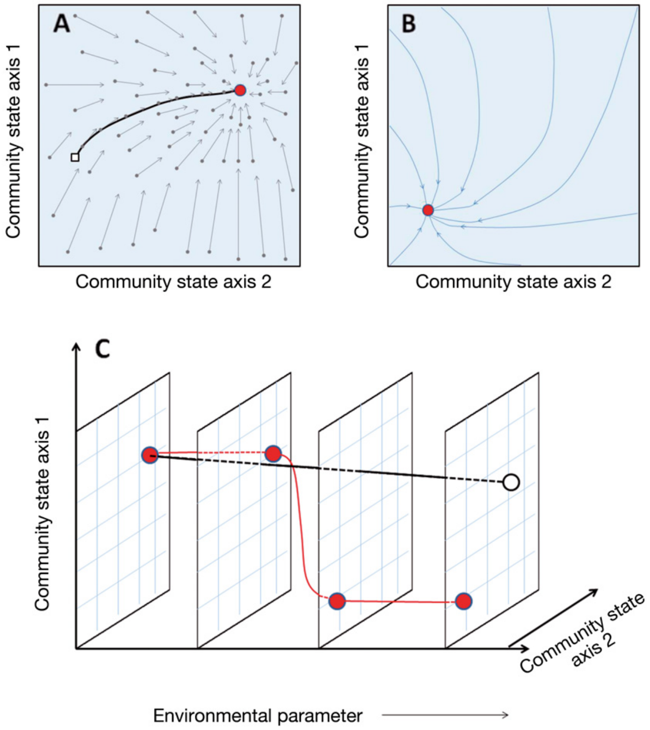


Fig. 2. Phase portrait and phase shift. (A) Phase portrait of a community showing attractor (red circle), vector field (gray arrows) in the state space (blue shading), and a possible starting point (open square) for a trajectory of succession (solid black line). (B) Phase shift of community state associated with environmentally driven changes in the vector field (i.e. interactions between species and their environment). Red circle: attractor, blue arrows: successional trajectories in the state space (blue shading). (C) The dynamic range of shifts in phase portraits of a community as a function of environmental change. Two examples of different phase-shift trajectories are shown. Solid red circles and red line: a threshold phase shift occurring between the middle 2 environments. Open circles and black line: a linear phase shift (circles: attractors for each phase portrait at a specific value of an environmental parameter along the abscissa, lines: dynamics of changes in the phase portrait as a function of environmental change). Modified from Abraham & Shaw (1992)

Second, the successional trajectories (black line in Fig. 2A) a community follows in phase space are deterministic (assuming no intervening perturbations), although the starting point immediately following a disturbance may be random (i.e. stochastic, or of variable type and magnitude). Stochastic perturbations during succession are jumps to different points in the phase portrait and result in mosaics of patches of varying age. Each potential trajectory during succession is the smooth curve that results from the integration of tangent vectors (gray vectors associated with the black line in Fig. 2A, one vector for each point in the phase space) that drive the system toward its attractor (Abraham & Shaw 1992). In ecologists' terms, the vector field (the collection of gray arrows in phase space) represents the instantaneous rates of change in community state at each point in phase space caused by interactions of species with their environment and with each other. The direction and magnitude of a vector represent the net effect of different types and strengths of interspecific interactions unique to that assemblage and environment. This abstraction of the vector field underlies a central theme in community ecology: At a site with a specific set of environmental conditions under which a single stable community can persist, interactions among species under those conditions will always lead to the same equilibrial assemblage (Lewontin 1969).

Phase shifts and alternative stable states

Phase shifts and alternative stable states are equilibrial views of community structure. Many ecologists view equilibrium as an inaccurate characterization of reef ecosystems; however, as Petraitis et al. (1989) pointed out, the debate over whether particular systems are equilibrial or non-equilibrial is largely artificial. Both views emphasize the operation of the same underlying processes, but at different spatial and temporal scales. The influence of scale and the possibility of dynamic equilibria make it very difficult to distinguish equilibrial from non-equilibrial systems and phase shifts from alternative stable states.

Phase shifts

Environmentally driven changes in the vector field imply changes in the strength or nature of species interactions. Changes in the vector field alter successional trajectories and the equilibrium of the phase portrait. A change in the phase portrait of a community associated with environmental change in space or time is a phase shift (Fig. 2B). For example, the change in abundance and composition of species associated with the transition from a sheltered bay to a rocky headland is a phase shift in space. Ecologists have tended to emphasize phase shifts in time, especially for cases in which environmental changes, perhaps accrued over time, have caused abrupt and dramatic changes in species composition. An important example is the transition from corals to macroalgae observed on some coral reefs (Hughes 1994, Petraitis & Hoffman 2010, this Theme Section). The essential feature characterizing a phase shift is that the shift in the community assemblage is caused by a persistent change or trend in the environment, because under each specified set of environmental conditions, there is only a single attractor, or equilibrial community.

Phase portraits of different environments arrayed along an axis integrating that environmental change reveal the dynamic range of a phase shift (Fig. 2C; Petraitis & Dudgeon 2004). The biotic changes may constitute large or small changes in a community, and there is no criterion for the extent of alteration required to call a change a phase shift (Rogers & Miller 2006, Bruno et al. 2009). Essentially, if one specifies *a priori* the minimum amount of change in a community ecologically meaningful and such a change can be detected statistically, then there is evidence of a phase shift. A large phase shift precipitated by a small change in a single environmental parameter — a threshold phenomenon—is easily detected because a slight environmental change causing dramatic changes at the community level is likely to occur in a short time. At the other end of the spectrum, a small change in a community as a function of environmental change may be barely detectable, particularly if the rate of change in the environment is slow (black line in Fig. 2C).

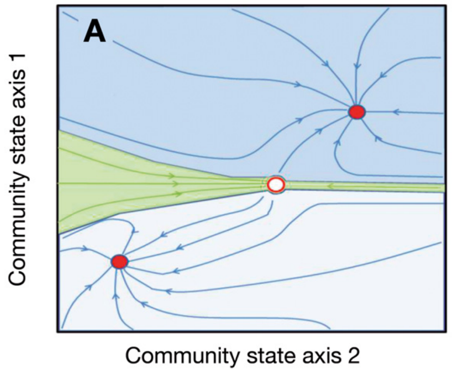
Concepts of resilience (Lewontin 1969 [therein called 'relative stability'], Holling 1973, Grimm & Wissel 1997, Nyström et al. 2008) are inextricably linked with phase shifts. Lewontin (1969) conceptualized the resilience of a system using the now-traditional ridge-and-valley phase portrait, with a rolling ball representing the trajectory of the community. The ball rolls towards the stable state, represented by the lowest, least energetic point on the landscape. Resilience is positively related to the steepness and depth of the basin(s) of attraction, with steep and deep basins being more resilient than shallow ones. The notion of a community losing resilience is depicted by the shallowing and flattening of the basin of attraction in which the community resides (Nyström et al. 2000, Beisner et al. 2003). This change in the phase portrait is caused by environmental change: the movement of the system along the abscissa of Fig. 2C to a new phase portrait, in which changes in the vector field (e.g. shorter vectors, less determinism, different trophic structure, etc.) cause the community to move within the basin of attraction more easily. Shallow phase portraits are those near the threshold for which any further loss of resilience with environmental change will shift the equilibrium to a new location, corresponding to a different community. Thus, lowered resilience is associated with greater likelihood of phase shifts.

The term 'regime shift' has recently become popular, particularly in the literature on fisheries and pelagic ecosystems (Hare & Mantua 2000). Regime shift is generally used synonymously with phase shift. Like phase shift, regime shift is used to describe changes in either biotic or abiotic conditions, or both (Hare & Mantua 2000, Scheffer et al. 2001, Kaiser et al. 2005). The 2 terms mean the same thing and they are distinctly different from alternative stable states. A number of recent papers have incorrectly defined phase shifts as alternative states and regime shifts as alternative stable states (Beisner et al. 2003, Hughes et al. 2005, Nyström et al. 2008). Redefining these widely recognized ecological terms ignores precedent (Lewontin 1969, Connell & Sousa 1983, Peterson 1984, Sousa & Connell 1985), divorces coral reef science from the broader field of community ecology, and is retarding the progress of the discipline.

Alternative stable states

The distinctive feature of alternative stable states is the presence of >1 basin of attraction in a given phase portrait (Fig. 3A; cf. Fig. 2, in which only 1 basin occurs in any phase portrait). In ecological terms, this means that a single set of environmental conditions can support >1 successional end-state (Lewontin 1969, May 1977, Connell & Sousa 1983, Peterson 1984, Sousa & Connell 1985, Petraitis & Dudgeon 2004, Schröder et al. 2005). In practice, any significant differences between abiotic conditions occupied by alternative states in space or time must demonstrably be caused by different resident populations rather than originating extrinsically (Sousa & Connell 1985). Reef scientists have often ignored the requirement that multiple assemblages (or points in phase space) must be stable under a single set of environmental conditions, thereby confusing phase shifts with alternative stable states. Contrary to the view of Beisner et al. (2003), community changes that result from trends of environmental change are not alternative states; they are merely phase shifts, which essentially amount to natural demonstrations of the control of populations by abiotic and biotic factors.

The theory of alternative stable states implies that the outcome is contingent upon the starting conditions—the basin of attraction in which the starting point is located. What processes cause communities to move from one basin of attraction to another? Petraitis & Latham (1999) described hypothetical scenarios in which a pulse of recruitment or mortality might move the system between basins of attraction in the absence of environmental variability. Lewontin (1969) and May (1977) recognized that natural environments are variable. Slight fluctuations in time that are associated with the natural range of environmental conditions, or



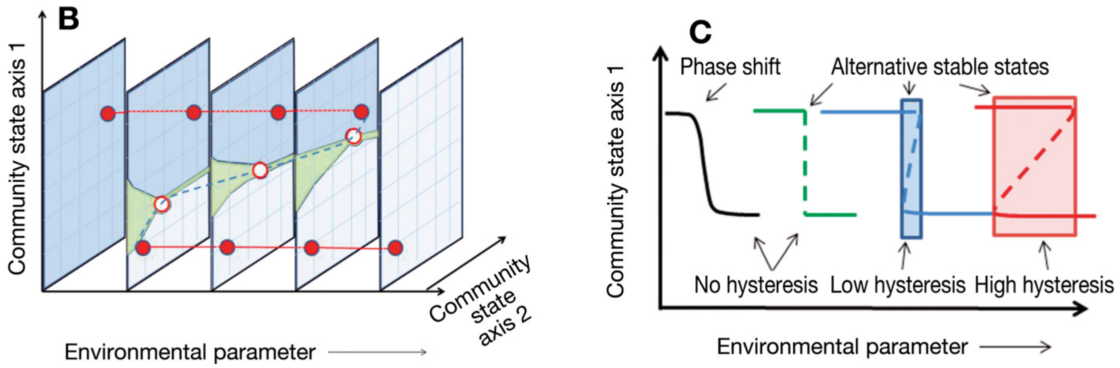


Fig. 3. Alternative stable states. (A) Phase portrait plotted in 2 dimensions showing 2 alternative stable states. There are 2 separate basins of attraction (shaded light blue/grey and blue), with dark blue arrows in each indicating successional trajectories towards their respective attractors (solid red circles). The separatrix between the alternative states (often visualized as a ridge or saddle, and here shaded green) has an unstable equilibrium point (open red circle), departures from which can lead to either alternative state. The dark green arrows within the separatrix are trajectories leading to the unstable equilibrium. The separatrix is depicted as a broad surface simply to illustrate that it need not be a line. (B) Several phase portraits plotted in 2 dimensions and arrayed along the axis of a key environmental parameter, showing single equilibrial states at low and high values of the environmental parameter, and multiple stable equilibria at intermediate values. The blue dashed line connecting unstable equilibria of different phase portraits is the breakpoint (May 1977) or threshold curve (Petraitis & Hoffman 2010). The environments over which multiple stable equilibria exist determine hysteresis in the system. Note that basins of attraction and separatrices may display different shapes in different phase portraits. (C) Variable hysteresis in different systems, ranging from none (phase shift or multiple stable states in a single environment), to small (multiple stable states only over a small number of distinct environments, blue-shaded region), to large (multiple stable states over many distinct environments, red-shaded region). Solid lines: stable equilibria at particular values of environmental parameters. Dashed lines: breakpoint curves, which are ridges of unstable equilibria distinguishing stable states in each environment. In contrast to hysteresis shown by shaded regions, the stable equilibria outside of shaded regions represent resistance of community state to environmental change. Panels (A) and (B) modified from Abraham & Shaw (1992)

perturbations (stochastic or otherwise), can cause spectacular, discontinuous shifts in state variables, moving the system across the separatrix (the saddle) between basins of attraction, but the environment is effectively the same before and after the event (Lewontin 1969). May's (1977) conceptualization differs and can be visualized by arraying phase portraits determined for each environmental condition along an environmental axis (Fig. 3B). This is the now-familiar S-shaped curve, characterized by 2 discontinuity thresholds at given values along the environmental axis, and the separatrix (the dashed line), which is the boundary between basins of attraction.

The range of environments (or sets of parameter values) over which alternative stable states are possible determines the extent of hysteresis in the system (Fig. 3C). By hysteresis, we mean (1) the lack of change in community state following manipulation of parameters within the range of values between different critical environmental conditions that cause forward and backward switches of state; and (2) the different paths followed by communities upon crossing the thresholds for forward and backward switches (Scheffer et al. 2001). If a wide range of environments characterizing an ecosystem can support alternative states, then hysteresis is strong and even large directional shifts along the environmental axis of interest may be insufficient to tip the system to an alternative state. On the other hand, if alternative states occur only within a narrow range of environments, then hysteresis is weak and the system can be tipped back to an alternative state far more easily. Finally, and critically, if alternative states exist in only a single environmental condition, or if there are no alternative states in any environment, then there is no hysteresis in the system. In either case, a reversal of direction along the environmental axis will initiate restoration of the prior community, and forward and backward trajectories will differ only trivially. Establishing the extent of hysteresis is essential to ecosystem management; it is critical to establish the environmental range (if any) over which alternative states are possible.

Demonstrating alternative stable states

There are 2 robust approaches to demonstrating the existence of alternative states. The first is to show by experiment that a pulse perturbation (sensu Bender et al. 1984) can cause a switch between different, stable community assemblages at the same site in the absence of persistent environmental changes (Connell & Sousa 1983, Peterson 1984). Conditions before and after pulse perturbations can be the same because by definition, the pulse is an ephemeral event between periods of the same environmental regime. Press perturbations, on the other hand, are inappropriate for demonstrating alternative stable states because by definition environmental conditions before and after the perturbation are different. Moreover, an argument for alternative stable states requires a demonstration that any positive feedbacks that stabilize the currently resident community and resist invasion by the alternative community are biotically driven and constitute the sole source of modifications of the physical environment (Peterson 1984, Sousa & Connell 1985, Schröder et al. 2005).

The criterion for spatial scale over which alternative states occur is the minimum area required for populations of dominant species to be self-sustaining (Connell & Sousa 1983). The criterion for temporal stability of alternative states has been more controversial. Petraitis & Dudgeon (2004) and Petraitis et al. (2009) argued that demonstrating resilience of invading assemblages to small perturbations was preferable evidence of stability to the temporal criterion of Connell & Sousa (1983), which is the time to self-replacement of the longest-lived component of the community. In this sense, and contrary to the views of others (e.g. Scheffer et al. 2001, Bellwood et al. 2004), community resilience is positively correlated with alternative stable states where they occur. The designs and analytical approaches required for valid experimental tests are reviewed by Petraitis & Dudgeon (2004) and demonstrated by Petraitis et al. (2009).

The second approach is indirect and more difficult to execute. As Petraitis & Hoffman (2010) point out, a system with multiple stable states in >1 environment must have at least 2 discontinuous thresholds, each at a unique value along an environmental axis, to generate the S-shaped curve of Fig. 3C. One could infer the existence of alternative stable states from experimental evidence showing a switch from one state to another at a specified value of an environmental parameter and the switch back to the first state at a different parameter value. An experiment of this sort is unlikely to be performed for ethical and logistical reasons, because the scale and magnitude of the required pulse perturbation(s) are unknown. No other type of evidence is admissible (Petraitis & Dudgeon 2004, Petraitis et al. 2009).

Recent efforts to characterize reef communities as exhibiting alternative, stable, hard-coral and non-coral states have attempted to circumvent the difficulties of direct tests and to explain the long-term persistence and apparent stability of non-scleractinian community states relative to that of scleractinians. These studies have focused on 3 lines of evidence (Mumby 2009): empirical identification of positive feedbacks, demonstration of hysteresis, and modeling. None of these lines of evidence in isolation, however, indicates the existence of alternative stable states. We evaluate feedbacks and hysteresis here, and defer discussion of modeling to a later section.

Positive feedbacks are thought to be especially important in establishing one successional outcome in an environment that could support different successional outcomes, but they are not in and of themselves evidence for alternative stable states. Some reef scientists consider positive feedbacks to be signatures of alternative states, but they are ubiquitous in ecological systems (Bruno & Bertness 2001). In the context of alternative stable states, they must also explain all differences in abiotic conditions between states (Sousa & Connell 1985).

Likewise, evidence of hysteresis is not evidence for alternative stable states for reasons of logic, interpretation, and practicality. The logical problems are twofold. First, alternative states may occur without hysteresis (Fig. 3C, see also Petraitis & Hoffman 2010). Second, tests of hysteresis are tautological because they implicitly assume that multiple stable states occur across a range of environments prior to demonstrating their existence in any single environment.

Tests of hysteresis may also suffer from problems of biased interpretation. There is a misconception that phase shifts are easily reversible (see Mumby 2009), whereas alternative states are not. This is not necessarily true. Phase shifts may be far more difficult to reverse than alternative states if they are the products of large and persistent environmental changes that are not easily reversed, such as a spill of toxic chemicals. Moreover, if the environment has changed in several parameters, which may be independent or negatively correlated, then reversal of a phase shift through attempted environmental restoration is unlikely. Failure to appreciate these possibilities may lead to the interpretation of community stasis as only being the result of hysteresis.

Finally, there are practical difficulties that further complicate the interpretation of hysteresis in experimental outcomes. The magnitudes of environmental pulses that are necessary to cross ecological thresholds are usually unknown. Manipulation of environmental parameters may be of insufficient magnitude to cause a switch. In such cases, experimental tests of hysteresis rely on negative evidence — no community response to environmental manipulation — for which the probability of a Type II error is, therefore, also unknown. Moreover, misconstruing the identity of the parameter putatively causing a switch between states will yield no community change following manipulation. Inferring alternative states from such a result will obviously be faulty because the hysteresis will be illusory.

PHASE SHIFTS AND ALTERNATIVE STABLE STATES ON CORAL REEFS

Petraitis & Dudgeon (2004) reviewed evidence of changes in community state in tropical reef ecosystems around the world in the context of whether those changes represented either phase shifts or alternative stable states. Three key points from that review are relevant here. First and most important, the authors found no evidence in support of the hypothesis that coral and macroalgal assemblages represent alternative stable states of reef communities from studies published through 2003. Second, these studies, and studies published after 2003, frequently blurred the distinction between phase shifts and alternative stable states and erroneously concluded that coral reef systems represented alternative stable states (e.g. Nyström et al. 2000, 2008, Scheffer et al. 2001, Elmhirst et al. 2009, Norström et al. 2009, Riegl et al. 2009). Third, cases of persistent shifts from coral to macroalgal assemblages tended to be isolated in specific areas (Ninio et al. 2000), whereas other areas showed no such shifts over ecological time scales that were relatively long (Connell et al. 1997, Bruno et al. 2009).

Intensified study of coral reefs, which is largely driven by concern about the effects of climate change, warrants a fresh assessment of whether the observed changes represent phase shifts or alternative stable states. Below we evaluate several cases from the recent and older literature that have been proffered as demonstrations of alternative stable states. With one exception, the evidence corroborates the conclusions of Petraitis & Dudgeon (2004).

Chronic perturbations, time and alternative states

The first reference to alternative community states on coral reefs of which we are aware is from Lighty (1980). He inferred that stress conditions introduced by off-bank transport of turbid and episodically cooled waters in the late Holocene led to the demise of the *Acropora*-dominated Abaco reef system in the Bahamas. In this scenario, mortality of the cold-sensitive acroporids — the elkhorn coral *Acropora palmata* and the staghorn coral *A. cervicornis* — around 3000 yr ago was followed by conversion to an alternative community state dominated by macroalgae and octocorals, which persists to this day (Lighty 1980, A. C. Neumann pers. comm.). The failure of the acroporids to recover can be directly attributed to the northerly location of the Abaco reef system and its continual exposure to cold-water stress. Do the coral- and macroalgae-dominated phases actually constitute alternative stable states? The only valid test would be to remove the chronic perturbation and observe whether or not the community would respond by returning to coral dominance.

The last few decades may have provided a natural test of the hypothesis of alternative stable states. The cold-sensitive *Acropora* spp. have recently expanded northward in the western Atlantic region in association with decadal-scale increases in annual sea surface temperature. Acroporid corals have appeared where they had not lived for the past few thousand years (Precht & Aronson 2004). This includes the return of *A. palmata* to the Abaco reef tract (Precht & Aronson 2006a). The millennial-scale responses of the Abaco reefs to changing environmental conditions are clearly phase shifts, and there is no evidence for alternative stable states.

In a similar vein, both species of *Acropora* have moved up and down the east coast of Florida, apparently in response to millennial-scale warming and cooling trends, respectively (Precht & Aronson 2004). During the early to middle Holocene (9 to 5 kyr ago), warmer oceanic conditions off the eastern Florida Peninsula favored the accretion of an *Acropora*-dominated barrier-reef tract up to 10 m thick, ranging as far north as Palm Beach County (Lighty et al. 1978). As temperatures cooled after the mid-Holocene, the northern limit of reef growth regressed southward to the present-day limit of the Florida Reef Tract, south of Miami. As temperatures have increased again in recent years, acroporids have re-expanded northward. Reef-coral assemblages dominated by living thickets of *A. cervicornis* were discovered off Fort Lauderdale in 1998 (reviewed by Precht & Aronson 2004). Although the temporal scale of the phase shifts has been large, it appears that when the abiotic conditions have been suitable, acroporid reefs have dominated. When conditions have deteriorated, other taxa such as octocorals, sponges, and macroalgae have persisted. Millennial-scale persistence in this case should not be confused with the existence of alternative stable states.

Houtman Abrolhos Islands, Western Australia

Hatcher (1992) argued that environmental conditions were broadly similar along the Houtman Abrolhos archipelago off Western Australia. Reef areas were dominated by either macroalgae (kelps) or hard corals, which Hatcher (1992) interpreted as representing alternative stable states. Smale et al. (2010), however, showed that kelps, hard corals, and other benthic epifauna in the Houtman Abrolhos changed predictably along a latitudinal gradient. Furthermore, kelp- and coral-dominated communities expanded and contracted their geographic ranges in response to historical climate change (Greenstein & Pandolfi 2008). As in eastern Florida and the northern Bahamas, environmental tracking on long temporal scales is very different from the stability of community types.

Kaneohe Bay, Hawaii

Kaneohe Bay is a classic example of cases where environmental changes have caused phase shifts. Wastewater input resulted in nutrient enrichment, causing a transition from coral to macroalgal dominance (Banner 1974). After >2 decades of discharge, 2 sewage outfalls were diverted from the bay in 1977–1978. The diversions were followed by rapid and dramatic declines in nutrient levels. There was a correspondingly rapid return to coral dominance (Maragos et al. 1985). If the reef ecosystem in Kaneohe Bay existed in alternative stable states, the reduction of nutrients through improvements in water quality should not have resulted in a rapid shift back to the coral-dominated configuration, regardless of ensuing complications (Hunter & Evans 1995, Stimson & Conklin 2008).

Uva Island, Panama

The 1982–1983 El Niño event dramatically affected community composition and net production of calcium carbonate on the reef at Uva Island, off the Pacific coast of Panama (Eakin 1996). Following mass mortality of the dominant branching corals *Pocillopora* spp., population densities of the herbivorous echinoid *Diadema mexicanum* increased dramatically and remained high until the 1990s. The abundant *D. mexicanum* rapidly bioeroded the reef framework, and their grazing on coral spat resulted in recruitment failure. Bellwood et al. (2004) cited this situation as an example of an alternative stable state representing one end-result of reef degradation: the bioeroded urchin barren. Eakin (2001) had already noted, however, that although coral cover remained low (<10%) through the period of elevated sea urchin density, *Pocillopora* slowly recovered in the mid- and late 1990s as sea urchin densities declined. Reef dynamics at Uva Island represented a phase shift and were not consistent with the hypothesis of alternative stable states.

More recently, Fong et al. (2006) reported a transition from coral to macroalgal dominance at Uva and nearby Cavada Island following the 1997–1998 El Niño–Southern Oscillation (ENSO). Macroalgae persisted for several years afterwards despite the presence of consumers by virtue of their association with an unpalatable cyanobacterial epiphyte. The results of short-term press experiments manipulating nutrients and grazing were intriguing but still inadequate to infer alternative states (Fong et al. 2006). The extent of changes in the post-ENSO abiotic environment was also unclear.

Discovery Bay, Jamaica

The dynamics in reefs along the north coast of Jamaica, and especially the reef at Discovery Bay, have been generalized as a model of reef decline for the Caribbean region over the past few decades. Some of these generalizations have been correct but other conclusions from Jamaica have been applied inaccurately to the rest of the Caribbean (Precht & Aronson 2006b, Bruno et al. 2009). After repeated disturbances, including Hurricane Allen in 1980; outbreaks of corallivores and coral disease in the early 1980s; Hurricane Gilbert in 1988; a number of coral bleaching events in the late 1980s; and the regional, disease-induced mass mortality of the herbivorous sea urchin *Diadema antillarum* in 1983–1984 (Lessios 1988), coral cover on Jamaican reefs fell from >40 to <10% (Liddell & Ohlhorst 1992, Hughes 1994). Macroalgae became the dominant benthic functional group, exceeding 60% absolute cover in many places. Although these disturbances and their immediate effects were well documented, several reef scientists have asserted that the decline of reefs in Jamaica was ultimately caused by overfishing (Knowlton 1992, Hughes 1994, Nyström et al. 2000, Jackson et al. 2001), which, they have suggested, laid the foundation for ecosystem collapse. In the overfishing scenario, large predators were depleted centuries ago, and fishers subsequently overexploited herbivorous fishes. Finally, the mass mortality of *D. antillarum*, the grazing activity of which had masked the loss of herbivorous fishes (Jackson et al. 2001), triggered a proliferation of macroalgae that flipped the reefs into an alternative stable state (Knowlton 1992, Palumbi et al. 2008, and many others). Edwards & Gomez (2007, p. 7) stated:

> In 1983, there was a mass die-off of the *Diadema* urchins from disease, with densities being reduced by 99%. At this point, the last bastion of herbivorous control was breached and firstly shallow reefs and then deeper reefs were taken over by macroalgae. By the late 1980s, the reefs had largely shifted to an alternative stable state with 70–90% algal cover. From a restoration point of view, this alternative state is probably an order of magnitude harder to restore than the various degraded versions of the coral dominated system that persisted before the *Diadema* die-off. To regain the original state, not only is there a need for management measures (passive restoration) to shift conditions [back to high coral cover], but there is likely to be a need for some large active restoration disturbance (fisheries management and/or urchin culture to restore herbivory) to remove macroalgae and add corals before the system is likely to have any chance of flipping back.

The scenario is plausible, but is it accurate for Jamaica, let alone the wider Caribbean?

Populations of *Diadema antillarum* along much of the north coast of Jamaica have recovered patchily since the late 1990s, resulting in significant top–down changes to the benthic community in these areas of recovery (Woodley 1999, Aronson & Precht 2000, Edmunds & Carpenter 2001, Cho & Woodley 2002, Bechtel et al. 2006, Idjadi et al. 2010). Carpenter & Edmunds (2006) reported similar observations from reefs elsewhere in the Caribbean.

At Dairy Bull reef near Discovery Bay, the benthic community had completely returned to the coral-dominated state by 2005 (Fig. 4), with a species composition closely resembling the pre-1980 community (Idjadi et al. 2006), following recovery of the local *Diadema antillarum* population to half of their pre-mortality density (Edmunds & Carpenter 2001). Coral populations collapsed again to even lower abundance than before the reversal, following the bleaching event of 2005 (Quinn & Kojis 2008). The community has since returned once again to the coral-dominated state (Fig. 4; Crabbe 2009). There were no detectable changes in fish populations or improvements in water quality between 1980 and the late 1990s (Cho & Woodley 2002, Webber et al. 2005, Greenaway & Gordon-Smith 2006, Hardt 2008). The reversion to coral dominance at Dairy Bull and other reefs appears to be predicated almost exclusively on the recovery of *D. antillarum*, which can singlehandedly drive reductions in macroalgae and recovery of coral populations to their initial abundance and species composition.

Connell & Sousa (1983) proposed that alternative stable states should be recognized based on the generation times of the affected organisms. The apparent rapidity of the recent coral-to-macroalgae transition contrasts with the much longer time that presumably will now be required for coral recovery at many other sites. It is tempting to infer that time to transition is directly related to resistance to transition and, therefore, to conclude that the system exhibits hysteresis (McManus & Polsenberg 2004, Norström et al. 2009); however, asymmetries in the observed times required for transitions between states do not necessarily indicate hysteresis. Jackson and colleagues (Jackson & Johnson 2000, Jackson et al. 2001, Pandolfi et al. 2003) have argued that there was a delay of at least several centuries between the time humans began interfering with coral reefs and the time those reef communities finally collapsed in the 1980s. If this surmise is correct, and if time is a valid proxy for resistance to transition, then the multicentennial transition from coral to

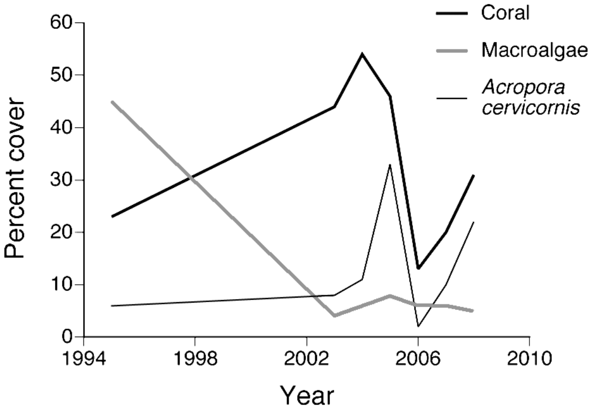


Fig. 4. Temporal trends in the total cover of hard corals, macroalgae, and *Acropora cervicornis* at Dairy Bull, a reef site on the north coast of Jamaica. Data from Idjadi et al. (2006) and Crabbe (2009)

macroalgal dominance was much more difficult than the decadal-scale recovery of corals that was noted, for example, at Dairy Bull. Of course, time to recovery is not related to difficulty of transition, so the time course of a transition has no bearing on hysteresis or alternative community states. The biotic stability of coral reefs on centennial, millennial, and longer time scales is most parsimoniously viewed as an indication of the stability of environmental drivers (Aronson et al. 2002a, 2002b, 2005), in the absence of evidence to the contrary (Ivany et al. 2009).

Coral and macroalgal dominance cannot be alternative stable states, as Mumby and colleagues claimed they are, if restoring grazing pressure reverses the recent shift from coral to macroalgal dominance, as they also suggested (Mumby 2006, Mumby et al. 2007a, Mumby & Harborne 2010). Instantaneous observations have shown that reefs exist along continua of coral and macroalgal cover (Bruno et al. 2009), supporting the phase-shift interpretation. In response, Mumby (2009) advanced the intriguing suggestion that alternative stable states could be apparent on ecological scales but latent on microecological scales. This idea may have merit, but Bruno et al. (2009) cannot be construed as corroborating the alternative-states hypothesis when their data support the phase-shift interpretation.

In summary, hurricanes and other disturbances killed the corals along the north coast of Jamaica. The decimation of *Diadema antillarum* facilitated an increase in macroalgae because there were few other herbivores present, although observations on other Caribbean reefs have shown that mass coral mortality alone is sufficient to precipitate the transition from coral to macroalgal dominance (Aronson & Precht 2006). Finally, the return of *D. antillarum* a mere 1.5 decades later restored the coral-dominated state. This appears to have been a simple phase shift, in which the macroalgal state was not a stable alternative (Knowlton 2006), and no evidence of ecologically significant hysteresis was noted. The increase in macroalgae and the loss of coral cover were easily reversed when only one of several disturbances—the exogenously caused loss of *D. antillarum*—was alleviated.

Other examples of community shifts on coral reefs

Reef scientists have been documenting temporary, post-disturbance shifts to macroalgal dominance for half a century. A large literature from the 1960s and 1970s describes the effects of coral-killing disturbances, including storms and predator outbreaks, on reef community structure in both the Caribbean and the Indo-Pacific (Chesher 1969, Endean & Stablum 1973, Stoddart 1974, Connell & Slatyer 1977, Connell 1997, Diaz-Pulido et al. 2009). Belizean reefs responded to extensive damage from Hurricane Hattie in 1961 with a shift from corals to macroalgae, >2 decades before the *Diadema antillarum* mass mortality. Macroalgae dominated for >1 decade before corals recovered on these unfished reefs (Stoddart 1963, 1969, 1974). Whether macroalgal dominance represented a phase shift or more simply a successional stage remains unresolved.

More recently, high sea surface temperatures in December 2005 to January 2006 triggered mass coral bleaching and mortality on *Acropora*-dominated reefs of the Keppel Islands in the southern Great Barrier Reef (Diaz-Pulido et al. 2009). The reefs rapidly shifted to macroalgal dominance. Corals then recovered rapidly through asexual re-expansion of the remaining fragments, outcompeting the macroalgae in <1 yr. As in the case of Hurricane Hattie, succession appears to be the most parsimonious hypothesis.

The fished reefs of Moorea, French Polynesia have been subjected on a decadal scale to recurrent disturbances, including cyclones, outbreaks of the crown-of-thorns starfish *Acanthaster planci*, and temperature-induced coral bleaching. Long-term monitoring and experimentation have documented rapid excursions from, and returns to, coral dominance (Done et al. 1991, Adjeroud et al. 2005, 2009, Berumen & Pratchett 2006). The volatility of benthic assemblages at Moorea in response to frequent disturbance again supports an inference of succession. The hypothesis of alternative stable states is not supported, and the same can be said for reefs in the shelf lagoon of the Belizean barrier reef (Aronson et al. 2002a, 2002b) and the Great Barrier Reef (Emslie et al. 2008).

A common argument in the recent literature is that macroalgae-dominated reefs are a relatively new phenomenon, that they are becoming more frequent, and that they are a sign of anthropogenic degradation of reef ecosystems. In contrast, a recent meta-analysis of the frequency and magnitude of coral-to-macroalgae phase shifts showed that they are much less common and less geographically extensive than generally assumed: only 1 to 2% of the world's reefs surveyed between 1996 and 2006 were dominated by macroalgae (Bruno et al. 2009). This study also indicated that there has been no measurable trend toward macroalgal dominance on coral reefs since 1995. Likewise, a recently published meta-analysis of trends in coral and macroalgal cover on Caribbean reefs (n = 1962) found that regional and subregional mean values of macroalgal cover have not changed since the mid-1980s (Schutte et al. 2010). The regional mean macroalgal cover from 2001 to 2005 was 15.3%, which hardly suggests a Caribbean-wide phase shift to macroalgal dominance.

It bears repeating that transitions from coral dominance do not necessarily lead to macroalgae-dominated systems. Results of phase shifts include reef communities that are dominated by sea anemones (Chen & Dai 2004), corallimorpharians (Loya 2004), sponges (Aronson et al. 2002b), and octocorals (Davis 1982).

Ship groundings

Ship groundings have long been put forth as potential examples of alternative stable states resulting directly from human disturbance to coral reefs. Four years after a ship grounding on the Great Barrier Reef, Hatcher (1984) noted that persistent macroalgal dominance in the absence of a measurable wreck-derived influence provided circumstantial evidence that it represented an alternative stable state. The metal hull of the grounded vessel remained, however, and it now seems likely that iron leaching from the vessel's corroding hull stimulated and maintained the macroalgal bloom; similar phase-shift responses have been reported from other ship-grounding sites at which corroding metal debris remained (Schroeder et al. 2008, Work et al. 2008). These examples suggest that removing ships grounded on coral reefs should reduce the potential of a phase shift to dominance by macroalgae and other undesirable taxa.

How do reefs respond to ship groundings from which the ship has been removed? If a ship grounding flattens the topography of a highly structured reef habitat, and if topographic complexity does not recover through coral growth, the community can develop so as to converge on that found in natural hardground habitats. Hardground communities typically consist of flat limestone pavements dominated by turf and crustose coralline algae, gorgonians, and isolated coral colonies. This is precisely what happened at the 'Wellwood' ship-grounding site in the Florida Keys (Aronson & Swanson 1997a, Precht et al. 2001). In 1984, the 122 m freighter MV 'Wellwood' struck and flattened a 1500 m^2 section of the shallow spur-and-groove zone at Molasses Reef, which at the time was dominated by topographically complex stands of *Acropora palmata*. Aronson & Swanson (1997a,b) surveyed the 'Wellwood' site in 1995 to 1996 at 4 to 7 m depth and found it to be quantitatively more similar to reference sites that were hardgrounds than to undamaged, reference sections of spur-and-groove habitat adjacent to the grounding. Abiotic conditions were essentially the same before and after the damage.

One of the hardground reference sites, Pickles Reef, which in 1995 was thought to represent a natural hardground, turned out to be the site of 2 earlier ship groundings: 1 in ~1800 and the other in 1894. Scattered debris from the two 19th-century groundings was still visible, but the Pickles Reef reference site was otherwise indistinguishable from a second, truly natural hardground site used as reference. The hardground at Pickles Reef was bounded laterally by spur-and-groove habitat, which was dominated by *Acropora palmata*. Pickles Reef provides strong circumstantial evidence that ship groundings can produce long-lived hardgrounds, and it is plausible that these hardgrounds resist conversion back to spur-and-groove habitats on a decadal to centennial time scale. Spur-and-groove and hardground communities of the Florida Keys are candidates for alternative stable states, although once again resistance has not been demonstrated. Alternative states or not, restoring ship-grounding sites clearly must include reestablishing topographic complexity (Precht et al. 2001).

THEORETICAL CONSIDERATIONS

For the most part, studies of the recent shift from corals to macroalgae have been non-experimental, unreplicated, and uncontrolled. Executing well-designed experiments would be a challenge and would require at least several years before strong inferences could be drawn. Such difficulties have motivated modeling studies of community dynamics. A recent quantitative model characterized Caribbean reefs as switching between alternative, stable, coral and macroalgal states with changes in the intensity of herbivory (Mumby et al. 2007a, Mumby 2009); however, there are 2 fundamental problems with this and related models (Elmhirst et al. 2009). These problems call into question the utility of the models for resolving the issue of phase shifts and alternative states.

First, the axes of environmental parameters (e.g. those displayed along the abscissa of Fig. 3B) represent only extrinsic environmental features. Biotic interactions, such as grazing rate, are components of the vector field in any given phase portrait, i.e. under any specific set of physico-chemical conditions grazing rate is dynamically coupled to the system (Schröder et al. 2005). The use of grazing intensity as the environmental parameter upon which to delineate multiple stable points is, therefore, inappropriate; rather, the variation in grazing intensity is described by variation in vectors within phase portraits. Indeed, using any parameter that is dependent on another state variable of the system merely shifts the question to a different level: Does the consumer in question ever naturally exist at multiple stable equilibria in one environment? Both Paine (1977) and Connell & Sousa (1983) recognized this problem and persuasively argued that communities with high and low abundances of consumers (or high and low predation intensities) cannot be regarded as stable alternatives, because when consumers increase in abundance they regulate prey abundance, leading the system (in this case) to a coral-dominated community. The results of Mumby's model show the expected pattern of return to coral dominance as grazing intensity increases. The question is whether variation in grazing intensity (or, as a proxy, grazer abundance) in the model is itself stable at any value (Knowlton 1992, Palumbi et al. 2008), or whether it simply reflects the natural variability that is expected during the protracted increase in the density of *Diadema antillarum* from 1983 to the present.

The second problem is that the empirical values used to parameterize Mumby's model are based on independent data sets from Jamaica that spanned the 1970s to the 1990s. In other words, the parameters reflect rates of processes in very different abiotic environments that might favor either corals or macroalgae but do not represent combinations of parameter values that could actually occur in any single natural environment. This homogenization of parameters is tantamount to ignoring the same-environment criterion for testing alternative stable states and distinguishing them from phase shifts.

IMPLICATIONS FOR MANAGEMENT

The ecological imprint of catastrophic disturbances can persist for a very long time without necessarily moving the affected community into an alternative stable state. Despite the recognition of shifting baselines in the recent literature on coral reefs, it is peculiar that reefs in Jamaica and elsewhere in the Caribbean were characterized as being locked into an alternative stable state within a decade after the confluence of a number of catastrophic perturbations (e.g. Knowlton 1992). Had the expectations for recovery from these combined disturbances initially been more realistically scaled in decades to centuries, it is doubtful that coral reef ecologists would still be developing models to explore how to overcome putative hysteresis (see also Emslie et al. 2008).

Herbivore addition and exclusion experiments performed by Sammarco (1982a, 1982b) on patch reefs in Discovery Bay in the 1970s suggested that declining herbivory relative to the space available for colonization promoted algal growth and decreased coral recruitment. As *Diadema antillarum* decreased, macroalgal biomass increased. Once the urchins were restored, the system returned to its original composition. The response of the benthos to urchin abundance was similar in small-scale plots and whole-reef manipulations. Although no one could have predicted the compounded, catastrophic disturbances that rocked the reefs along the north coast of Jamaica in the decade following Sammarco's work, his manipulative studies should have allowed reef scientists to predict the responses of the benthos to changes in herbivory in space and time. Given that these catastrophic disturbances occurred, the increase in macroalgae that followed the loss of *Diadema* and the subsequent reduction of macroalgae following the recovery of *Diadema* highlight the predictive value of scaling up small-scale ecological experiments. For unknown reasons, this most appropriate guide to predicting the future of Jamaican reefs was overlooked by most reef scientists.

The reaction of ecologists and managers to the 1988 forest fires that burned in Yellowstone National Park serves as an excellent terrestrial counterpoint to the example of Caribbean reefs. The fires occurred during an extreme year and were the largest observed since the park was established in 1872. The last comparable fires had occurred at ~1700 (Romme 1982, Romme & Despain 1989). Had the expectation for recovery from the 1988 conflagration been scaled in years to decades, there would have been a public outcry for active intervention and restoration. A demographic analysis of trees in the adjacent unimpaired forests was combined with the life-history strategies of the affected species to develop an accurate recovery model (Romme & Turner 2004). The model predicted that it would take at least 80 to 100 yr for the forest canopy to close and for the forests to resemble their pre-burn configuration and architecture. Despite a number of ecological surprises during the last 2 decades (Turner et al. 2003), the forests of Yellowstone are on track to recover within the century (Romme & Turner 2004).

'The straw that broke the camel's back' is an ancient metaphor of threshold behavior that has been used in recent years to describe the supposed hysteresis and existence of alternative stable states on coral reefs. In the case of Jamaica, the alleged last straw after centuries of overfishing was the catastrophic loss of *Diadema* in 1983–1984 (Knowlton 2001). When that last straw was removed by the return of *Diadema* in the late 1990s, however, the camel stood up: the benthic assemblage came bounding back on its own.

The management implications of this recovery are twofold. First, the idea that without active restoration the reef will remain locked in a macroalgal state is incorrect. Why is this important? Improving fishery resources through the implementation of gear changes and establishment of marine protected areas in coastal Jamaica is a worthy management goal (Woodley & Sary 2000, Watson & Munro 2004). However, even at very small scales, it is a costly proposition with a poor chance of changing the trajectory of the benthic community at the landscape scale or in an ecologically relevant time frame. Second, even without their full complement of taxa and functional groups, coral reefs are not locked in alternative stable states. They can recover by alleviating the responsible stressor(s) or restoring the perturbed aspect(s) of the system (Precht & Aronson 2006b, Idjadi et al. 2010).

In an attempt to communicate the urgency of the coral reef crisis, some authors have overemphasized the danger of irreversible thresholds (Bellwood et al. 2004). If it is all over, then apart from ethical considerations (to which we wholeheartedly subscribe), what is the 'ecological' value of protecting parrotfish and other herbivorous fishes? If on the other hand, protecting herbivores will have a salutary effect (Mumby et al. 2007b, Mumby & Harborne 2010), then the damage is not irreversible as has been claimed. Single-taxon management, when used in conjunction with other management measures, can be a powerful and relatively inexpensive approach to achieving certain goals of reef conservation (Power et al. 1996, Simberloff 1998, Hilborn 2004, Aronson & Precht 2006). For instance, no-take restrictions on parrotfish populations could limit macroalgal growth and promote coral recovery on some reefs. Protection of parrotfish, combined with a network of Sanctuary Preservation Areas (SPAs), in the Florida Keys National Marine Sanctuary could be one reason for the low algal cover on Florida's reefs (Bruno et al. 2009). Throughout the Caribbean, however, it appears that *Diadema* are far more effective than fish at reducing macroalgae and enhancing coral recruitment (Sammarco 1980, 1982b, Carpenter 1986, Hawkins & Roberts 2004, Carpenter & Edmunds 2006, Idjadi et al. 2010), so they could serve as a focal point for local conservation and management efforts, especially on reefs that are severely overfished (e.g. Macia et al. 2007). Finally, where reefs have lost their major framebuilding corals and structural complexity, restoration of foundation species is particularly important because they can facilitate the colonization of other species by maintaining or providing critical microhabitat (Halpern et al. 2007, Precht et al. 2010).

CONCLUSIONS

For coral reef scientists, the concept of alternative stable states simplifies a highly complex system of interactions, feedbacks, and measurable characteristics, yielding a dichotomy based on 1 or 2 key parameters. One class of the dichotomy (the coral-dominated community) is valued whereas the other (macroalgae-dominated or coral-impoverished community) is considered degraded and undesirable, with innuendos of humanity's moral turpitude. Reef scientists have abstracted a minimalist picture of reefs flipping between the 2 extremes and then drawn on it a baroque overlay of mechanisms that lock those reefs into one state or the other. The science has been unduly influenced by the narrative that emerged from Discovery Bay, but the scenario is not even accurate for that best-studied of reefs.

The distinction between phase shifts and alternative stable states is no semantic quibble. It is a critical issue in ecology that must be resolved if we are to diagnose the situation correctly and manage coral reefs effectively. The questions that remain are: (1) whether we can restore reef environments in the face of climate change; and (2) whether we will choose to invest in the required restoration.

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Interactions between disturbance and dispersal reduce persistence thresholds in a benthic community

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ABSTRACT: Interactions between the scale of dispersal and the disturbance regime can lead to radical shifts in the ability of organisms to colonize patches and persist within a landscape. We varied the spatial and temporal rates of disturbance and the connectivity between patches in a model of a patch landscape to illustrate thresholds of community persistence for a marine benthic community. We used model parameters representative of a New Zealand marine biogenic-structured community for which recovery after the cessation of disturbance has been observed within ~15 yr. Model results suggest functional extinction of these biogenic communities under many disturbance regimes, and homogenization of the landscape to a community dominated by opportunistic species. Dispersal limitation increases in importance for recovery as the disturbance regime strengthens, indicating thresholds in the tolerable disturbance regime based on the dispersal potential of the dominant biogenic species. Limited sensitivity of our model results to different functional forms of the recovery trajectory and colonization neighborhood suggest that these results can be extrapolated to other biogenic structure-dominated communities with recovery rates of a similar order of magnitude. Our results demonstrate that the scale of the disturbance regime and dispersal processes are fundamentally coupled, and knowing the scales of both processes is imperative when predicting change in the structure and diversity of benthic communities threatened by cumulative change.

KEY WORDS: Disturbance · Colonization · Dispersal · Connectivity · Landscape · Spatially explicit model · Patch dynamic · Thresholds · Resilience · Persistence

INTRODUCTION

All marine benthic communities consist of mosaics of patches with different histories of disturbance, colonization, and succession (Johnson 1970, Pearson & Rosenberg 1978, Rhoads et al. 1978, Paine & Levin 1981, Pickett & White 1985, Hall 1994, Zajac 2008). In these communities, dispersal between patches will influence recovery and landscape-scale responses to changes in the disturbance regime (Palmer et al. 1996, Whitlatch et al. 1998, Thrush & Whitlatch 2001, Pascual & Guichard 2005). It is clear that marine landscapes are highly diverse, with high spatial variability, and abundant biogenic structures produced by both epifauna and infauna (Ellingsen et al. 2007). Even on the vast continental shelf and slope, small-scale heterogeneity is extensive and there is no evidence for panmixia (Levin et al. 2001, Levin & Dayton 2009). Given the lack of general information on marine ecological dynamics as compared to terrestrial systems, the question arises as to whether we can use limited natural history information to populate landscape models to assist in ecosystem-based management of marine landscapes (Thrush & Whitlatch 2001, Jennings et al. 2005, Kaiser et al. 2006).

Both natural and anthropogenic disturbances have the potential to result in habitat fragmentation and long-term degradative change in marine systems (Paine & Levin 1981). Natural disturbances to the seafloor range from large and relatively infrequent events,

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e.g. large storms and hurricanes (Connell 1978) to small, frequent disturbances, e.g. ray foraging pits and wave disturbances (Sousa 1984, Thrush et al. 1991). In contrast, anthropogenic disturbances by benthic fishing gear, eutrophication, and sedimentation are often widespread and frequent relative to natural disturbances in the marine environment (Turner et al. 1999, Thrush & Dayton 2002). Examples include estimates of as much as 20% of the New Zealand continental shelf trawled each year (Cryer et al. 2002) and the entire shelf off northern California trawled between 1.5 and 3 times per year (Friedlander et al. 1999). The general pattern, repeated across broad spatial scales, is that high rates of disturbance reduce the abundance of structure-forming species, resulting in homogeneous, simple, low diversity communities, and the loss of large and long-lived sedentary species that have disproportionately high contributions to ecosystem function (Dayton et al. 1995, Scheffer et al. 2001, Thrush et al. 2001, Thrush & Dayton 2002).

Our understanding of resilience to disturbance in marine systems is limited (Thrush et al. 2009). Here we define resilience following Suding & Hobbs (2009) as the amount of disturbance a system can endure while retaining the same ecological structure, function and feedbacks. After disturbance results in the clearing of a patch in a marine system, it is often unsuitable for immediate colonization by the dominant structure-forming species (Wilcox et al. 2006, Zajac 2008). For example, marine structure-forming species in soft sediments such as corals, sponges, oysters, and bryozoans may require hard substrate such as shells for colonization (Hewitt et al. 2005). While the exact nature and prevalence of successional processes is still debated (Zajac 2001, Menge et al. 2005), time to recovery has both an element of life history of the dominant species, in terms of how long it takes to reach maturity and the organism's dispersal ability, and elements of community interactions such as competition and facilitation. Though the particular species and interactions vary between marine communities, increases in complexity of habitat structure (both infaunal and epifaunal), biogeochemical processes, and species interactions with time from disturbance are common to most marine systems (Pearson & Rosenberg 1978, Rhoads et al. 1978, Hall 1994, Newell et al. 1998, Zajac 2001), particularly in soft sediments. These similarities suggest that a conceptual model of a generalized recovery trajectory can advance our understanding of the role of disturbance on marine community dynamics (Fig. 1).

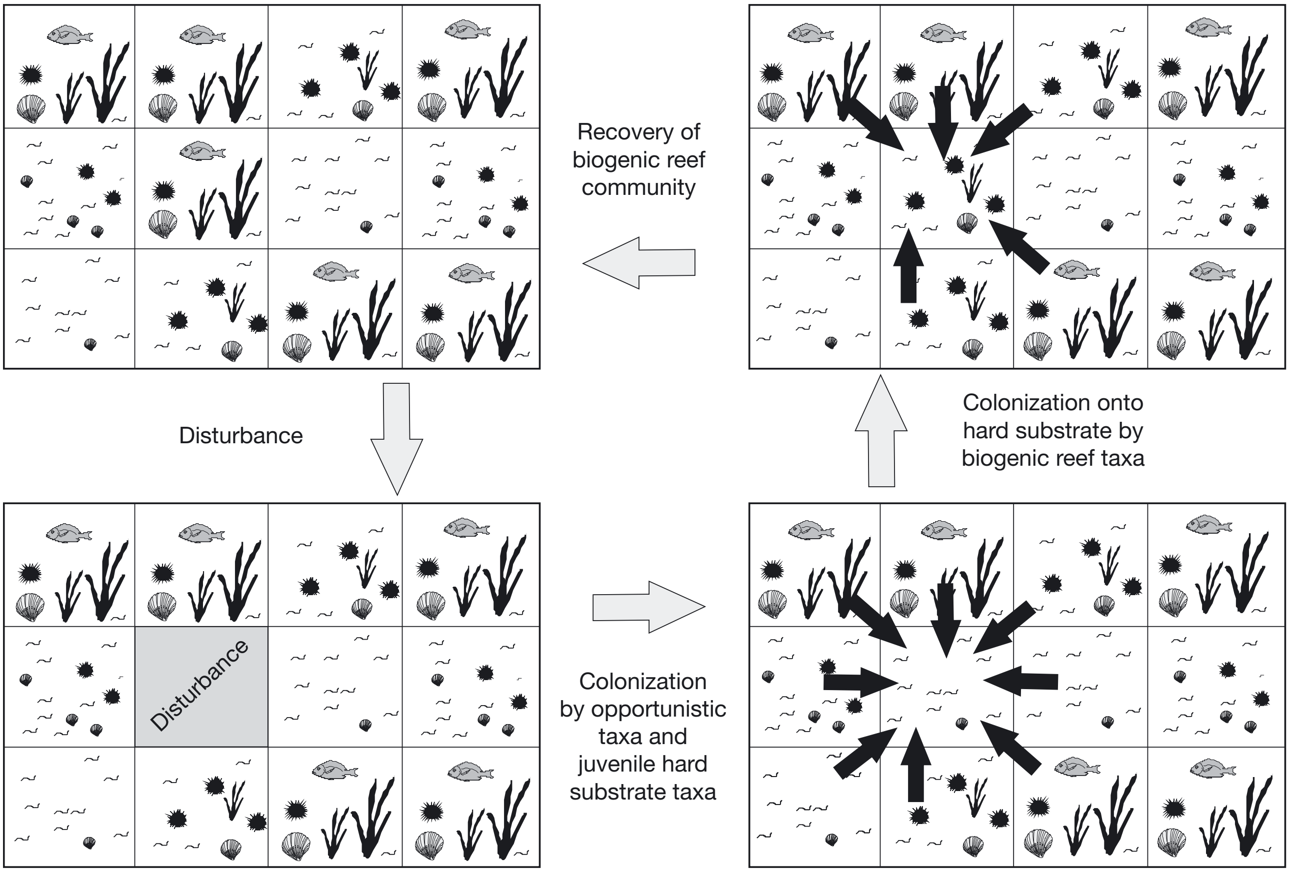

Fig. 1. Schematic of mosaic of biogenic habitat patches undergoing disturbance and recovery

The likely time to recovery of impacted areas is also related to the magnitude of changes to the landscape (Rhoads et al. 1978, Thrush et al. 2008), such that recovery to a mature community becomes less likely as the disturbance size and frequency increase, reducing the abundance and proximity of potential colonists. Patches may also exhibit variability in their ability to serve as sources and sinks for colonization due to transport processes interacting with landscape features that modify the likelihood of successful colonization (Dias 1996, Pulliam 1996, Lundquist et al. 2004). Unfortunately, dispersal and colonization processes are one of the most poorly known aspects of marine ecosystems (Cowen & Sponaugle 2009). The extent to which patch colonization is by local, regional, or global dispersers has large implications for community dynamics and resilience to disturbance (Palmer et al. 1996). While some species do have long-lived larvae and global dispersal potential, short-dispersing fauna and flora are also common, particularly in soft-sediment ecosystems (Grantham et al. 2003). In fact, reviews of larval dispersal suggest that sessile structural species such as sponges and corals generally have the lowest dispersal potential (Kinlan & Gaines 2003).

To better manage marine systems, we must understand how the scale of connectivity and the temporal and spatial scales of disturbance (and resulting landscape fragmentation) interact as a framework for predicting the implications of more complex variability in colonization potential. Here we create a model to develop a general framework for disturbance and recovery dynamics in marine landscapes. We parameterize our model to represent the complex mosaic of biogenic habitat types typically found in marine benthic ecosystems, using rates from a well-observed system (Cranfield et al. 2003, Cranfield et al. 2004). A previous model of marine benthic landscapes, conceptually adapted from a successional model of forest disturbance (Turner et al. 1993), suggested temporal and spatial rates of disturbance at which benthic communities could persist, assuming no restrictions on colonist dispersal (Thrush et al. 2005). Our objective is to determine how incorporating restricted colonist dispersal decreases the range of spatial and temporal rates of disturbance under which benthic communities can persist. In effect, we demonstrate how the disturbance regime and dispersal processes interact to determine when complex mosaics of communities tip into states characterized by simple, homogeneous landscapes.

METHODS

Our spatially explicit patch dynamic model was created to illustrate the interaction of the disturbance regime and colonization processes in regulating community dynamics and landscape structure in marine benthic systems. Here, we consider a marine benthic community dominated in terms of habitat structure by relatively long-lived species that would typify bryozoan reefs, sponge gardens, bivalve beds, or other important biogenic features that have become increasing rare with increases in anthropogenic disturbance (Rothschild et al. 1994, Cranfield et al. 1999, Thrush & Dayton 2002, Thrush et al. 2005). The landscape is modelled as a mosaic of habitat patches at varying ages from newly disturbed to mature structured habitat and thus represents a common perspective on benthic soft-sediment communities (Zajac 2008). We examine how the percent cover of mature biogenic habitat responds to varying spatial and temporal rates of disturbance and resulting levels of fragmentation (e.g. large solitary disturbances versus multiple smaller disturbances) within the landscape. We relate the percent cover of mature biogenic habitat to both thresholds in habitat dominance (disturbance combinations that result in percent cover by mature biogenic habitat of >50% of the total landscape), and thresholds of functional extinction (disturbance combinations that result in percent cover by mature biogenic habitat of <10% of the total landscape). We further define persistence thresholds as those disturbance rates below which mature biogenic habitat is not retained in the model landscape. Rates of recovery after fishing disturbance have varied with distance from and size of neighboring patches (Cranfield et al. 2003, 2004) suggesting that local dispersal between patches is important in determining patch recovery. Spatially-explicit dispersal is incorporated into the model by varying the size of the local neighborhood around disturbed cells from which colonists could be sourced.

We first describe our standard model structure and the parameters used to define disturbance and recovery processes based on a New Zealand marine benthic community dominated by biogenic structure-forming species. This standard model simulates landscapes with unrestricted colonization, and assumes no spatial dependence of colonization on proximity to occupied or mature habitat to represent an open system of interacting disturbed and recovering patches. Within this standard model structure, we vary spatial and temporal rates of disturbance to predict disturbance scenarios under which a large proportion of the landscape (e.g. 50%) is dominated by mature benthic communities, and disturbance scenarios under which we predict functional extinction, i.e. <10% of the landscape is dominated by mature benthic communities. We then modify this standard model to incorporate spatial restrictions in colonization to represent a system of patches with differing connectivities, repeating all disturbance combinations for twelve colonization scenarios that vary in the size of the surrounding neighborhood that serves as a colonist source for each cell. Finally, we test the sensitivity of model results to different realizations of the successional recovery process, and the neighborhood and age-dependent rules for source populations that govern colonization of disturbed cells.

Biogenic reef community. We developed a general model of community dynamics based on observed recovery rates for a well-studied biogenic reef community, a New Zealand shallow (depth <100 m) bryozoan reef community (Cranfield et al. 1999, 2003, 2004) (Table 1). Similar community dynamics and recovery rates occur for other biogenic reef communities, e.g. Chesapeake Bay oyster reefs (Rothschild et al. 1994, Lenihan 1999). The mature stage is defined by biogenic habitat attributes, and time to recovery from disturbance of this biogenic reef was estimated at 15 yr, at least in terms of the growth to reproductive stage of the habitat dominant species. Field observations show disturbed patches to typically progress through a series of successional stages of increasing habitat structure (Pearson & Rosenberg 1978, Rhoads et al. 1978, Cranfield et al. 2004, Zajac 2008) (Table 1, Fig. 1). In the system we are modelling (dominated by epifaunal habitat architects), initial colonization is by opportunistic infaunal taxa such as small polychaetes or amphipods. This pioneer stage is followed by colonization of hard substrate forming species such as juveniles of large suspension feeding bivalves. Once these hard substrate fauna have matured, colonization onto hard substrate and then growth of dominant biogenic reef fauna occurs; without presence of these hard substrates, biogenic reef fauna do not colonize the surrounding soft sediments (Table 1).

Table 1. Recovery dynamics of biogenic reef communities in a conceptual model of community stages. Age: age of cell in model

Age (yr)	Examples
Pioneer	
1	Small polychaetes and amphipods
Juvenile hard substrate	
2–5	Colonization by hard-substrate forming species: large suspension feeding bivalves, juvenile burrowing crustaceans, juvenile sponges, large crustaceans
Mature hard substrate	
6–14	Mature stage of adult bivalves and encrusting fauna (sponges, hydroids, tunicates), large burrowing species and other species affiliated with habitat structure, deep burrows, and bioturbation. Colonization onto hard substrate by juveniles of dominant mature biogenic reef fauna: erect bryozoans and sponges
Mature biogenic reef	
15+	Mature bryozoans forming complex biogenic reef

While we conceptually define the recovery trajectory as representative of different successional stages that increase sequentially with time, in effect the model recovery trajectory includes only a time to recovery of a mature biogenic community. Our designation of different successional stages is implicit, but not an essential part of the model structure. We recognize that ecological interactions (e.g. priority effects, inter- and intraspecific competition, facilitation) can influence the trajectory of communities over time, both in terms of the temporal scale of recovery and the endpoint community that is attained (Farrell 1991, Tanner et al. 1996, Dudgeon & Petraitis 2001, Menge et al. 2005). Later, we test sensitivity of model predictions to different realizations of the recovery trajectory (see 'Methods—Model sensitivity'), though still assuming the same endpoint biogenic community, allowing us to generalize across some potential ecological interactions that can change the temporal scale and magnitude of recovery.

Standard model structure. The model consists of a 100 × 100 cell grid, with each of the 10 000 cells representing a habitat patch at a certain age. Conceptually, each cell represents a large enough area to sustain a biogenic reef community, and be reproductively successful such that the cell can serve as a colonist source to other cells. While the model is scale invariant, we conceptualize each grid cell to represent an area of ~100 × 100 m, a realistic patch size for this biogenic reef community that historically has occupied 100s of km^2 (Cranfield et al. 2003). While dispersal distances for species in this biogenic reef community have not been explicitly quantified, differences in recovery rates of disturbed patches separated from source reefs by distances of <5 km suggest that dispersal in the range of 1 to 20 cells (100 m to 2 km) is a likely estimate for many of the dominant biogenic species (Cranfield et al. 2003, 2004).

The model was initialized with all cells representing a mature state. After a disturbance occurred, a disturbed cell was redesigated cell age 1, representing a pioneer community of immediate post-disturbance state. Disturbances and corresponding source areas for colonization were simulated assuming periodic boundary conditions (e.g. a torus). The age of each undisturbed cell was sequentially increased after each time step (corresponding to years). In the standard model, recently disturbed pioneer cells (age 1) increased sequentially in age with no spatial restrictions on colonization. We simulated the proportion of patches at each age in the landscape over 300 time steps, which was sufficient time to eliminate transient dynamics due to the initialization of the cells. We use the mean proportion of patches at each age in the final 50 time steps ($t = 250$ to 300) to compare between simulations.

Disturbance. Disturbances were randomized across the landscape in continuous square blocks of sizes representing different percentages of the landscape disturbed and at time steps corresponding to the frequency of disturbance. Disturbance rates ranged in spatial scale from 0 to 100 % of the landscape disturbed in each time step, and in temporal scale from 0 to 20 individual disturbance events per year. Disturbance frequencies <1 were accumulated over consecutive time steps (e.g. a frequency of 0.1 equates to 1 disturbance event once in 10 yr). Disturbances were created at random locations using a random number generator, and all cells were equally likely to be disturbed regardless of disturbance history. Simulations using different values of the seed for the random generator showed variation of <1 % in mean proportion of mature cells after 300 time steps; thus results using only 1 seed are presented here. Disturbed cells were reduced to pioneer stage 1, representing homogenization of habitat within the entire cell, such that no mature individuals remain to supply colonists to disturbed cells. While different types of disturbance (natural and anthropogenic) occur in most ecological systems, for simplicity we assume that only 1 type of disturbance is operating at the scale of the model, rather than disturbances with different frequencies and spatial extents operating concurrently.

Patch colonization. To examine how restricted colonization processes interact with the level of landscape fragmentation created by each of the disturbance scenarios, we added spatial restrictions on colonization to the standard model structure, limiting colonization of disturbed cells to those within a minimum distance to a colonist source. Colonization of a previously disturbed cell (age 1) occurred if there was at least 1 cell within the cell's neighborhood equal to or greater than the required source age. The neighborhood of each cell was defined by all surrounding cells within a particular dispersal distance (dd, number of cells from center). Dispersal distances thus corresponded to square neighborhoods centered on each cell of side length $(2\text{dd} + 1)$ and neighborhood area of $[(2\text{dd} + 1)^2 - 1]$. The source age was defined as age 6, representing the presence of mature hard structure-forming species that could serve as source populations for the initial colonization of disturbed cells. We simulated 12 dispersal distances (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 15, 20), with corresponding neighborhoods covering 0.08, 0.24, 0.48, 0.80, 1.20, 1.68, 2.24, 2.88, 3.60, 4.40, 9.60, and 16.80 % of the total landscape, respectively. We repeated the full set of disturbance combinations (spatial scale: 0 to 100 %, temporal scale: 0 to 20 events per year) for each dispersal distance. We examined spatially dependent colonization of only pioneer (i.e. recently disturbed) cells, though similar restrictions with aging of 'older' patches dependent on proximity to source patches showed qualitatively similar results as the scale of dispersal was varied (C. Lundquist unpubl. data).

Model sensitivity. Actual recovery trajectories and colonization dynamics with respect to the size and age-structure of colonist source populations are rarely quantified for marine benthic communities (though see Kaiser et al. 2006 for a review of community recovery rates after the cessation of fishing, and Ellis et al. 2008 for estimates of recovery rates for some benthic phyla). As these recovery rates have not been quantified for the biogenic reef community that we model here, we examine sensitivity of the model to different functional representations of the recovery trajectory and of the influence of patch neighborhood on colonization success. For example, it is unlikely that patch successional processes proceed linearly from one stage to the next (Johnson & Miyanishi 2008); rather we expect that inter- and intraspecific interactions result in nonlinearities in the recovery of patches, as well as the potential for multiple endpoint communities (Farrell 1991, Dudgeon & Petraitis 2001, Zajac 2001, Menge et al. 2005, Caplat & Anand 2009). Similarly, we compared different realizations of dispersal and colonization processes that regulate the local abundance of colonists, e.g. whether recovery and/or colonization is dependent on the presence of a single neighbor or the successional status of the entire local neighborhood.

To analyze the sensitivity of landscape dynamics to the recovery trajectory, we varied the mathematical representation of recovery over time, and the relative dependence of recovery on neighborhood composition. Four recovery functions were used: (1) neighborhood-independent sequential function (the standard model structure); (2) neighborhood-dependent step function; (3) neighborhood-dependent linear increase; (4) neighborhood-dependent logistic increase (Fig. 2). In the neighborhood-independent recovery, cells were aged sequentially by 1 at each time step. For neighborhood-dependent cases, recovery functions were based on the proportion of occupied cells (cells of age >1) in each cell's neighborhood, based on the dispersal distance modeled in each simulation. We chose sensitivities in recovery based on variability of 50 % of the standard (Type 1) sequential recovery rate. For the step function, cells increased in age by 0.5 (50 % less than baseline) if the percent occupied was <20 %; 1 if percent occupied was 20 to 50 %; and 1.5 (50 % higher than baseline) if percent occupied was >50 %. The linear function had a minimum value of 0.5 with 0 % occupancy and a high value of 1.5 with 100 % occupancy within each cell's neighborhood. The logistic recovery curve used a sigmoid function fit to the same minimum and maximum values as the linear function.

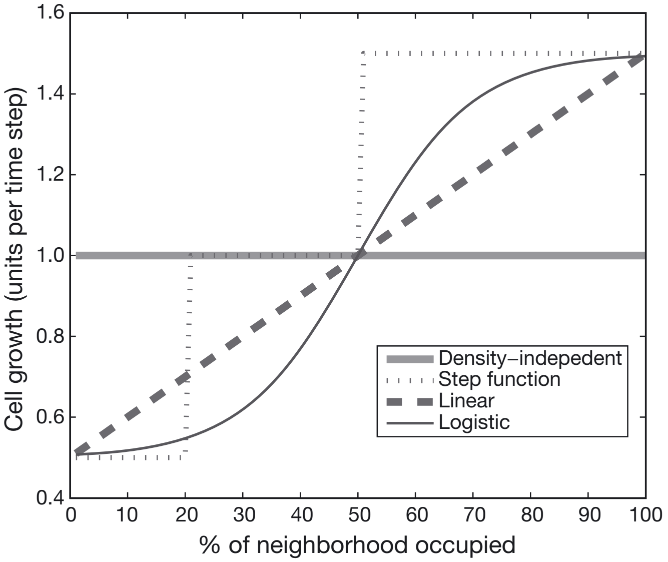

Fig. 2. Functional forms of recovery trajectory used in sensitivity analysis

To analyze the influence of different model realizations of the colonization neighborhood on modeled landscape dynamics, we compared 3 mathematical representations of cell colonization: (1) maximum cell age within neighborhood (the standard colonization option, described previously); (2) percentage of neighborhood occupied; and (3) percentage of neighborhood in mature state. For the first, colonization of a previously disturbed cell (age 1) occurred during that time step if a cell was within a minimum proximity to a colonist source, i.e. there was at least 1 cell within the cell's neighborhood equal to or greater than the required source age, with the standard colonization option being source age = 6. Within this first sensitivity analysis, we also varied the minimum source age to further investigate the dependence of model results on the presence of neighboring mature biogenic or hard-structured habitat. We analyzed 2 additional colonist source ages, representing colonist age of a mature biogenic reef (source age = 15), and of all non-disturbed cells being able to contribute to the colonist source pool (source age = 2). For the second colonization scenario, colonization of a previously disturbed cell occurred during that time step if at least 20% of the neighborhood was occupied (age > 1). For the third colonization scenario, colonization occurred if at least 20% of the neighborhood was in a mature community state (age 15 or greater). For the second and third colonization scenarios, the 20% metric was chosen based on representation of both an ecologically relevant amount of mature biogenic reef habitat, and not being overly restrictive in requirements of mature habitat (e.g. many combinations of disturbance rate did not result in >50% mature habitat remaining).

RESULTS

Our model results showed one of 2 patterns in community dynamics for each individual simulation. Simulations either reached a relatively steady proportion of cells in each successional stage, or simulations reduced to a homogeneous 100% pioneer stage over the course of the simulation. Ecologically, we interpret dominance by the pioneer stage as the degradation of the benthic community mosaic into a landscape lacking the heterogeneity generated by long-lived, biogenic habitat-forming species.

For simulations that result in the first pattern of a stable stage distribution (and that did not result in extinction of the mature habitat-forming communities), the combinations of spatial and temporal frequencies of disturbance were surprisingly restricted, even for simulations with no spatial restrictions on colonization. Contour plots of combinations of spatial and temporal rates of disturbance that resulted in 50 and 10% mature habitat illustrate further reductions in the domain of suitable disturbance regimes when comparing the standard model results to scenarios with restricted colonization, and as the size of the colonist neighborhood (dispersal distance) was decreased (Fig. 3).

To examine changes in thresholds of persistence of mature habitat, we plotted changes in mature and occupied habitats for constant disturbance frequencies of 1 disturbance event per year, while varying the spatial extent of disturbance (Fig. 4). We define persistence thresholds as combinations of the spatial extent and frequency of disturbance where the percentage of mature (or occupied) habitat becomes zero. Simulations with local dispersal (dd = 1) show persistence thresholds at <10% of the landscape disturbed per year. As colonist source neighborhoods increase to include regional neighbors, no decrease from maximum possible occupied habitat is shown until disturbance rates of >20% per year, with thresholds of persistence of occupied habitat increasing to ~35% with the largest dispersal distance simulated (dd = 20) (Fig. 4). In comparison to the unrestricted dispersal scenarios, the percent mature curve is nearly identical to the 'dd = 20' scenario, while percent occupied for the unrestricted dispersal scenarios is represented by the 45° line, i.e. the 45° line represents (1 – the total disturbance rate) per time step. Thus, even regional dispersal simulations that assume minimal spatial restrictions on dispersal demonstrate significant declines from the maximum possible occupied and mature habitat.

To examine thresholds in persistence, functional extinction and dominance, we compared simulations that varied colonist neighborhoods (Fig. 5). As results for unrestricted simulations were visually similar to the 'dd = 20' scenarios at the resolution presented here, we present only the 'dd = 20' scenario. Relative changes in the percentage of occupied habitat were larger than those changes in the percentage of mature habitat as the size of the colonist neighborhood was increased for most disturbance combinations (Fig. 5). These results illustrate combinations of spatial and temporal rates of disturbance at which mature biogenic habitat are unlikely to persist, even with unrestricted dispersal. The range of 'successful' combinations of spatial and temporal disturbance frequency (i.e. resulting in non-zero cover of mature or occupied habitat) increased as colonist neighborhood increased (Fig. 5).

Sensitivity analyses demonstrate the importance of connectivity in interpreting disturbance/recovery processes, with simulations that modelled restricted dispersal being more sensitive to differences between mathematical representations of intrinsic patch dynamics (Fig. 6). Model results showed minimal sensitivity to functional form of the recovery (successional) trajectory, with <10% variability in the percent of mature habitat between the 4 functional forms simulated, illustrated for 3 colonist neighborhoods (Fig. 6a). In all cases, the step function showed a slightly larger percentage of mature habitat (Fig. 6a). Sensitivity to source age was more apparent in simulations with localized dispersal than in less restricted dispersal simulations (Fig. 6b). Simulations with restricted dispersal showed largest decreases in mature habitat when source colonists were restricted to mature habitat (source age 15), and less severe decreases when source colonists were restricted to hard structure habitat (source age 6, the standard case), relative to simulations where colonist sources included all undisturbed cells (source age 2) (Fig. 6b). Finally, sensitivity to colonization rule was minimal for less restricted dispersal scenarios, but showed large decreases in percent

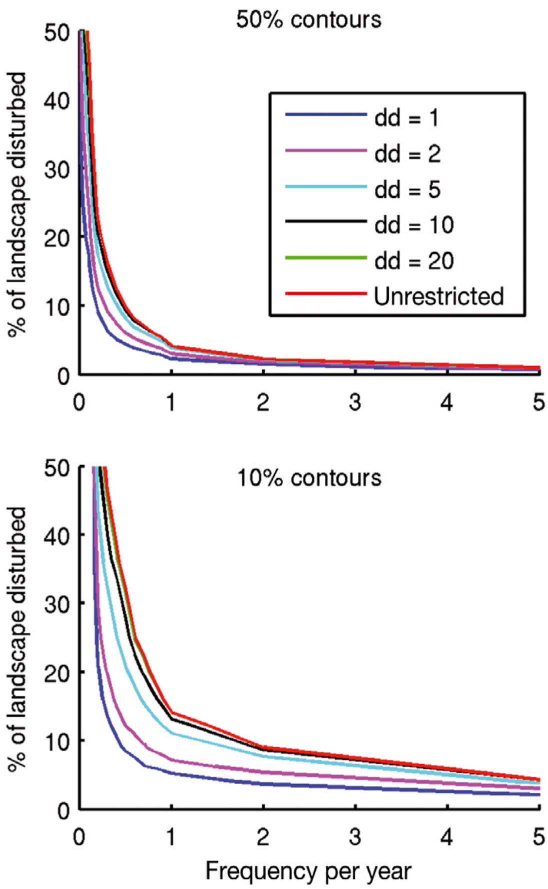

Fig. 3. Contour plots of 50 and 10% of the landscape maintained in mature habitat across the range of spatial and temporal scales of disturbance. Results are based on the standard model options for recovery (sequential) and colonization (max. age of cells within neighbor, source age = 6 yr). Contours are shown for dispersal distances (dd) = 1, 2, 5, 10, and 20 cells, and for the standard model with unrestricted colonization. Note the overlap of contours for dd = 20 and the unrestricted dispersal scenarios

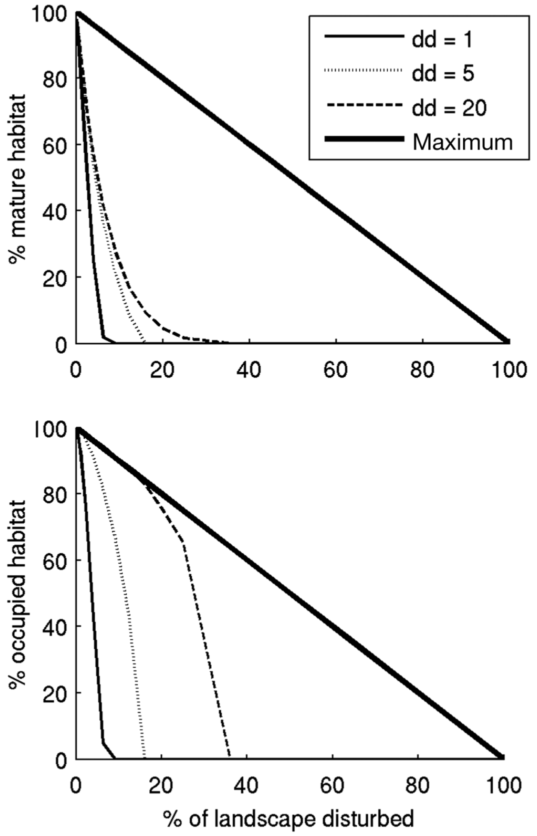

Fig. 4. Comparison of (a) % mature and (b) % occupied habitat for simulations with constant frequency of 1 disturbance yr^{-1}, and varying spatial extent of disturbance, for 3 sizes of colonist neighborhood (1, 5, and 20 cell dispersal distances). Thick line symbolizes max. possible % of occupied or mature cells for each disturbance rate (e.g. max. occupied habitat for simulations with a disturbance rate of 20% of the landscape yr^{-1} is 80%). Results are based on standard model options for recovery (sequential) and colonization (max. age of cells within neighborhood, source age = 6 yr)

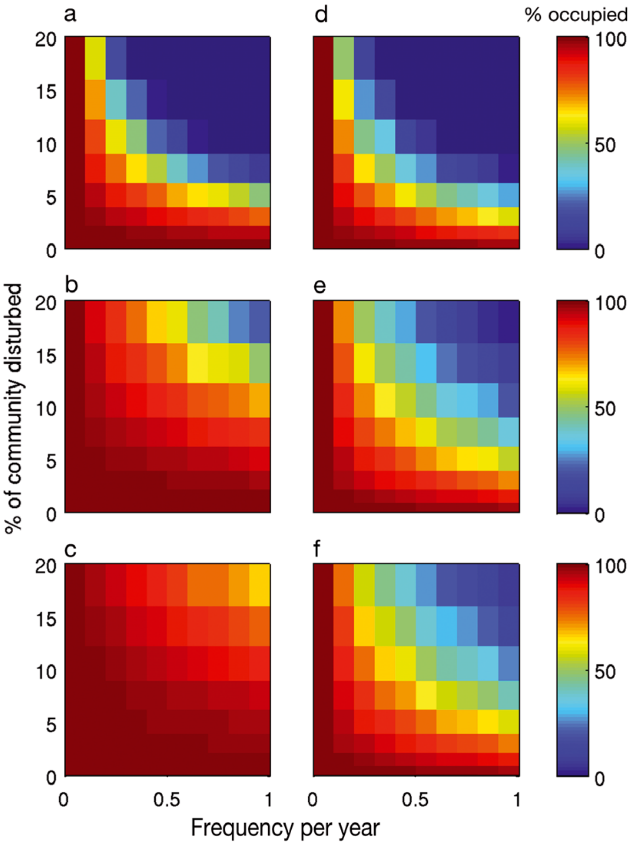

Fig. 5. Contour plots of the percentages of occupied (a,b,c) and mature biogenic habitat remaining (d,e,f) for different combinations of temporal frequency and spatial extent of disturbance, illustrated for dispersal distance = 1 (a,d); dispersal distance = 5 (b,e); and dispersal distance = 10 cells (c,f). Results are based on the standard model options for recovery (sequential) and colonization (max. age of cells within neighbour, source age = 6 yr). Red shading indicates persistence of occupied (or mature) habitat under that disturbance combination, while blue shading indicates that occupied (or mature) habitat is unlikely to persist under that disturbance combination

mature for localized dispersal scenarios for colonization rules where colonization was dependent on presence of at least 20% mature habitat (Fig. 6c). Simulations with 20% occupied rules and maximum age rules showed similar results.

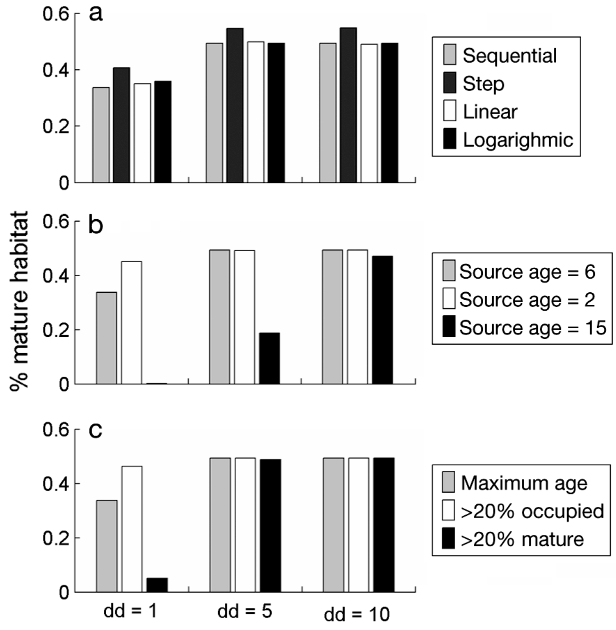

Fig. 6. Sensitivity to model parameters, illustrated for % mature habitat for colonist neighborhoods of dispersal distances of 1, 5, and 10 cells. (a) Functional form of recovery (standard option—sequential; step; linear; logarithmic); (b) source age for colonization based on max. neighbor age (standard option—source age = 6; source age = 2; source age = 15 yr); and (c) colonization rule (standard option—max. neighbor age with source age = 6 yr; >20% occupied; >20% mature). All simulations illustrated using disturbance rate of 5 disturbances each of 1% of total landscape yr^{-1}

DISCUSSION

The resilience of communities dominated by large, long-lived species is threatened by increasing disturbance rates (Scheffer et al. 2001, Thrush & Dayton 2002, Bremner et al. 2005, Thrush et al. 2006). Disturbance fragments the landscape, reducing both the proportion and proximity of mature habitat that provides colonists (With & King 1999). Feedbacks between disturbance regimes and dispersal and colonization processes underlie changes to resilience (Pascual & Guichard 2005, Thrush et al. 2009). Here, we highlight a feedback mechanism between landscape connectivity and fragmentation by disturbance that further reduced the cover of mature biogenic habitat. This result is in part due to the contribution of time-dependent colonization processes on community recovery such that disturbance rates are too high for patches to recover to the minimum age and thus serve as a colonist source (Ellner & Fussmann 2003). Here, our model illustrates a persistence threshold, dependent on the particular connectivity matrix that declines faster than would be predicted from the disturbance rate alone.

As mature stages of many marine biogenic communities exhibit restricted dispersal (Osman & Whitlatch 1998, Kinlan & Gaines 2003), our results indicate that thresholds in community persistence will be exceeded at lower disturbance rates for these biogenic-structured communities. As colonist source neighborhoods were decreased in the model scenarios to represent more restricted dispersal indicative of these biogenic communities, the domain of disturbance rate resulting in functional extinction of biogenic structured habitat increased. Other landscape models have demonstrated interactions between dispersal and patch dynamics, such that the total abundance of habitat or spatial configuration often determines habitat thresholds below which dispersal behavior has a strong influence on community dynamics (With & Crist 1995, Wiens et al. 1997, With et al. 1997, Flather & Bevers 2002, Johst et al. 2002, With & King 2004). Similarly, metapopulation and metacommunity models emphasize the need to consider both the relative influence of regional versus local processes and intrinsic patch dynamics to predict extinction risk (Loreau & Mouquet 1999, Loreau et al. 2003, Cardinale et al. 2004, Kallimanis et al. 2005, Laird & Schamp 2008). Field experiments highlight a variety of processes influencing recovery that often involve interactions between dispersal and intrinsic process in a scale-dependent fashion, for example, edge effects (terHorst & Dudgeon 2009); habitat stability (Thrush et al. 1996); and the response of opportunistic species (Norkko et al. 2006). As dispersal behavior, the scale of dispersal, and the relative contribution of local versus regional colonist sources are often poorly known, understanding that large, long-lived communities will be more strongly affected by increasing rates of disturbance improves our ability to predict resilience of communities under increasing rates of anthropogenic disturbance (Thrush et al. 2006, 2009).

Our results support numerous theoretical and empirical demonstrations of the importance of habitat structure for ecosystem function of marine benthic communities (Turner et al. 1999, Thrush et al. 2001, Diaz et al. 2003). Relevant processes dependent on structural attributes include age-dependence to arrive at mature biogenic structured communities and a dependence on the existence of mature structured communities for colonization to occur (Scheffer et al. 2001, Ellner & Fussmann 2003). Unfortunately, the importance of habitat structure and associated successional processes required for biogenic habitats to be created are often ignored in theoretical models of metapopulations and metacommunities (Wilcox et al. 2006).

Our model simulations encompassed many realistic rates of natural and anthropogenic disturbance, so the large range of solutions that represented functional extinction of biogenic reef communities was unexpected. High intensity disturbances are likely to be unsustainable for complex, biogenic-structured communities dominated by long-lived and poor dispersing species. The potential for historical anthropogenic disturbance rates to have tripped thresholds for persistence of these biogenic communities is likely to contribute to the problem of demonstrating differences between control and fished areas in some locations subject to trawling (Dayton et al. 1995, Daan et al. 2005, de Juan et al. 2007). In addition, our model demonstrates inequalities in the influence of spatial and temporal disturbance on landscape dynamics, such that results differed between simulations with the same total annual disturbance rate, but different spatial and temporal combinations of disturbance (i.e. 10% disturbed once per year versus 1% disturbed 10 times per year). These results imply that the rate of disturbance has a much more complex interaction with successional processes via habitat connectivity, and the configuration and fragmentation of the landscape resulting from the particular disturbance regime.

Our model incorporated many simplifying assumptions that in most cases make our results a conservative estimate of the impacts of disturbance on marine landscapes. For example, we assumed no spatial correlation in disturbance, though most marine disturbances are spatially correlated, e.g. trawling disturbance with aggregated distribution of trawl effort (Friedlander et al. 1999). Sedimentation events from terrestrial runoff also have a higher probability of impacting certain areas in estuaries and coastal zones, although impacts change considerably depending on wind and tidal conditions (Thrush et al. 2004). Similarly, fishing disturbances may exacerbate other processes (such as land-based increases in sedimentation or eutrophication) that otherwise decrease resilience to disturbance (Lenihan 1999, Crain et al. 2008). Natural disturbance rates are also expected to vary in size, with an '1/f noise' nature such that most disturbances are small and few are large (Pascual & Levin 1999, Denny et al. 2004, Fisher et al. 2008), rather than the constant size/frequency of disturbance modelled in each simulation here. We speculate that impacts of correlated disturbances would depend strongly on connectivity within the landscape, and the relative proportion and configuration of the landscape that is left undisturbed (Kallimanis et al. 2005). In contrast, we predict that including concurrent disturbance impacts of different temporal and spatial scales (including that of multiple stressors) would have additive or multiplicative results on model predictions as the disturbance regime is increased (Crain et al. 2008). Finally, we simulated only 'square' disturbances; we predict that varying the shape of disturbances via configurations with larger perimeter to area ratios could interact with disturbance frequency to increase or decrease landscape fragmentation, depending on the size of the disturbance relative to the total area of the landscape, and thus modify the range of feasible disturbance regimes (Liddel 2001, Fonseca et al. 2004, Langmead & Sheppard 2004).

Other assumptions are likely to have more variable effects. For example, we assumed that disturbances resulted in complete clearing of a cell such that no macro-organisms remain to facilitate colonization by pioneers. Organisms that escape the disturbance impact, e.g. juveniles that are left intact, or adults that are damaged but regenerate, could dampen threshold effects. Experimental manipulations in benthic systems have shown the importance of historical community presence in determining colonization after disturbance (Tanner et al. 1996, Dudgeon & Petraitis 2001). We also assumed that there were no differences in dispersal rate between successional community stages, though it is likely that mature structural species will have lower dispersal rates than highly mobile pioneer species (Osman & Whitlatch 1998, Grantham et al. 2003, Kinlan & Gaines 2003). We also did not consider variations in suitability of each patch for colonization, although a number of processes will affect successful settlement, e.g. hydrodynamic forces, habitat selection, and settling behavior (Butman 1987). This may explain the small amount of change in community dynamics we observed after increasing the colonist source pool from ~17 % of the total landscape (corresponding to a radius of 20 cells out from a disturbed cell) to a global colonist neighborhood consisting of the entire landscape.

In general, our results show the importance of the degree of neighborhood connectivity in defining a community's ability to persist in the face of disturbance. These results can easily be extrapolated to a spatial management context for other biogenic-structured communities with similar times to recovery to determine relevant rates of disturbances that result in functional extinction (or alternatively, which rates result in a minimum proportion of mature community persisting across a landscape). Vice versa, we could utilize the observed proportion of various successional stages at a location to determine the likely disturbance rate or dispersal kernels. It is important to understand the response of sensitive biogenic habitats to disturbance-mediated changes in the connectivity of habitat patches, and the dependence of these habitats on proximity to colonist sources for resilience to and recovery from disturbance. Anthropogenic impacts are continually increasing, including impacts of climate change on coastal habitats (Harley et al. 2006), though the expected change in disturbance rates due to climate change is unknown. Our approach, linking connectivity and disturbance rates, can further aid in determining patterns of biodiversity, production, ecosystem function, and resilience across ecological scales (Leibold et al. 2004, Karlson 2006, Thrush et al. 2009).

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Modeling of priority effects and species dominance in Long Island Sound benthic communities

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ABSTRACT: Spatially structured communities are common in many systems, including the marine benthos where sessile species compete for substrate. Which species colonizes a habitat first may determine species coexistence or dominance. The strength of this priority effect will vary as a function of the interaction between life history processes and disturbance events at different spatial and temporal scales. On a local scale, disturbance tends to open up space, allowing new propagules to arrive, while on a regional scale, it has the potential to reduce source populations and the colonization ability of dispersal-limited species. Differences in larval longevity will have a direct influence on dispersal distance, the relative timing of colonization, and the impact of priority effects, especially when interacting with different disturbance regimes. This study presents a modeling exercise to highlight this synergy and its implications for invasive species and ecosystem management. Four life histories were simulated, representing species from the 4 common community states of Long Island Sound, USA: resident bryozoans, invasive ascidians, mussels, and the ascidian *Diplosoma listerianum* that is restricted to years with abnormally warm winters. Brooding species took longer to exert dominance than broadcast spawners, but were more resilient to disturbance, having less local extinctions. Simulations showed that the combined effects of dispersal ability and disturbance could allow the maintenance of diversity on a regional scale regardless of the identity of locally dominant species. Priority effects are only present when the system experiences localized disturbance regimes, such as predation.

KEY WORDS: Community threshold · Dispersal · Life history · Model

INTRODUCTION

Studies on patterns of species dominance have focused on competitive exclusion (Tilman 1980), tradeoffs between species' competitive and colonizing abilities (Yu & Wilson 2001), or simple stochastic events (Caswell 1976). Often, however, these mechanisms can also have profound effects on communities, which may in turn cause shifts in species compositions (Ricklefs & Schlutter 1993, Holyoak et al. 2005). The synergistic effect of stressors and the particular characteristics of a community can make it difficult to predict responses of coexisting species, as community structure often shows rapid transitions (Sutherland & Karlson 1977, Scheffer & Carpenter 2003, Petraitis & Methratta 2006, Houseman et al. 2008).

The turning points or thresholds where species composition changes from one state to another allow different community structures in similar habitats (Sutherland 1974, Scheffer et al. 2001, Folke et al. 2004). These thresholds are often caused by environmental conditions and a secondary effect from the internal dynamics of the community (e.g. changes in the abundance of a dominant competitor or predator). Detecting thresholds in field studies can be difficult because they require a thorough understanding of the natural systems where they occur, and can often involve multiple mechanisms operating at different spatial and tempo-

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ral scales (Connell & Sousa 1983, Andersen et al. 2009, Petraitis & Hoffman 2010 this Theme Section). For example, disturbance (Connell 1978) can have strong effects on diversity (i.e. number of species in a community) but may affect species differently depending on the spatial scale over which it operates (Munguia & Miller 2008). When an environmental (abiotic or biotic) mechanism such as disturbance can elicit different responses from coexisting species due to different life history properties, we expect different thresholds to be present within an ecosystem (Dudgeon & Petraitis 2001, Andersen et al. 2009).

In spatially structured habitats (i.e. metacommunities) where local communities share a regional species pool, mechanisms structuring diversity can also be scale dependent (Petraitis & Latham 1999, Dudgeon & Petraitis 2001, Holyoak et al. 2005). Disturbance can occur at the within-community patch scale (e.g. Connell 1978, Sousa 1980), create fragmented communities and ecosystems affecting inter-patch movement (e.g. Huxel & Hastings 1999, Fahrig 2003) or be responsible for the destruction of communities and the potential extinction of population sources (e.g. Munguia & Miller 2008). Disturbances occurring at different spatial scales will have different effects on a region's diversity. Disturbance at the local scale (i.e. within a community) has been shown to have a hump-shaped influence on the diversity of competing species (known as the 'intermediate disturbance hypothesis', Connell 1978); often the response and recovery from these disturbances towards low diversity communities dominated by a few species is relatively fast (Sousa 1980). Alternatively, when disturbance occurs at the regional scale, communities can take longer to recover to the pre-disturbance state, depending on the severity of the event. Regional disturbances have the potential of wiping out populations and driving species to extinction, and can include large-scale events such as storms or oil spills. If habitats with similar environmental conditions can have different species composition (e.g. Sutherland & Karlson 1977, Petraitis & Methratta 2006), then it is crucial to understand the mechanisms driving differences in species distributions. Instead of focusing on the community response to disturbance, studies could focus on the environmental thresholds (Folke et al. 2004, Hughes et al. 2005) that produce changes in species dominance and the variance in community composition (Houseman et al. 2008).

A large body of work has focused on alternative states, where small changes in environmental conditions can shift community structure (e.g. Petraitis & Latham 1999, Scheffer & Carpenter 2003). These changes are so small that they often allow alternative communities to occur simultaneously under the same conditions within a region (e.g. Sutherland 1974, Petraitis & Methratta 2006). In any of these states, there is often a dominant species that drives differences in community structure among habitats. However, predicting which species (i.e. state) will occur is not an easy task since it involves addressing appropriate spatial scales, disturbance rates, successional stages and species life histories (Petraitis & Latham 1999).

Marine species thrive in spatially structured habitats because they often have 2 life history stages that act at different spatial scales: an among-habitat or regional scale experienced by the disperser (often larvae or juveniles; Roughgarden et al. 1985, Roughgarden et al. 1988), and a local scale experienced by the sedentary stage. This sedentary stage is often represented by sessile adults in species such as bryozoans, ascidians, sponges, barnacles and mussels. Marine species can also have differences in adult longevity relative to disturbance and larval recruitment, which can affect population dynamics at both local and regional spatial scales (e.g. Osman & Whitlatch 1998, Munguia et al. 2007). Therefore, the spatial arrangement of habitats can be crucial for population dynamics and diversity patterns (e.g. Hughes et al. 2005), where communities are part of a mosaic of different habitats as well as sites within the same habitat (Leibold et al. 2004).

An essential resource for many sessile marine species is the hard substrate to which they attach permanently as adults (e.g. Osman 1977). Most coastal regions are a patchy network of hard rocky habitats and soft mud and sand habitats, with sessile species being generally adapted to live in and compete for only one of the habitat types. In many sites, dominance by a single species can be observed as mussel beds, barnacle zones, oyster reefs, bryozoan reefs, or even patches of invasive ascidians (e.g. Whitlatch & Osman 1999, Petraitis et al. 2003, Cocito 2004, Paine & Trimble 2004, Osman et al. 2010 this Theme Section).

Within such space-limited communities, the timing of disturbance relative to recruitment can result in priority effects if the early arriving species can dominate the local habitat and exclude other incoming species (Fukami 2004, Shurin et al. 2004). When priority effects occur, they tend to diminish diversity at a local scale and regional mechanisms are needed to counter these and maintain the regional species pool. For example, if disturbance occurs locally across the region and is coupled with adequate connectivity (i.e. dispersal of species) among different habitats, then different local priority effects should allow the simultaneous occurrence of multiple communities within the region. Such patterns were observed in settling plates that were in close proximity, yet showed different species composition (Sutherland 1974), reflecting the local–regional dynamics that recent theory is proposing (Shurin et al. 2004). Therefore, while local diversity may be low due to priority effects, regional diversity may remain relatively high by allowing different dominant species and communities in different sites.

Because the first step in the colonization of any habitat by any sessile species is the arrival and recruitment of planktonic larvae, the timing of the availability of open space relative to the settlement of larvae of each species are critical to the success of each species (e.g. Osman 1977, Sutherland & Karlson 1977, Sousa 1984). With differences in reproductive cycles among species and the concurrences of habitat availability, priority effects would seem a likely mechanism for producing local dominance within the ecosystem. Further, given the large spectrum of individual life histories among the often hundreds of competing species within many of these marine systems, there is the potential for priority effects to produce a patchwork of different dominant species. This is likely to be enhanced by the spatial and temporal variation in disturbances that make open substrate available.

Within eastern Long Island Sound (USA), we have identified 4 distinct subtidal epifaunal invertebrate communities that are easily distinguished by the taxa that dominate them (range: 30 to 100 % cover, but often over 50 % cover; Osman et al. 2010): (1) a native community frequently found in coastal areas and often dominated by resident bryozoans (e.g. *Schizoporella errata*), (2) a community dominated by invasive ascidians (e.g. *Botrylloides violaceus* and *Styela clava*), most commonly seen in man-made structures such as harbors, marinas, and other sites under human influence, (3) a community dominated by mussels and algae (e.g. *Mytilus edulis* and *Laminaria longicrurus*) that periodically replaces bryozoan or ascidian communities, and (4) an ascidian community dominated by the invasive colonial ascidian *Diplosoma listerianum* that is restricted to warm-winter years (mean temperature > 4°C).

Data collected over the past 15 yr (e.g. Osman & Whitlatch 1995, 1996, 1998, 2004) have shown that these 4 states all exhibit a level of resilience that allows them to be maintained for years, if not indefinitely, by interacting physical and biological processes such as disturbance and dispersal ability (Osman et al. 2010). These same processes are also responsible for switches in community composition, but changes appear to require unique sets of abiotic and biotic stresses or disturbances. Switches between states occur over time periods of months to years over equally variable spatial scales that can span from a few meters to kilometers (R. W. Osman & R. B. Whitlatch unpubl. data). These processes (Osman et al. 2010) vary from those that are local and operate fast (e.g. predation by different predator guilds or localized disturbance events) to those that are regional and operate much more slowly (e.g. climate change or gradual anthropogenic impacts such as changes in land use). Local stresses can result in the different communities co-existing at sites near one another. Stresses occurring at regional scales can produce broader regional switches in threshold conditions, but are of potentially variable duration. Therefore, this system has interacting effects of stresses with fast, intermediate, and slow rates of action on the switching among community states at local and regional scales.

The main objective of this study was to model whether disturbance at local and regional spatial scales would cause different patterns of dominance and extinction. These dominance patterns were linked to the 4 species representative of the community states observed in the Long Island Sound. We also provide a discussion of potential consequences for resource management under local and regional disturbance scenarios.

We simulated 2 spatial levels of disturbance to examine how variation in scale affected species interactions and the connectivity among habitats. First, we wanted to know if different spatial scales of disturbance affected representative locally dominant species. We tested whether priority effects (Shurin et al. 2004) could constrain the arrival of new species into individual habitats, and whether disturbance at different spatial scales could counter priority effects. We were particularly interested in whether life history traits were correlated with species' dominance and community responses to disturbance. Local disturbance would cause mortality and make resources (substrate space) available at a particular locality, while regional disturbance would have a similar effect across all sites or habitats. A community affected by local disturbance should be vulnerable to invasion by recruits produced at other, undisturbed sites within the region. The resilience of this community and the priority of its dominant species will depend on the ability of the dominant species to recruit locally and outcompete invaders from within the region for the newly available resources (e.g. Andersen et al. 2009). With regional disturbance affecting all species and sites, dispersal may allow all dominant species to remain even if local priorities break down. Our objective was to model the general problem of disturbance at different spatial scales.

METHODS

Model. A simulation model was used to generate community patterns during succession. A network of 4 local communities was colonized by 4 species in the species pool and the model tracked all 16 local populations (Fig. 1). The model used modified Lotka-Volterra

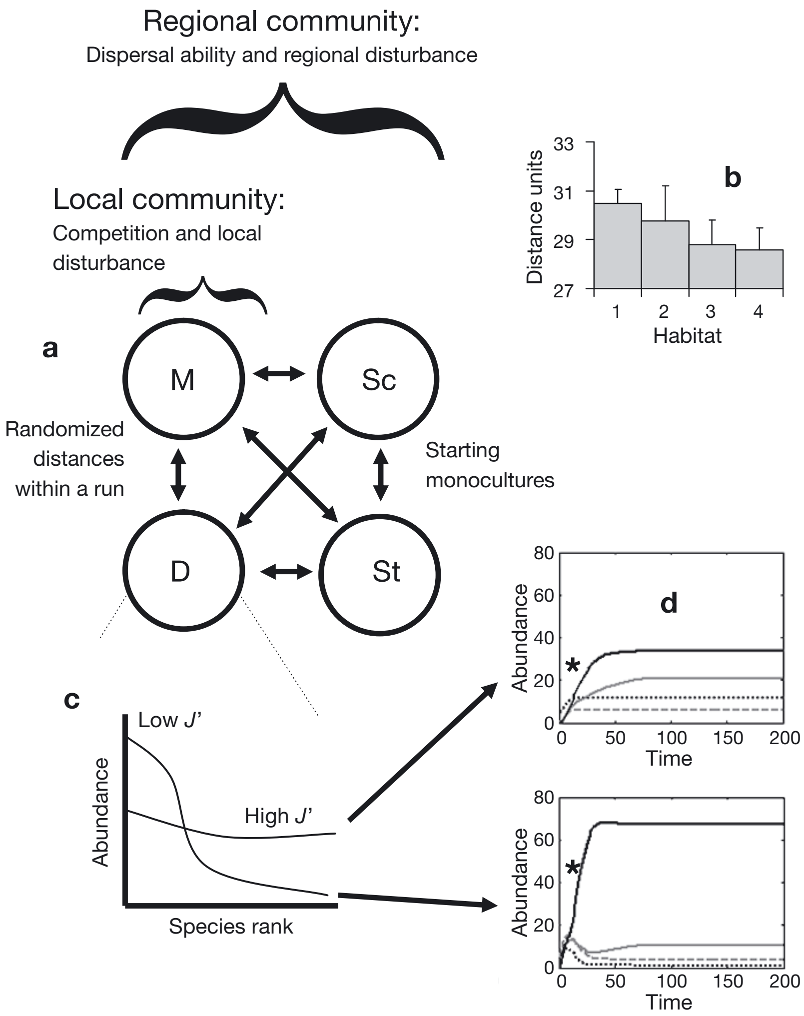

Fig. 1. Diagram of the simulation model. (a) Within each local community (large circle), a single species started as a monoculture (M: *Mytilus edulis*, Sc: *Schizoporella errata*, St: *Styela clava*, D: *Diplosoma listerianum*). These monocultures were allowed to grow and disperse to other sites, affecting diversity both within a single habitat and within the region. (b) Each locality had a predefined location, where, on average, Habitat 1 was the most isolated and Habitat 4 was the least isolated. There was a small amount of variation in distance between sites in each iteration (error bars represent 1SE from 200 iterations); however, the starting location of each monoculture was randomized to avoid confounding effects between distance and life histories. (c) Diversity (represented as evenness, J') would be low if a single species dominated, or would be high if species had similar abundance levels. (d) Abundance–time plots where each curve is a different species. Asterisk depicts the point in time when the dominant species at each locality showed maximum population growth rate during each simulation. Evenness was calculated for this point in time to understand the state of the community in terms of diversity when a species was set to dominate a habitat

equations, in which species were affected by density dependence and shared a local carrying capacity K (set at 100 ind.). The system was spatially explicit, with distances between habitats being defined at the start of each iteration. A transition matrix (T, Appendix 1) was used to generate population dynamics for 4 species i in 4 communities j. Each cell within T was defined by the birth rate of species i (b_i) and the dispersal rate (d_i) weighted by the distance between community j and every other community:

$$T_{ij} = b_i - [\, b_i \times d_i \,/\, \Sigma \text{ distances to } j\,] \tag{1}$$

where distance is a positive integer with a ceiling of 60 (e.g. distance between j and j = 1, and values would increase to represent increasing distances). For example, a population with a high dispersal rate would be able to seed far away habitats but would have a relatively low self-seeding ability. Therefore, dispersal ability is spatially explicit and the distance to the source population affects the arrival of propagules at a novel habitat. The spatial layout among habitats was maintained constant (e.g. Habitat 1 was always the most isolated, Fig. 1). However, in every iteration, the actual distance varied slightly (up to 5%), as well as the starting location of each species (i.e. the most isolated species was not always the most isolated) among iterations. This approach provided variability that could affect connectivity and prevented site effects where the results obtained could be due to the location of a particular habitat and not due to the species' life histories.

We simulated 4 species and 4 habitats, where the vector N contained each species' population in each habitat (i.e. 16 cells). This population-explicit approach allowed us to keep track of immigration and emigration effects through the T matrix (Appendix 1). Simple matrix multiplication allowed us to simulate changes in each habitat as a function of both within and among habitat influences:

$$N_{ij}(t{+}1) = N_{ij}(t) + T_{ij} \times N_{ij}(t)\,((K - N_{ij}(t) - \sum_{s \neq i}[N_j(t)_s \times \alpha_s])/K) \tag{2}$$

where N_{ij} is the abundance of species i in community j at time t, and $N_j(t)_s$ is the sum of species abundances in

Table 1. Life history parameters of the 4 species used in the model. 'Birth' represents the number of propagules per individual that are seeded into the larval pool. Within each time step, birth rate would be multiplied by a random number between 0 and 1 to generate random variability in propagule output, thus making *Mytilus* offspring production more variable than that of *Diplosoma*. 'Dispersal' represents the probability that any individual may be able to reach a new habitat within the next time step. 'Alpha' is the competitive ability of each species to maintain or displace individuals from a particular local habitat. 'Death' is probability of dying in the absence of predators, disturbance or competitors. Populations had a 5% probability of dying every time step; when populations were affected by 'death', 10% of the population would be removed from that locality. Thus, 'death' is a relatively small event (0.05 × 0.1) affecting adult individuals of a population. See Fig. 1 for full species names

	Birth	Dispersal	Alpha	Death
Mytilus	100	0.8	0.2	0.05
Styela	50	0.5	0.2	0.05
Schizoporella	5	0.3	0.6	0.05
Diplosoma	1	0.1	0.8	0.05

community j excluding species i. Interspecific competition, α_s, was defined as a vector where each species s ($s \neq i$) had a different value (Table 1). Competition affected N_{ij} depending on the competitive strength and abundance of coexisting species; there was no explicit intraspecific competition taking place in the model. Mortality, m_i, occurred before the next time step (i.e. affected established individuals). Every local population had a 5% chance of being affected by death, and if death occurred, 10% of the population would be removed (Table 1). Therefore, the steps of the model were: (1) production of propagules within each population, (2) dispersal to different habitats depending on their dispersal ability, (3) recruitment depending on the space available, and (4) disturbance (if present) followed by random mortality before the next time step. Mortality was random, with the same rate being used for all species. Our focus was on added mortality resulting from disturbance and its effects on the community. Abundances would never become negative, as the model would convert such values to zero.

Each run of the model started with monocultures of the 4 species (set at 5 ind. species^{-1}) in each local community (starting at 5% of the local carrying capacity). Simulations were followed for 200 time steps, which was enough time to observe changes in community composition and for any single species to achieve dominance in any of the sites. As a general reference, each local community can be assumed to inhabit ~25 m^2 where individuals present can certainly exert competitive dominance and export offspring (e.g. Osman 1977, Petraitis et al. 2003). Conversely, the regional scale can be assumed to represent an area of ~3000 km^2 where localized disturbances can vary within the region, but all sites would be subjected to a larger regional disturbance. We can assume that every 4 time steps constitutes a year; however, the model is designed for generality aiming to understand dominance patterns by sessile species with different life histories (Levins 1966). Along the same lines of generality, the 4 modeled species fell on a gradient of birth rates and competitive ability representing the dominant species of each of the 4 states (Table 1). The model was written in MATLAB (Mathworks). An earlier version of the model was presented at the ICES annual conference (unpubl.; available at www.ices.dk/products/AnnualRep/ASCproceedings/2007/Annual%20Science%20Conference%202007/CM-2007/A/A0207.pdf).

Long Island Sound species simulation. For the models, we chose 4 species, each representing 1 of the 4 threshold community states for fouling communities in eastern Long Island Sound (Osman et al. 2010): (1) *Mytilus edulis* for the mussel-dominated state, (2) the bryozoan *Schizoporella errata* for the native community state, (3) the solitary ascidian *Styela clava* for the invasive ascidian state, and (4) the colonial ascidian *Diplosoma listerianum* for the *Diplosoma*-dominated state. We used known life histories (see Osman et al. 2010) to parameterize each species in the model to reflect relative (but not absolute) differences in their life histories as well as life histories of other species in the community they each represent. Based on these hypothesized differences in model variables, we were interested in addressing how regional and local disturbance affect dominance patterns in systems analogous to shallow-water benthic communities. Species were defined by dispersal ability, birth rate, mortality rate, and competitive ability (Table 1). These life history parameters provide a typical range along a gradient of dispersal ability and competitive ability, similar to observed competition–colonization tradeoffs (e.g. Yu & Wilson 2001). First, the mussel (*M. edulis*) represented the mussel–alga community. It was the best disperser in the model given that it produces a large number of larvae that can remain in the water column for 15 to 30 d (Newell 1989) but have little chance of recruiting back into the parent population. Its competitive ability is modest in that mussels do not really overgrow any of the other species (although they have the potential to maintain space because they are long-lived), and they suffer high mortality from predators and storms. The potentially long-lived (up to 20 yr, Newell 1989) and slow growing mussel therefore shows the lowest population growth rate of the 4 species.

Secondly, *Schizoporella errata*, a locally dominant encrusting bryozoan represented the bryozoan-dominated native community. This species has short-lived planktonic larvae that generally recruit in minutes to hours (e.g. Ryland 1970, Watts & Thorpe 2006). Because of its potential to recruit back into a local population and its relatively fast colony growth rate, it shows a relatively high population growth rate.

The solitary ascidian *Styela clava* represented the invasive ascidian community (Berman et al. 1992). This species has external fertilization, producing larvae that develop and recruit in <24 h. Thus, it disperses more broadly than the bryozoan and has less ability to recruit back into local populations. Its competitive ability is similar to that of mussels as it cannot overgrow other species, but it can hold on to space. It appears to live for 1 to 2 yr but is subject to high recruit mortality. Its population growth rate was represented as intermediate between those of the mussel and the bryozoan.

Finally, the colonial ascidian *Diplosoma listerianum* represented the 4th community state, where it is the sole dominant species (e.g. Harris & Tyrrell 2001, Altman & Whitlatch 2007), particularly following warm winters (mean winter temperatures <4°C inhibit recruitment, Stachowicz et al. 2002). It has short-lived larvae that often recruit minutes after release and thus has a high probability of recruiting back into a local population. Colonies also have the highest growth rate and these combine to give it the highest local population growth rate. It is also the superior competitor that is able to overgrow each of the other species. Predation on new recruits and relatively short-lived adult colonies affect its mortality rate.

Questions tested. ***What are the effects of local and regional disturbances on species dominance patterns?*** In order to test the effects of disturbance at different spatial scales on dominance events, we used 3 different scenarios with the model. First, we ran the population dynamics model without any disturbance events. Then we simulated disturbance occurring at the scale of the region, e.g. affecting all 4 habitats (Fig. 1) at the same time. Every 4 time steps, all populations would suffer 70% mortality. Finally, local disturbance occurred at the same frequency as regional disturbance, i.e. every 4 time steps, and a single habitat was affected (the selection of the habitat was random every time). All of the species present in that habitat were affected by the disturbance, suffering 70% mortality. These disturbance rates were chosen because they were sufficient to create variability without inducing chaotic population fluctuations.

What are the effects of dominant species on local and regional diversity? We wanted to examine how community structure affected dominance (abundance > 50% of carrying capacity) and extinction events for each life history type. At the end of the simulations, the model would identify species that dominated each habitat and it would then backtrack events through time to identify large changes in population dynamics. For any given population that dominated a habitat, we recorded the state of the community when the greatest population growth occurred between 2 time steps by calculating an evenness index (Fig. 1). The greatest population growth rates tended to occur within the first half of the time steps if disturbance was not present; however, when disturbance was present, such positions would vary in time among simulations, reflecting stochastic localized extinction events. When a population went extinct, we calculated the evenness of the community when the lowest population growth occurred. This was used to represent the state of a community when a species was driven to extinction; this approach helped in determining whether such extinction events were driven by dominant species (low diversity), by a large number of equally abundant species (high diversity), or whether extinction was just a function of disturbance and was independent of the state of the community.

RESULTS

Effects of local and regional disturbances on dominance patterns

In the simulations without disturbance, the 4 sessile species showed few dominance events (Fig. 2a), and species tended to reach similar abundance levels in most runs. In this scenario, neither the starting monoculture (Fig. 1) nor the type of life history affected the resulting dominance pattern. All 4 species were more dominant at sites where they started as monocultures (a reflection of priority effects), but this was not that much greater than switches to dominance by other species (Fig. 2a). The overriding outcome was the lack of dominance as well as little resilience. In the local disturbance scenario, the original monocultures persisted (Fig. 2b) and resisted dominance from other species, contributing to resilience of local dominants. The only exception was the original *Mytilus edulis* habitat, which was dominated by the other 3 species in ~40% of the model runs. When regional disturbance events occurred (Fig. 2c), the relative frequencies were similar to no-disturbance simulations, except that there was a large increase in the proportion of runs exhibiting dominance events. There was no clear pattern between life histories and the proportion of runs where each species dominated. Species varied in the amount of time (from 9 to 50 time steps) they required to achieve dominance, with the broadcast spawning spe-

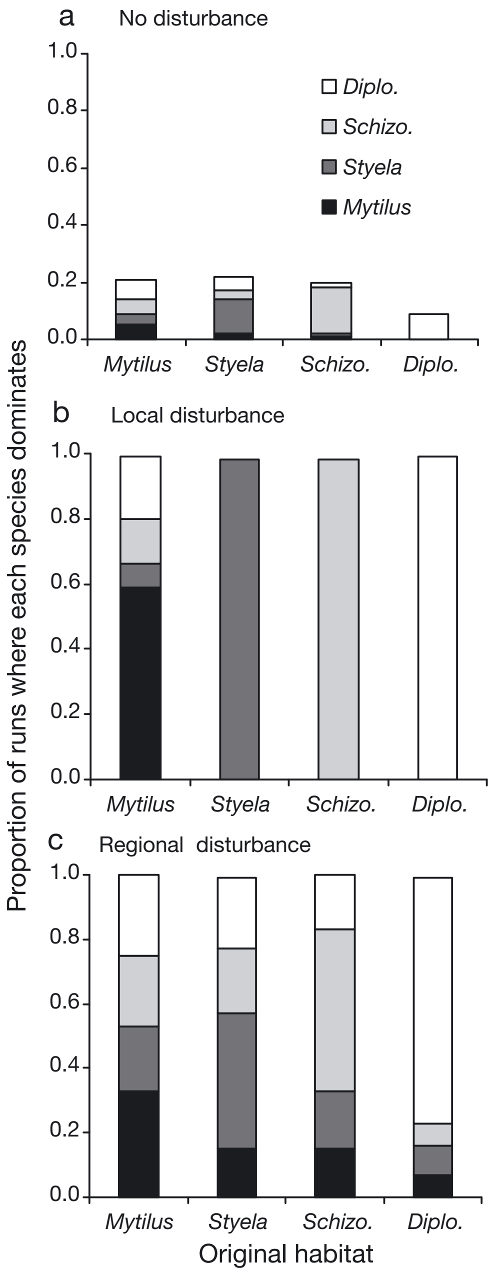

Fig. 2. Frequency of dominance events (>50 % abundance) for each of the 4 simulated species partitioned by habitat. Simulations started with a monoculture at low abundance in each of the 4 habitats (original habitat, *x*-axis). A bar represents the proportion of runs that had a dominance event for each species. (a) Under no disturbance conditions, all 4 species have few dominance events; in the majority of the runs, species are able to coexist at similar abundance levels; further, only *Diplosoma* is able to dominate original *Diplosoma* habitat. (b) Under local disturbance events, the initial monocultures persist, not allowing other species to exert dominance, except for the habitat with original mussel monocultures, where other species are able to dominate. (c) Under regional disturbance events, species show a large number of dominance events, with broadcast spawners being less dominant than brooders. There is little predictability as to which species dominates each habitat. See Fig. 1 for full species names

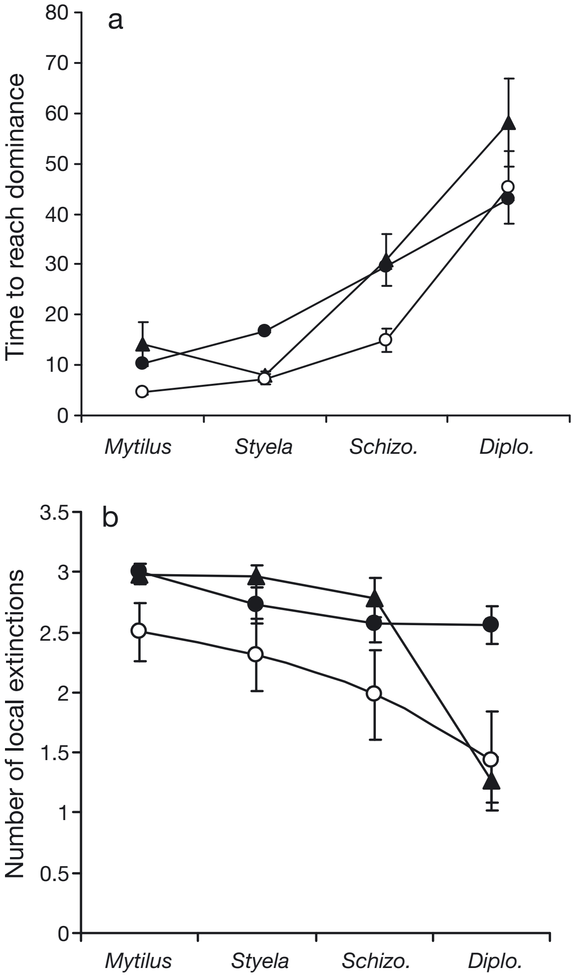

Fig. 3. (a) Average number of time steps to reach dominance, and (b) average number of local extinctions shown by each of the 4 species, under different disturbance scenarios: no disturbance (▲), regional disturbance (○), and local disturbance (●). Values are means of 1000 runs, and error bars represent ±1 SE. See Fig. 1 for full species names

cies (*M. edulis*) being the fastest to achieve dominance and the brooding (*Diplosoma listerianum*) species being the slowest (Fig. 3a). This behavior was observed regardless of the disturbance level.

The number of local extinctions varied among the disturbance levels. In simulations without disturbance, *Diplosoma listerianum*—a species with limited dispersal but high competitive ability—had the least number of extinctions, while the other species suffered a large number of extinction events (Fig. 3b). With regional disturbance, there was a gradual decrease in extinctions with a decrease in dispersal ability, and *D. listerianum* had the same number of extinctions as in the no-disturbance scenario. With local disturbance however, all 4 species had a similar number of extinctions, regardless of life history.

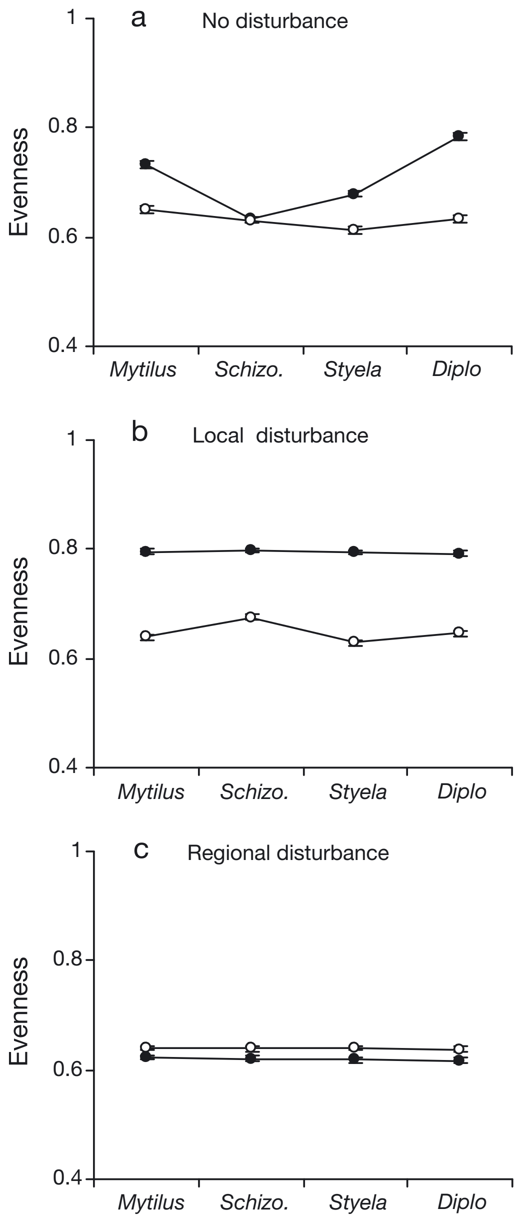

Fig. 4. Community structure (represented as evenness) at the time when a species started becoming dominant (●) or started becoming extinct (○) in the 3 scenarios. Values are means of 1000 runs. See Fig. 1 for full species names

Effect of dominant species on local and regional diversity

Without disturbance (Fig. 4a) and with local disturbance (Fig. 4b), community evenness was generally much higher at the time of dominance than when extinction occurred. The only exception was for *Styela* under conditions of no disturbance. During regional disturbance events (Fig. 4c), evenness did not differ between times of extinction and times of dominance. Evenness that led to extinction was fairly consistent across species and disturbance conditions, but evenness that led to dominance varied (Fig. 4). This suggests that regional disturbance has an overall negative effect on evenness, while local disturbance may actually increase evenness.

DISCUSSION

Sessile marine species can rapidly increase in population growth and generate dominance, which may exclude other sessile species (e.g. Paine & Levin 1981, Keough 1984). Our simulations show that priority effects can take place with the typically dominant species of eastern Long Island Sound even when these species have differing life histories. However, in this system there are a large number of dominant species in different sites, which are mixed with a number of less abundant species (Osman et al. 2010). Therefore, priority effects are not creating competitive exclusion, and our modeling suggests that for sessile marine species, the combined effects of dispersal ability and disturbance can allow the maintenance of diversity on a regional scale regardless of the identity of locally dominant species.

Priority effects were only present when the system experienced localized disturbance regimes, such as predation. Predators of settling larvae and post-settlement life stages of sessile species can limit recruitment to localized patches of habitats, as has been shown experimentally with ascidian recruits (Osman &Whitlatch 2004). Predation can limit a species' distribution, and can drive prey to local extinction; in the simulations, local disturbance was not able to exclude species from the regional species pool. On the contrary, it seems that predation or localized disturbance can enhance priority effects in benthic communities (Fig. 2) and increase overall diversity (Fig. 4). Houseman et al. (2008) showed that variance in community composition was greatest when disturbance and constant resource availability were present in plant communities, and Bull & Bonsall (2010) found that localized predation in metapopulations can reduce regional extinction. Their results suggest that such variance gave rise to different dominance patterns and in turn different community states. Similarly, under large-scale disturbance events that affect eastern Long Island Sound, such as ice scouring or fluctuating winter temperatures, species still exhibit local dominance but it is harder to predict which species will dominate locally. In the Gulf of Maine, there is a strong interaction between top-down and bottom-up effects driving benthic communities (Witman et al. 2003). A large mussel recruitment event led to a 15-yr shift in species composition via changes in local trophic interactions; however, at broader spatial scales, species composition was highly variable due to the changes in bottom-up and top-down stressors. Similarly, in our model, priority effects were no longer present in the system given the random dominance patterns driven by regional disturbances. Therefore, local disturbance produces high resilience through localized recruitment, but maintains system-wide evenness (Fig. 2), whereas regional disturbance reduces evenness and creates less resilience in the system.

The 4 different life histories that we used in the model represent a range of local propagule retention that can be observed in many sessile benthic communities (e.g. Osman 1977, Keough 1984, Hunt & Scheibling 1997, Munguia 2004). It is interesting to note that the extremes of this range of life histories varied in their response to local and regional disturbance. These 2 life history extremes seem to resemble local patch dynamics (Leibold et al. 2004), a potential scenario also found in homogenous habitats where there are tradeoffs in species' competitive and dispersal abilities. These tradeoffs allow for coexistence at regional scales, but tend to create low diversity levels at local scales (e.g. Chesson 2000, Yu & Wilson 2001, Shurin et al. 2004). Relative to *Diplosoma listorianum*, *Mytilus edulis* tended to be less dominant at local scales at the end of the simulation (Fig. 2); however, it achieved dominance faster (Fig. 4a) and was more susceptible to local extinctions regardless of the disturbance scenario (Fig. 3b), suggesting that it was being outcompeted. Mussels tend to be the competitive dominant in most systems where they occur on the intertidal and are not subjected to high levels of predation (e.g. Paine & Levin 1981); however, in the Long Island Sound as in other parts of New England, this species shows episodic recruitment events that are reflected in large variations in abundance (Witman et al. 2003). Extinction rates are linked to the lack of local recruitment (Fig. 3); lecithotrophic species seem to be affected by local disturbance since local disturbance may allow the maintenance of priority effects by suppressing recruitment of the best competitors (Fig. 1; e.g. Connell 1978).

The state of the community is correlated with dominance and extinction patterns among the different life histories. When a particular species shows maximum positive growth, communities tend to have a more even distribution of individuals among the species present than when a species goes locally extinct. This suggests that the dominant species does not have an immediate negative effect on the community; rather, species are still present and there is no exclusion of less abundant species when habitats are homogenous. Interestingly, under the no-disturbance scenario, communities had different evenness during the beginning of a dominance event, where the extreme life histories showed the highest evenness values. Petraitis et al. (2003) showed similar results from empirical data, where species occurrence (barnacles, mussels and predatory snails) was scale dependent. This variation in abundance is analogous to our variation in dominance patterns, and reflects the complex interactions between stressors that drive community patterns observed in terrestrial systems (Houseman et al. 2008). In intertidal communities, barnacle and mussel recruit survivorship varied when disturbance was applied in the intertidal through clearings of different sizes; but more importantly, snail densities were not affected by disturbance size (Petraitis et al. 2003). In our simulations, under regional and local disturbance regimes, differences in evenness among life histories disappeared; however, the evenness level varied in magnitude between extinction and dominance events for each species. Such patterns suggest that regional disturbance provides a larger amount of stochastic variation and minimizes priority effects regardless of life history, while local disturbance generates a broader gap in the state of the community between dominance and extinction events. If a particular species dominates a habitat, it shows the greatest population growth when the community has an even distribution of individuals across the species present. For example, in small reef communities where disturbance was not present within a region, each local community exhibited strong priority effects (Munguia 2004). Our results suggest that local disturbance contributes to both the maintenance and resilience of local threshold states, which in turn affects regional diversity (e.g. Folke et al. 2004). Alternatively, regional disturbance events in our model increase local dominance at the expense of diversity, suggesting a more negative impact including possible extinctions.

Ecosystem management and species invasions under priority effects

If life histories are correlated with dominance patterns, then refocusing conservation strategies on life histories and dominance could prove more fruitful than trying to sustain individual species' populations. Coastal ecosystems are under constant change, either through anthropogenic modifications of the landscape (Armaitiene et al. 2007), seasonal events such as changes in temperature or storms (Paperno et al. 2006), or increasing species arrivals to the region (Silliman & Bertness 2004). Given the large variation in life history traits present in a given ecosystem, it may be more feasible to consider managing life histories rather than particular species or aiming for specific diversity levels. This simple simulation showed the synergistic interaction between the scale of disturbance and an array of life histories in giving rise to priority effects of sessile species. Given the correlation between life histories and dominance patterns, we suggest that thresholds may be used in conservation efforts within localized habitats. Anticipating unwanted changes, or buffering the effects of such changes, regardless of the mechanistic source, could be a management strategy focusing on such thresholds (Hughes et al. 2005).

For example, management strategies can influence localized disturbance events, whether it is the closure of a particular area to fishing, allowing predators to increase in numbers, or active removal of particular target species (Pinnegar et al. 2000, Micheli et al. 2005). Pinnegar et al. (2000) show how localized management (particularly closures and regulation of artisanal fisheries) can produce shifts in species composition in hard-bottom habitats around the world. However, managing large regional disturbance events seems more difficult and there seems to be less data available. In our simulations, regional disturbance was a periodic event; if we can monitor such periodicity in natural systems, then we can maximize efforts at local scales, managing source populations for example, that would produce enough propagules to seed the rest of the region in between disturbance events. Habitat management focusing on local communities (which can equate to native or key species in a given region) may be the best approach even with regional disturbances such as climate change. This approach might also be easiest for management for 2 reasons: (1) dominant species, groups or communities can be set as identifiable goals, (2) while potential stressors can be easily identified (Garrabou et al. 1998, Silliman & Bertness 2004, Armaitiene et al. 2007). Finally, if maintaining diversity of a regional system is the desired goal, then management should focus on maintaining communities with different dominant species or evenness in different sites. However, it is important to note that the dominance events in our model may not be related to the more rigorous mechanisms associated with alternative states theory; clear identification of patterns and processes are required when managing thresholds (Folke et al. 2004, Andersen et al. 2009).

Here we have shown that priority effects act in conjunction with the scale at which disturbance regimes may be present in an ecosystem and can affect community structure of sessile benthic species. When resources are limiting, such as hard substrate for benthic species, local dominance tends to occur, excluding other species and driving diversity down. However, while a dominance event may occur more frequently under local disturbance, these dominance events arise from scramble competition (e.g. Sousa 1980) at the local scale, with all species present in a community having relatively equal abundance levels. The rate to achieve dominance tends to be slower with brooding species, and this should be considered when attempting to manage novel invasive species such as *Diplosoma listerianum* and *Didemnum* sp. that have recently appeared in the Long Island Sound (Osman & Whitlatch 2007).

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Appendix 1. Setup of the transition matrix, *T*

$$\underset{\textbf{16 x 16 matrix}}{\boldsymbol{T}} = \left|\begin{array}{cccccccccccccccc}
a1 & a2 & a3 & a4 & 0\ldots &&&&&&&&&&& \\
b1 & b2 & b3 & b4 & 0\ldots &&&&&&&&&&& \\
c1 & c2 & c3 & c4 & 0\ldots &&&&&&&&&&& \\
d1 & d2 & d3 & d4 & 0\ldots &&&&&&&&&&& \\
0 & 0 & 0 & 0 & a1 & a2 & a3 & a4 & 0\ldots &&&&&&& \\
. & . & . & . & b1 & b2 & b3 & b4 & 0\ldots &&&&&&& \\
. & . & . & . & c1 & c2 & c3 & c4 & 0\ldots &&&&&&& \\
. & . & . & . & d1 & d2 & d3 & d4 & 0\ldots &&&&&&& \\
&&&&&&&& a1 & a2 & a3 & a4 & 0\ldots &&& \\
&&&&&&&& b1 & b2 & b3 & b4 & 0\ldots &&& \\
&&&&&&&& c1 & c2 & c3 & c4 & 0\ldots &&& \\
&&&&&&&& d1 & d2 & d3 & d4 & 0\ldots &&& \\
&&&&&&&&&&&& a1 & a2 & a3 & a4 \\
&&&&&&&&&&&& b1 & b2 & b3 & b4 \\
&&&&&&&&&&&& c1 & c2 & c3 & c4 \\
&&&&&&&&&&&& d1 & d2 & d3 & d4
\end{array}\right| \qquad \underset{\textbf{16 x 1 vector}}{\boldsymbol{N}} = \left|\begin{array}{c}
A1 \\ A2 \\ A3 \\ A4 \\ B1 \\ B2 \\ B3 \\ B4 \\ C1 \\ C2 \\ C3 \\ C4 \\ D1 \\ D2 \\ D3 \\ D4
\end{array}\right| \begin{array}{c}
\text{Species 1 Community 1} \\ . \\ . \\ . \\ . \\ . \\ . \\ . \\ . \\ . \\ . \\ . \\ . \\ . \\ \\ \text{Species 4 Community 4}
\end{array}$$

The transition matrix is expressed as a series of non-zero matrices along the diagonal. Each row is unique for a particular species (letters) because it incorporates that species'dispersal ability, while each element within that row is unique for a particular habitat (numbers) given its differences in dispersal ability

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Linking fisheries, trophic interactions and climate: threshold dynamics drive herring *Clupea harengus* growth in the central Baltic Sea

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ABSTRACT: How multiple stressors influence fish stock dynamics is a crucial question in ecology in general and in fisheries science in particular. Using time-series covering a 30 yr period, we show that the body growth of the central Baltic Sea herring *Clupea harengus*, both in terms of condition and weight-at-age (WAA), has shifted from being mainly driven by hydro-climatic forces to an inter-specific density-dependent control. The shift in the mechanisms of regulation of herring growth is triggered by the abundance of sprat, the main food competitor for herring. Abundances of sprat above the threshold of ~18×10^{10} ind. decouple herring growth from hydro-climatic factors (i.e. salinity), and become the main driver of herring growth variations. At high sprat densities, herring growth is considerably lower than at low sprat levels, regardless of the salinity conditions, indicative of hysteresis in the response of herring growth to salinity changes. The threshold dynamic accurately explains the changes in herring growth during the past 3 decades and in turn contributes to elucidate the parallel drastic drop in herring spawning stock biomass. Studying the interplay between different stressors can provide fundamental information for the management of exploited resources. The management of the central Baltic herring stock should be adaptive and take into consideration the dual response of herring growth to hydro-climatic forces and food-web structure for a sound ecosystem approach to fisheries.

KEY WORDS: Condition · Weight-at-age · WAA · Ecological threshold · Inter-specific density-dependence · Hydro-climate · Herring · Sprat · Ecosystem-based fisheries management · Alternative dynamics

INTRODUCTION

Disentangling the combined effects of food-web structure and trophic interactions, climate changes and anthropogenic pressures (e.g. fishing) on population dynamics is of central importance for the understanding of ecosystem functioning, and thus the management of exploited resources. The quantification of the biotic and climatic effects on ecosystem dynamics, however, is often complicated by nonlinear relationships or discontinuous responses of populations and communities to the driving forces (Scheffer & Carpenter 2003).

Herring *Clupea harengus* is a key species in the Baltic Sea ecosystem, as important prey for cod *Gadus morhua* (Bagge 1989) and a plankton-zoobenthos feeder (Casini et al. 2004). Moreover, herring is one of the most important commercial species in the area, heavily exploited by the 9 countries surrounding the Baltic Sea (EC 2008).

Since the late 1970s, the central Baltic herring stock has undergone a marked decline in stock size. How-

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ever, the drop in biomass has been more noticeable than the decrease in abundance (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m413p241_supp.pdf), which is partly explained by a parallel drastic decline in mean body weight (ICES 2009a). The decrease in individual herring weight was formerly hypothesised as a major effect of either climate-related hydrographic changes (i.e. decrease in salinity, Rönnkönen et al. 2004) or increased competition with the enlarged sprat *Sprattus sprattus* population (Cardinale & Arrhenius 2000), both negatively affecting the main planktonic food for herring.

In the Baltic Sea it has been shown that both top-down and bottom-up controls (including hydro-climatic forces) can act simultaneously on different trophic levels (e.g. Alheit et al. 2005, Casini et al. 2008), but also that their relative strength can vary over time as a consequence of changes in the food-web structure (Casini et al. 2009). Specifically, zooplankton dynamics in the offshore areas is mainly regulated by hydrological forcing when the stock size of sprat is below a specific abundance threshold, whereas it is driven by sprat predation when the abundance of this major planktivore exceeds such a threshold (Casini et al. 2009). Similar dual ways of ecosystem functioning and trophic control have been also found for different species in other aquatic (Litzow & Ciannelli 2007, Stige et al. 2009) as well as terrestrial (e.g. Wilmers et al. 2006) systems.

In this study we extend the concept of ‘threshold dynamics’ in the Baltic Sea from Casini et al. (2009) a step further, to investigate the body growth of the central Baltic herring. We show that the 2 apparently contrasting hypotheses of herring growth regulation (hydro-climatic factors and inter-specific density-dependence) are not mutually exclusive, providing evidence that the strength of the 2 forces on herring growth varies depending on food-web structure and interaction strength between competing species.

MATERIALS AND METHODS

Time-series of Baltic sprat stock abundance was retrieved from stock assessment official reports (ICES 2009a). Recently compiled herring biological data (individual total length, total weight and age) covering the period 1978 to 2008 were collected during the autumn international acoustic survey (ICES 2009b) by Latvia and Sweden in offshore areas of the central Baltic Sea (the Gotland Basin, ICES Subdivision 28, Fig. 1).

For the estimation of condition we used the double-logarithmic length-weight regression, in line with previous studies on clupeid growth in the Baltic Sea (e.g. Möllmann et al. 2003, Casini et al. 2006). Condition was estimated from the year-specific ln(L)-ln(W) regression as the weight in grams at the length of 180 mm, which corresponded to the mean length of herring in our dataset.

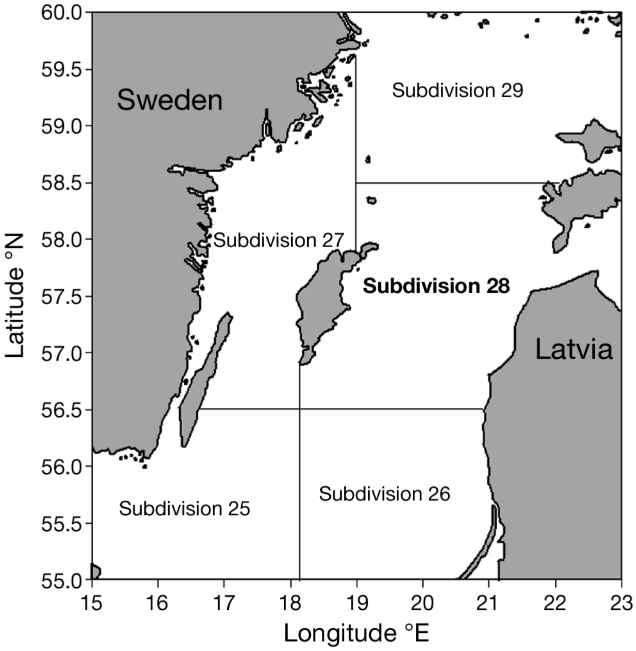

Fig. 1. Central Baltic Sea: ICES Subdivision 28 was the area of fish sampling

Fish weight-at-age (WAA) is theoretically a result of forces acting over subsequent years from hatching to the date of collection. However, the trends in WAA were very similar among all age-classes, with simultaneous inter-annual variations (Fig. 2). This strongly suggests that changes in external conditions affect similarly the whole population at the same time. Therefore, for the purpose of our analyses we averaged the WAA of age 2+ fish, which represent the part of the population that will spawn in the following spring (i.e. at age 3+). At age 3+, central Baltic herring are fully reproductive (ICES 2009a) and therefore their mean body weight may have an effect on the stock recruitment success (Cardinale et al. 2009). Fish older than 5 yr were excluded since in some years they were scarcely represented in our samples (<10 ind.).

Condition and WAA (hereafter referred as growth parameters) were used as indicators of the biological state of the fish at each specific year, and not as proxies for developmental/ontogenetic processes for which growth rate in length would have been more indicative (e.g. Winters & Wheeler 1994).

To account for potential differences between countries in biological parameters (length and weight

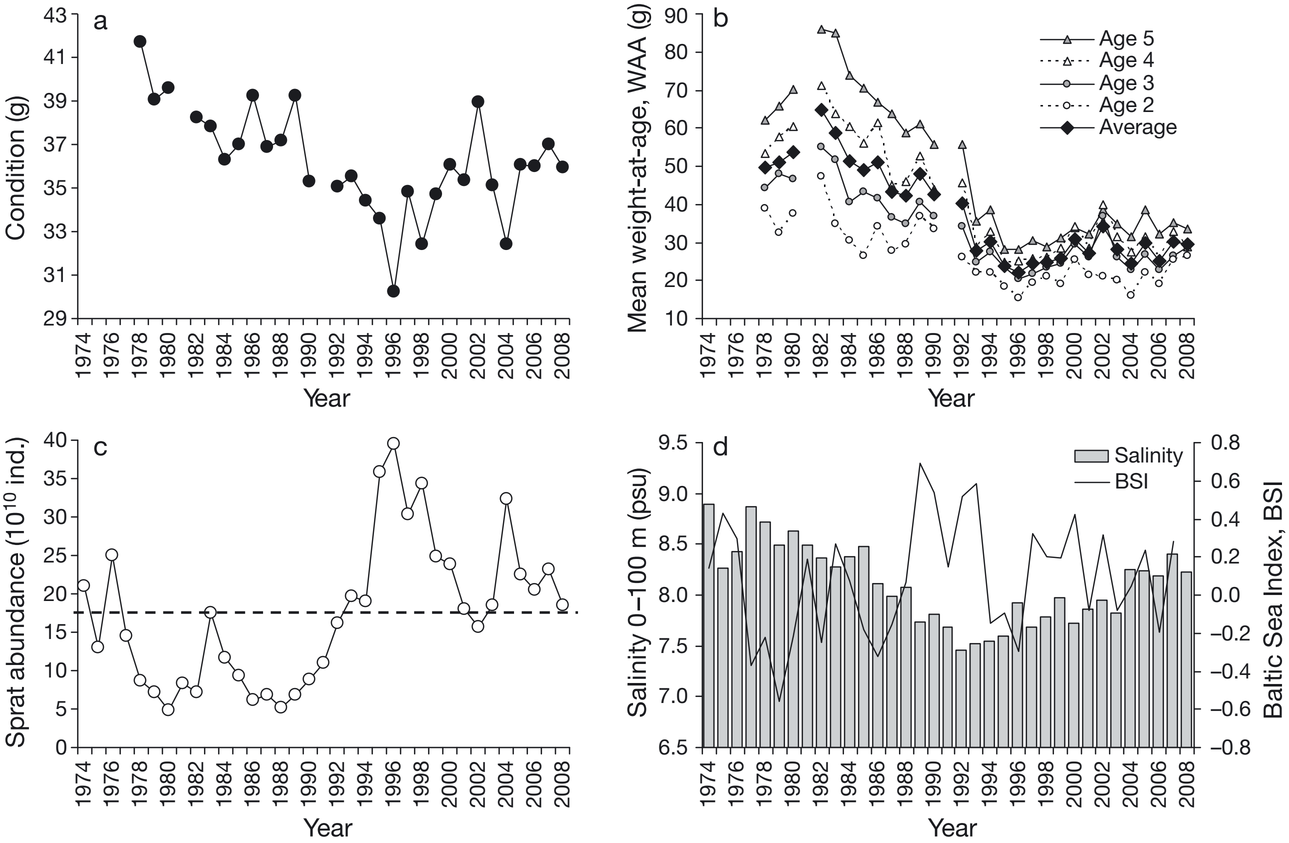

Fig. 2. Temporal trends of parameters used in the analyses: (a) herring condition, (b) herring weight-at-age (WAA), (c) sprat stock abundance, (d) salinity between 0 and 100 m, and Baltic Sea Index, BSI (a proxy for the regional climate)

measurements as well as age estimations), and in turn growth calculation, a Generalized Linear Model (GLM) was used to predict the year effect on herring condition and WAA after scaling out the country effect. Condition data were normally distributed and, thus, the normal distribution was used in the GLM. For WAA, on the other hand, a Gamma distribution was preferred to account for the moderate skewness in the distribution of the data.

In the analyses we used growth data from ICES Subdivision 28, because this area was used in previous studies investigating herring growth (e.g. Möllmann et al. 2003, Casini et al. 2006) and ecosystem dynamics (Casini et al. 2008, 2009) and, therefore, constitutes a valid standpoint for comparison. Moreover, Subdivision 28 corresponds to the geographical centre of distribution of the herring and sprat stocks used in this study.

Salinity data for this area were provided by the Swedish Meteorological and Hydrological Institute (SMHI, freely available at www.smhi.se). The average of salinity in May and August integrated between 0 and 100 m depth (samples at surface and at 10 m depth intervals) was used in the analyses. Spring and summer are the main feeding seasons for both herring and sprat in the central Baltic Sea (e.g. Szypuła et al. 1997), and spring is also the main reproduction period for the copepod *Pseudocalanus* spp., one of the main prey for both fish species (Möllmann et al. 2003, Casini et al. 2004). Therefore, spring-summer can be considered a critical period determining fish condition and WAA later in early autumn (Casini et al. 2006). Salinity is related to the Baltic Sea Index (BSI), a regional climate proxy closely coupled with the NAO (North Atlantic Oscillation). BSI is defined as the difference of normalized sea level pressure anomalies between Szczecin (Poland) and Oslo (Norway) (Lehmann et al. 2002). Positive values of both indices correspond to a dominance of westerlies over the Baltic and increased rainfall and runoff, whereas a negative index corresponds to easterlies (Hänninen et al. 2000, Lehmann et al. 2002).

The relationship between herring growth (in terms of condition and WAA) and the predictors was first analysed with Generalized Additive Models (GAMs). The following additive formulation was used:

$$y = a + s_1(V_1) + \ldots + s_n(V_n) + \varepsilon \qquad (1)$$

where a is the intercept, s the thin plate smoothing spline function (Wood 2003), $V_1 \ldots V_n$ the predictors and ε the random error. As predictors, we used sprat stock abundance and salinity. These parameters were chosen because of their acknowledged importance for herring growth in the Baltic Sea, acting on the main planktonic prey for herring (Möllmann et al. 2003, Rönkkönen et al. 2004, Casini et al. 2006). We did not test for intra-specific density-dependence (i.e. effect of herring abundance on herring growth) as no evidence has been found for such relationship (Rönkkönen et al. 2004, Casini et al. 2006). The lack of intra-specific density-dependence is also supported by the absence of a negative relation between herring abundance and zooplankton in the offshore areas of the central Baltic Sea (Casini et al. 2008), that could be due to the omnivorous nature of herring which also feed on nektobenthos (Casini et al. 2004), reducing the interaction strength with zooplankton. Unfortunately, nektobenthos time-series covering our study period are not available for this area and could not be used in the growth models. The numerical dominance of sprat compared to herring in a large part of the study period (ICES 2009a) could also partly explain the lack of detectable intra-specific density-dependence within the herring population.

Furthermore, to test for the existence of a potential 'phase transition' (Litzow & Ciannelli 2007) in the response of growth to the predictors, we applied a Threshold Generalized Additive Model (TGAM, Ciannelli et al. 2004) to condition and WAA. This kind of non-additive model can be formulated as:

$$y = a + \begin{cases} s_{1,1}(V_1) + \ldots + s_{1,n}(V_n) + \varepsilon & \text{for } V_x > t \\ s_{2,1}(V_1) + \ldots + s_{2,n}(V_n) + \varepsilon & \text{for } V_x \le t \end{cases} \qquad (2)$$

where 2 specific additive formulations are adopted for different values of the threshold variable V_x. We tested the occurrence of a threshold on sprat abundance, under the assumption that the zooplankton community in the offshore Baltic Sea is dominated by environmental variability for low abundances of sprat, while it is driven by the dynamic of this pelagic fish when its abundance is high (Casini et al. 2009).

TGAMs are an extension of non-parametric regression techniques (Hastie &Tibshirani 1990) and were chosen here for their ability to represent an abrupt change in the relationships between dependent and independent variables (i.e. a phase transition) at a specific threshold value. The threshold value was selected minimizing the Generalized Cross Validation score (GCV) of the whole model (Ciannelli et al. 2004). The searching algorithm runs the model for 100 possible threshold values between the 0.1 lower and the 0.9 upper quantiles. To evaluate the robustness of the estimated threshold, we performed a sensitivity analysis (Saltelli et al. 2000). Our objective was to test the dependency of the identified threshold value to the specific set of data and years available. We generated 1000 random replicates of the dataset, for different proportions of the original dataset. Then, a TGAM was fitted on each replicate and the corresponding threshold estimated. Residuals of the TGAMs were analysed to inspect for potential deviation from the normality assumption and other anomalies in the data or in the model fit (i.e. autocorrelation) using graphical methods (Cleveland 1993). Autocorrelation of the model residuals was examined using the autocorrelation function (ACF).

The normal distribution was used in the condition models, whereas a Gamma distribution was preferred for the WAA models due to the moderate skewness in the distribution of the data. Additive and threshold formulations were compared using the Akaike Information Criterion (AIC, Akaike 1973). To calculate the AIC for TGAMs, an extra penalty was introduced to account for the threshold parameter.

Additionally, an estimate of the significance of the threshold was obtained through a wild bootstrap approach (Mammen 1993). In this case, a null scenario of no-threshold effect was simulated reshuffling the threshold variable. Then, the same threshold model formulation was fitted and the penalized maximum log-likelihood (PML) of the model was calculated. This procedure was repeated 1000 times reshuffling the threshold variable in each bootstrap sample. In this way we obtained a reference distribution of the PML for the null scenario of no-threshold effect. Finally, the bootstrap estimate of the p-value for the threshold was calculated as the percentage of the PML values of the reference distribution for the null scenario that was larger than the original model PML.

The strength of the link between herring growth and sprat abundance (as well as salinity) in the 2 configurations identified by the TGAM was also assessed, by quantifying the probability density distribution of the correlation coefficients obtained by bootstrap resampling (Casini et al. 2009). This analysis involved a random pairwise sampling with replacement where each time-series was resampled 5000 times. The number of elements in each bootstrap sample equals the number of elements in the original dataset. The probability density distribution of the corresponding correlation coefficients was then computed using nonparametric kernel smoothing (Casini et al. 2009). In the simple linear correlation analyses, the potential occurrence of temporal autocorrelation in the growth time-series was tested in the 2 configurations using the autocorrelation function (ACF).

RESULTS

Time-series of herring condition and WAA are presented in Fig. 2a,b. Condition showed a continuous decline from the late 1970s, reaching a minimum in 1996. Thereafter, herring condition increased, although oscillating at relatively low levels. WAA showed a similar pattern, except the decline started some years later than for condition, and the increase after 1996 was not as marked as for condition. WAA trends showed a tight covariation among all age-classes, with inter-annual changes coincident for the whole population. Sprat stock was mostly at low levels between the late 1970s and the early 1990s, followed by a drastic increase that peaked in the years 1995 to 1996. Subsequently, the sprat stock has oscillated at relatively high levels (Fig. 2c). Salinity between 0 to 100 m showed a constant decrease from the 1970s to the early 1990s, followed by a steady increase, and eventually reached values almost as high as at the beginning of the time-series (Fig. 2d). Salinity was significantly correlated with the winter Baltic Sea Index ($r = -0.43$, $p = 0.012$; after correcting for temporal autocorrelation by first-order differencing, $r = -0.38$, $p = 0.028$), evidencing the strong influence of atmospheric oscillations on the hydrological processes in the Baltic Sea (Hänninen et al. 2000, Lehmann et al. 2002).

In general, both for the GAMs and TGAMs, the effect of sprat abundance on herring growth was stronger than the effect of salinity (Table 1). The 2 predictors were significant in all the models, except salinity in the GAM for WAA. Threshold models performed generally better than additive formulations both in terms of deviance explained and AIC (Table 1). However, the improvements including a threshold were more evident for the WAA model than for the condition model, which showed a weaker non-additivity in the dynamics (Table 1), as also shown by the shallower minimum in the GCV profile (see Figs. 3b & 4b). The PML calculated on the original data was smaller than the lower 5% of the PML distribution for the bootstrap under the no-threshold null hypothesis in both the condition and WAA models (Fig. S2 in the Supplement). Consequently, the thresholds identified were considered statistically significant for both growth parameters. In addition, the same significant threshold value of ~18×10^{10} sprat individuals was obtained for both the response variables (Table 1). For sprat abundances lower than the identified threshold (low-sprat configuration), salinity showed a significant positive relationship with both condition and WAA. In contrast, for sprat abundances higher than the identified threshold (high-sprat configuration), a significant negative effect of sprat on herring growth was found (Table 1, Figs. 3c,d & 4c,d). The TGAM formulation correctly captured the general pattern of herring condition along the whole time period investigated (Fig. 3a). The model performed better during the second half of the time series, tightly modelling the wide inter-annual fluctuations that characterized herring condition. The TGAM formulation well described the rapid drop in WAA observed in the mid 1990s and the following fluctuations around values almost half of those observed at the beginning of the time-series (Fig. 4a). The model underestimated 1982 to 1983 values and overestimated the peak in WAA observed in 2002. The residuals of the TGAMs did not violate the normality assumption and did not present temporal autocorrelation (Fig. S3 in the Supplement).

The sensitivity analysis showed that a decrease in the dataset size did not affect the median of the estimated threshold in the TGAMs (Fig. 5). A reduction of the dataset size down to 72% of the original size had only minor effect on the precision of the threshold estimate in the WAA model. A sensible loss in the precision of the estimate was observed only for levels <70% of the dataset size, with an asymmetric dispersion

Table 1. Generalized Additive Model (GAM) and Threshold Generalized Additive Model (TGAM) analyses. For each model, deviance explained (Dev. Expl.), Akaike Information Criterion (AIC) and no. observations (n) are given. For each predictor, effective degrees of freedom (edf) and significance value (p) are provided. For TGAMs, threshold value (t) and no. of observations above and under the threshold are also given (n(t)). WAA: weight-at-age

Model	Herring response	Threshold (t)	Dev. Expl.	AIC	n	Factors	*F*	edf	p	n (t)
GAM	Condition	–	77.3	102.07	29	Salinity	3.55	2.22	0.0295	–
						Sprat	15.13	1.72	< 0.0001	–
	WAA	–	79.0	189.90	29	Salinity	1.95	1.71	0.149	–
						Sprat	18.79	2.05	< 0.0001	–
TGAM	Condition	17.85	81.4	101.67	29	Salinity for sprat < t	5.75	2.76	0.0045	16
						Sprat for sprat ≥ t	22.14	2.82	< 0.0001	15
	WAA	17.85	88.8	173.96	29	Salinity for sprat < t	9.86	1.00	0.0044	16
						Sprat for sprat ≥ t	47.33	2.95	< 0.0001	15

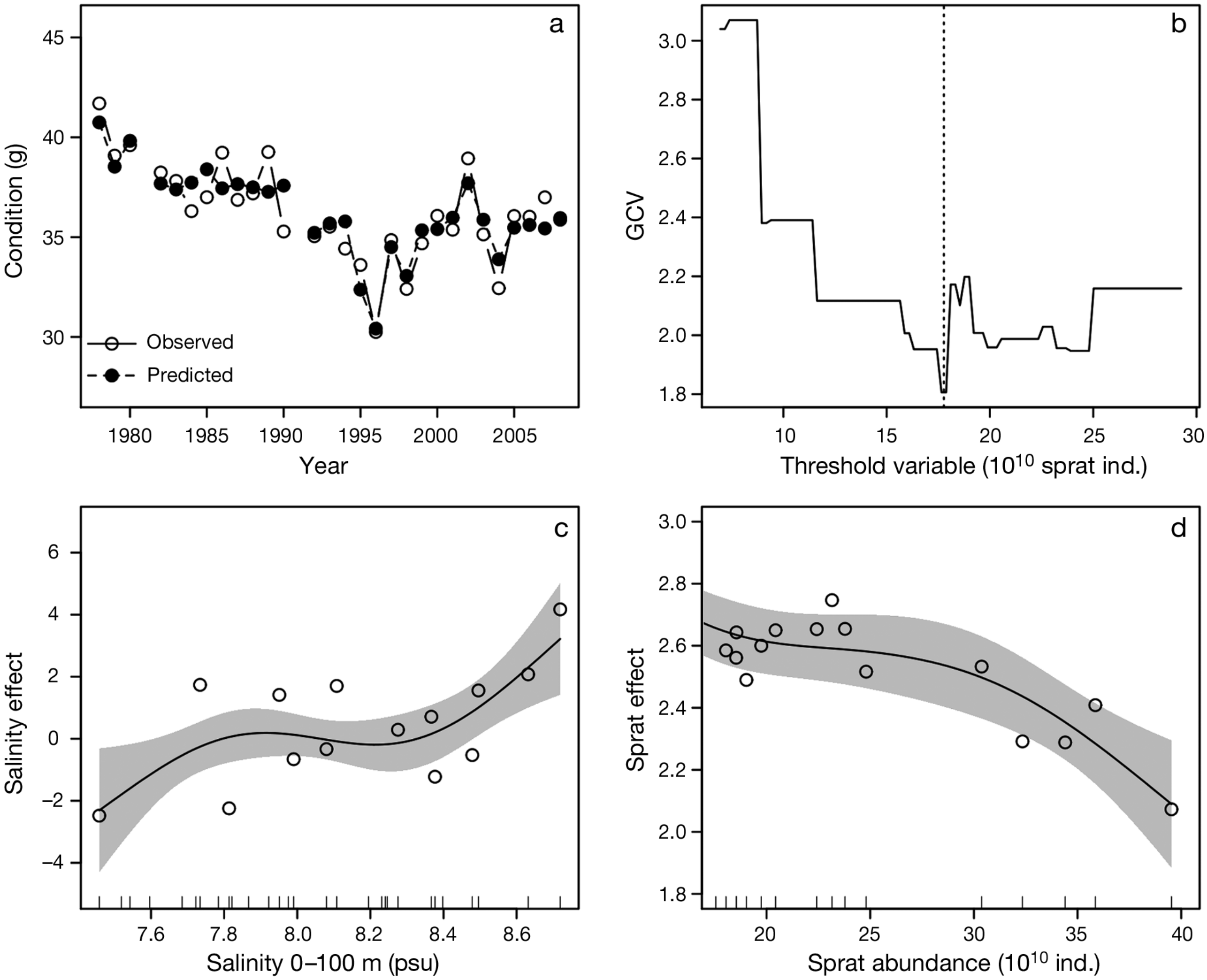

Fig. 3. Threshold Generalized Additive Model (TGAM) for herring condition. (a) Time-series of observed values and values predicted by TGAM, (b) Generalized Cross Validation (GCV) score profile as function of threshold variable (sprat abundance) with vertical dotted line = estimated threshold, (c) effect (unitless) of salinity on condition, (d) effect of sprat abundance on condition. Grey-shaded regions represent 95 % confidence intervals

towards low threshold estimates. The sensitivity analysis on the condition model showed a more symmetric dispersion but poorer stability in the estimates of the threshold. Threshold estimates showed a visible dispersion already omitting 7 % of the original condition dataset (Fig. 5).

The linear relationships between variations in herring growth and the predictors (salinity and sprat abundance) in the 2 configurations identified by the TGAM are shown in Fig. 6 (condition) and Fig. 7 (WAA). Considering the whole period, the analysis evidenced a strong negative Pearson's correlation coefficient between sprat abundance and growth parameters. However, the analysis of the relationship in the low-sprat configuration did not provide statistical support that variations in herring growth are related to sprat abundance, as illustrated by the simple linear correlations and the probability density distribution of correlations coefficients (Figs. 6a,c & 7a,c). On the other hand, in the high-sprat configuration, the link was significantly enhanced and herring growth was closely coupled to sprat variations (Figs. 6a,c & 7a,c). Reversed results were found in the assessment of the link between herring growth and salinity. In fact, considering the whole period, the analysis showed a positive Pearson's correlation coefficient, which increased in the low-sprat configuration (Figs. 6b,d & 7b,d). In contrast, in the high-sprat configuration, no relationship between salinity and herring growth was noticeable (Figs. 6b,d & 7b,d). Herring growth showed lower values in the high-sprat configuration than in the low-sprat configuration, regardless of the salinity level. In

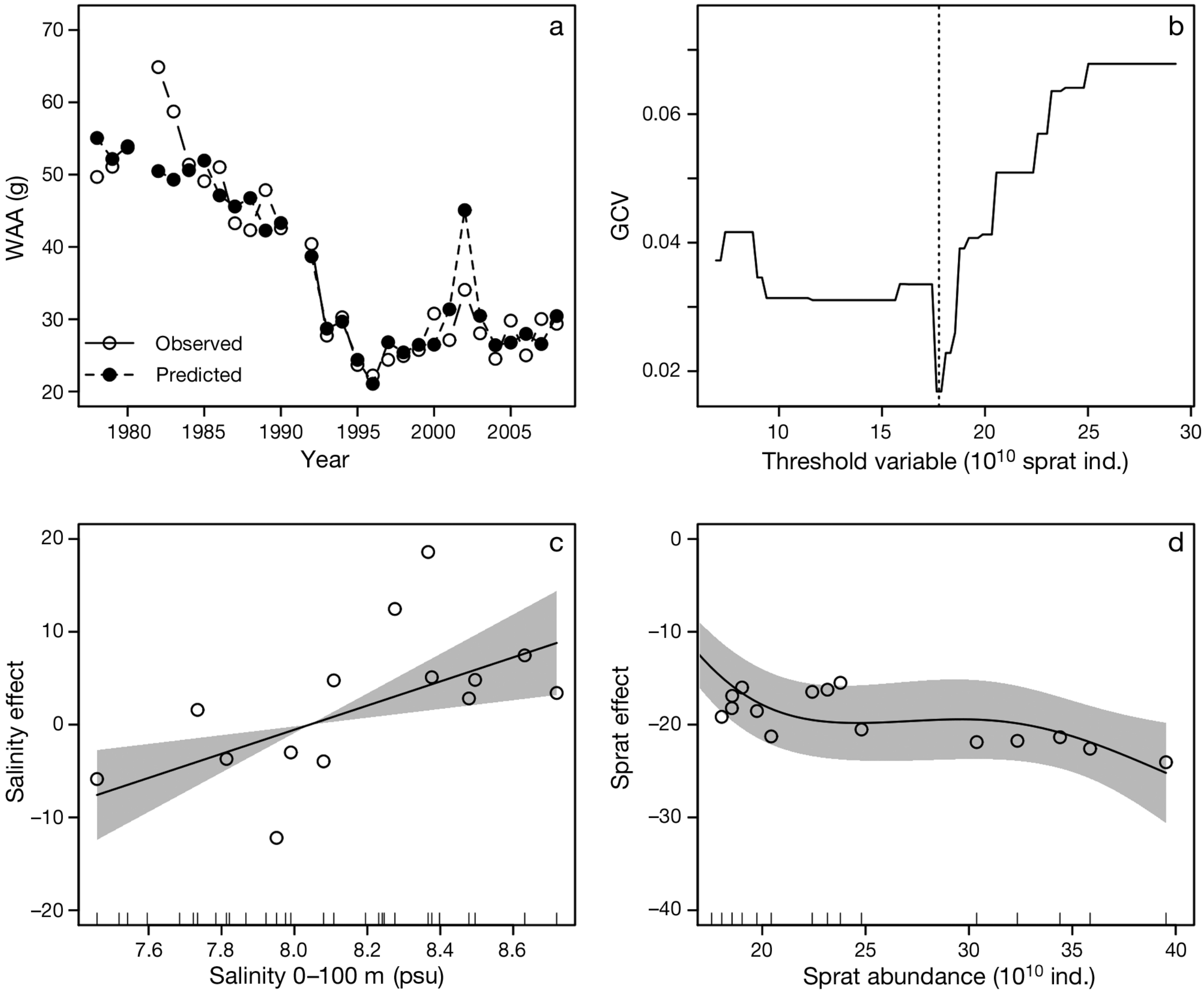

Fig. 4. TGAM for herring WAA. (a) Time-series of observed values and values predicted by TGAM, (b) GCV profile as function of threshold variable (sprat abundance) with vertical dotted line = estimated threshold, (c) effect of salinity on WAA, (d) effect of sprat abundance on WAA. Grey-shaded regions represent 95 % confidence intervals

general, the improvement of the relationship between growth and sprat abundance in the high-sprat configuration (and between growth and salinity in the low-sprat configuration) was more evident for herring WAA than condition, as shown by the Pearson's correlation coefficients and their probability density distributions. The growth time-series did not present temporal autocorrelation in either of the 2 configurations (Fig. S4 in the Supplement).

DISCUSSION

In this study, we have shown that the main factors driving herring growth in the central Baltic Sea may switch following changes in other key food-web components. Specifically, we found that the dominant factors affecting variations in the growth of herring switched from salinity to inter-specific competition depending on the size of the sprat population. Therefore, during the past 3 decades, a combination of changes in hydro-climatic factors and trophic interactions after the sprat outburst, has led to a drastic reduction in the individual growth of herring.

The factors affecting the body growth of other herring populations worldwide have been intensively investigated. These factors range from internal population control, e.g. intra-specific density-dependence (Winters & Wheeler 1994, Tanasichuk 1997, Shin & Rochet 1998, Melvin & Stephenson 2007), physical forcing as wind-induced turbulence (Shin & Rochet 1998), to temperature (Watanabe et al. 2008) and/or

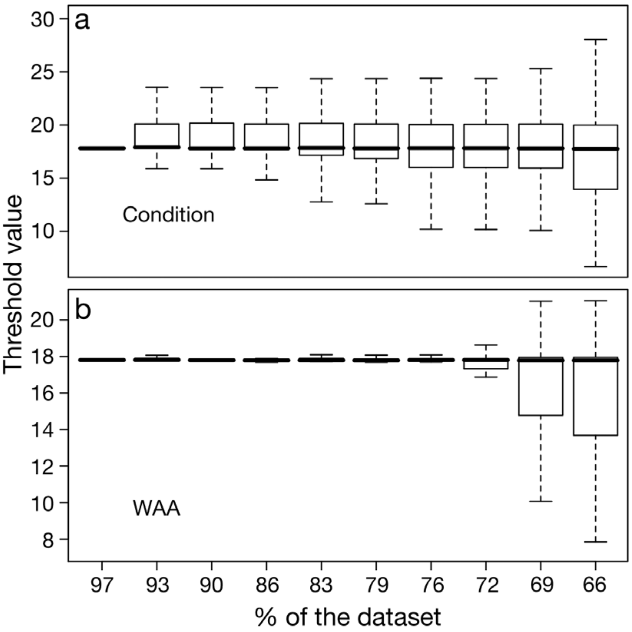

Fig. 5. Sensitivity analysis for (a) herring condition and (b) WAA. Boxplot of threshold values estimated sampling different proportions of original dataset (randomly sampling from 97 to 66% of the time-series). Bold lines identify the median, and box-whiskers = approximate 2-side 95% confidence interval and first and third quartiles

anthropogenic stress as fishery-related size selection (Wheeler et al. 2009). Density-dependence and hydroclimatic forces have also been suggested to act at different temporal (Heath et al. 1997) and spatial (Husebø et al. 2007) scales.

Compared to other herring stocks, the central Baltic Sea herring population inhabits an enclosed brackish environment, which makes organisms particularly sensitive to large salinity variations determined by climate-mediated irregular water inflows from the North Sea and precipitation (Voipio 1981, Lehmann et al. 2002). Moreover, the large diet overlap between herring and sprat in this region (Casini et al. 2004) produces a strong inter-specific feeding competition among clupeids. Accordingly, the growth of the central Baltic Sea herring has been previously linked to salinity variations and sprat stock size (Möllmann et al.

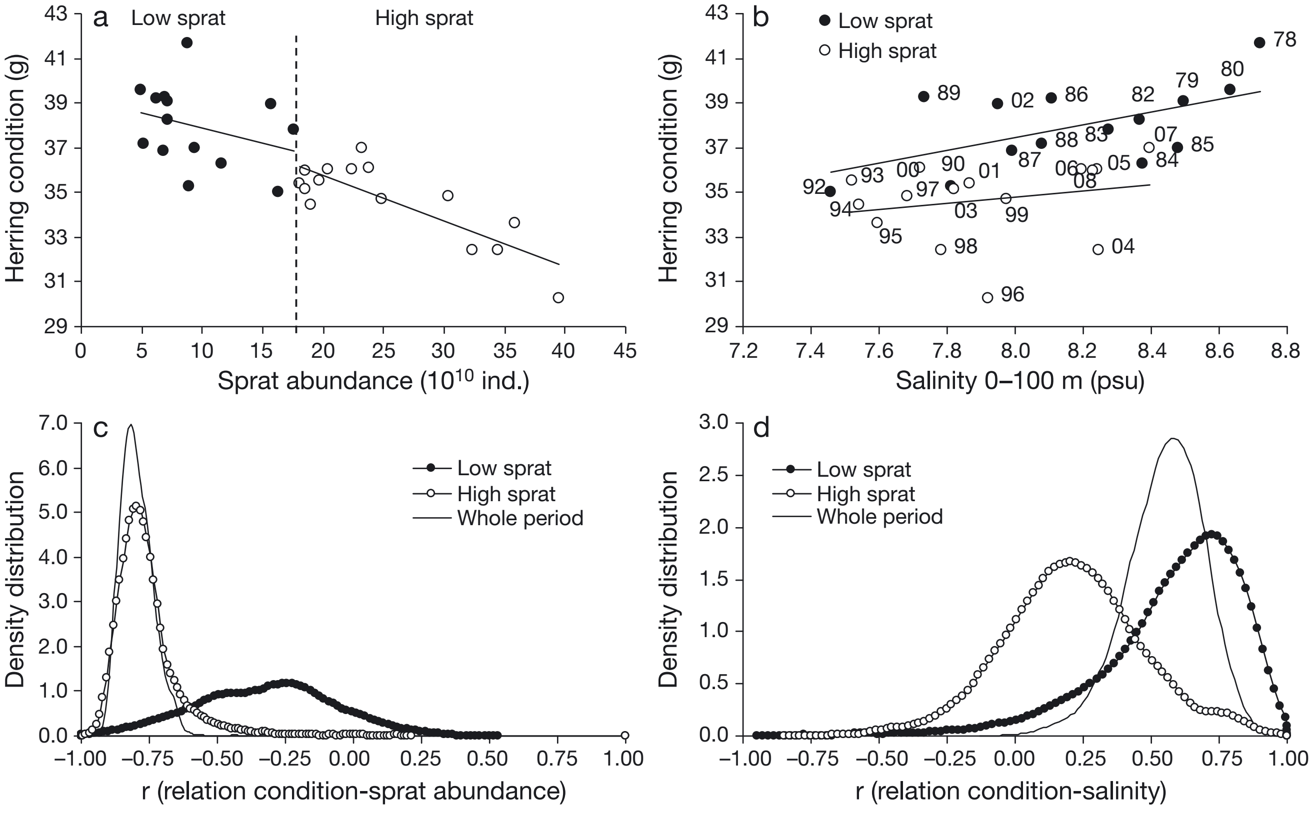

Fig. 6. Alternative dynamics in regulation mechanism of herring condition. (a) Relationships between sprat abundance and herring condition in the 2 configurations. Low-sprat: r = –0.56, p = 0.27; high-sprat: r = –0.82, p = 0.00022; whole period: r = –0.82, p < 0.0001; (b) relationships between salinity and herring condition in the 2 configurations. Low-sprat: r = 0.58, p = 0.030; high-sprat: r = 0.22, p = 0.43; whole period: r = 0.54, p = 0.0024. Nos. (each point) = observation year. (c,d) Density distribution of correlation coefficients between herring condition and sprat abundance, as well as salinity, in the 2 configurations and whole study period

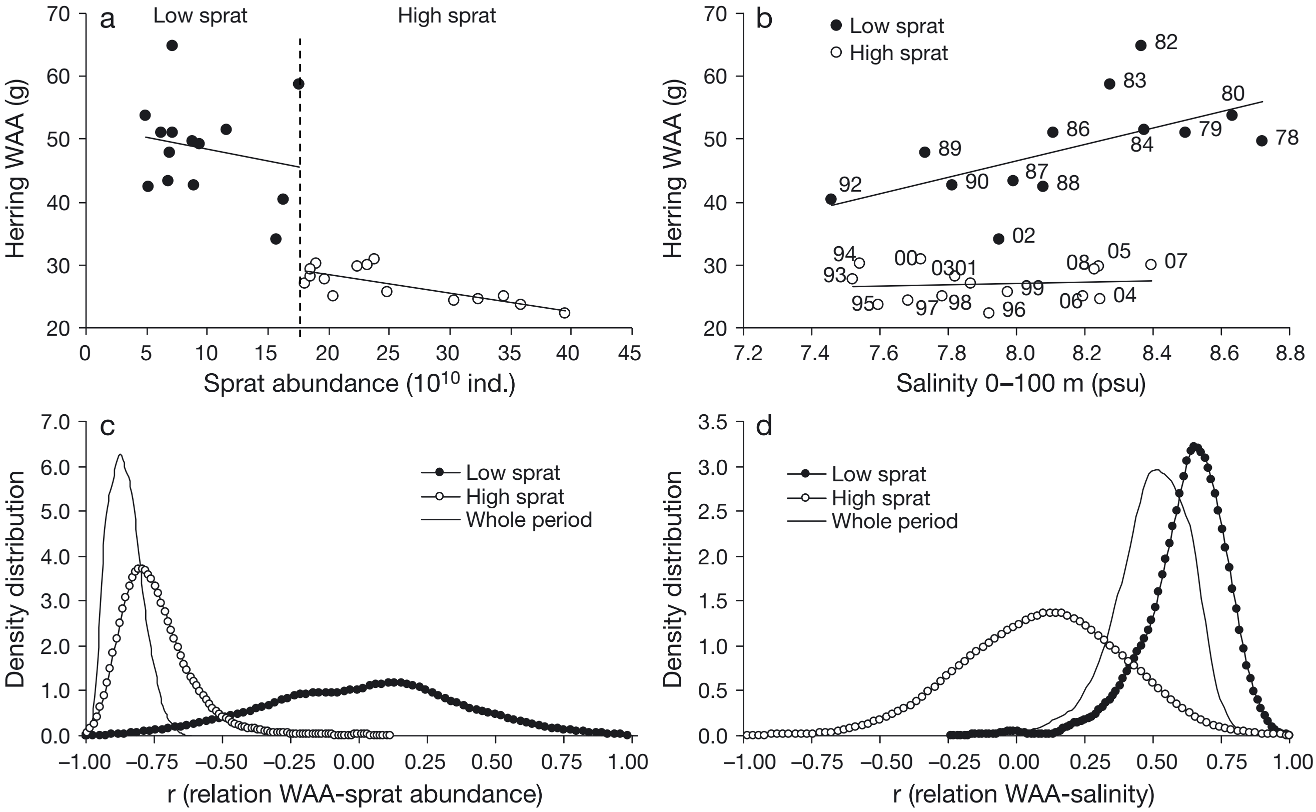

Fig. 7. Alternative dynamics in regulation mechanism of herring WAA. (a) Relationships between sprat abundance and herring WAA in the 2 configurations. Low-sprat: r = –0.20, p = 0.49; high-sprat: r = –0.76, p = 0.001; whole period: r = –0.81, p < 0.0001; (b) relationships between salinity and herring WAA in the 2 configurations. Low-sprat: r = 0.60, p = 0.032; high-sprat: r = 0.11, p = 0.69; whole period: r = 0.53, p = 0.0031. Nos. (each point) = observation year. (c,d) Density distribution of the correlation coefficients between herring WAA and sprat abundance, as well as salinity, in the 2 configurations and whole study period

2003, Casini et al. 2006), both factors acting on the abundance of one of the main preys for herring, the copepod *Pseudocalanus* spp. In particular, while the growth and reproductive performance of this zooplankter are enhanced by high salinity, sprat predation can operate a top-down control on this food resource (Möllmann & Köster 2002, Renz & Hirche 2006). Our results add to this general ecological understanding a crucial aspect, showing that the relative strength of the 2 main drivers (i.e. salinity and inter-specific competition) on herring growth may switch depending on the stock size of the sprat, the main planktivorous fish in the offshore areas of the central Baltic Sea. We specifically identified an ecological threshold of ~18 × 10^{10} sprat individuals which separated one low-sprat configuration characterized by a close link between herring growth and salinity variations, and one high-sprat configuration in which herring growth appears decoupled from salinity and becomes strongly controlled by inter-specific density-dependence.

The ecological explanation of this switch in the main regulatory mechanisms of herring growth is provided by Casini et al. (2009) who showed that the external drivers of zooplankton dynamics switch from hydroclimatic forcing to predation pressure depending on the population size of sprat. Also for zooplankton, the shift from one regulation mechanism to the other is triggered when the sprat population exceeds the threshold of ~17 × 10^{10} sprat individuals (Casini et al. 2009), very close to the threshold found in our study. In particular, at low levels of sprat population, *Pseudocalanus* spp. appears to be driven by salinity variations, a link that is disrupted when the abundance of sprat exceeds the ecological threshold (Casini et al. 2009).

The evidence provided by our investigation in combination with Casini et al. (2009) underlines that in low diverse systems, as the Baltic Sea, variations in key species such as sprat can have implications for ecosystem functioning detectable across trophic levels. Specifically, although salinity is an important factor for herring condition and WAA (e.g. Flinkman et al. 1998, Möllmann et al. 2003, Rönnkönen et al. 2004), our study provides evidence that food-web interactions, i.e. competition with sprat, can dampen the positive effect of high salinities, and become the main regulator of herring growth. This is exemplified by the increase in salinity from the beginning of the 1990s, which was not translated into the expected increase in herring growth (especially WAA), despite the high biomass of the primary producers (Casini et al. 2008). This demonstrates the occurrence of a discontinuous pattern (i.e. hysteresis) in the response of herring growth to salinity variations (Fig. 8) that may be indicative of alternative stable states in the system (Scheffer & Carpenter 2003). The shift between the 2 configurations during the past 3 decades has been triggered by the dramatic increase in the sprat stock, which has been linked before to predation release from cod (Casini et al. 2008) whose stock decreased due to high fishing pressure (ICES 2009a) and adverse hydro-climatic factors (i.e. low salinity and anoxic conditions in the deep waters) (Köster et al. 2005). However, the rise in temperature, which enhances sprat egg and larval survival, has also contributed to the sprat stock increase (Nissling 2004, Alheit et al. 2005).

The occurrence of shifts in the functioning of marine ecosystems has been generally seldom reported, although some examples exist (e.g. Hunt et al. 2002, Ciannelli & Litzow 2007, Stige et al. 2009). In the Gulf of Alaska it was found that the Pacific cod–prey interaction is either top-down or bottom-up regulated depending on temperature conditions and community state (Litzow & Ciannelli 2007). Hunt et al. (2002) also suggested that temperature and ice dynamics modulate the strength of top-down and bottom-up forces on the recruitment of walleye pollock population *Theragra chalcogramma* in the Barents Sea. Stige et al. (2009), on the other hand, showed for the Barents Sea that at low densities of planktivorous fish (capelin *Mallotus villosus*) the climate forcing on zooplankton is stronger, similar to what we found in our study for herring growth. In our study, however, we also indicate a putative ecological threshold (~18 × 10^{10} ind. sprat) responsible for the shift in the control of herring growth.

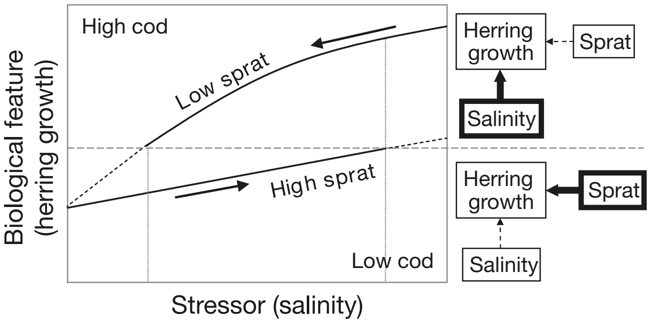

Fig. 8. Discontinuity (hysteresis) in the response of herring growth to variations in salinity. In low-sprat configuration, salinity explains changes in herring growth, whereas in high-sprat configuration the link between herring growth and salinity becomes weaker and inter-specific density-dependence becomes the main factor affecting herring growth

The threshold dynamic evidenced in our study by the TGAMs was more evident for herring WAA than condition, as shown by all the statistics used in the analyses. Although at the moment we do not have robust elements to provide a comprehensive explanation for this difference, the common threshold identified indicates that common mechanisms are behind the threshold dynamic of both growth parameters. It is worth noting that using additive models (GAMs) sprat abundance was the main explanatory factor, whereas salinity appeared of minor importance. Also using TGAMs, the strength of the relationship between sprat abundance and herring growth in the high-sprat configuration appeared higher than the relationship between salinity and herring growth in the low-sprat configuration. These considerations point to that, while a significant threshold was identified by our analyses, the density-dependent mechanism seems overall to have been the major regulator of herring growth during the past 3 decades.

The direct effect of fishing on the body size of target organisms has been shown by several studies (Shin et al. 2005). Also for the central Baltic Sea, it may be suggested that the high fishing mortalities during the 1980s and 1990s (ICES 2009a) have contributed to the reduction in the mean size of herring by selecting the larger individuals (e.g. Vainikka et al. 2009). However, the increase in fishing mortality could be partly an effect, and not only a cause, of the decrease in individual herring size (ICES 2009a). In fact, for a given catch in biomass, a decrease in fish individual weight would imply a higher number of fish caught every year. We opted, therefore, not to introduce fishing mortality as a potential predictor in our analyses. The question whether changes in fishing mortality are mainly a cause, or a result, of the variations in herring mean size is worth further investigation.

The central Baltic herring stock decreased steadily from the end of the 1970s (ICES 2009a). The drop in WAA and condition of the spawners could have indirectly contributed to the general decrease in the herring stock, by hampering the population recruitment success (Cardinale et al. 2009), likely through reduced fecundity and hatching success of the eggs (Laine & Rajasilta 1999). The decrease in herring body growth also directly contributes to explain the sharper decrease in herring spawning stock biomass, than in stock abundance, since the early 1980s (Fig. S1 in the Supplement). This is because a decrease in the mean weight is automatically translated into a reduction in biomass, for comparable levels of abundance. However, the change in age structure of the spawning population towards a relatively higher abundance of younger spawners (ICES 2009a) has likely also contributed to the drastic decrease in spawning stock biomass.

The results presented here have important implications for an ecosystem-approach to fisheries management. The threshold in the mechanisms of regulation of herring growth implies that effective management should take in consideration both hydro-climatic circumstances and food-web structure, and be adaptive to their variations with prompt management actions. We have specifically detected here a clear-cut and easy-to-understand threshold value which could be used to reach the goal of a healthy central Baltic herring stock. The restraint of the sprat population below the abundance threshold would release herring from inter-specific competition and enhance herring growth, increasing spawning stock biomass and stock reproductive potential. The best way to achieve this goal is to allow the Baltic cod stock to recover to a level capable of controlling the sprat population.

Acknowledgements. This paper is dedicated to the memory of our colleague and dear friend Johan Modin, who inspired Fig. 8.

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Conditional responses to increasing scales of disturbance, and potential implications for threshold dynamics in soft-sediment communities

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ABSTRACT: Disturbance-recovery experiments conducted across environmental gradients can reveal the relative importance of processes, feedbacks and threshold conditions that sustain ecosystem functioning and resilience. In the present paper we argue that threshold responses to disturbance (e.g. marked non-linear shifts in abundance of important species) are scale-, context- and species-dependent. In order to test the context-dependency in recovery dynamics of soft-sediment benthic communities, we conducted a large-scale sublittoral experiment investigating patterns in recovery of 2 functionally different groups of deposit feeders (surface vs. subsurface deposit feeders; Hydrobiidae vs. Oligochaeta) with increasing spatial scales of hypoxic disturbance in the Baltic Sea. Plots (1, 4 and 16 m^2) were defaunated at 4 sandy sites (5 m depth) that varied in exposure to wind-waves, and subsequent recovery of macrofaunal abundances was monitored over 15 mo, focusing on post-larval recolonisation. Recovery patterns were site-specific, depended on the scale of disturbance, and indicated a shift in the relative importance of smaller-scale biological factors to broader-scale physical factors, i.e. waves, currents and sediment transport, when moving from sheltered to more exposed sites. We found group-specific responses, related to mode of living (epifaunal/infaunal) and dispersal potential. In addition, Hydrobiidae exhibited opportunistic population increases in response to disturbance, likely due to increased food availability. The results highlight the importance of interactions between environmental factors, and understanding natural-history characteristics and relative mobility of different taxa, when assessing both the resilience and the recovery of benthic communities.

KEY WORDS: Disturbance · Conditional recovery patterns · Scale · Soft-sediment communities · Opportunistic responses · Food availability

INTRODUCTION

Abrupt changes in ecosystem qualities can occur as a result of extreme environmental forcing, as a consequence of changing intrinsic dynamics or the interaction of factors (Groffman et al. 2006, Scheffer et al. 2009, Swift & Hannon 2010). Soft-sediment habitats are often considered disturbance-dominated systems and recovery rates and patterns may provide important insights into the potential for broad-scale and abrupt changes in the structure and function of benthic communities. For example, theoretical predictions show that rates of recovery from small-scale perturbation could indicate how close to a threshold a system is (van

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Nes & Scheffer 2007, Scheffer et al. 2009). Changes in spatial structure across landscapes can affect connectivity and local recovery that produce broad-scale changes in community structure (Pascual & Guichard 2005), and field studies of benthic communities show that following disturbance, the rates and patterns of recovery are both scale-dependent and influenced by site-specific environmental factors (Zajac et al. 1998, Thrush et al. 2003). In addition, faunal responses to disturbance are species-specific, with the potential for opportunistic population increases in response to release of available food resources or release from predation or competition pressure (Norkko et al. 2006b, Van Colen et al. 2008). Thus disturbance-recovery experiments can reveal processes, feedbacks and threshold conditions that are important for ecosystem resilience and can thus provide important insights into the functioning and appropriate management of ecosystems (Thrush et al. 2009).

Knowledge of natural history and the role of particular types of organisms in the ecosystem is critical for predicting species- and species-environment interactions that could lead to threshold responses (Dayton 2003). Aggregation, patchiness and the spatial distribution of a population may provide information on the mechanisms structuring the population, as these patterns are modified by both biotic and abiotic factors (Thrush 1991). Density-dependent shifts in species-interaction strength, direction and feedback are likely to influence recovery patterns and community dynamics after disturbance. For example, species may aggregate around patchy food resources released by the disturbance and then change their degree of aggregation during recovery (Norkko & Bonsdorff 1996a, Norkko et al. 2006b).

In soft-sediment communities, dispersal is a key process, often involving many different life stages, with different dispersal scales and mechanisms (Whitlatch et al. 1998), highlighting the need to include demographics in studies of disturbance and recovery. Depending on the mode of colonisation (e.g. large-scale settlement of pelagic larvae, post-settlement dispersal with sediment bedload transport, or adult crawling/swimming), if the size of disturbed patches exceeds the scales of dispersal of specific species, then the system may be predisposed to tip into an opportunism-dominated community state. However, in marine systems many details of dispersal and colonisation are relatively poorly known (Cowen & Sponaugle 2009). Nevertheless, dispersal potential is dependent on both species' and habitat characteristics; for example, Valanko et al. (2010) showed that in non-tidal areas, infaunal species are less likely to disperse with sediment bedload transport compared with epifaunal species.

Species with strong functional roles that may influence resource availability in recovering patches, but that are also affected by environmental forces (Norkko et al. 2006a), are likely to exhibit scale-dependent responses important in maintaining ecological resilience (Thrush et al. 2009). In a species-poor ecosystem with low levels of functional diversity and complementarity, once a threshold that reflects the sensitivity of a functional group or taxon to a stressor is passed then major changes in recovery dynamics and ecosystem function are to be expected. For example, in the Baltic Sea, feedback loops between degraded benthic communities, hypoxia and internal nutrient loading from the sediments are implicated in the continued large-scale eutrophication of the ecosystem (Karlson et al. 2007, Vahtera et al. 2007).

As species–environment relationships are likely to change across larger-scale gradients in environmental factors (e.g. wave exposure, salinity, nutrient status), experiments should be conducted across environmental stress gradients to improve predictive capacity and to disentangle the combined effects of human-induced and natural stress factors (Hewitt et al. 2007, Thrush et al. 2009). In sublittoral habitats, large-scale experiments conducted across gradients of environmental variables are rare and much of our current knowledge about disturbance-recovery dynamics in soft-sediment communities stems from manipulative experiments in intertidal areas (Thrush et al. 1996, Norkko et al. 2006b, Van Colen et al. 2008, although see Zajac & Whitlatch 1982 for a shallow subtidal study) or before-after sampling efforts in relation to dredging or other large-scale impacts (Dauer & Simon 1976, Pearson & Rosenberg 1978). Therefore the scale-dependence and relative importance of ecological mechanisms and processes in sublittoral, coastal systems deserves additional attention. In this context, experiments conducted over multiple sites will facilitate assessment of the relative importance of broad-scale environmental patterns and small-scale mechanisms, and enhance the generality of the findings, which is crucial for our ability to predict change (Thrush et al. 2000).

In the present paper we highlight the importance of considering the context-dependency of threshold dynamics in light of disturbance-recovery ecology. If the disturbance approaches or exceeds some threshold level, the benthic community may exhibit a threshold response (i.e. marked non-linear shifts in abundance, diverging recovery trajectories and/or changes in interactions between important species). More specifically we argue that such changes in system dynamics are scale-, context- and species-dependent. The critical disturbance size may be site-dependent due to interactions with the physical characteristics of a site (e.g. currents, waves, sediment grain size characteristics) and dependent on the timing of disturbance in relation to seasonal recruitment patterns, with potentially profound implications for subsequent community assembly. Changes in recovery dynamics may thus indicate that the disturbance has exceeded a threshold level.

We designed a sublittoral disturbance-recovery experiment to investigate patterns in the recovery of macrofaunal abundances after increasing spatial scales of hypoxic disturbance, focusing on post-larval recolonisation. Recovery was assessed in terms of abundances and size-frequency distributions in relation to natural seasonal fluctuations in undisturbed control areas. The experiment was conducted at 4 sublittoral sites that represent gradients of increasing exposure to wind-waves (the major hydrodynamic force in our studied system) and increasing sediment grain size. We focused our analysis on the 2 numerically dominant groups of deposit feeders: hydrobid mudsnails that are mobile as adults and live on the sediment surface versus infaunal oligochaetes with limited larval dispersal and comparatively more sedentary adult stages. Both groups have the potential to utilise food resources released by the disturbance. The following predictions were tested:

(1) Recovery was predicted to be faster at more exposed sites, where currents and wave-action aid the dispersal of fauna into the disturbed area.

(2) Recovery was predicted to depend on the scale of disturbance and to be faster in smaller disturbed areas.

(3) Recovery was predicted to be faster in mobile epifauna, compared with infauna.

(4) Recovery mechanisms were predicted to differ between the 2 taxonomic groups and the relative importance of these mechanisms was predicted to change across the environmental gradients in the study area.

The results of the 15 mo experiment were analysed with emphasis on the interactions between natural-history characteristics in these contrasting deposit-feeders and environmental site-specific variables such as sediment characteristics and wave exposure. Thus, the aim was to provide insight into the recovery dynamics for important deposit-feeders in soft-sediment systems. By understanding context-dependent shifts in the recovery processes, we may more generally predict threshold responses.

MATERIALS AND METHODS

Study area. The field experiment was conducted in the northern Baltic Sea, in the outer archipelago near Tvärminne Zoological Station (59° 50′ N, 23° 14′ E), Finland (Fig. 1). Four coastal sites 1 to 5 km apart were chosen to encompass a range of exposure to wind-waves, with exposure increasing from Sites A to D. Salinity is around 6 and there are no tides in the area. All sites were at about 5 m depth and had sandy sediments (organic content <1%), with a range in grain size corresponding to the wave climate and exposure at each site (see Table 1). Macrofaunal communities were dominated by typical brackish water taxa such as

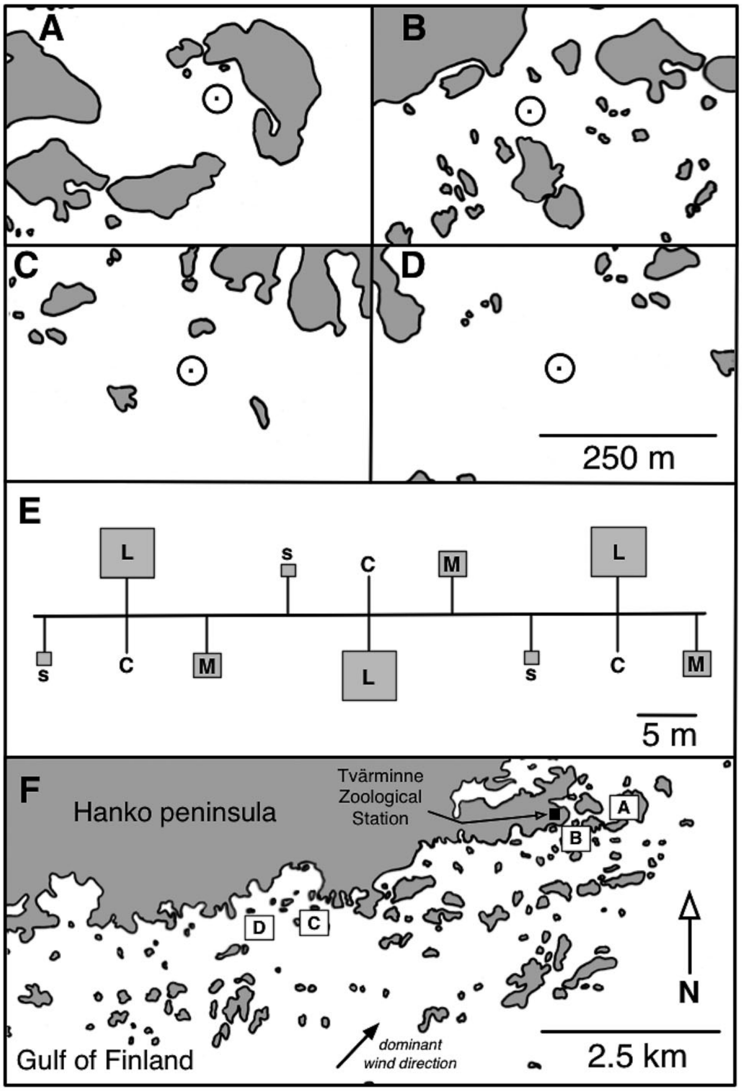

Fig. 1. (A–D) Location of study Sites A to D; (E) experimental design employed at each site, with arrangement of plots along 50 m transect at each site, where C = Control, S = Small, M = Medium and L = Large, corresponding to 0, 1, 4 and 16 m^2 disturbance plots respectively; and (F) position of study sites in relation to one another off southwestern Finland. Wind-wave exposure increases from Sites A to D

oligochaetes, the hydrobid mudsnails *Hydrobia ulvae* and *Potamopyrgus antipodarum*, the bivalve *Macoma balthica*, and the polychaetes *Hediste diversicolor* and *Marenzelleria* sp.

Experimental setup. The disturbance experiment simulated patchy coastal hypoxia induced, for example, by drifting algal mats (Norkko & Bonsdorff 1996a, 1996b). Hypoxic disturbance was initiated by covering experimental plots with plastic, and all manipulations and sampling were done using SCUBA. At each site, disturbance plots of 1, 4 and 16 m^2 and control plots (hereinafter referred to as Small, Medium, Large and Control) were each replicated 3 times (Fig. 1). The location of different treatment replicates was stratified along a 50 m transect to ensure that potential underlying spatial patterns of fauna or environmental factors, not visible from the sediment surface, would not affect the interpretation of recolonisation patterns. The plots were defaunated by covering the sediment surface with black low-density polyethylene (LDPE) plastic to induce anoxia to underlying sediments. The edges of the plastic sheets were held in place with metal rods secured with 30 cm metal pegs, which prohibited any water exchange from underneath the plastic. Plots were covered for a 16 d period to ensure complete defaunation and the experiment started by carefully removing the plastic in late July.

Macrofauna. After defaunation, macrofaunal community data was collected from defaunated and control plots to track faunal recovery dynamics over 15 mo, focusing on post-larval recolonisation, but also including the peak in seasonal recruitment the year after the disturbance (all sites sampled at 0, 0.5, 1, 3, 10, 12 and 15 mo, with time 0 corresponding to 31 July 2006). Three replicate cores (diameter 5.6 cm, depth 15 cm) were taken within a central area (0.25 m^2) of each plot on each sampling occasion. Cores were never taken from the same exact location within this central plot area over the course of the experiment. Sediment bedload traps were used to compare relative dispersal rates for Hydrobiidae and Oligochaeta in Control and Large plots (see Valanko et al. 2010). Traps were not deployed in the Small and Medium plots, as they might have introduced a relatively large artefact in these plots. The traps (diameter 3.7 cm, depth 29 cm, aspect ratio 7.8:1) were slotted into pre-deployed outer sleeves, flush with the sediment surface. At each site a total of 5 traps were deployed in the Control areas (1 near each of the 3 Control plots + 2 extra), while 1 trap was deployed in the centre of each Large plot (i.e. 3 per site). The traps were deployed for 48 h at each site on each sampling occasion.

The core and trap samples were preserved in 70% ethanol and stained with Rose Bengal before enumeration of all macrofaunal taxa. To include small recruits, the samples were elutriated by first suspending the sediment in a bucket of spinning water and decanting off the supernatant through a 200 µm sieve (repeated 5 times), and then checking the remaining sediment for any larger animals.

We focused on the recovery patterns of 2 key taxa, Hydrobiidae and Oligochaeta. Hydrobiidae are surface detritivores/grazers that actively crawl on the sediment surface. In contrast, Oligochaeta are burrowing detritivores. *Hydrobia ulvae* veligers may be planktonic, while *H. ventrosa* do not have planktonic larvae. The Oligochaeta considered here produce egg capsules that hatch without a planktonic stage. In order to focus on the recolonisation by post-settlement and adult stages, the experiment was started after the major seasonal peak in settlement for both groups. The abundance of the mudsnails *H. ulvae*, *H. ventrosa*, and *Potamopyrgus antipodarum* was pooled (hereinafter collectively referred to as Hydrobiidae). *H. ulvae* was the dominant mudsnail at all sites throughout the study. *P. antipodarum* contributed about 5% at Site A and 10 to 40% at the other sites. *H. ventrosa* contributed <1% at all sites. Oligochaeta were not identified to species level. However, tubificid oligochaetes such as *Clitellio arenarius* and *Limnodrilus* sp. typically dominate shallow sandy habitats in the northern Baltic Sea.

Sediment properties. As a measure of food available to near-surface deposit feeders, sediment chlorophyll *a* (chl *a*) samples were taken from each plot on each sampling occasion with a 2.1 cm diameter core. The top 1 cm of sediment was sliced off the cores, stored at –20°C and freeze-dried prior to analysis. Chl *a* was extracted from sediments in 90% acetone for 24 h and measured spectrophotometrically. An acidification step was included to separate degradation products from chl *a* (Sartory 1982).

Sediment grain size was measured from 5 replicate core samples (diameter 2.1 cm, depth 5.0 cm) collected once from each site in undisturbed areas. Hydrogen peroxide (6%) was used to dissolve organic material. Grain sizes were separated into <63, 63–250, 250–500 and >500 µm fractions using respective sieves and dry weight was obtained for each fraction (48 h at 60°C).

Stable isotope analysis of *Hydrobia ulvae* and sediment. In order to investigate whether recolonisation patterns of *H. ulvae* over different spatial and temporal scales could be linked to food availability, stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) of surface sediments and *H. ulvae* were measured on 4 different occasions at Site A, the most sheltered site. This site was targeted as it had the highest abundance of Hydrobiidae. Sediment samples were obtained from each plot with a 2.1 cm diameter core. *H. ulvae* were hand-picked by divers from each plot using a pipette

(10 adult individuals pooled per plot). All individuals were identified live under the microscope and only adults of the numerically dominant *H. ulvae* were included in the analyses. The mudsnails were left in filtered seawater for 3 h to empty their guts and were then dried at 60°C for 48 h. To remove carbonates from the shells, the crushed samples were acidified in 2 N HCl (Herman et al. 2000). After the acid was removed with a pipette, the homogenate was rinsed with distilled water and dried at 60°C overnight. The sample was re-homogenised and 1 mg weighed into a tin capsule for analysis. For analysis of sediment stable isotope signatures, the top 0.5 cm of the sediment was sliced off and dried at 60°C for 48 h. The sediment was ground to a fine powder and passed through a 500 µm sieve to remove coarse sand. A subsample was acidified with 2 drops of 1 N HCl and dried at 60°C overnight. The sample was re-homogenised and 30 mg weighed into a tin capsule for analysis.

Stable isotopes of *Hydrobia ulvae* were analysed at the Institute for Environmental Research, University of Jyväskylä, using a FlashEA 1112 elemental analyser coupled to a Thermo Finnigan DELTA$^{\text{plus}}$ Advantage mass spectrometer (Thermo Electron). Sediments were analysed at the University of California Davis Stable Isotope Facility, using a PDZ Europa ANCA-GSL elemental analyser coupled to a PDZ Europa 20-20 mass spectrometer (Sercon). In both cases, PDB limestone and atmospheric nitrogen were used as standards for δ^{13}C and δ^{15}N, respectively. Isotopic ratios, expressed in delta (δ) notation, were calculated relative to the standards using the formula:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N}\ (‰) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3; \quad \text{where } R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C} \text{ or } {}^{15}\mathrm{N}/{}^{14}\mathrm{N} \tag{1}$$

Data analysis. Two-way ANOVA was used to analyse treatment-related differences in sediment chl *a* within each site over the first 3 mo of the experiment. Treatment and sampling time were treated as fixed factors because we chose scales of disturbance to encompass different adult mobility scales of resident organisms and dates to reflect specific times in the strong seasonal cycle in the Baltic. One-way ANOVA was used to analyse general differences in sediment chl *a* between sites over the first 3 mo of the experiment (data from Control plots only, all times pooled). Prior to ANOVA analyses, data were examined for homogeneity of variances (Levene's) and normality (Kolmogorov-Smirnov). Initial analyses of abundances of Hydrobiidae and Oligochaeta across treatments, sites and times (fixed factors) were performed within a generalised linear modelling framework (McCullagh & Nelder 1989, Crawley 1993). Preliminary inspection of abundance patterns over time in the experimental plots revealed that recovery was not consistent across sites (as expected) and further analyses of recovery and treatment effects were done on a site-by-site basis. Variance-to-mean ratios were used as a measure of spatial aggregation of Hydrobiidae and Oligochaeta in different treatments at different sites over time. Kolmogorov-Smirnov 2-sample tests were used to compare size frequency distributions in Hydrobiidae between sites and treatments. Relative dispersal rates were calculated for Hydrobiidae and Oligochaeta from number of individuals caught in a trap per day divided by number of individuals in corresponding cores, i.e. traps in Control plots divided by densities in Control cores and traps in Large plots divided by densities in cores from the same Large plots (in this non-tidal system, animals at 5 m depth were unlikely to passively move >2 m over the 48 h trap deployments, which occurred under relatively calm wind conditions). Two-way ANOVA with treatment and sampling time as fixed factors was used to test differences in relative dispersal for the 2 taxa separately, after testing the assumptions of homogeneity of variances and normality. Linear regression was used to analyse trends in stable isotope signatures of *Hydrobia ulvae* and sediment across different-sized disturbed plots.

RESULTS

Visual observations and sediment chl *a*

Defaunation was successful at all sites. The sediment underneath the plastic sheets was black all the way to the plot edges, with large numbers of dead or moribund adult bivalves (mainly *Macoma balthica* and *Mya arenaria*) and polychaetes (mainly *Hediste diversicolor* and *Marenzelleria* sp.) on the sediment surface. These specimens were gone within 1 to 2 d, indicating that this very transient additional food resource was efficiently utilised by fish (*Platichthys flesus* and *Perca fluviatilis*) observed near the plots immediately after removal of the plastic.

Two weeks after the disturbance, the disturbed plots were visibly greener than the control plots at all sites, indicating fast growth of microphytobenthos. This pattern was still noticeable the following spring, 10 mo after the disturbance. Despite the obvious growth of microalgae, no significant treatment effects were detected in the sediment chl *a* values at any of the sites over the first 3 mo of the recovery (2-way ANOVAs, $p > 0.05$, data not shown). This is probably because the sample integrated chl *a* over the top 1 cm of the sediment, instead of targeting only the very top sediment surface, where the microalgae are most abundant. The greener appearance in the disturbed plots was likely due to a combination of higher amounts of available sediment nutrients and lower rates of bioturbation and grazing in these plots compared with the Control plots, resulting in more microphytobenthos remaining in the top millimetres of the sediment surface. Although no differences were found between treatments at any of the sites, there were clear differences in the general levels of sediment chl *a* between the respective sites (Control plots, 1-way ANOVA: $F_{3,35} = 49.58$, $p < 0.001$; Table 1), with the lowest levels at Sites A and D, and the highest levels at Sites B and C.

Table 1. Environmental characteristics at the experimental sites. Sediment grain size fractions and median grain size refer to the top 5 cm of the sediment (n = 5). Sediment (Sed.) chl *a* is the average (±SD, n = 9) of the top 1 cm in Control plots in July to October of the first year of the study

Site	Sediment grain size (% dry wt)				Median grain size, d_{50} (mm)	Sed. chl *a* (µg g^{-1} dry wt)
	Silt and clay (<63 µm)	Fine to very fine sand (63–250 µm)	Medium sand (250–500 µm)	Coarse sand (>500 µm)		
A	6.6	78.3	12.0	3.1	0.14	11.4 ± 0.5
B	1.8	36.5	58.0	3.6	0.29	23.6 ± 1.0
C	0.8	28.4	33.6	37.2	0.39	19.6 ± 3.2
D	0.4	8.8	35.6	55.2	0.60	14.1 ± 2.4

Site- and taxon-dependent recovery patterns

Patterns of recovery after anoxia differed between sites, between scales of disturbance, and also between Hydrobiidae and Oligochaeta (Table 2, Fig. 2). Abundances varied between sites and over the duration of the experiment also in the Control plots (Table 2). Analysis of abundance patterns for Hydrobiidae and Oligochaeta clearly indicated that the results of the experimental treatments were site-dependent. Significant interactions between Treatment and Sites, and Treatment and Time nested within Site were also

Table 2. Abundances of Hydrobiidae and Oligochaeta (ind. $core^{-1}$, diam. 5.6 cm) per site, months after disturbance and disturbance treatment (mean ± SE, n = 9). Months after disturbance correspond to the following dates: 0 = 31 Jul 2006, 0.5 = 12 Aug 2006, 1 = 29 Aug 2006, 3 = 17 Oct 2006, 10 = 9 May 2007, 12 = 25 Jul 2007 and 15 = 9 Oct 2007. Small = 1 m^2, Medium = 4 m^2, Large = 16 m^2. Wind-wave exposure increases from Sites A to D

Site	Month	Hydrobiidae				Oligochaeta			
		Control	Small	Medium	Large	Control	Small	Medium	Large
A	0	4.1 ± 0.9	0	0	0	11.8 ± 3.0	0	0	0
	0.5	5.3 ± 1.1	4.9 ± 1.2	3.4 ± 1.0	1.3 ± 0.4	8.6 ± 2.6	4.8 ± 1.0	4.9 ± 1.0	2.4 ± 0.6
	1	8.1 ± 1.5	17.3 ± 2.4	14.7 ± 3.1	16.1 ± 1.8	13.7 ± 1.9	6.7 ± 1.2	10.0 ± 1.5	5.0 ± 0.9
	3	16.1 ± 2.4	17.1 ± 2.0	29.7 ± 3.3	24.0 ± 2.9	24.0 ± 2.5	15.7 ± 1.5	15.6 ± 2.3	21.0 ± 3.2
	10	6.2 ± 0.7	19.7 ± 4.2	15.9 ± 2.3	24.7 ± 5.0	7.0 ± 1.3	10.2 ± 2.0	10.1 ± 2.1	13.9 ± 2.7
	12	10.6 ± 1.9	18.7 ± 4.0	18.2 ± 2.5	23.0 ± 2.4	7.3 ± 1.2	10.7 ± 1.4	6.1 ± 1.2	3.0 ± 0.4
	15	10.1 ± 1.4	10.7 ± 1.3	10.3 ± 1.6	10.3 ± 1.0	10.2 ± 1.7	10.6 ± 1.5	7.9 ± 1.9	6.9 ± 1.3
B	0	2.8 ± 0.7	0	0	0	14.7 ± 2.9	0	0	0
	0.5	4.9 ± 1.2	3.6 ± 0.9	4.4 ± 1.6	4.9 ± 1.1	32.6 ± 10.1	5.1 ± 1.2	6.7 ± 2.8	10.3 ± 3.0
	1	11.7 ± 1.8	12.8 ± 3.4	8.1 ± 1.8	9.2 ± 1.8	8.8 ± 1.9	6.3 ± 2.5	9.8 ± 3.7	10.1 ± 3.4
	3	18.6 ± 1.8	23.2 ± 3.3	24.2 ± 2.5	21.3 ± 2.2	11.7 ± 2.9	7.1 ± 1.1	4.9 ± 1.1	8.0 ± 1.6
	10	9.7 ± 1.9	17.0 ± 4.5	11.7 ± 1.9	11.0 ± 2.4	14.6 ± 2.2	7.7 ± 1.2	11.0 ± 1.2	6.6 ± 1.4
	12	8.2 ± 1.6	11.2 ± 1.5	14.8 ± 2.2	9.7 ± 1.7	4.9 ± 1.8	9.3 ± 2.4	2.8 ± 0.8	7.4 ± 2.3
	15	35.4 ± 4.7	35.7 ± 4.0	42.6 ± 3.9	30.3 ± 3.3	8.7 ± 1.5	9.3 ± 1.7	16.8 ± 3.4	11.6 ± 1.6
C	0	3.8 ± 0.5	0	0	0	16.4 ± 2.1	0	0	0
	0.5	3.4 ± 1.0	4.1 ± 1.4	3.0 ± 0.5	2.4 ± 0.8	32.1 ± 7.3	17.9 ± 3.3	30.7 ± 2.3	22.6 ± 2.5
	1	5.0 ± 0.7	7.8 ± 1.3	5.7 ± 0.8	4.1 ± 0.5	35.0 ± 10.9	15.4 ± 9.9	11.9 ± 1.5	8.3 ± 2.2
	3	5.4 ± 0.6	7.3 ± 1.2	10.7 ± 1.4	8.0 ± 0.9	14.1 ± 2.8	5.6 ± 1.8	3.6 ± 0.6	7.4 ± 1.2
	10	6.0 ± 1.0	4.0 ± 1.0	4.7 ± 0.7	3.8 ± 0.7	16.2 ± 4.4	3.6 ± 1.0	5.9 ± 2.1	5.6 ± 1.2
	12	6.7 ± 1.2	7.2 ± 1.3	9.1 ± 1.7	10.4 ± 1.5	12.9 ± 2.8	15.2 ± 4.7	11.4 ± 3.7	7.7 ± 2.6
	15	23.0 ± 2.7	24.9 ± 1.6	28.3 ± 4.9	36.1 ± 3.2	27.2 ± 6.1	15.3 ± 1.4	12.1 ± 1.9	19.3 ± 5.8
D	0	1.8 ± 0.5	0	0	0	39.3 ± 6.8	0	0	0
	0.5	5.2 ± 1.0	4.7 ± 0.7	6.6 ± 1.4	4.8 ± 1.0	50.2 ± 10.3	28.9 ± 7.1	17.2 ± 3.2	18.7 ± 3.4
	1	15.1 ± 1.5	8.6 ± 1.0	6.6 ± 1.7	7.0 ± 1.2	27.9 ± 4.0	13.1 ± 2.2	11.8 ± 1.4	20.1 ± 4.0
	3	17.9 ± 2.9	15.9 ± 2.0	12.6 ± 2.1	17.4 ± 2.8	49.1 ± 9.1	29.1 ± 3.6	27.9 ± 3.1	44.0 ± 8.1
	10	11.6 ± 2.6	10.6 ± 2.2	10.3 ± 1.5	6.9 ± 1.5	24.3 ± 2.7	19.6 ± 4.4	11.2 ± 3.4	12.2 ± 4.6
	12	13.6 ± 3.0	13.9 ± 1.0	16.4 ± 2.7	12.8 ± 1.4	47.0 ± 3.6	28.7 ± 3.8	23.7 ± 6.3	25.7 ± 3.2
	15	43.4 ± 2.5	53.6 ± 4.3	50.4 ± 3.0	44.6 ± 4.6	12.8 ± 3.0	14.6 ± 3.3	14.0 ± 1.9	12.6 ± 2.9

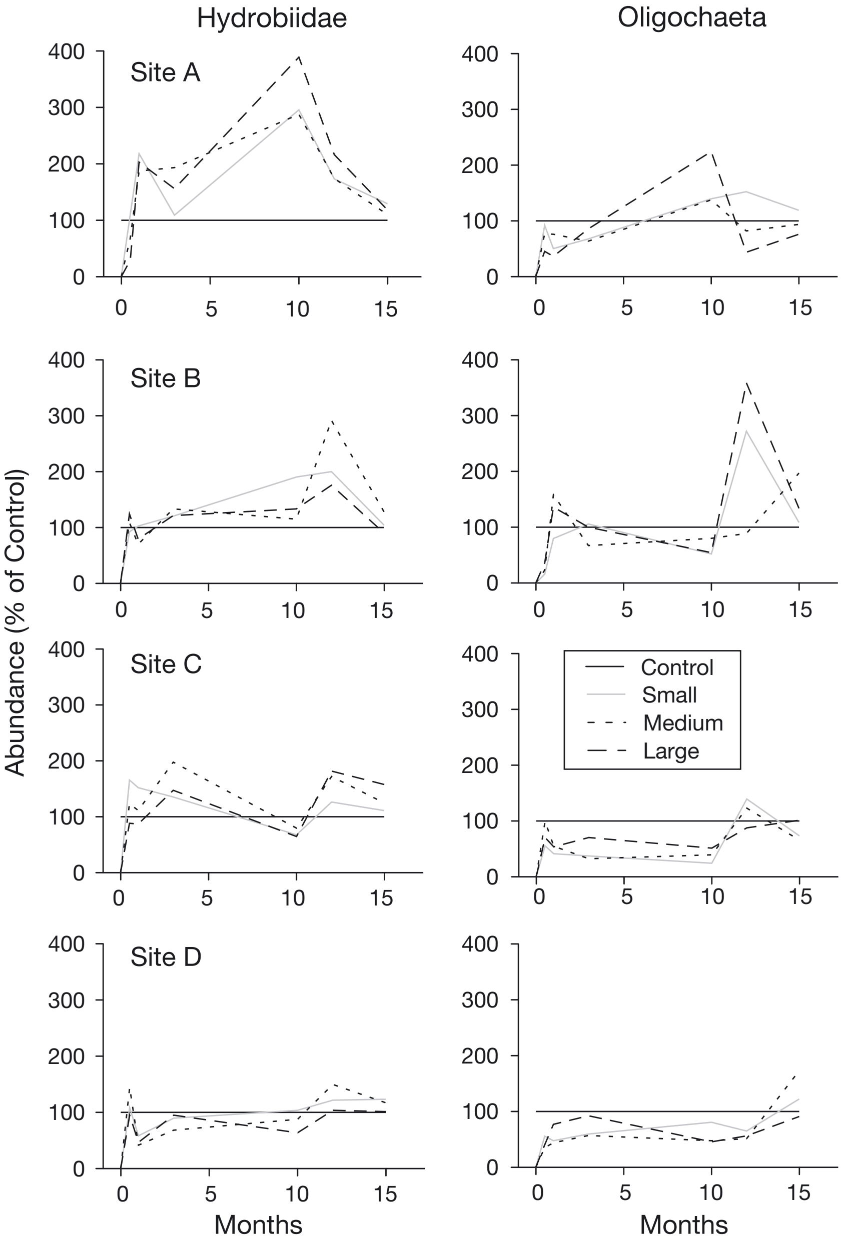

Fig. 2. Abundance of Hydrobiidae (left panels) and Oligochaeta (right panels) at Sites A to D (top to bottom panels) in different treatments over time after disturbance (0 = end of July), expressed as the average of the percent of the Control in the 3 blocks. See Table 2 for actual abundance values

apparent (Table 3). Hydrobiidae rapidly colonised disturbed plots at all sites. In addition, they exhibited opportunistic responses to the disturbance, which were most pronounced at the most sheltered site (Site A) and then gradually disappeared towards the most exposed site (Site D) (Fig. 2). At Site A, Hydrobiidae exhibited an opportunistic overshoot of up to 400 % (cf. Control and Large plot densities). Averaged over all the disturbed treatments and 1 to 15 mo of recovery, the abundance of Hydrobiidae in the disturbed treatments was 198, 137, 127 and 92 % of the Control abundance at Sites A, B, C and D, respectively, i.e. the mudsnails exhibited a decreasing opportunistic response with increasing exposure. Overall, the highest abundances of Hydrobiidae at Site A were found in the Large and Medium plots, with the persistence of the opportunistic response increasing with scale. At the other sites the differences between Small, Medium and Large plots were relatively small for Hydrobiidae.

Oligochaeta did not exhibit a strong opportunistic response, and at the more exposed sites, remained below Control levels until 1 yr after the disturbance (Fig. 2). Averaged over all the disturbed treatments and 1 to 15 mo of recovery, the abundance of Oligochaeta in the disturbed treatments was 97, 132, 67 and 74 % of the Control abundance at Sites A, B, C and D, respectively, i.e. the recovery of the infaunal Oligochaeta was clearly delayed compared with the epifaunal Hydrobiidae. Again, the effect of the scale of disturbance was minor. No significant correlation was found between abundances of Hydrobiidae and Oligochaeta in any of the treatments, at any site or any time ($p > 0.05$).

Variance-to-mean ratios, patchiness and aggregation

Variance-to-mean ratios of the abundances of Hydrobiidae and Oligochaeta were calculated for each plot (3 replicate cores) and the average of these was plotted for each treatment over time (Fig. 3). Hydrobiidae had highly aggregated patterns (variance-to-mean ratio $\gg 1$) in the disturbed treatments at Site A, where the mudsnails exhibited opportunistic responses. Ratios were generally lower in the Control plots throughout the 15 mo experiment. Similar patterns were found at Site B. These patterns changed when moving towards the more exposed sites. At Site C differences between treatments were smaller (except for the last sampling occasion) and, in contrast to the 2 more sheltered sites, the mudsnails were comparatively more aggregated in the Control plots compared to the disturbed plots at Site D. This indicates that broader-scale physical factors, i.e. waves, currents and sediment transport, resulted in a more

Table 3. Significance of Site, Treatment, Time within Site and interaction effects on the abundance of Hydrobiidae and Oligochaeta (generalised linear model)

Factor	df	χ^2	p
Hydrobiidae			
Site	3	1655.24	0.0001
Treatment	3	165.28	0.0001
Time(Site)	20	61184.40	0.0001
Site × Treatment	9	407.47	0.0001
Treatment × Time(Site)	60	3424.16	0.0001
Oligochaeta			
Site	3	14353.11	0.0001
Treatment	3	3504.02	0.0001
Time(Site)	20	20381.74	0.0001
Site × Treatment	9	835.44	0.0001
Treatment × Time(Site)	60	9585.27	0.0001

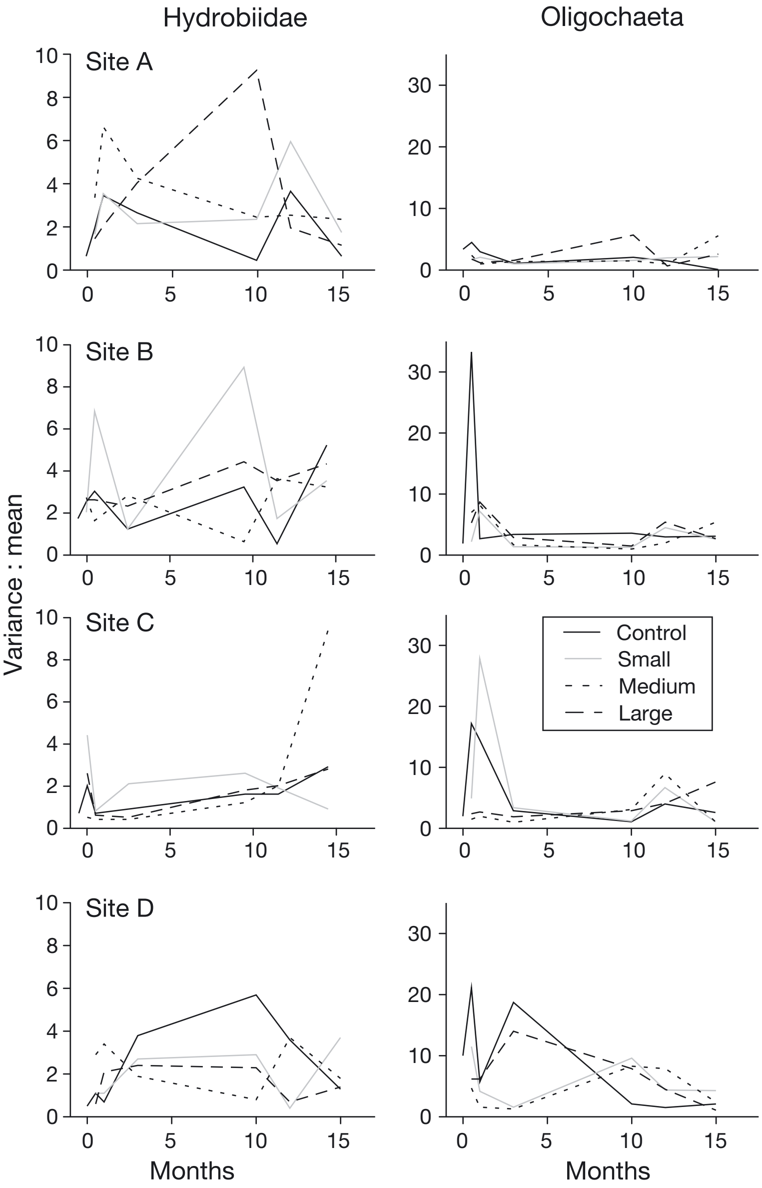

Fig. 3. Variance-to-mean ratios of Hydrobiidae (left panels) and Oligochaeta (right panels) at Sites A to D (top to bottom panels) in different treatments over time after disturbance (0 = end of July). Note the different scales for Hydrobiidae and Oligochaeta

homogeneous recolonisation of the disturbed plots at Sites C and D compared to the more sheltered Sites A and B.

Oligochaeta exhibited contrasting patterns, with the lowest levels of aggregation at Site A and then clearly higher levels of aggregation and stronger differences between treatments over time towards Site D. No consistent differences between treatments were observed, indicating that factors other than those directly related to wind-wave exposure were more important in driving spatial patterns in this infaunal group compared with the epifaunal Hydrobiidae.

Size frequency distribution of Hydrobiidae

The size frequency distribution of Hydrobiidae was assessed in Control and Large plots for the extremes on the exposure gradient, i.e. the most sheltered (Site A) and the most exposed site (Site D). These 2 sites had similar levels of sediment chl *a*, but contrasting grain size (Table 1). Size frequency distributions differed between treatments and between sites (Fig. 4). After 1 mo, patterns were similar at both sites, with a dominance of smaller size classes overall and very few larger individuals in the Large plots (Kolmogorov-Smirnov tests, differences between Control and Large plots: Site A: $D = 0.254$, $p = 0.007$; Site D: $D = 0.191$, $p = 0.065$). For example, at Site A 78% of the individuals in the Control plots were <1.2 mm, whereas in the Large plots 97% were <1.2 mm. Corresponding values for Site D were 74% and 87% in Control and Large plots, respectively. After 3 mo, the dominance by smaller size classes persisted at Site A, although at this time no significant difference between Control and Large plots was detected ($D = 0.113$, $p = 0.219$). At Site D, however, the size structure had become more even in both Control and Large plots (Fig. 4), but again with no significant difference between the treatments ($D = 0.133$, $p = 0.136$). Size patterns in Small and Medium plots mirrored the Large plots at both sites (data not

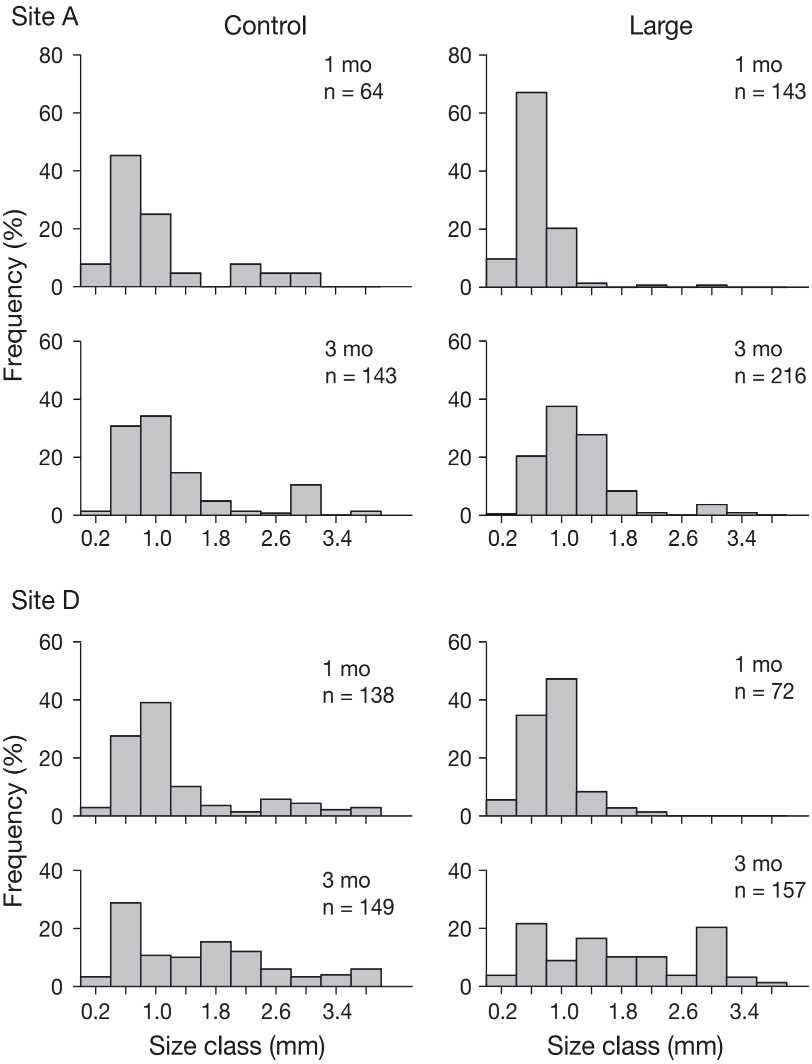

Fig. 4. Size frequency distribution (%) of Hydrobiidae in Control (left panels) and Large (right panels) plots 1 mo and 3 mo after disturbance at the most sheltered (Site A, top 4 panels) and the most exposed site (Site D, lower 4 panels). The 3.8 mm size class includes all mudsnails >3.8 mm shell length

shown). The size distribution of Hydrobiidae in Control plots differed between the 2 sites at both 1 and 3 mo (1 mo: $D = 0.250$, $p = 0.009$; 3 mo: $D = 0.281$, $p < 0.0001$). No significant differences between treatments were found at either site at any of the subsequent sampling occasions ($p > 0.05$).

Relative dispersal rates

Differences in dispersal potential can help explain differences in recovery patterns between taxa. Relative dispersal rates estimated with bedload traps (ind. trap^{-1} d^{-1} ind. core^{-1}) were in general higher in Hydrobiidae compared with Oligochaeta, here again exemplified by results from 1 and 3 mo after disturbance (Fig. 5). At Site A relative dispersal rates for Hydrobiidae were higher in Control compared with Large plots (2-way ANOVA: Treatment: $F_{1,12} = 15.45$, $p = 0.0020$; Time: $F_{1,12} = 0.54$, $p = 0.4734$; Interaction: $F_{1,12} = 1.15$, $p = 0.3041$). The lower dispersal over Large plots was most likely due to less foraging and more time spent feeding on the abundant microphytobenthos (visibly greener sediment in the disturbed plots). Correspondingly, it is likely that relatively more Hydrobiidae in the Control plots actively crawled into the traps in search of food. This difference between Control and Large plots decreased over time and was not significant at 3 mo ($p > 0.05$). Interestingly, the low relative dispersal rates of Hydrobiidae in the Large plots at Site A corresponded with opportunistic responses (i.e. high abundances) in the Large plots at both 1 and 3 mo. Similar patterns were observed at Site B (Treatment: $F_{1,12} = 7.59$, $p = 0.0176$; Time: $F_{1,12} = 3.07$, $p = 0.1054$; Interaction: $F_{1,12} = 5.53$, $p = 0.0366$). Also at Sites C and D, relative dispersal rates of Hydrobiidae were higher in Control compared with Large plots at 1 mo, with the difference decreasing at 3 mo, but these differences were not significant ($p > 0.05$).

Relative dispersal rates for Oligochaeta were generally lower, with no consistent pattern between sites or over time (Fig. 5). Overall relative dispersal at Site A was higher at 1 mo than at 3 mo (2-way ANOVA: Treatment: $p = 0.4712$; Time: $p = 0.0348$; Interaction: $p = 0.5608$), but no significant differences between treatments were observed at any of the sites. Nevertheless, in contrast to Hydrobiidae, relative dispersal in Oligochaeta was often higher (although not significantly) in Large plots compared with Control plots, suggesting fundamentally different response patterns between the 2 taxonomic groups. Since the number of traps per site was low (for logistical reasons), the power to detect significant differences was also low, but the results are nevertheless useful for helping to understand recovery patterns.

Stable isotopes of mudsnails and sediment

Stable isotopes of *Hydrobia ulvae* and surface sediment were measured in different plots at Site A during the first 3 mo of the experiment. No significant trends between treatments or over time were found for $\delta^{13}C$ in

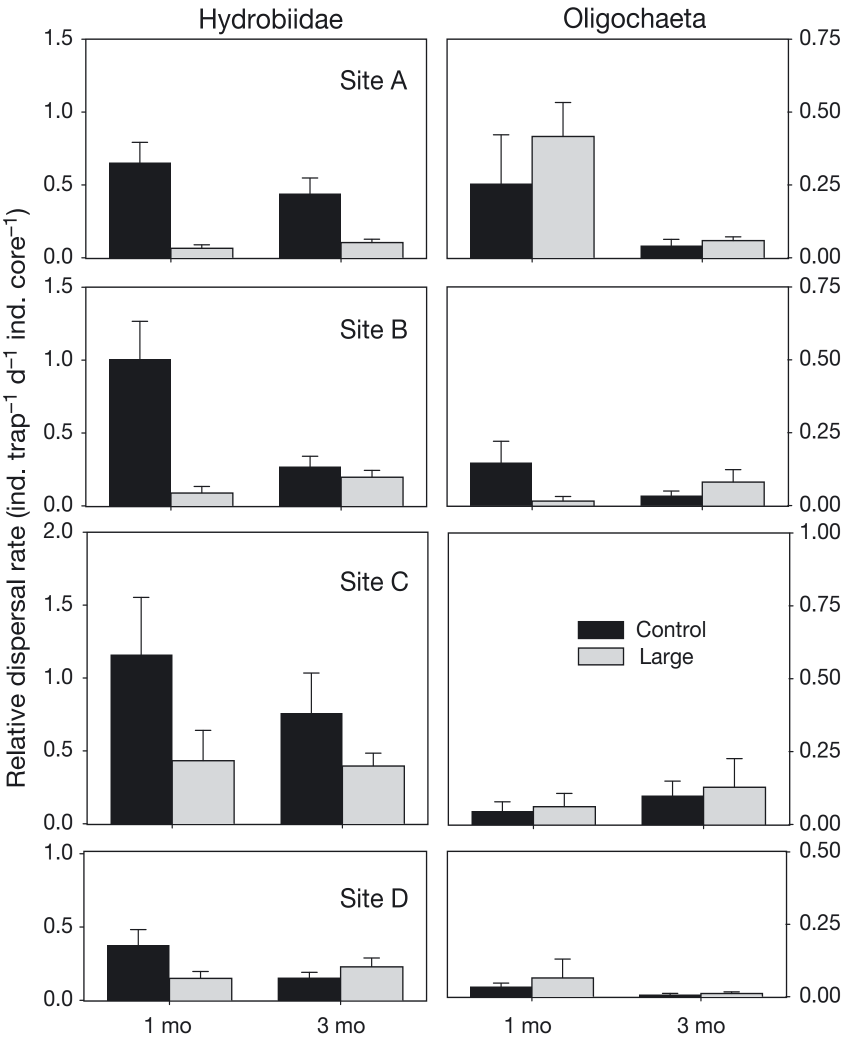

Fig. 5. Relative dispersal rates of Hydrobiidae (left panels) and Oligochaeta (right panels) at Sites A to D (top to bottom panels) in Control (n = 5) and Large (n = 3) plots 1 mo and 3 mo after disturbance. Note the different scales for Hydrobiidae and Oligochaeta

either *H. ulvae* or sediment, with average δ^{13}C values of −20.7 ± 0.5 and −22.3 ± 0.4, respectively. Differences between treatments and over time were small for both *H. ulvae* and sediment also for δ^{15}N. However, a significant trend of slightly higher δ^{15}N in both *H. ulvae* and sediment in the disturbed plots was found after 3 mo (Fig. 6), corresponding to the visual observations of stronger microalgal growth in the disturbed plots. The slightly higher δ^{15}N of the sediment in the disturbed plots indicates a greater proportion of recycled nitrogen in the disturbed plots and this was mirrored in the δ^{15}N of the *H. ulvae*, indicating that the mudsnails indeed are staying and feeding inside the disturbed plots, likely benefiting from the abundant microphytobenthos on the sediment surface (Fig. 6).

DISCUSSION

Disturbance events in coastal ecosystems are increasing in spatial and temporal extent, and the integrity of seafloor ecosystems is dependent on the inherent ability of the benthic communities to recover from these disturbances. We used a subtidal disturbance-recovery experiment with the aim of identifying the context-dependency and relative importance of the underlying mechanisms in the recovery process. Our results showed that recovery patterns after disturbance were indeed highly context-dependent, as patterns were both site- and taxon-specific (Fig. 7).

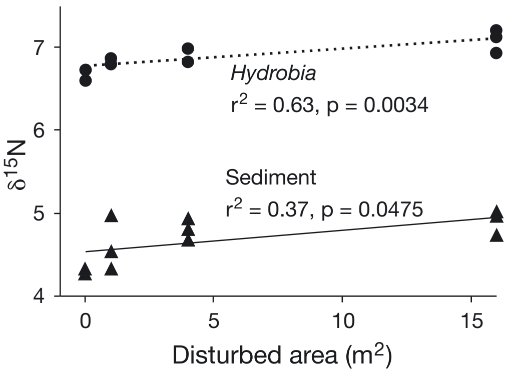

Fig. 6. Stable isotope signatures (δ^{15}N) in *Hydrobia ulvae* (●) and surface sediment (▲) across different-sized disturbed plots at Site A, the most sheltered site, 3 mo after disturbance. Results of linear regression analyses are reported

We predicted that recovery would be fastest at the most exposed site, with hydrodynamic forcing (waves, currents) aiding recolonisation. Contrary to predictions, however, initial increases (after 1 mo of recovery) in abundances and overall recolonisation rates were faster at the more sheltered sites, particularly for the surface-dwelling Hydrobiidae. This was likely due to high microphytobenthic production (resulting from disturbance-induced release of sediment nutrients), which to a greater extent remained in the disturbed plots at the sheltered sites, where it was efficiently colonised particularly by actively crawling Hydrobiidae. This release of resources thus facilitated the initial recolonisation and even produced a long-lasting overshoot in abundances compared with the Control

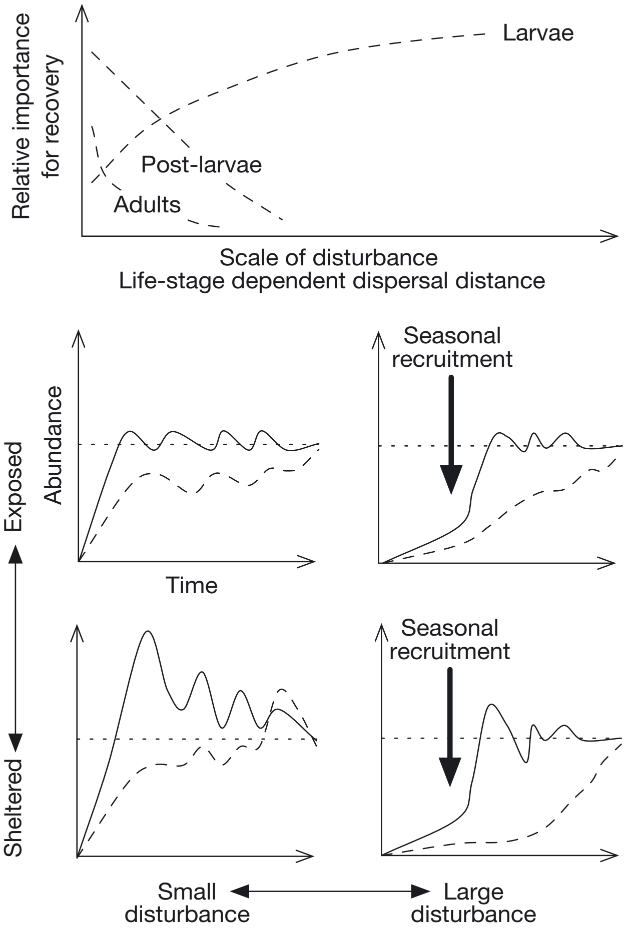

Fig. 7. Conceptual model of the relative importance of adults, post-larvae and larvae for the recovery dynamics after increasing spatial scales of disturbance (top panel). As the scale of disturbance exceeds post-larval dispersal ranges, the recovery becomes dependent on seasonal recruitment. Hypothetical recovery trajectories after disturbances in sheltered and exposed systems with low functional diversity (lower 4 panels) are exemplified by a mobile opportunistic species with planktonic larvae (——) and a sedentary brooding species (– – –). A normalised control community is shown (-----)

plots. Importantly, such an overshoot does not necessarily imply recovery, but rather is indicative of a prolonged disturbance effect (Norkko et al. 2006b, Van Colen et al. 2010). It is likely that these taxa would recover faster at more exposed sites if the scale of disturbance exceeded the range of post-larval dispersal.

In line with our predictions, the epifaunal Hydrobiidae recovered faster than the infaunal Oligochaeta, which can be attributed to the generally greater mobility of epifaunal taxa compared with infaunal taxa, and the tendency of Hydrobiidae to rapidly aggregate around patches of food and utilise abundant microphytobenthos (Norkko & Bonsdorff 1996a, Herman et al. 2000, Norkko et al. 2000). In a short-term experiment (5 d of recovery after drift algal disturbance, 0.25 m^2 plots), Norkko & Bonsdorff (1996a) also found that Hydrobiidae abundances recovered faster than Oligochaeta and also increased above abundances in ambient undisturbed areas, highlighting the differences in active versus passive dispersal/recolonisation between these 2 groups. The present experiment highlights that these are not transient patterns but may persist for over a year. Importantly, they may also be highly site-dependent. The relative dispersal rates also indicated that Hydrobiidae were more mobile than Oligochaeta. Many species of Oligochaeta reproduce asexually, lack a planktonic larval stage or are brooders, although some adults may migrate by swimming in response to resource depletion (Nilsson et al. 2000). This reproductive behaviour could also partly explain the slower recovery in Oligochaeta, but the rapid influx of Hydrobiidae may have interfered with the establishment of juvenile Oligochaeta on the sediment. Oligochaeta recovery may, however, be rapid in patches where egg capsules survive anoxic events and hatch (Norkko & Bonsdorff 1996a). Our experiment did not start until just after the main seasonal recruitment peak, so post-larval dispersal was likely the main mechanism of recolonisation for both Oligochaeta and Hydrobiidae, until possible larval recruitment the following year. The timing of opening up our experimental plots to recolonisation also coincided with the seasonal maximum extent of drifting algal mats in the northern Baltic (Norkko & Bonsdorff 1996b). While the temporal variability of surface deposit feeders may also be greater than for subsurface feeders due to differences in the stability of food resources (Levinton & Kelaher 2004), these effects may be site-dependent, as indicated by the high degree of change in spatial aggregation over time of Hydrobiidae compared with Oligochaeta at the most sheltered site, while at the most exposed site we found the opposite pattern: Oligochaeta exhibited the lowest levels of aggregation at the most sheltered site and then more aggregation and stronger differences between treatments over time towards the more exposed sites (Fig. 3).

Interestingly, the Hydrobiidae exhibited marked opportunistic responses to the disturbance, which lasted for a whole year, particularly in the largest disturbed plots at the most sheltered site. The size structure analyses of Hydrobiidae showed that the opportunistic response was mainly driven by juveniles. However, for the population to be considered fully recovered, the proportion of adult individuals needs to increase in the recovering plots, as Cardoso et al. (2005) reported for *Hydrobia ulvae*, and which in the present study was observed after 3 mo of recovery (Fig. 4). Norkko et al. (2006b) found similar scale-dependent opportunistic responses to disturbance by the amphipod *Corophium volutator* in intertidal areas on the Swedish west coast, also in connection with blooms of microphytobenthos in the disturbed areas.

Although the sediment was visibly greener in our disturbed plots, we were not able to quantitatively link the faunal responses to changes in sediment chl *a*, most likely due to the rather crude method of chlorophyll sampling, i.e. integrating over the top 1 cm, instead of targeting only the sediment surface. The lack of strong disturbance effects in the stable isotope signatures of *H. ulvae* and sediment indicates that the opportunistic patterns observed at Site A were not due to differences in the source of food between treatments, although the isotope results did indicate a greater proportion of recycled nitrogen in the disturbed plots. It is therefore likely that either increased food availability or release from competition or predation facilitated the opportunistic response, and that the mudsnails therefore preferentially spent more time in the disturbed plots, as also indicated by our relative dispersal rate patterns. Such interactions between localised resource inputs and mobile consumers may explain high spatial variability in the community (Levinton & Kelaher 2004).

Our findings thus highlight the importance of conducting relevant field experiments across environments, in order to aid our capability to predict community changes. Predicting abrupt change can be about defining threshold conditions in environmental stressors, but it is also about understanding the interactions between taxa that influence community dynamics. Our results also highlight the importance of including taxon-specific responses, and understanding natural-history characteristics of populations, when assessing the resilience of different benthic communities (Fig. 7). As the Hydrobiidae and Oligochaeta in this area are amongst the numerically dominant groups, their population dynamics and recovery rates and patterns are of importance for the trophic functioning of the coastal ecosystem. In addition, this system lacks large habitat modifiers or ecosystem engineers, which could potentially modulate the community response to disturbance (Zajac et al. 1998, Norkko et al. 2006a, 2006b, Van Colen et al. 2010).

Coastal marine ecosystems are affected by a combination of multiple human impacts (Costanza et al. 1997, Lotze et al. 2006) and one pressing issue is defining how close to a threshold a system is (Thrush et al. 2009). The multiple stressors influence species-habitat relationships, which in turn change along natural environmental gradients. Therefore location × treatment interactions are common in experimental studies. Although experiments for logistical reasons are often conducted in one location only, this significantly limits the generality of the findings (Thrush et al. 2000). By using locations arrayed along relevant environmental gradients, however, it is possible to quantify why these locations respond differently (Hewitt et al. 2007). It is also necessary to consider which spatial scales the different factors involved in the recovery process operate and interact over (Zajac et al. 1998). Disturbance may release resources, which have transient or longer-lasting effects on the communities depending on the different species' abilities to exploit them (Kelaher & Levinton 2003, Holt 2008, Van Colen et al. 2010). Disturbance also creates patchy communities, in both time and space, with threshold effects likely when the scale of disturbance exceeds post-settlement dispersal ranges of the key species (Fig. 7). Although some scale-dependent recovery patterns were observed in our experiments for the bivalve *Macoma balthica* (A. Norkko et al. unpubl.) for example, no long-lasting threshold responses over the spatial scales of disturbance we studied here were apparent for Hydrobiidae or Oligochaeta, most likely because the spatial extent of the disturbance was still relatively limited and within the potential range of post-larval, juvenile or adult dispersal along the sediment surface (either active movement or with the sediment bedload transport). A threshold or shift in mechanisms of recovery will therefore likely occur when the disturbance exceeds post-larval dispersal potential and becomes dependent on seasonal recruitment of planktonic larvae (Fig. 7). In line with our predictions, we found that the importance of small-scale, local and biological factors in the recovery process was greater at the sheltered sites, while there was a switch to greater importance of physical, broader-scale, regional factors at the more exposed sites (e.g. waves, currents). A sudden shift in the interactions between these factors was however not identified, as the factors changed gradually along the environmental exposure gradient. Context-dependency and generality are often viewed as opposing forces, but incorporating the shifts in the relative importance of different biological and physical factors in driving recovery patterns and understanding the underlying mechanisms of context-dependent patterns will help inform our understanding and prediction of generality and potential thresholds in disturbance-recovery dynamics.

Thresholds in community structure or functioning are reached when recovery patterns after disturbance are sufficiently perturbed (Thrush et al. 2009). For example, in the Baltic Sea, the low salinity limits the number of species available for recolonisation and due to low functional redundancy, such a species-poor system affected by increasing hypoxia is potentially continuously close to a resilience threshold. Recovery to the same depauperate community after hypoxia may be relatively rapid in a degraded system characterised by small, rapidly growing species (Thrush & Whitlatch 2001, Troell et al. 2005), and recovery is thus easier to predict in a low-diversity system (Fig. 7). In a more diverse system, disturbance may result in dramatic shifts in species composition, as there are greater ranges in life-history characteristics and recolonisation potential. A more diverse system, with overlapping and seemingly redundant functions, does theoretically have an overall greater resilience (Peterson et al. 1998). In both kinds of systems, a slowing rate of recovery may be a sign of declining resilience in the system and may foreshadow an approaching threshold condition and subsequent regime shift (van Nes & Scheffer 2007).

Information on natural-history characteristics and functional diversity in the communities and gradients in environmental conditions should all be used to make informed predictions about changes in the resilience of coastal ecosystems. Also, the importance of *in situ* measurements and interdisciplinary field experiments for understanding benthic ecosystem function should be stressed, as the interactions between the fauna, the sediment and the environment are complex and context-dependent, with potential for highly nonlinear responses to environmental change (Norkko et al. 2006b, Van Colen et al. 2010). The challenge is still to move from hindsight to more predictive science (Thrush et al. 2009) and it is clear that modelling efforts will need to include and synthesise information gathered from numerous empirical studies, conducted in a wide range of environments.

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Empirical evidence of an approaching alternate state produced by intrinsic community dynamics, climatic variability and management actions

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ABSTRACT: A major challenge to ecologists is identifying factors that make a system susceptible to regime shifts or state transitions. Theory and modelling have suggested a number of indicators to warn of approaching tipping points, but empirical tests of their validity are few. We tested 2 indicators, change to a key species and increased temporal variability, in a harbour, a system type rarely studied for regime shifts and alternate states. Long-term monitoring over 20 yr on a number of intertidal sandflats allowed us to document change and determine potential contributing factors. We detected decreasing abundance in the key species and increased temporal variability (flickering) of community composition before a trophic and functional change to an alternate community type. Detection of these indicators occurred despite cyclic patterns in community and population dynamics and a relatively fast and permanent change of one external condition (nutrients). We provide evidence that this shift was the product of a relatively small change in management of sewage disposal, combined with climate dynamics and mediated through changes in a key species, a tubeworm that provides biogenic habitat structure, stabilises sediment and affects dispersal and recruitment. These factors all interacted to escalate the effect of the relatively small changes in nutrients across a tipping point.

KEY WORDS: Tipping point · Thresholds · Key species · Regime shift · Macrofauna

INTRODUCTION

In the last 2 decades there has been increased documentation of regime shifts in ecological systems. These phenomena occur when a system passes a threshold and fundamentally changes in structure and function (Hughes et al. 2005, de Young et al. 2008). Now, however, the challenge has shifted from documenting shifts to identifying factors that make a system susceptible to rapid changes in a world of multiple stressors and non-linear dynamics. A strict mathematical evaluation of the size of the basins of attraction needed to mathematically define alternative states in ecological systems might be difficult for natural systems where observational and process noise are present (Sugihara 1994). Nevertheless, 2 promising indicators of impending regime shifts or state change are large changes in the abundance of key species (Thrush et al. 2009) and increased temporal variability (flickering; Oborny et al. 2005, van Nes & Scheffer 2005, Carpenter & Brock 2006, Scheffer et al. 2009) in key factors that drive ecosystem dynamics. However, empirical tests of such indicators are rare.

Regime shifts in marine systems are commonly documented for coastal and shelf-depth systems (Edwards & Richardson 2004, Ware & Thomson 2005, Casini et al. 2009) rather than estuarine and harbour systems. This is surprising given the degree of anthropogenic activity that has impacted estuarine and harbour ecosystems over human history (Thrush et al. 2004, McCormick-Ray 2005, Altieri & Witman 2006, Lotze et al. 2006). Although these are easy marine ecosystems to sample, part of the problem is the practicality of collecting broad-scale ecological data with a historical focus on point-source impacts, rather than cumulative and broad-scale change. While the major agents of

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change in estuaries worldwide (fishing, nutrient and sediment loading and habitat change) are generally considered to occur along spatial gradients, the potential for cumulative effects and multiple stressor interactions is high, with such interactions likely to result in sudden rather than gradual change (Thrush et al. 2008a,b, Thrush & Dayton 2010).

Key species sensitive to a stressor may affect resilience and precipitate large changes (Thrush et al. 2009). Species that dominate local function are known from many systems, with individual species driving ecosystem responses. Such species may not characterise all elements of functional performance, but their importance can be easily quantified. In soft-sediment habitats, common in estuarine systems, changes in species that influence sediment stability or nutrient processing are thought to result in major shifts in ecosystem performance and the ability of the system to resist stress (Lohrer et al. 2004, Norkko et al. 2006, van Nes & Scheffer 2007). For example, the loss of suspension-feeding bivalves has been suggested to profoundly change trophic relationships and ecosystem function (Nichols et al. 1986, Airoldi et al. 2008). Species that create structure in what would otherwise be a homogenous plain of mud and sand are important in modifying boundary flows and sediment transport and creating habitats for other organisms (Thrush 1991, Zajac et al. 2003, Levin & Dayton 2009). In particular, polychaete tube mats have been shown to be important to benthic community composition and sediment stability (Fager 1964, Mills 1969, Levin 1982, Noji & Noji 1991, Thrush et al. 1996, Friedrichs et al. 2000). However, functionally important species, even when dominant, are not necessarily resistant to stress (Allison 2004, Schiel et al. 2006), and interactions between anthropogenic and natural change are increasingly being reported (e.g. van de Koppel et al. 2001, Cranfield et al. 2003, Frank et al. 2005, Coco et al. 2006, Heithaus et al. 2008, Casini et al. 2009, Volkenborn et al. 2009).

Detecting change in any natural ecosystem must be done against a background of variability, and to date, the usefulness of increased temporal variability as an indicator of an approaching threshold has been demonstrated only by numerical simulation (Carpenter 2003, Carpenter & Brock 2006). Empirical time series are generally considered too noisy for this concept to be of use (Collie et al. 2004, de Young et al. 2008, but see Zaldivar et al. 2008). Estuaries, in particular, have for a long time been considered highly dynamic due to temporal variation in environmental conditions. Nevertheless, stable, resilient communities at multiple sites over time scales that exceed the life span of many common macrofaunal species were detected in a harbour ecosystem (Manukau Harbour, 37° 57′ S, 174° 42′ E) on the west coast of New Zealand, despite climate-driven interannual variability in wind-wave disturbances (Turner et al. 1995). Since then, continual bimonthly monitoring over 20 yr (1987–2007) at 2 sites (AA and CB, Fig. 1) demonstrate ongoing stability, despite temporal dynamics in a number of the species being related to the El Niño Southern Oscillation (ENSO) (Hewitt & Thrush 2009b).

However, at a third site (CH, Fig. 1), monitored bimonthly between 1987–1996 and 1999–2007, a marked shift in community composition occurred after cessation of oxidation pond discharge in April 2001. The shortest distance from the monitored site to the discharge point was 7 km which, given the complexity of harbour hydrodynamics and the timing of discharge from the oxidation ponds, represents a minimal distance. The oxidation pond discharge had been a low level source of enrichment for over 20 yr. Prior to the cessation in oxidation pond discharge, this large sandflat (3 km^2) was dominated by the tube-mat forming polychaete *Boccardia syrtis* which disappeared post-cessation. Tube-mat forming macrofauna, when densities are high, can play significant roles in soft-sediment habitats. Specifically, *B. syrtis* performs important functions in stabilising sediment and influencing the dispersal of post-settlement individuals (Cummings et al. 1996, Thrush et al. 1996), and a previous survey in Manukau Harbour suggested a response to the slight enrichment provided by the sewage discharge (Ellis et al. 2000). Cessation also decreased water column nutrients and chlorophyll *a* (chl *a*) (Wilcock & Martin 2003). Thus, we anticipated that the lowered organic content would result in a decreased tube-mat and concomitant changes in community structure and function to an alternate state. The major question asked of the data was whether we

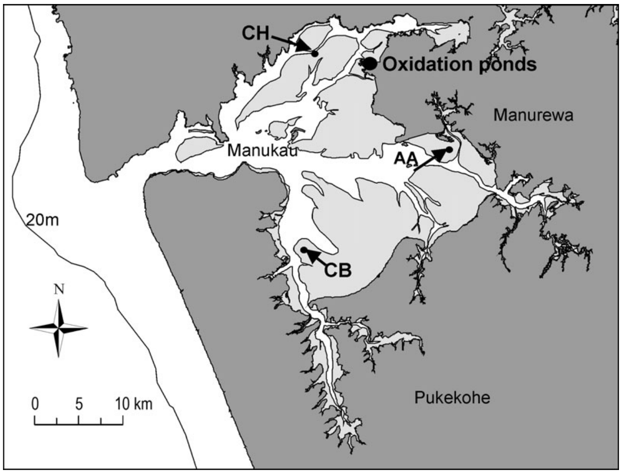

Fig. 1. Location of sites (CH, AA and CB) and sewage discharge (oxidation ponds) in the intertidal part of Manukau Harbour (shaded light grey), New Zealand

would observe increased temporal variability in community composition before this trophic and functional change occurred.

MATERIALS AND METHODS

Sampling was conducted at three 9000 m^2 sites within Manukau Harbour (349 km^2), with sites >10 km apart (Fig. 1). The sites were all situated on large, relatively homogeneous, intertidal sandflats at the mid-tide level, whose physical appearances were reasonably similar across the sites. Manukau Harbour has 2 main hydrodynamic areas: the southern half, within which AA and CB are located, and the northern half, where CH is located. Two of the sites (AA and CB) were sampled every 2 mo between October 1987 and February 2003. The other site (CH) was sampled every 2 mo between October 1987 and October 1996 and then again between April 1999 and February 2007.

Twelve replicate cores were taken from each site on each sampling occasion in the following way. The site was divided into 12 equal area sectors and 1 core sample (13 cm diameter, 15 cm depth) was taken from a random location within each sector. To limit the influence of the small-scale spatial autocorrelation (Thrush et al. 1989) and preclude any localised modification of populations by previous sampling events, core samples were not positioned within a 5 m radius of each other or any samples collected in the preceding 6 mo.

After collection, the macrobenthos were separated from the sediments by sieving (500 µm mesh) and preserved with 70% isopropyl alcohol in seawater. Macrofauna were then identified to the lowest practical level (generally species), and counted. Taxon abundances from all replicates taken at a single time and site were averaged.

Non-metric multidimensional scaling on Bray-Curtis similarities based on untransformed data was used to graphically represent changes in communities at the 3 sites over time. Differences in community composition between different periods were assessed using analysis of similarities (ANOSIM) using PrimerE (Clarke & Gorley 2006) for each site separately. Temporal variability in community compositions was assessed for each year using average Bray-Curtis dissimilarities (similarity percentage [SIMPER]; PrimerE; Clarke & Gorley 2006) and the index of multivariate dispersion (PrimerE; Warwick & Clarke 1993) based on square root-transformed data.

From 1999 to 2007, the following variables were available (as monthly point measurements) that were likely to respond to the change in wastewater treatment: water column ammoniacal-nitrogen, nitrate-nitrogen, soluble and total phosphorus and dissolved oxygen concentrations; and sediment chl *a* concentrations. Two measures of ENSO were also available: the Southern Oscillation index (SOI; Troup SOI, see www.bom.gov.au/climate/glossary/soi.shtml; McBride & Nicholls 1983); and Z1, an index of atmospheric pressure variation across New Zealand that encapsulates the strength of the westerly winds (Salinger & Mullan 1999). These ENSO measures were converted to 2 yr moving averages as they proved most useful in predicting temporal variations in species abundances (Hewitt & Thrush 2009b). Cross correlation analysis was used to determine the lag period between these variables and the abundance of common taxa. These variables were included as explanatory variables, along with the abundance of *Boccardia syrtis*, in multiple regressions predicting the abundance of common taxa and in a redundancy analysis. Forward selection was used to determine the important environmental variables for the canonical correspondence analysis. Variables were eliminated from regression models using backwards selection with an exit value of $p > 0.15$ (Crawley 1993). Initially, multiple regressions included an autoregressive term; however, this was never significant. Model variables were also permuted and end models checked for best fit using adjusted r^2 and Akaike's Information Criterion values. Co-linearity diagnostics and variance inflation factors were examined (Belsley et al. 1980), homogeneity of variance was evaluated by plotting residual versus predicted values and normality was assessed via normal probability plots. Log-transformations and Poisson error structures were used as required. The relative importance of variables in the final models to the predicted species abundance was assessed using their standardised slope estimates.

RESULTS

Community dynamics

Stable communities were observed at the 2 continuously monitored sites within the harbour (AA and CB), with no significant differences observed between the time periods 1987–2000 and 2003–2007 ($p > 0.05$). The ordination space occupied by the full time series was only slightly greater than that apparent in the first 5.5 yr of monitoring (Fig. 2). However, the ordination space occupied by the site near the oxidation ponds (CH) changed markedly, with community compositions of the time periods 1987–2000 and 2003–2007 being significantly different from each other ($p < 0.05$) (Fig. 2). Immediately after the cessation (2001–2002), the community composition swung between the initial and new states and was not significantly different from

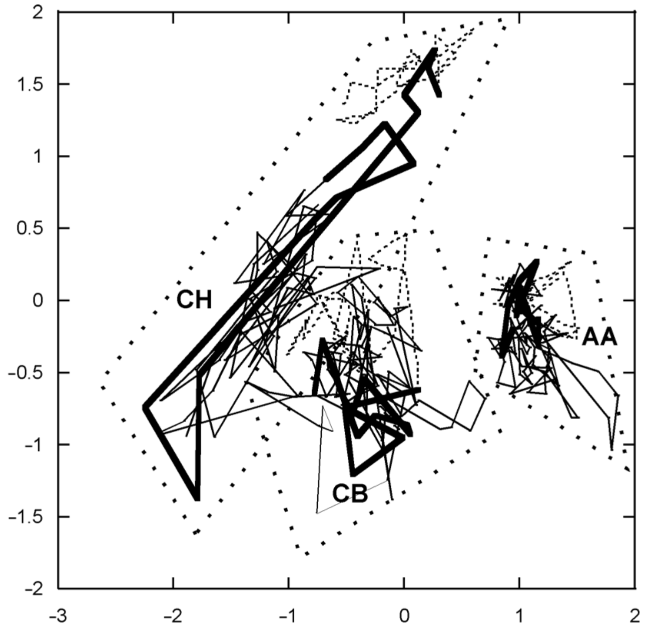

Fig. 2. Ordination space covered by community data for all sites. Sampling times between 1987 and 2000 are connected by thin lines, 2001 and 2003 are connected by thick lines and 2003 and 2007 are connected by dotted lines. The area covered by each space is delineated by a thick dotted line

either time period ($p > 0.05$). Importantly, this transition phase encompassed more of the ordination space, emphasising high community variability, than either the initial or new phase.

The increased temporal variability at CH apparent in the ordination plot, for the 2 yr immediately after the management action (Fig. 2), is endorsed by significant increases in within-year dissimilarity and multivariate dispersion ($p = 0.001$ and 0.012, respectively) (Fig. 3). The new community state was less temporally variable than the initial community.

The community pre-2001 was dominated by the tube-mat forming *Boccardia syrtis*, which exhibited both seasonal and multi-year temporal variation (Fig. 4). A number of other polychaetes and juveniles of the bivalve *Macomona liliana* were also numerically dominant (Table 1). Interface feeders (species that switch feeding mode between suspension and deposit feeding), deposit feeders, predators/scavengers and suspension feeders were all represented in the 10 most dominant taxa, with average numbers of 61, 20, 12 and 7 individuals per core, respectively. Immediately after the management action, species composition and the functional traits of the community changed somewhat (Table 1), with average abundances of interface feeders, deposit feeders, predators/scavengers and suspension feeders in the top 10 dominant taxa being 53, 25, 8 and 12 individuals, respectively. A number of species, mainly crustaceans, became highly temporally variable in abundance. Finally, a new community stabilised, dominated by a mix of deposit-feeding polychaetes and crustaceans, with some juveniles of the deposit-feeding bivalve *Soletellina siliqua* (Table 1). A major change in habitat occurred: from the tube-worm dominated state to one of destabilized sediment, with few protruding structures and surficial pits and holes, dominated by deposit feeders (average of 87 individuals in top 10 most dominant taxa). A trophic shift also occurred, with no interface or suspension feeders occurring in the top 10 taxa.

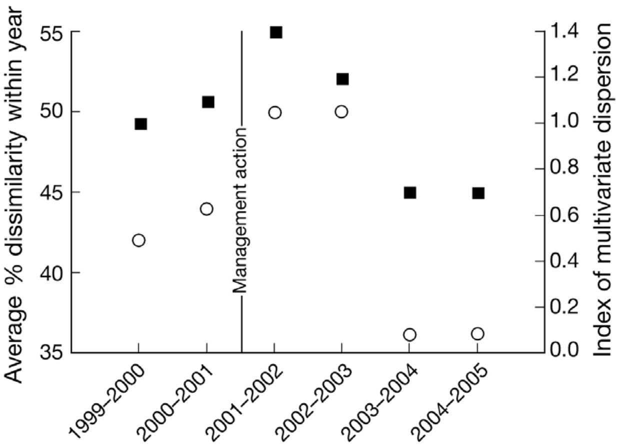

Fig. 3. Annual temporal variability in community structure, calculated as (○) average Bray-Curtis % dissimilarity and (■) index of multivariate dispersion from April to February, based on square root-transformed data at Site CH before and after the management action

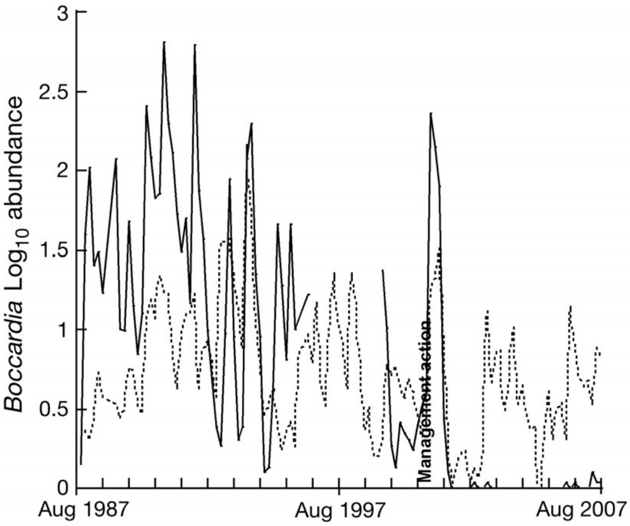

Fig. 4. *Boccardia syrtis*. Time series of abundances (log$_{10}$-transformed) at the 2 sites at which it was abundant, (——) site CH and (······) site CB

Table 1. Characteristics of the 10 most abundant taxa found during 3 different time periods: initial (1987–2000), between (2001–2002) and post (2003–2005) cessation of oxidation pond discharge. Abundance is given followed by the rank in parentheses. –: Zero abundances

Taxon	Habitat	Feeding mode	Period		
			Initial	Between	Post
Boccardia syrtis	Tube-dweller	Interface (mainly deposit)	1114 (1)	454 (1)	–
Heteromastus filiformis	Mobile, all sediment depths	Deposit	262 (2)	21 (7)	10 (8)
Nemerteans	Mobile, all sediments	Predator/scavenger	106 (3)	36 (6)	40 (3)
Sphaerosyllis semiverricosa	Mobile, all sediments depths	Predator/scavenger	96 (4)	–	–
Euchone sp.	Tube-dweller	Suspension	65 (5.5)	110 (2)	–
Magelona dakini	Mobile, sediment depths <2 cm	Deposit	65 (5.5)	95 (3)	316 (1)
Tanaidacea	Mobile	Suspension	48 (7)	–	–
Macroclymenella stewartensis	Tube-dweller	Deposit	45 (8)	19 (8)	34 (4)
Macomona liliana	Limited mobility	Interface (mainly deposit)	36 (9.5)	11 (10)	–
Glycinde trifida	Mobile, all sediment depths	Predator/scavenger	36 (9.5)	–	–
Paracalliope novaezelandiae	Mobile, surface-dweller	Deposit	–	67 (4)	–
Colurostylis lemerum	Mobile, surface-dweller	Desposit	–	40 (5)	43 (2)
Toridoharpinia hurleyi	Mobile, surface-dweller	Scavenger	–	15 (9)	–
Soletellina siliqua	Limited mobility, surface deposit feeder	Deposit	–	–	20 (5)
Mysidacea	Limited mobility, surface-dweller	Deposit or predator/scavenger	–	–	19 (6)
Waitangi brevirostris	Mobile, all sediment depths	Deposit	–	–	16 (7)
Syllis spp.	Mobile, all sediment depths	Predator/scavenger	–	–	8 (9)

Interestingly, the previous dominant species did not necessarily become more temporally variable, partly because many of them already had pronounced seasonal and multi-year cycles (Hewitt & Thrush 2007). However, 27 % of species that had been previously low in abundance (mean < 1 individual per core) now exhibited erratically higher abundances (i.e. increased mean and standard deviation). Many species, including some of the initial dominants, did not appear during the same seasons in which they were previously abundant. Species richness was markedly lower in the new community: annual average number of species varied from 35.2 to 42.3 in the initial years, 36.2 and 31.8 immediately prior to and after cessation, respectively, and 18.8 to 23.2 thereafter. The number of infrequently occurring taxa did not change, although most of these that were present during the initial period disappeared and were replaced by new species, 25 % of which did not stabilise into the new community.

Table 2. Concentrations (mean ± SE) of sediment chlorophyll *a* (chl *a*) and water column nitrate, ammonium and soluble phosphorus found during 3 periods: initial (1987–2000), between (2001–2002) and post (2003–2005) cessation of oxidation pond discharge. For sediment chl *a*, values are only available from 1999

Period	Sediment chl *a*	Water column		
		Nitrate	Ammonium	Phosphorus
Initial	17.5 ± 3.1	0.20 ± 0.07	0.37 ± 0.07	0.11 ± 0.007
Between	10.7 ± 0.4	0.10 ± 0.02	0.08 ± 0.02	0.10 ± 0.03
Post	7.7 ± 0.5	0.09 ± 0.01	0.08 ± 0.01	0.06 ± 0.005

Potential drivers of changes in population dynamics

Changes in water column nutrients and chl *a* content consistent with decreased sewage input were recorded in the vicinity of Site CH (Table 2; Wilcock & Martin 2003), and many of the changes in species abundances were to species expected to respond to such changes. For example, suspension feeders could be expected to decrease with decreases in water column chl *a*, and key polychaetes (e.g. *Boccardia syrtis* and *Heteromastus filiformis*) should also respond negatively to subtle decreases in organic loading (Ellis et al. 2000).

The redundancy analysis demonstrated that 66 % of the variability in community composition could be explained by the 2 ENSO variables, sediment chl *a* content, water column nitrate concentrations and $\log_{10}$-transformed densities of *Boccardia syrtis*. The canonical axes were significant at a p-level of 0.002.

Multiple regressions revealed that temporal variation in the abundance of only one species (*Colurostylis lemerum*) was not explainable by any of the predictor variables. Significant predictors for other species included variables reflecting changes in ENSO, the wastewater treatment or the abundance of *Boccardia syrtis* (Table 3). None of the species had ENSO variables alone selected as important predictors. Four of the species did not have *B. syrtis* abundance as an important predictor; for the others, the relative importance of *B. syrtis* relative to the other predictors varied from 20 to 100 %.

Table 3. R^2 and relative importance of variables predicting the abundance of species over time between 1999 and 2007 at Site CH for models using variables representing the El Niño Southern Oscillation (ENSO), changes to the wastewater treatment (sediment chlorophyll *a* [chl *a*]) and water column soluble phosphorus (SP), ammoniacal nitrogen [NH_4] and nitrate-nitrogen [NO_3]) and the $\log_{10}$ abundance of *Boccardia syrtis* (Boc). The relative importance of each variable was calculated from its standardised parameter estimate. –: Variable was not important. Full statistical results are in Appendix 1. All taxa common in one or more years were analysed

Taxon	R^2	ENSO	Chl *a*	SP	NO_3	NH_4	Boc
Colurostylis lemurum	<0.10	–	–	–	–	–	–
Orbinia papillosa	0.28	–	–	44.4	–	31.5	24.1
Aglaophamus macroura	0.37	30.5	69.5	–	–	–	–
Nucula hartvigiana	0.37	53.3	–	–	–	–	46.7
Waitangi brevirostris	0.40	30.9	–	30.9	–	38.2	–
Sphaerosyllis semiverricosa	0.41	–	–	–	–	15.4	84.6
Magelona dakini	0.42	20.0	–	–	–	–	80.0
Macroclymenella stewartensis	0.46	30.9	–	–	–	41.5	27.6
Austrovenus stutchburyi	0.48	13.8	–	29.6	42.1	14.5	–
Soletellina siliqua	0.48	20.5	–	–	79.5	–	–
Heteromastus filiformis	0.52	29.7	–	–	–	–	71.3
Owenia fusiformis	0.59	22.8	–	–	–	56.5	20.7
Macomona liliana	0.69	–	73.7	–	–	–	26.3
Euchone sp.	0.85	15.7	–	–	–	–	84.3
Glycinde trifida	0.78	–	–	–	–	–	100.0

DISCUSSION

We observed a large change in an intertidal soft-sediment macrofaunal community preceded by 2 yr of high annual temporal variability in community composition. This increase in variability or flickering was detected despite natural seasonality in community and population dynamics. The changes appeared driven by subtle shifts in environmental drivers interacting with facilitation by the *Boccardia syrtis* tube mat, in a way consistent with complex system dynamics involving interactions across time scales and feedbacks (Pascual & Guichard 2005, Rietkerk & van de Koppel 2008). We suspect that this process was primarily driven from the bottom up. While there are large predators in this system, e.g. shorebirds and rays, densities of shore birds continued to be low and the rays actually feed on the tube-mat.

The temporal change in community structure and function was coincident and mechanistically concordant with a management action that resulted in small decreases in organic and primary nutrient loading and a prolonged ENSO event that affected temporal dynamics of a number of species throughout the harbour (Hewitt & Thrush 2009b). While there is yet no definition of the spatial and temporal extent of a change that represents an alternate state, we feel that the observed strong change in community composition and function that lasted for over 5 yr, albeit at one large sandflat, qualifies. Specifically, the change in community composition was accompanied by a change in biogenic habitat structure, with the removal of an extensive tube-mat that was likely to have consequent changes to bioturbation rates, hydrodynamics and food sources for fish and birds. A trophic and feeding shift also occurred with numbers of predators/scavengers decreasing and deposit feeders increasing. Other monitored sites, located in a different hydrodynamic area of the harbour, did not exhibit similar changes

Increases in both spatial and temporal variance have been suggested as a potential predictor of approaching tipping points and regime shifts (Oborny et al. 2005, van Nes & Scheffer 2005, Brock & Carpenter 2006, Carpenter & Brock 2006, Scheffer et al. 2009). However, the numerical model simulations that have suggested these indicators are dependent on a high level of mechanistic knowledge. Few empirical studies have assessed the value of these indicators, although increased spatial variance in community composition variables during transition between alternative states has recently been observed in 2 systems (Litzow et al. 2008). Our results assess temporal variance and provide evidence of an increase in temporal variance for the 2 yr of the transition followed by a decrease to below the initial degree of variability. Interestingly, this increase in temporal variability of community composition was not a simple reflection of increases in the temporal variability of dominant species. Both increases and decreases in seasonal variability of dominants were observed, similar to the effect of stressors on the spatial variability of macrobenthic species abundances (Hewitt & Thrush 2009a).

Both the community change and the increased variance preceding it were detected despite natural variation in species abundances at a number of scales (from seasonal patterns to multi-year cycles). In Manukau

Harbour, 18 to 38% of common species exhibit seasonality, although most of these seasonal patterns were not consistent in timing or magnitude from year to year, and 15 to 26% of common taxa exhibited multiyear cycles in abundance from 3 to 9 yr in length (Hewitt & Thrush 2007). These temporal patterns were explainable to varying degrees by variables representing ENSO and smaller-scale location-specific environmental variables (up to 80 and 55% explained, respectively; Hewitt & Thrush 2009b). The natural variability in species abundances we observed over time did not always reflect highly variable communities, suggesting that species interactions are important in stabilising community dynamics (van Nes & Scheffer 2005). Species interactions, together with temporally small environmental shifts related to storm events, probably account for the unexplained variability in our regression analyses.

Regime shifts and tipping points are probably common in estuaries, as indicated by the number of studies reporting strong anthropogenic impacts, although in this case such a reaction was unexpected. While the management action itself was profound (removal of sewage ponds and increased sewage treatment), fast and permanent, the effect of the oxidation ponds had previously not been demonstrated to be large nor the spatial footprint to encompass our monitoring site 7 km away (3 to 5% increase in sediment organic content only within 1400 m; Ellis et al. 2000). Moreover, the resultant changes to water column nutrients were small relative to other reported eutrophication problems. We suggest 2 potential reasons for the large community composition, trophic and functional responses.

First, a tipping point can often result from a combination of gradual changes and a shock or interactions between intrinsic temporal dynamics and cumulative effects (Biggs et al. 2009). In our case it seems likely that the small change in water column nutrients interacted with ENSO-driven variation, producing a greater effect than would have been observed from either driver on their own. This highlights the importance of considering anthropogenic effects as occurring on the wave of natural changes, rather than expecting natural variability to obscure detection of anthropogenic effects or to assume that anthropogenic effects expected to be small or similar in size to natural variability will have little or no consequences. It also highlights the profound implications that changes to climate and climatic variability may be expected to have on the resilience of ecosystems to other anthropogenic impacts and management actions.

Second, the changes to water column nutrients did not have a simple direct effect; rather, effects for some species appeared mediated through changes to the tube-mat. Species that generate spatial structure are expected to play a key role in regulating positive interactions between fast and slow processes and are thus likely to be key in defining complex dynamics and resilience (Dayton 2003, Rietkerk & Van de Koppel 2008, Thrush et al. 2009). *Boccardia syrtis* population dynamics are complex; beyond the correlation with ENSO cycles, the species exhibits 5 to 7 yr cycles that are not synchronous across the harbour, suggesting some strongly intrinsic control. Both through stabilising sediment and through the tube structure affecting recruitment, *B. syrtis* could have strong interactions with other species in the community. The system is therefore a cyclic one, where it could be postulated that the intrinsic seasonal and multi-year cycles in *B. syrtis* abundance result in the community oscillating to the border of the basin of attraction of an alternative attractor (Scheffer et al. 2009).

While the mechanistic details for this regime shift may well be system-specific, involving interactions of tube-mats, sediment stability and subtle changes in organic loading, it is unlikely that tube-dwellers are the only key species likely to have this effect. Removal of any species that provide structure in soft-sediment systems or species that provide high levels of bioturbation (van Nes & Scheffer 2007, Lohrer et al. 2008) or benthic–pelagic coupling (Airoldi et al. 2008) are likely to have far-reaching effects. When such species exhibit sensitivity to environmental or anthropogenic stressors, regime shifts may occur (Thrush et al. 2009). Suding et al. (2008) emphasised the importance of considering both functional and environmental response traits when predicting system responses to change. However, ecological surprises are common, and at least in some circumstances due to complex dynamics, emphasising the importance of developing and empirically testing indicators of approaching thresholds, tipping points or regime shifts (Doak et al. 2008, Thrush et al. 2009).

CONCLUSIONS

In our system, the effects of ENSO and the preference of *Boccardia syrtis* for slightly enriched sediment, together with the intrinsic population dynamics of *B. syrtis* and the intrinsic species interactions between it and the rest of the community, acted to escalate the effect of the relatively small changes in nutrients across a tipping point. We were lucky to have sufficiently good spatially and temporally resolved ecological and environmental data to detect and tease apart the mechanisms of change. The length of time series needed for detection of such changes is inevitably dependent on the resolution of the data and must exceed the length of dominant cyclic patterns (~9 yr for our data; Hewitt & Thrush 2007). However, despite the noisy nature of real-world data, we could detect changes that foreshadowed a regime shift, which should be encouraging for both empirical researchers and management agencies.

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Appendix 1. Full statistics for the multiple regression analyses reported in Table 3. El Niño Southern Oscillation variables are the Southern Oscillation index (SOI) and Z1, changes to the wastewater treatment are sediment chlorophyll *a* (chl *a*) and water column soluble phosphorus (SP), ammoniacal nitrogen (NH_4) and nitrate-nitrogen (NO_3), and the $\log_{10}$ abundance of *Boccardia syrtis* is represented as Boc. Lag: lags in months when a variable was lagged; MS: mean squares or deviances; test-value: χ^2 or *F*-value

Taxon	Source	Lag	df	MS	Test-value	p
Orbinia papillosa	Model		3	8.821	26.46	<0.0001
	Error		34	2.033		
	Intercept		1	0.338	0.22	0.6386
	NH_4	12	1	0.047	14.04	0.0002
	SP	6	1	0.089	7.44	0.0064
	Boc		1	0.060	4.67	0.0307
Aglaophamus macroura	Model		2	0.497	9.32	0.0006
	Error		32	0.053		
	Chl *a*	4	1	0.024	–2.81	0.0084
	SOI		1	0.012	2.34	0.0254

Appendix 1 (continued)

Taxon	Source	Lag	df	MS	Test-value	p
Nucula hartvigiana	Model		2	21.993	11.25	0.0001
	Error		39	1.955		
	Intercept		1	0.566	–1.39	0.1723
	Z1	4	1	0.091	3.53	0.0011
	Boc		1	0.094	2.99	0.0048
Waitangi brevirostris	Model		3	2.139	6.58	0.0016
	Error		29	0.325		
	Intercept		1	0.305	4.82	<0.0001
	NH_4		1	0.108	–1.87	0.0719
	SP	2	1	0.067	–2.59	0.0149
	SOI		1	0.079	2.14	0.0407
Sphaerosyllis semiverricosa	Model		2	0.067	13.62	<0.0001
	Error		39	0.005		
	Intercept		1	0.014	–0.65	0.5203
	NH_4	4	1	0.005	3.97	0.0003
	Boc		1	0.005	2.24	0.0308
Magelona dakini	Model		2	1.078	15.11	<0.0001
	Error		41	0.071		
	Intercept		1	0.051	44.12	<0.0001
	SOI		1	0.014	1.62	0.1138
	Boc		1	0.018	–4.87	<0.0001
Macroclymenella stewartensis	Model		3	45.058	10.05	<0.0001
	Error		35	4.482		
	Intercept		1	0.906	0.21	0.8385
	NH_4	10	1	0.220	–4.09	0.0002
	Z1	4	1	0.154	4.35	0.0001
	Boc		1	0.214	2.78	0.0087
Austrovenus stutchburyi	Model		4	0.250	7.84	0.0001
	Error		34	0.032		
	SP	4	1	0.020	2.38	0.0230
	SOI		1	0.009	2.33	0.0257
	NO_3	10	1	0.021	3.25	0.0026
	NH_4	8	1	0.015	1.50	0.1430
Soletellina siliqua	Model		2	28.782	57.56	<0.0001
	Error		38	1.611		
	Intercept		1	0.222	108.45	<0.0001
	NO_3	6	1	0.223	15.96	<0.0001
	Z1	6	1	0.048	17.57	<0.0001
Heteromastus filiformis	Model		2	41.882	22.66	<0.0001
	Error		42	1.849		
	Intercept		1	0.332	0.55	0.5838
	SOI		1	0.090	1.64	0.1084
	Boc		1	0.097	3.63	0.0008
Owenia fusiformis	Model		3	31.080	16.09	<0.0001
	Error		33	1.932		
	Intercept		1	0.696	–2.07	0.0460
	Boc		1	0.110	1.75	0.0898
	NH_4	6	1	0.133	3.88	0.0005
	Z1	12	1	0.117	1.77	0.0865
Macomona liliana	Model		2	105.404	210.81	<0.0001
	Error		33	27.800		
	Intercept		1	0.187	0.02	0.8889
	Boc		1	0.038	6.78	0.0092
	Chl *a*	2	1	0.048	34.64	<0.0001
Euchone sp.	Model		2	2.926	101.51	<0.0001
	Error		34	0.029		
	Intercept		1	0.085	–1.06	0.2968
	Z1	12	1	0.014	1.99	0.0549
	Boc		1	0.013	11.95	<0.0001
Glycinde trifida	Model		1	1195.017	152.04	<0.0001
	Error		42	7.860		
	Intercept		1	0.460	2.05	0.0466
	Boc		1	0.187	12.33	<0.0001

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Thresholds and multiple community states in marine fouling communities: integrating natural history with management strategies

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ABSTRACT: The epifaunal communities characteristic of the southern New England, USA, region between eastern Long Island Sound, CT, and Cape Cod, MA, comprise a complex system in which different mechanisms at certain threshold levels can cause the establishment of 4 distinct community states: (1) a diverse native community dominated by bryozoans and sponges most commonly found in open coast areas, (2) an invasive ascidian community characteristic of marinas and areas of coastal development, (3) a mussel-dominated community occurring after massive recruitment and (4) an ascidian community dominated by *Diplosoma listerianum* that occurs only in years following warm winters. Each of these states is fairly resilient, but the spatial extent and duration of each state can be highly variable. Transitions among the states occur if some set of threshold conditions are surpassed and reasonable predictions can be made based on knowledge of the natural history of the species within the system. Two sets of processes seem to control the resilience of each state and the thresholds beyond which a transition to a new state occurs: (1) fast and local processes such as within-population recruitment, predation or bioengineering by mussels and (2) slow regional processes such as climate change, coastal development or habitat restoration. Of these, coastal development and restoration efforts are under management control and could have large effects on these community states, in particular the native community. However, we may not be able to influence large-scale regional processes such as climate change that may favor non-native communities. Nevertheless, the different community states can be used as indicators of both local and regional management success and allow local management efforts to be put in the context of larger scale shifts in threshold conditions that affect regional community patterns.

KEYWORDS: Threshold dynamics · Fouling community · Ascidians · Bryozoans · Mussels · Climate change · Coastal development · Invasive species

INTRODUCTION

Ecosystems are increasingly stressed by co-occurring phenomena over a wide range of temporal and spatial scales. Understanding and predicting the impacts of these multiple stresses necessitate the integration of observation, experimentation and modeling across different scales (e.g. Shurin et al. 2004, Holyoak et al. 2005). In the study of community dynamics, metapopulation and metacommunity theories now link local and regional scales with contributions such as habitat isolation, dispersal limitation, habitat destruction, differences in local and regional disturbances, or fragmented landscapes becoming important (e.g. Nee & May 1992, Moilanen & Hanski 1995, Ellien et al. 2000, Leibold et al. 2004, Cadotte 2007, Gouhier & Guichard 2007, Munguia &

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Miller 2008). Environmental and resource management strategies must also be cognizant of the connections between community patterns and processes and broader ecosystem functions across multiple scales.

An important aspect of dynamics at multiple scales is the degree to which systems at any scale exist in different states with transitions among these occurring once some set of threshold conditions is surpassed. Such transitions can result in potentially catastrophic changes with negative economic consequences (reviewed by Muradian 2001), and may even rival historical changes resulting from severe climate shifts in which past or future communities have no recent analogs (Williams & Jackson 2007, Stralberg et al. 2009). Here we integrate the results of over 25 yr of experimental and observational studies of subtidal epifaunal communities that are characteristic of the southern New England, USA, region between eastern Long Island Sound, CT, and Cape Cod, MA. We explore how critical knowledge of organisms' natural history can be coupled with threshold dynamics and multiple community states within a spatial landscape. We also examine how such an approach might aid in evaluating resource management decisions.

Resilience or resistance to change caused by environmental perturbations (e.g. Pimm 1984, O'Neill et al. 1986, Tilman & Downing 1994) is a critical part of threshold dynamics and the existence of multiple community states (e.g. Holling 1973, Sutherland 1974, 1990). A resilient system can maintain one configuration despite a variety of stresses, but once displaced beyond a threshold by strong or persistent stresses, a new configuration can ensue that will exhibit its own resilience and resistance to change. The reduction in stress or return to previous environmental conditions may be insufficient to overcome the resilience of the new state.

The factors associated with critical thresholds have often been related to nutrient inputs that cause a switch in the composition of primary producers and cascading trophic changes (e.g. Scheffer et al. 2000, Carpenter 2001, Gunderson 2001). However, communities can exhibit different states not necessarily associated with large changes in the ecosystem's primary producers (e.g. Connell & Sousa 1983, Peterson 1984, Sutherland 1990, Knowlton 1992, Chase 2003, see Petraitis & Dudgeon 2004 for a review and critique). Coupling community switches with resilience at local, habitat and regional scales can produce a system of multiple, patchy community states within the overall dynamics of the system. If recruitment at the local or patch scale is sufficient to maintain the community over multiple generations and dispersal among patches remains relatively low so as to not override local resilience, the metacommunity structure of the regional system can be maintained (Holyoak et al. 2005); otherwise the system would behave as one large homogenous local community (Mouquet & Loreau 2003).

The differences in the ecology and natural history of the species that make up each local community are critical in determining the temporal and spatial scales and the predictability or regularity of stresses that ultimately produce thresholds. For example, in most epifaunal communities, species vary in their longevity with generation times of months to years, dispersal by free-living larvae that exist for minutes to weeks can vary from <1 m to ≫10 km, and resultant populations can have spatial extents from small patches of boulders to many km^2. The same stress (e.g. low winter temperature) can occur only once in the lifetime and probably at a particular life stage of an annual species, while a longer-lived species may encounter this stress multiple times and at multiple ages. Thus, the species composition and structure of the different community states will determine the complexity of the threshold conditions and related dynamics both locally and regionally. Such complexity challenges environmental management efforts, but the distribution of distinct, easily recognized community states may be used in developing management plans and measuring their success on local to regional scales.

Although our knowledge of the southern New England sessile invertebrate system is far from complete, our goal is to use observational and experimental data to characterize community states that are defined by different dominant species and the threshold conditions that result in switches among these states. We will: (1) characterize and review the diversity of natural histories of species within these communities and how these contribute to at least 4 dominant states; (2) examine the processes that contribute to transitions among these states and define thresholds; (3) test the system stability, state resilience and conditions necessary for change; and (4) examine the application of these dynamics to general management problems.

NATURAL HISTORY AND ITS INFLUENCE ON DOMINANCE

Regional species pool

In southern New England, sessile invertebrates often dominate natural rocks, reefs, seagrasses and algal substrates as well as artificial man-made structures such as piers, jetties and pilings. Within the region there are >200 sessile species in more than 10 phyla, including individual and colonial species with a diversity of life histories and abilities to respond to environmental changes on a variety of temporal and spatial scales. Table 1 illustrates the range of life-history characteristics of some representative sessile species, many

Table 1. General characteristics of common sessile invertebrate species within the southern New England shallow water epifaunal community. Recruitment times are based on 9 yr of weekly data collected at the Breakwater site. S: solitary; C: colonial; SF: suspension feeding; ZP: zooplankton predator; max.: maximum; diam.: diameter

Species	Solitary/ colonial	Colony growth form	Individual max. size	Larval		Recruitment		Adult	
				Feeding	Period	Range	Peak	Feeding	Period
Sponges									
Halichondria bowerbanki	C	Variable	Single cell	No	<1 d	May–Dec	Jun, Sep	SF	yr
Hydroids									
Tubularia larynx	C	Vine-like	>1 cm tall	No	<1 d	–	–	ZP	mo–yr
Obelia sp.	C	Vine, arborescent	<1 mm	Yes[a]	d–wk	May–Oct	May, Sep	ZP	mo–yr
Polychaetes									
Spirorbis spp.	S	-	1 mm diam.	No		May–Dec	Sep	SF	mo
Hydroides dianthus	S	-	>10 cm long	Yes	1–3 wk	May–Oct	Sep	SF	mo–yr
Barnacles									
Balanus spp.	S	-	>1 cm diam	Yes[a]	d–wk	May–Nov	Aug	SF	yr
Molluscs									
Mytilus spp.	S	-	>10 cm long	Yes	~4 wk	Jun–Sep	Jun	SF	yr
Bryozoans									
Cryptosula pallasiana	C	Encrusting	~1 mm	No	min–h	May–Dec	Jul–Sep	SF	yr
Schizoporella errata	C	Encrusting	~1 mm	No	min–h	Jun–Nov	Jul	SF	yr
Microporella ciliata	C	Encrusting	~1 mm	No	min–h	Jun–Oct	–	SF	yr
Bugula turrita	C	Arborescent	~1 mm	No	min–h	Jun–Nov	Aug–Sep	SF	mo–yr
Bowerbankia gracilis	C	Vine-like	~1 mm	No	min–h	Jun–Oct	Jul–Aug	SF	mo–yr
Membranipora membranacea	C	Encrusting	~1 mm	Yes	d–wk	Jul–Oct	Sep	SF	Unknown
Ascidians									
Botryllus schlosseri	C	Encrusting	~1 mm	No	min–h	May–Nov	Aug	SF	mo–1 yr
Botrylloides violaceus	C	Encrusting	~1 mm	No	min–h	Jun–Dec	Jul–Sep	SF	mo–1 yr
Diplosoma listerianum	C	Encrusting	~1 mm	No	min–h	Jun–Dec	Sep	SF	mo–1 yr
Molgula manhattensis	S	-	>2 cm diam.	No	<1 d	Jun–Oct	Aug–Sep	SF	1–2 yr
Ascidiella aspersa	S	-	>5 cm tall	No	<1 d	Jun–Dec	Jul–Oct	SF	1–2 yr
Ciona intestinalis	S	-	>10 cm tall	No	<1 d	May–Oct	Jul–Aug	SF	1–2 yr
Styela clava	S	-	>15 cm tall	No	<1 d	Jun–Oct	Jul–Oct	SF	1–2 yr

[a] During at least 1 planktonic stage

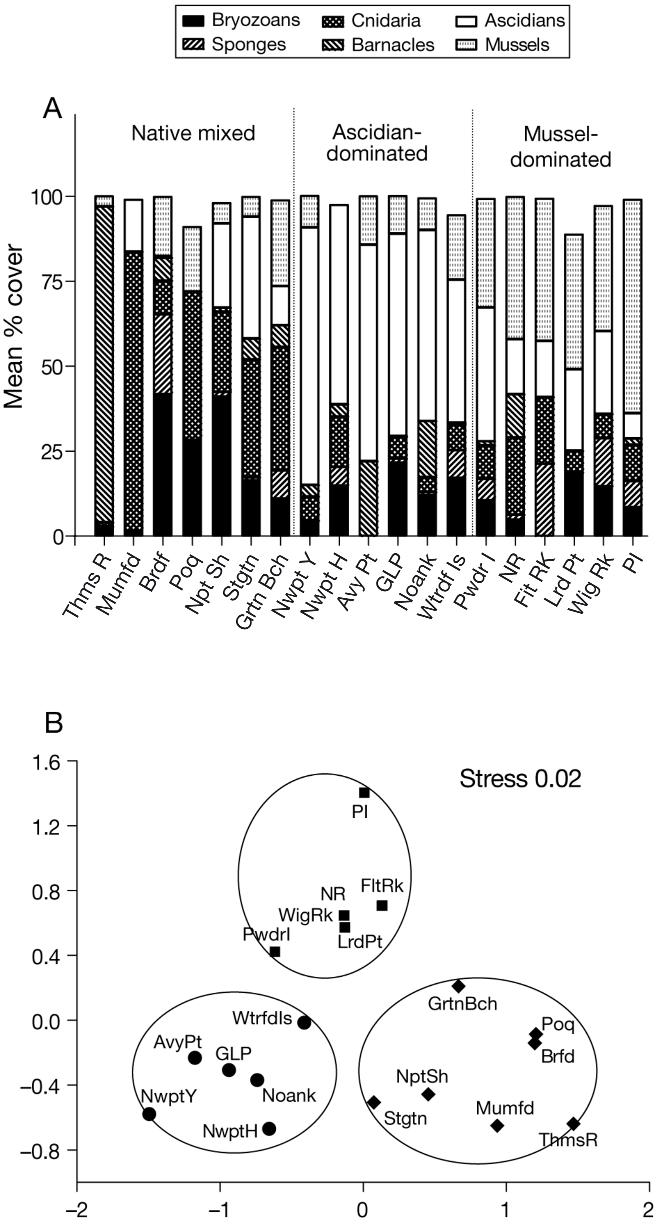

Fig. 1. Dominance variability of benthic sessile invertebrates among 19 sites surveyed in eastern Long Island Sound and Narragansett Bay in 2004. (A) Each bar shows the mean % cover for each taxa at the site. Means are based on analyses of a minimum of 20 random photos of 140 cm^2 of the substrates at the site. A grid with 120 points was overlain on each digital photo using ImageJ software and the taxa under each point was counted. (B) Multidimensional scaling (MDS) analysis (using Primer 6) of mean % abundances of taxa at each site. Thms R: Thames River; Mumfd: Mumford Cove; Brfd: Branford; Poq: Poquonnock River; Npt Sh: Newport Shipyard; Stgtn: Stonington; Grtn Bch: Groton Beach; Nwpt Y: Newport Yacht Club; Nwpt H: Newport Harbor; Avy Pt: Avery Point; GLP: Groton Long Point; Noank: Noank; Wtrfd Is: Waterford Island; Pwdr I: Powder Island; NR: Niantic River; Flt Rk: Flat Rock; Lrd Pt: Lord's Point; Wig Rk: Wigwam Rock; PI: Pine Island. The 3 Newport sites are in Narragansett Bay and the remaining sites are in Long Island Sound

of which can be dominant on individual substrates. Although the individuals or colonies of some species can survive for decades, most live for less than 1 yr. This makes the communities incredibly dynamic with some populations turning over annually and species composition on individual substrates fluctuating continually. Nevertheless, the diversity on individual substrates can remain quite stable despite species turnover rates of >10% mo^{-1} and can usually recover after major disturbances (e.g. Osman 1977, 1978). Despite fluctuations in dominance on individual substrates, within a site the community is usually comprised of a fairly constant subset of the total species available regionally. We have observed distinct, identifiable and resilient communities at many sites with dominance by one or a few taxa that has remained stable for >15 yr (authors' pers. obs.). In numerous transplant experiments (Osman & Whitlatch 1998, 2004), we found that for treatments in which site conditions were maintained, communities reverted to dominance patterns of each site. We have also witnessed rapid and dramatic shifts in dominance and population and/or community dynamics at some sites as a consequence of the occasional massive recruitment of mussels (see 'Mussel community') or year-to-year and decade-to-decade climate changes (e.g. Stachowicz et al. 2002a). In field experiments we have also produced consistent shifts in dominance by altering the recruitment of invasive non-native species or exposure to predators (Osman & Whitlatch 1998, 2004, 2007).

Within the region we have identified 4 distinct subtidal, epifaunal invertebrate community states that are readily distinguished by the taxa that dominate them: (1) a diverse native community dominated by several species of bryozoans and sponges that is characteristic of more open coastal areas; (2) a community dominated by invasive ascidians that is most commonly seen in harbors, marinas and other sites impacted by humans; (3) a mussel/algal community that can periodically replace the native or invasive-dominated communities; and (4) an ascidian community dominated by the invasive colonial ascidian *Diplosoma listerianum* that is restricted to years following warm winters (Stachowicz et al. 2002a). Fig. 1A illustrates the variability in species dominance patterns among 19 sites surveyed in 2004 in eastern Long Island Sound and Narragansett Bay. The results of a multidimensional scaling analysis (Fig. 1B) of mean percentage of total epifaunal cover by each of the taxa at each of the sites (algae and unoccupied substrate excluded) indicated that each of the sites displayed dominance indicative of one of the 3 states (*Diplosoma* state excluded, see '*Diplosoma* community'). It is important to note that representatives of all of the dominant taxa occur at most sites and that the native community can vary greatly among sites.

Observations and experiments over the past 20 yr have shown that the 4 community states exhibit a level of resilience that allows them to be maintained for years, if not decades, by interacting physical and biological processes (Osman & Whitlatch 1995, 1996, 1998, 2004, Stachowicz et al. 1999, 2002a,b). However, we have observed or experimentally produced switches among states over time periods of months to years over variable spatial scales. The switches appear to require unique sets of environmental changes or stresses (Fig. 2). The stresses vary from those that are local and operate relatively quickly (e.g. predation by different predator guilds) to those that are regional and operate much more slowly (e.g. climate change). Local stresses can cause certain threshold conditions to be exceeded, resulting in the different communities coexisting at sites <1 km apart. More regional stresses operating at variable rates are likely to produce broader regional switches in threshold conditions. How these stresses interact is shaped by the natural histories of the species comprising each of the alternate community states.

Native community

The native community can be quite variable with dominance varying among sites (Fig. 1). Although the 'native' status of a few of these species may be presently unclear, all have been in the region for well over 100 yr (Sumner et al. 1911). Bryozoans and sponges are the most common dominants, but cnidarians (anemones, hydroids and the coral *Astrangia poculata* can all contribute) and occasionally barnacles or serpullid polychaetes can also dominate particular substrates. Local recruitment, especially for the bryozoans and sponges, is an important component in maintaining dominance (e.g. Caley et al. 1996). Many of the species have short-lived larvae (Table 1) that quickly recruit to available habitat. This enables populations and communities to be maintained at sites by the continual replacement of each generation by subsequent generations of recruits produced from within the site. This is coupled with extremely high mortality of new recruits of competitively superior ascidians inflicted by small invertebrate predators such as the gastropods *Mitrella lunata* and *Anachis* spp. as well as benthic-feeding fish (Osman & Whitlatch 1995, 1996, 1998, 2004). Colonial bryozoans are more immune to predation on recruits and juvenile colonies than many of the other competing taxa (Osman & Whitlatch 2004). Sponges, anemones and *A. poculata* may also suffer less predation than other taxa, whereas less dominant species such as hydroids, barnacles and mussels often have specific predators, especially on adults. The intense predation on ascidian recruits removes these taxa before they can be established and contributes to the maintenance of native communities, especially those dominated by bryozoans. We have conducted experimental studies at one open-coast site (Pine Island) for over 15 yr and have observed bryozoan dominance on natural substrates for much of this time (>10 yr), as well as this dominance continually developing on experimental substrates exposed at this site (e.g. Osman & Whitlatch 1998, 2004). Other studies have observed similar bryozoan dominance at sites within this region despite high species turnover rates (e.g. Osman 1977, 1978). However, at the Pine Island site, a shift away from bryozoan dominance resulted from a massive recruitment of and subsequent dominance by mussels (see 'Mussel community').

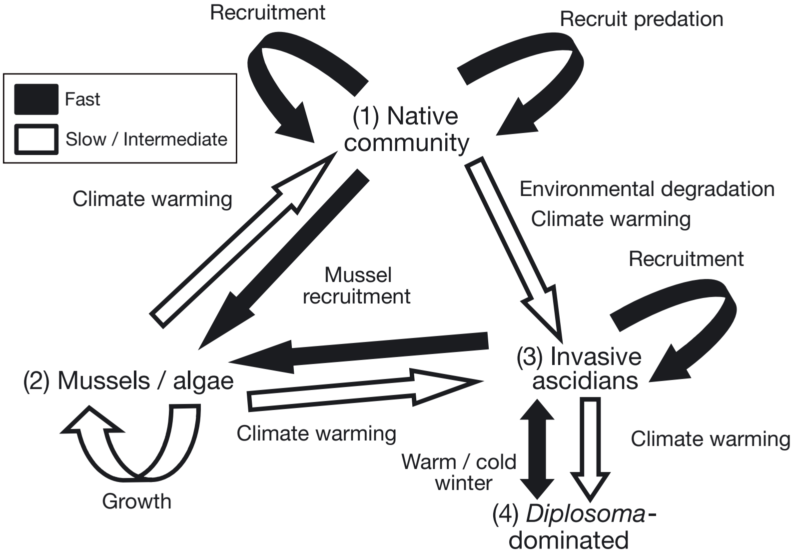

Fig. 2. The 4 different community states: (1) the native community, (2) mussels/algae, (3) invasive ascidians (4) a state dominated by *Diplosoma listerianum*. Arrows represent the changes from one community state to another with the hypothesized processes labeled. The speed at which transitions may occur is indicated by arrow shading, with black indicating relatively fast rates and white indicating relatively slow or moderate rates. Arrows looping back to a state indicate processes contributing to resilience

Invasive ascidian community

The ascidian-dominated community seems to be maintained by local recruitment. The majority of dominant species (i.e. *Botrylloides violaceus*, *Styela clava*, *Ascidiella aspersa*, *Diplosoma listerianum*, *Didemnum vexillum*) have all invaded the region within the last 35 yr (Carlton 1989, Berman et al. 1992, Harris & Tyrrell 2001). All the colonial ascidians release fully developed larvae that can recruit immediately. Studies of similar species (e.g. Olson 1985, Davis & Butler 1989) have shown that most larvae settle within 10 m of parental colonies, and in field experiments we have observed the highest recruitment <1 m from parental colonies or source areas (Osman & Whitlatch 1998). Larvae of solitary ascidians develop from externally fertilized eggs in <24 h and can therefore travel farther than larvae of colonial ascidians before recruiting (e.g. Svane & Young 1989), but new recruits and juveniles of these species are preyed upon by a variety of benthic invertebrate and fish predators (Osman & Whitlatch 1995, 1996, 1998, 2004). This community exhibits long-term dominance and resilience in areas where predators are absent or in very low abundance (e.g. Osman & Whitlatch 2007). In southern New England, these areas typically include marinas, industrial areas and other sites heavily impacted by humans. Other areas, such as seagrass beds, in which substrates (grass blades) are regenerated annually and predator abundances appear to remain low, can also develop ascidian-dominated communities if sources of recruiting larvae are close.

Mussel community

The mussel-dominated community can be spatially extensive and has the potential to displace either of the previously described communities. The establishment of this community state appears dependent on a massive influx of larval recruits (Fig. 2). The causes of such massive recruitment events may be variable, but they are almost certainly the result of broad regional conditions (e.g. Witman et al. 2003). We have observed 2 large-scale mussel recruitment events, one successful and the other not. In 1994 we observed overwhelming recruitment of mussels, but only inside experimental cages protected from predators. When the cages were removed, all mussels were quickly consumed over a 1 to 2 wk period (Osman & Whitlatch 1998). In 2000, a more regional recruitment event occurred with recruitment so large that mussel beds extended beyond hard substrate areas onto adjacent sandy sediments. At Pine Island, the bryozoan community which existed before the recruitment event was replaced. The mussels were removed from sandy areas by winter storms in the first year and were greatly reduced by storms or predators (e.g. crabs, sea stars and diving ducks) at most sites by the end of the second year. Several local, but persistent, mussel patches seen in 2004 (Fig. 1) remained at the Pine Island site until August 2006. The mussels eventually became covered by the macroalga *Laminaria* sp. and a storm resulted in the removal of almost all of the mussels and kelp. A bryozoan-dominated community has become re-established at this site. In this instance, the mussels did not displace the ascidian communities at any of the sites where we continuously monitor recruitment (Avery Point since 1991, Noank and Groton Long Point since 2001; Fig. 1), possibly as a consequence of the inability of the mussels to attach to the ascidians or predation by the ascidians on mussel larvae.

Diplosoma community

The *Diplosoma*-dominated community only occurs at some of our sites after warm winters and replaces the normal ascidian-dominated community (Fig. 2). This species is dependent on annual recruitment and when the mean winter temperature is below 4°C there is almost complete recruitment failure (Fig. 3). We conducted an extensive survey of sites (Fig. 1) in 2004, the second of 2 yr with cold winters; *Diplosoma* was only found at 2 sites and it represented <1% of the fauna at these sites. Without new recruits the species disappears from the local system (Stachowicz et al. 2002a)

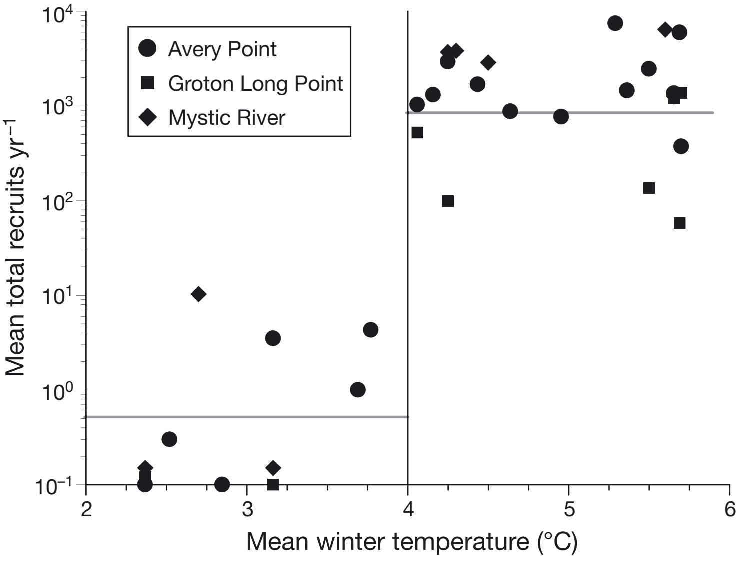

Fig. 3. *Diplosoma listerianum*. Mean total annual recruitment of *D. listerianum* on panels at 3 different field sites as a function of mean winter temperature. Horizontal grey lines = means above and below the 4°C temperature threshold. Recruitment was generally lower at Groton Long Point, but recruitment was almost absent at all sites when mean winter temperature was below 4°C. Recruitment was measured at Avery Point since 1991 and the other 2 sites since 2001. Years through 2008 are shown. Sea surface temperature data were collected at Millstone Point, Waterford, CT, and supplied by the Dominion Nuclear Environmental Laboratory

and the system returns to its normal complement of fouling species. However, when present this species becomes dominant in both the ascidian community on hard substrate as well as in seagrass beds.

TRANSITIONS AMONG COMMUNITY STATES

Given the dynamic nature of these communities and the relatively short-lived nature of most species, recruitment is a dominant aspect in both maintaining particular states and the transition to a new state. For states to be maintained and remain resilient over multiple generations, recruitment of existing species back into the local community is essential. In addition, there appear to be key processes that contribute to the resilience of particular community states; recruit predation for the resilience of native communities, mussel community resilience as a consequence of their habitat bioengineering (e.g. Seed & Suchanek 1992) and controlling of community processes (Witman et al. 2003), and continued warm winter water temperatures for the resilience of the *Diplosoma*-dominated community. Within this system there are several environmental changes that alone or in concert might overcome the resilience of one or more of the states and cause a switch to another (Box 1). Some processes are rapid and are more likely to be seen at a local scale, while others are slow and more prevalent over broader regional scales. Processes in both categories contribute to transitions from each of the states.

The native state has numerous species with lower competitive abilities relative to the invasive ascidians and mussels. It appears to be maintained by local recruitment and predation on ascidian and mussel recruits (Fig. 2), and a transition from this community requires a loss of predators or extremely high ascidian or mussel recruitment that overwhelms any predator control. In functional response experiments (Whitlatch & Osman 2009), we found that the maximum recruitment densities of ascidian species rarely exceeded the capacity of even one predator species to control it. In over 15 yr of observation and experimental studies we have never seen more than occasional ascidian

Box 1. Four rapid to intermediate rate processes and 4 slow to intermediate rate processes that affect community structure and stability in Long Island Sound (LIS) fouling communities. Note the interactions among processes operating at different rates as well as the differences in spatial scale

RAPID TO INTERMEDIATE RATE PROCESSES

Massive recruitment of mussels. This generally occurs over weeks. It is regional in scale, but can be habitat specific. It is the proximate cause of the switch to a mussel-dominated state. Causes are unclear but abnormally high recruitment of mussels has been associated with specific changes in the NAO (Fisher & Petraitis 2004).

Change in environmental stress. This fast to intermediate rate process is most likely to occur on local to intermediate spatial scales. Increased stress associated with changes in coastal development or decreased habitat quality is likely to result in reduction of predators maintaining native communities and increase the probability of a switch to an ascidian-dominated community. The reverse of this would be habitat restoration removing stresses and increasing the probability of recruitment of these predators and switching to a native community. An alternate is for habitat restoration to occur in areas without reducing coastal development stresses which may cause a switch in threshold but over a longer period of time.

Warm winters. The existence of a warm winter will have a fast to intermediate effect on a switch to *Diplosoma*-dominated community or the maintenance of an existing one. This will be region-wide in scope but only in habitats without recruit predators. The frequency of warm winters may also have an intermediate to slow effect on invader success and mussel recruitment.

Storm frequency and intensity. This process will also be related to winter severity and can contribute to a switch from a mussel-dominated state at a fast to intermediate rate.

SLOW PROCESSES

Climate change. Climate change operates at a slow rate but at a global scale. It has resulted in an increase of mean winter water temperatures in LIS and increases the probability of warm winters. Additionally, changing climate will have broader effects on the NAO (Ulbrich & Christoph 1999), regional weather patterns, and storm frequency.

North Atlantic Oscillation (NAO). The NAO accounts for a large amount of interannual variability in monthly sea level pressure over the North Atlantic (Rogers 1990) and the NAO index shows large variations on monthly to decadal or greater time scales. The index has been reported to exhibit 7 to 8 yr (Tunberg & Nelson 1998) and 20 yr (Rogers 1984) cycles. Changes in benthic communities (Tunberg & Nelson 1998, Hagberg & Tunberg 2000) and mussel recruitment (Fisher & Petraitis 2004) have been linked to the NAO index. Our observed high mussel recruitment in 1994 and 2000 correlate well with a 7 to 8 year NAO cycle.

Coastal development. The slow but ever increasing rate of development will increase the intensity and spatial scale of environmental stress as well as alter habitat distributions that are conducive to the different community states, especially increases in ascidian- and *Diplosoma*-dominated communities.

Habitat restoration. Habitat restoration is an intermediate to slow process that will affect habitat distributions, stress, and predator abundances. The ability of restoration efforts to cause switches among the community states will depend on the location and timing of these projects relative to other processes such as coastal development or climate-induced environmental changes.

colonies become established at sites with predator populations. Therefore, we see rapid processes such as changes in environmental stress that lead to the loss of the predators or massive recruitment (Box 1) as necessary for a transition from a native state. Slow processes such as coastal development could also cause this change by indirectly influencing stress.

The competitively superior invasive ascidians dominate the habitats in which they occur, provided there are no recruit predators. The return of predators could lead to a transition back to a native community state, but it is unclear whether this would be sufficient. Large populations of adult ascidians, which are generally immune to predators, reduce space available for recruiting native species or outcompete them. With broader ascidian age distributions and multiple generations at a site, a sufficient number of recruits could escape predators to maintain these populations. In transplant experiments (Osman & Whitlatch 2004), only large bryozoan colonies maintained dominance when transplanted to a predator-free site and adult ascidians transplanted to a predator site were generally unaffected. In transplant experiments examining the ability of the colonial ascidian *Didemnum vexillum* to invade native and ascidian communities (Osman & Whitlatch 2007), high recruitment of other ascidians in the ascidian community inhibited the invasion of this species significantly when compared to the native community. These results suggest that predators must first reduce ascidian recruitment substantially before native species can invade ascidian-dominated sites and become dominant. However, the large reproductive output and intense local recruitment of ascidians may make ascidian-dominated communities very resilient. Slow processes such as habitat restoration (Box 1) may be necessary for this transition.

Transition of the ascidian community to a *Diplosoma*-dominated state is dependent on recruitment after warm winters (Stachowicz et al. 2002a; Fig. 3). The probability of this occurring may be increasing with warming associated with climate change (Box 1). Based on annual differences (Fig. 3), the temperature threshold works rapidly and in both directions (Box 1). The resilience of a *Diplosoma*-dominated community if warm winters occurred year after year is less clear. We know that it can rapidly dominate substrate, but given its boom and bust pattern under present climatic conditions, we have no information on its ability to maintain dominance over long periods. Harris & Tyrrell (2001) have reported its autumn dominance over several seasons, suggesting that it may exhibit at least seasonal dominance over the long term.

To date there is little evidence of what controls the massive mussel recruitment events or their regional extent. Individual mussels can live many years and without losses can dominate a site for years. Losses are most likely to result from predation or physical dislodgement. Witman et al. (2003) found that several species of predators responded in ~1 yr to a massive region-wide recruitment of mussels and rapidly eliminated them at most sites in a period of <6 mo. We observed the dislodgement and removal of a dominant *Mytilus* population at our Pine Island site by a summer storm. Thus transitions from mussel dominance can be quite rapid but seem dependent on relatively major disturbances, i.e. either a surge in the numbers of predators or intense storms. Slow processes such as climate change or the NAO (Fisher & Petraitis 2004; Box 1) may affect the probability of a massive recruitment event occurring.

TESTING STABILITY, RESILIENCE AND PREDICTING TRANSITIONS

Given the complexity of the system (Fig. 2), we first examined the stability and resilience of the 4 community states using qualitative models (loop analysis) that do not depend on unknown quantitative relationships (e.g. Levins 1973, 1975, Jeffries 1974, Boling et al. 1975, Puccia & Levins 1985, Whitlatch & Osman 1994, Justus 2005). These models (Figs. 4 & 5, Tables 2 & 3) use a qualitative interaction matrix that links the components of a system and is then tested algebraically for stability. Interactions are defined as +1, −1 and 0, depicting positive, negative and no interactions between states, respectively. For example, predation is represented as positive for the predator and negative for the prey and density dependence is represented as a negative self-loop. These models allow for an easy representation of a system if enough natural history is known but there are insufficient data to build numerical models. We constructed both local and regional models and evaluated their stability (Dambacher et al. 2003) and the predicted responses to perturbations (Dambacher et al. 2002, 2005). Analyses were conducted using the online program of the Oregon State University 'Loop Group' (www.ent.orst.edu/loop/default.aspx). We used the stability of these models to test whether the system of 4 states represented in Fig. 2 could exist both locally and regionally. We used resultant model predictions of changes in a state as a measure of its resilience (positive response) or its potential transition to a different state (negative response).

The model in Fig. 4 represents the interactions among the 4 states at the local level: recruit predators prey on ascidians and *Diplosoma*, native species are outcompeted by the other 3 states, ascidians are outcompeted by mussels and *Diplosoma*, and all species are density dependent. This model is stable and, as shown in the prediction matrix (Table 2), any increase in the 4 dominant states results in a positive effect on that state, suggesting their resilience. Negative effects suggest that the native community can be lost under any environmental conditions, causing increases in any of the other 3 states, while the positive effect of predators indicates their role in native community resilience. Other negative effects also support the hypothesized transitions of ascidians to mussels and ascidians to *Diplosoma*. It is important to note that the model predicts changes to states, not the specific environmental threshold that might cause the change.

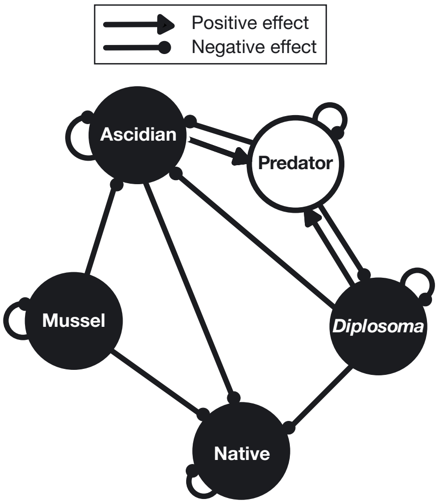

Fig. 4. Simple loop model representing the local dynamics comprised of the 4 alternate states shown in Fig. 2. The nodes and connectors between the different states represent simplified models used to test for stability with loop analysis. The local community structure is represented by the 4 community states (black circles), plus a single predator (white circle) eating ascidians and *Diplosoma listerianum*. Negative effects are represented by lines with circles and positive effects by arrows. Native species comprise the most susceptible state, which can transition to a mussel, ascidian or *Diplosoma* state. Negative self-loops represent negative density dependence. At the local scale, this model is stable and follows field observations

Table 2. Prediction matrix for the model shown in Fig. 4. The matrix shows the predicted change in each state as a consequence of an increase in each state in the first column. For example, an increase in the ascidian state is predicted to have a positive effect (+) on ascidians and predators, a negative effect (–) on *Diplosoma listerianum* and native species and no effect (blank cell) on mussels

Increase/Effect	Ascidian	*Diplosoma*	Predator	Native	Mussels
Ascidian	+	–	+	–	
Diplosoma	–	+			
Predator		–	+	+	
Native				+	
Mussel	–	+	–	–	+

Also, the model depicted in Fig. 4 is only one of many possible models, some of which may not be stable. For this reason we tested a number of alternative models which are shown in Supplement 1 available at www.int-res.com/articles/suppl/m413p277_supp.pdf). These models included changing or adding some negative links such as competition between mussels and *Diplosoma*, representing cold years by removing *Diplosoma*, or removing mussels to represent times when they were lost and did not recruit. All of these models were stable with some relatively minor changes in predictions. Only the removal of the density dependence of the 4 states (but not of the predators) resulted in ambiguous or unstable models.

To examine stability and resilience at a larger scale we created a simple regional system of 2 sites linked via the release of propagules from one site and recruitment to the other (Fig. 5, Table 3). The recruitment of the widely dispersing mussels can be seen as coming from a common larval pool with no direct links between the 2 sites. Links for the 3 other community states with more locally recruiting species were modeled as unidirectional positive effects representing rare transport of these larvae from one site to the other. This model is stable, but given its complexity we found that some changes in the dynamics, such as incorporating 2-way exchange of propagules between sites, would lead to model instability or ambiguity. Nevertheless, the model illustrates that the 4 dominate states can coexist on a more regional scale. The prediction matrix (Table 3) again suggests a fair degree of resilience for each of the states with increases having positive effects on that state. Except for mussels, increases in a community state at Site 1 also resulted in a positive effect at Site 2. As in the simpler model, the native community was predicted to decline with increases in mussels and *Diplosoma* and increase with increases in predators. Again, we explored alternate models (Supplement 1), principally changing one of the sites (e.g. removing predators, mussels or *Diplosoma*) to reflect the mosaic of sites that we observed in the field. We also incorporated a common larval pool for mussels to link the 2 sites. In almost all cases stability was maintained and all states were resilient in all stable models. Predicted changes showed minor variations but remained similar to those in Fig. 4 and Table 2.

Our goal with these models was to examine whether the 4 community states could co-exist on local and regional scales, whether each state has some degree of resilience and whether environmental changes that caused a positive change in one state could cause a transition in one or more of the other states. The results support all 3 of these and a system of multiple communities and threshold dynamics as represented in Fig. 2 seems at least probable. Can such a characterization be helpful in resource or environmental management?

APPLICATION TO MANAGEMENT

Epifaunal communities can have significant economic impacts through fouling, they can include commercially important species such as mussels or oysters and they are often diverse parts of most coastal ecosystems. Nevertheless, they are not generally targeted by management programs. Therefore, our goal is to use this system as an example and test of the potential application of thresholds in managing or restoring diverse and variable native communities. Suding & Hobbs (2009) outlined a framework for incorporating threshold dynamics in conservation and restoration with 4 steps: (1) pattern recognition, (2) identification of broad-scale drivers, (3) delineating feedback mechanisms and (4) model scenario building and testing. It is also important to recognize that the conditions for restoration will likely be different than those that produce the degradation of the system (Suding et al. 2004). Fig. 1 demonstrates that distinct communities and patterns of distribution can be recognized. Experiments, long-term studies, observations and cognizance of species' natural history (e.g. Table 1) have delineated the feedback mechanisms and potential drivers of the dynamics of thresholds between these recognizable states (Fig. 2, Box 1). The challenge is how the simultaneous existence of multiple community states with defined thresholds can be used to develop and test management scenarios.

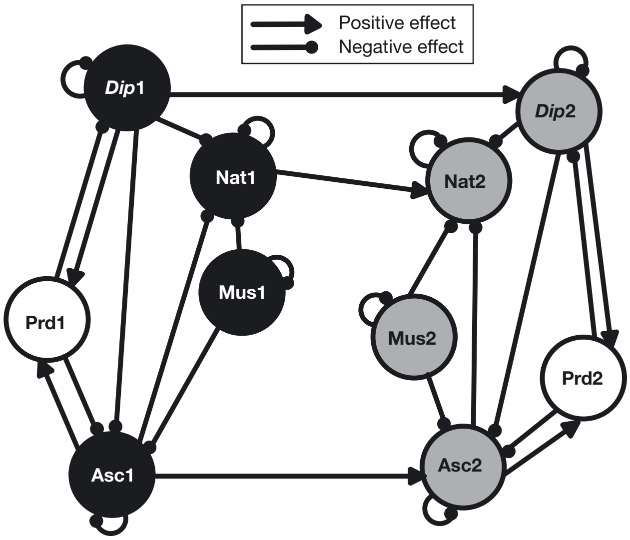

Fig. 5. Simplest loop model representing regional dynamics comprised of the 4 alternate states shown in Fig. 2, where the interactions observed at the local scale are expanded to 2 sites. The 2 sites have the same internal dynamics as represented in Fig. 4. Site 1 (black circles) represents an external source of native, ascidian and *Diplosoma listerianum* larval recruits for Site 2 (grey circles). Because mussels produce long-lived larvae that are widely dispersed, their recruits are presumed to come from a common larval pool and no direct connection between the sites is included. As depicted, this model is stable

Firstly, the 4 states themselves provide a clear means of assessing management success. Regardless of the management scenario being tested, evaluation is dependent on defining *a priori* a successful outcome. As seen in Fig. 1, dominance of native species, rather than complete absence of invasive species, may be the pragmatic goal. Because of the regional variability in the native community itself, scenarios must allow and plan for different local outcomes.

Secondly, the recognized dynamics provide a time scale for evaluating the success of any scenario. Recruit predation, mussel recruitment and mean winter temperature are all rapid processes and the outcome of a scenario involving any of these should be seen very quickly, perhaps within months. If restora-

Table 3. Prediction matrix for the model shown in Fig. 5. The matrix shows the predicted change in each state as a consequence of an increase in each state in the first column. For example, an increase in native species at Site 1 is predicted to have a positive effect (+) on native species at Site 1 and Site 2 and no effect (blank cell) on any of the other states

Increase/Effect	Nat1	Asc1	*Dip*1	Mus1	Prd1	Nat2	Asc2	*Dip*2	Mus2	Prd2
Nat1	+					+				
Asc1	–	+	–		+	–	+	–		+
*Dip*1		–	+			+	–	+		–
Mus1	–	–	+	+	–		–	+		–
Prd1	+		–		+	+	+	–		
Nat2						+				
Asc2						–	+	–		+
*Dip*2							–	+		
Mus2							–	+	+	–
Prd2						+		–		+

tion projects or coastal development do not immediately impact these rapid processes then changes may be much slower (Box 1) and harder to document. Nevertheless, since restoration or development should ultimately affect rapid processes such as predation or change in environmental stress, change should be quick once a threshold is crossed.

Thirdly, the recognized dynamics and simple modeling identify elements critical to any scenario. As an example, the qualitative models (Figs. 4 & 5, Tables 2 & 3, Supplement 1) demonstrate the importance of recruit predators to the resilience of the native community state or to restoring it. On the other hand, the lack of any predicted effect of increasing native species on the other states suggests that management must target changes beyond those that only have a direct impact on native species. If a major component of restoration is the movement or planting of desired species into an area, this may be inadequate if conditions that contribute to the resilience of the existing state are not changed. The inability of native species to remain dominant on substrates that are moved into a site without small predators and dominated by ascidians (Osman & Whitlatch 2004) serves as caution against the planting of seagrasses or oyster beds without considering the dynamics that contribute to the resilience of these habitats as well as the habitats they are replacing.

Fourthly, strong resilience of states and the potential for hysteresis implies that management scenarios and time frames for maintaining and restoring native communities will differ. If the invasive species have altered the system at regional or larger scales, novel approaches are likely to be necessary for restoration of the native community at even the local level (Suding et al. 2004, Norton 2009). A transition to the native species state will likely require the build-up of predators to a level that eliminates ascidian recruitment, the loss of adult ascidians which are present but relatively immune to predators, and larval recruits of native species reaching the target site or habitat. Each of these will require time, even if these processes are assisted in the restoration project. Maintaining a resilient native community may simply require protecting the target site and perhaps a buffer zone around it from impinging coastal development, allowing the predators and natural recruitment of native species within the site to work.

Fifthly, the spatial context of any management scenario is critical. The success of local management may depend on the source–sink relationships between a selected site and other locations within the region (Fig. 5, Table 3, Supplement 1). If coastal development contributes to the dominance of invasive ascidians, then the maintenance or restoration of a nearby site to the native state will require a different approach than at a more isolated site. Relative size of natural or restored sites will also be important. Establishing a small site with native community diversity within or adjacent to extensive coastal development may be difficult given the resilience of the invasive community and its ability to act as a source.

Finally, any management scenario must recognize the likelihood of uncontrollable shifts when threshold conditions are exceeded. The massive recruitment of mussels and shifts in *Diplosoma* dominance as a function of temperature are both changes in community state that can be anticipated but not really incorporated as a management goal. It can be recognized that if a restored site becomes dominated by mussels, storms or predators will likely cause it to shift back to a native community as long as conditions that prevent ascidian invasions remain. For example, in order to assure a return to a native state, it may be necessary to monitor recruit and predator abundance throughout the mussel state and reintroduce these predators if they are lost.

Thus, systems with threshold dynamics present both challenges and opportunities for management. The challenges include the focus on processes and linkages, the need to consider the resilience of surrounding unmanaged areas as well as the focal site(s), the need for separate restoration and management plans possibly focused on different processes, and incorporation of natural variability that may create a state different from either the restoration goal or the existing habitat state. The opportunities are the potential to define clearly success based on recognizable states and to set a realistic time period for evaluating success.

In summary, the southern New England epifaunal community is an example of a relatively complex system in which different mechanisms at certain threshold levels can cause the establishment of multiple community states. This complexity also causes the spatial extent and duration of each state to be highly variable. However, reasonable predictions can be made if the natural history of the system is well known. Processes occurring over short time scales (months to years) will determine transitions from one state to another; however, the long-term (> several yr) processes can be decisive in the overall spatial and temporal constancy of the different community states. These slow processes can be grouped into 2 categories, climate-related and anthropogenic. If we are interested in developing management strategies, we should be aware that coastal development and restoration efforts could have large effects on community states, as in the native community in this example. However, we may not be able to influence large-scale regional processes such as climate change that may favor non-native communities. Therefore, we need to consider and develop local management efforts to counter these larger scale shifts in threshold conditions that affect regional community patterns.

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Contribution to the Theme Section 'Threshold dynamics in marine coastal systems'

Predicting future ecological degradation based on modelled thresholds

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ABSTRACT: Threshold models are becoming important in determining the ecological consequences of our actions within the environment and have a key role in setting bounds on targets used by natural resource managers. We have been using thresholds and related concepts adapted from the multiple stable-states literature to model ecosystem response in the Coorong, the estuary for Australia's largest river. Our modelling approach is based upon developing a state-and-transition model, with the states defined by the biota and the transitions defined by a classification and regression tree (CART) analysis of the environmental data for the region. Here we explore the behaviour of thresholds within that model. Managers tend to plan for a set of often arbitrarily-derived thresholds in their natural resource management. We attempt to assess how the precision afforded by analyses such as CART translates into ecological outcomes, and explicitly trial several approaches to understanding thresholds and transitions in our model and how they might be relevant for management. We conclude that the most promising approach would be a mixture of further modelling (using past behaviour to predict future degradation) in conjunction with targeted experiments to confirm the results. Our case study of the Coorong is further developed, particularly for the modelling stages of the protocol, to provide recommendations to improve natural resource management strategies that are currently in use.

KEY WORDS: Coorong · Ecosystem states · Empirical anticipation · Environmental futures · Physico-chemical transitions · South Australia · Statistical modelling · Water allocation

INTRODUCTION

The management of coastal marine ecosystems such as estuaries is becoming increasingly based upon a mixture of empirical field monitoring and modelling of possible future ecological conditions. The importance of identifying thresholds for management is now more apparent than ever (Scheffer 2009, Suding & Hobbs 2009). The existence of such thresholds may be indicated by abrupt transitions from one ecosystem state to another, thus displaying regime shifts (deYoung et al. 2008) or catastrophic behaviour (Folke et al. 2004). These transitions are assumed to occur when the underlying physicochemical drivers within an ecosystem exceed a certain value (the threshold) that flips the system into a new, alternative state. Awareness of the possibility of these sudden transitions, including their implications for management, is currently high (e.g. van de Koppel et al. 2001, Lozano-Montes et al. 2008, Andersen et al. 2009, Scheffer et al. 2009). Searching for these thresholds involves detecting response to future climate change (Dakos et al. 2008, Scheffer 2009) or dire outcomes like benthic hypoxia (Conley et al. 2009) or coral reef loss (Mumby et al. 2007) that managers wish to avoid.

Current understanding of the role of thresholds is often based upon conceptual models of how the systems work (Dennison et al. 2007), in particular the key processes that give an ecosystem its distinctive character that is valued by the public. Many estuaries and coastal wetlands derive much of this character from the flows of fresh water coming downstream from their associated rivers. Excessive extraction of water upstream for human uses can, in turn, threaten an estuary's future and considerable progress has been made recently in modelling these relationships using relatively simple models (e.g. Kim & Montagna 2009, Lester & Fair-

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weather 2009a,b, 2010, Zweig & Kitchens 2009). Many of these modelling approaches, such as state-and-transition modelling, have implied thresholds associated with whatever environmental changes trigger the transitions between identified states. Especially of interest is how likely future climate change might influence flow regimes and consequential ecological effects (e.g. Powell 2008, Lester et al. 2009). These issues have long been recognised in freshwater ecology, where flows determine many aspects of ecosystem behaviour (Anderson et al. 2006), but the challenges of anticipating rare or extreme events are less routinely considered in marine ecology (but see Fuentes et al. 2006, Denny et al. 2009, Kimmel et al. 2009), despite the predicted increase of these events under climate change and their potential role in shaping ecosystems. The search for early-warning signals of thresholds is still in its infancy (Andersen et al. 2009, Scheffer et al. 2009), and so we believe that a variety of approaches needs to be explored and critically evaluated.

There is an inherent difficulty in predicting thresholds that are approaching but not yet apparent, but this is precisely what needs to occur to effectively manage non-linear systems. Previous work on the detection of upcoming transitions has focused upon recognising increasing variance of response variables as a threshold was approached (Carpenter & Brock 2006), shifts in spectral properties of time series near a threshold (Kleinen et al. 2003) or a slowing in rates of change (Dakos et al. 2008). Thus the focus is often upon the further moments of distributions of some variables (as opposed to just their means or central tendencies), where scientists become alert to increased overall variability within assemblages (Warwick & Clarke 1993) or changes in skewness (Guttal & Jayaprakash 2008). These properties have been demonstrated using deterministic models of response variables (e.g. Mumby et al. 2007, Carpenter et al. 2008) and, while threshold dynamics have been found to follow theoretical expectations, changes in many of these parameters have not been detected in simulated data prior to the threshold being crossed (e.g. see Carpenter et al. 2008). This means that they may be of limited use in predicting future transitions from measured or simulated time series of driving variables.

Over the last 10 yr, there has been a major decline in the ecological condition of the Coorong, the estuary and terminal lagoon system for Australia's largest river system, the River Murray (Brookes et al. 2009). This decline is due to prolonged drought combined with past management of the Murray-Darling Basin. In order to successfully manage these lagoons in the future, predictions are needed to evaluate the effects of possible management actions on the Coorong ecosystems under a variety of climatic scenarios. To provide such predictions, thresholds and concepts derived from the multiple stable-states literature have been used to model ecosystem response in the Coorong (Lester & Fairweather 2009b, 2010). The model itself is a state-and-transition model, with the states defined by the biotic assemblages found, and the transitions defined by a classification and regression tree (CART) analysis (De'ath & Fabricius 2000) of the physico-chemical data for the region (Lester & Fairweather 2009a,b, 2010). Thus these transitions between ecosystem states define the thresholds of interest for the Coorong, and can be used by managers to set objectives to manage towards or to define the limits of acceptable change.

We have been developing an understanding of thresholds for these ecosystem states in the Coorong lagoons subsequent to our initial modelling approach. The sensitivity of the ecosystem to and the behaviour near these thresholds is, however, currently unknown. Managers (in Australia at least) tend to manage to an often arbitrarily-defined set of limits in natural resource management. Here we explore how thresholds identified by analyses such as CART could be used to provide advance warning of upcoming ecological shifts. We use the Coorong model as an example to outline a more general protocol for assessing the utility of thresholds to derive leading indicators, focus upon modelling the states via that protocol and provide recommendations regarding targeted experiments to confirm our findings aimed at improving the natural resource management strategies currently in use.

A better understanding of these thresholds would aid managers in determining which changes within their dynamic system are worthy of concern. It would thus allow them to target monitoring to better detect when to act, and also fine-tune their actions based upon the outcomes of that monitoring. Here we explored threshold dynamics based on an existing ecological response model to identify whether any could be of assistance to managers. Thus the aims of the present study were to (1) describe the threshold dynamics within the ecosystem states model for the Coorong, with a view to predicting upcoming switches in state, and (2) evaluate a variety of approaches for how to assess which changes matter, and especially their utility for an early-warning capacity as leading indicators of ensuing change.

METHODS

Study area. The Coorong is the estuary at the terminus of the River Murray, the largest river system in Australia. The estuary is part of a Ramsar Convention-listed Wetland of International Importance, and provides important breeding and feeding habitat for many species of birds and fish (Brookes et al. 2009). The Coorong is a long, shallow lagoonal system, which is typified by a natural gradient in environmental conditions from an estuary around the Murray Mouth to hypersaline conditions at the southern, terminal end of the system, more than 100 km away. The Coorong can thus be divided into 3 regions: the usually estuarine Murray Mouth region at the northern end; and 2 lagoons separated by a constriction, the North and South Lagoons. River Murray flows can be regulated across a system of barrages at the northern end, with much smaller volumes entering the South Lagoon at Salt Creek, the Coorong's only tributary. Additional information on the characteristics of the system, including maps, are presented in Brookes et al. (2009) and Lester & Fairweather (2009b, 2010).

Ecosystem state model. An ecosystem response model was developed for the Coorong based on ecosystem states (Lester & Fairweather 2009a,b, 2010). The model is described in detail elsewhere (e.g. Lester & Fairweather 2009a) but is summarised to provide context for the further analyses of threshold dynamics presented here. The ecosystem states approach identifies clusters of biota that occur together in space and time and then finds thresholds for physico-chemical parameters that are associated with the presence of each cluster. Briefly, 2 data sets were compiled of the available biological and physico-chemical (or environmental) data, respectively. The biological data included survey data for fish, birds, benthic macroinvertebrates and macrophytes across 12 sites between 1999 and 2007. The environmental data included water quality and quantity, flow and meteorological variables over the same time period. Particular attention was given to including maxima, minima, lagged values and variances in the environmental data set (thus 230 variables in total), because mean variables are not always the best predictors of biological communities (Gaines & Denny 1993). The provenance of the data sets used and references to the collection methods are presented in Lester & Fairweather (2009b).

Clusters of co-occurring biota (including macrophytes, birds, fish and benthic macroinvertebrates) in space and time were identified from the biological data set using group-average clustering in PRIMER v6.0 (Clarke & Gorley 2006). Cluster membership was then used as the response variable for a CART analysis performed in CART Pro v6.0 (Steinberg & Golovnya 2007). CART analysis sequentially splits a response variable to maximise the difference between pre-defined groups by identifying thresholds (or splitting points) in the best of a range of independent variables (here the environmental data set) (Steinberg & Golovnya 2007). Thus the environmental conditions that were associated with each of the biotic clusters were identified. The biological data from cases in each CART terminal node were then tested for biological distinctness using analysis of similarities in PRIMER v6.0 (Clarke & Gorley 2006) and were combined when not statistically different. Predictive capacity was tested using cases withheld from the original model development and each group (or ecosystem state) was characterised based on its biological and environmental properties (e.g. using similarity percentage in PRIMER v6.0; Clarke & Gorley 2006).

For the Coorong, 8 ecosystem states were identified. Associated triggers in terms of physico-chemical parameters (with their relevant threshold values given in Table 1) were identified as average daily tidal range,

Table 1. The sequence of thresholds that determine each ecosystem state (see Lester & Fairweather 2009a, 2010 for a diagrammatic representation of the model and species lists for each state). A transition in ecosystem state will occur whenever one of the thresholds relevant for the original ecosystem state is crossed (as indicated by horizontal lines). Two horizontal lines are given for the maximum number of days since flow because that threshold appears in the model twice, '–' indicates that a threshold is not relevant for the ecosystem state in question. For example, no transition will occur from the Estuarine/Marine state if the water level, depth or salinity thresholds are crossed. Depth is from the previous year, consistent with the predictive variable identified in the ecosystem state model (refer to text for additional information). m AHD: metres above the Australian Height Datum, which approximates sea level

Ecosystem state	Relative state health	Tidal range (m)	Maximum no. days since flow	Water level A (m AHD)	Water level B (m AHD)	Depth (m)	Salinity (g l^{-1})
Estuarine/Marine	Healthy	>0.05	≤339	–	–	–	–
Marine	Degraded	>0.05	>339	–	–	>1.99	–
Unhealthy Marine	Degraded	>0.05	>339	–	–	≤1.99	≤64.5
Degraded Marine	Degraded	>0.05	>339	–	–	≤1.99	>64.5
Healthy Hypersaline	Healthy	≤0.05	≤339	>0.37	–	–	–
Average Hypersaline	Healthy	≤0.05	≤339	≤0.37	–	–	–
Unhealthy Hypersaline	Degraded	≤0.05	>339	–	>–0.09	–	–
Degraded Hypersaline	Degraded	≤0.05	>339	–	≤–0.09	–	–

the maximum number of days without barrage flows, 2 average annual water levels, average annual depth from the previous year (thus a temporal component was important here that was not so for other predictive variables) and average annual salinity. Various sequential combinations of parameter values for each of these 6 thresholds combine (Table 1) to predict the ecosystem state for a given case (note that the threshold for maximum number of days without flow of 339 appears twice in the model — once for cases with an average daily tidal range above the threshold, and once for those below the threshold — hence there are 6 thresholds that specify one of 8 possible states, rather than the 7 that would usually be required; see Lester & Fairweather 2009a,b for the model).

Because of the sequential nature of the thresholds in the ecosystem states model (a characteristic of the CART models upon which it is based; De'ath & Fabricius 2000), not all crossings of a threshold result in a change in ecosystem state. For example, changes in average annual salinity over the threshold do not result in ecosystem state changes unless depth from the previous year is less than 1.99 m, the maximum number of days since flow is greater than 339 and the average daily tidal range is greater than 0.05 m (Table 1). Table 1 illustrates this sequence of thresholds and allows the reader to determine when crossing a particular threshold will result in a change of state. In considering the threshold dynamics of the model, we have investigated both crossings of the threshold (whether or not an ecosystem-state change occurred) and only those crossings that resulted in a change in state (transitions), but have focused on the latter as most relevant to the management of the system.

Of the 8 possible ecosystem states, 5 occurred within the Coorong only when the threshold for the maximum number of days without barrage flow was exceeded. Based on modelled natural flows for the Murray-Darling Basin, end-of-system flows down the River Murray cease in only 1 % of years (CSIRO 2008), so we defined these 5 ecosystem states as being degraded. We believe that it is justified to consider a period of more than 11 mo without end-of-system flows as a degraded condition for the Coorong, and this is supported by the relatively simplified biotic assemblages associated with those 5 ecosystem states (see Lester & Fairweather 2009a,b for characteristics and species lists typical of each ecosystem state).

Each of the ecosystem states has been characterised based on its biological characteristics. As an example, the Average Hypersaline state (one of the healthy states lacking a tidal influence) was characterised by relatively low numbers of fish, including greenback flounder *Rhombosolea tapirina* and mulloway *Argyrosomus japonicus*. Correspondingly, few piscivorous bird species were associated with the state (with the exception of the Australian pelican *Pelecanus conspicillatus*). Instead, bird communities included waders (e.g. banded stilt *Cladorhynchus leucocephalus*, red-necked stint *Calidris ruficollis* and red-necked avocet *Recurvirostra novaehollandiae*) and waterfowl (e.g. grey teal *Anas gracilis*). *Ruppia tuberosa*, a macrophyte, had greater coverage here than for any other state for which data was available. There were relatively few benthic invertebrate taxa associated with this state, but chironomid larvae and amphipods occurred in high numbers. This state had moderate average salinities and low average depths, but freshwater flows occurred regularly. Water quality characteristics included high nutrient concentrations (e.g. total Kjeldahl nitrogen and ammonia), chlorophyll *a* and *b* concentrations and turbidity. In contrast, the Unhealthy Hypersaline state had higher average salinities, low average water levels and low variability in water levels with long periods since freshwater flows. Nutrient concentrations and turbidity remained high. Small-mouthed hardyhead *Atherinosoma microstoma* was the only fish species present in any large numbers. Avifauna were characterised by hoary-headed grebe *Poliocephalus poliocephalus*, Australian pelican (both piscivorous), banded stilt (a wader) and Australian shelduck *Tadorna tadornoides* (a waterfowl). This state supported a very limited diversity of invertebrates including polychaetes, but still had high numbers of chironomid larvae. Similar descriptions of the remaining states, along with tabulated average values for each, are presented in Lester & Fairweather (2009a).

Baseline scenario for the Coorong. In order to predict a sequence of ecosystem states for the region, the ecosystem states model was used in combination with a climate model, a river model and a hydrodynamic model for the region (Webster 2007, CSIRO 2008). A sequence of daily flows for the Coorong was developed using historical climate data with current infrastructure and extraction levels for the Murray-Darling Basin for the period of 1895 to 2008, largely in line with Scenario A in the Murray-Darling Basin Sustainable Yield Project (CSIRO 2008). This, coupled with average daily flows from the south via the Salt Creek tributary (from 2001 to 2008) and sea levels in Encounter Bay, was used as input to a hydrodynamic model developed for the Coorong (Webster 2007, Lester et al. 2009). The hydrodynamic model then predicted hourly water levels and salinities along the length of the Coorong over the 114 yr model run that were used as input to the ecosystem states model. The ecosystem states model predicted an annual time series of ecosystem states for each of 12 focal sites spread along the Coorong (see Lester & Fairweather 2009a, 2010 for additional detail). Thus the model predicted ecosystem states for a hypothetical 114 yr sequence that had historical climate variability but present-day infrastructure and extraction levels throughout. Such a sequence provides an understanding of the level of variability in ecosystem condition under a particular climate scenario, rather than attempting to replicate historical conditions exactly.

Threshold analyses. Some basic statistics were calculated for each threshold. These included the number of times each threshold was crossed under the baseline scenario simulation (described above), the return interval for crossing each threshold and the average number of years for which that threshold was exceeded (average exceedance interval).

The specific sites at which thresholds were crossed and the years in which each crossing occurred were also identified. Years in which thresholds were crossed at each site were identified using the R statistical environment v2.8.1 (R Core Development Team 2009). The years in which thresholds were crossed were also compared with lists of El Niño and La Niña years in Australia (BOM 2009). The El Niño Southern Oscillation (ENSO) affects large-scale Australian weather patterns, with drought periods associated with El Niño years and wetter periods with La Niña years. This pattern is in contrast to the associations seen in other parts of the world.

Determining rates of change: It is feasible that physico-chemical time series might exhibit different behaviour when they approach a threshold. Thus we wanted to see whether we could predict upcoming thresholds based on something simple, like changes in rates of change over time. Previous research on response variables suggests that rates of change slow as a threshold is approached (Dakos et al. 2008), and this may also be the case for predictive variables. A series of nested rates of change were developed for various time periods preceding each unique crossing of each threshold. For each site, rates of change were calculated for the week, month, year and decade prior to each threshold crossing. In order to preserve statistical independence, where a particular threshold was crossed at more than one site per year, only one site was selected at random for inclusion in the analysis. The site to be included was selected post hoc using a random number generator (having assigned each site a numeric tag). This site was included in the analysis and all other sites where the thresholds were crossed in the same year were excluded. Absolute values were taken for each rate of change, and the minimum, maximum and mean rates of change were calculated for each time step. Rates of change were calculated for each time period using linear regression in SYSTAT v.11 (SYSTAT 2004). Standardised rates of change were also computed by dividing each data point by the maximum rate of change observed within that time series. This scaling allowed comparison of trends for variables changing over different ranges. Confidence intervals were calculated for each rate of change (and standardised rate of change) by bootstrapping the mean rate of change using the 'boot' function in R.

Characterising transitions: Years in which individual sites crossed each threshold in the ecosystem state model were identified in the baseline scenario described above. For each, the value of the relevant parameter was recorded for the year in which the transition occurred and also for the following year to understand what values each variable takes immediately on either side of a threshold crossing.

Logistic regressions: Understanding the width of any transition zone for predictive variables around a threshold could assist in predicting whether upcoming transitions are likely. If these transition zones are sufficiently narrow, when values fall within that zone may be a good indication that a transition is imminent. Logistic regression is a classic method for exploring the shape of changes between binary variables, such as 2 ecosystem states governed by a threshold. Logistic regression was used for those thresholds that were crossed enough times to make analysis meaningful (here, a cut-off of more than 20 times over the 114 yr of the baseline scenario was used; see 'Results' for the number of times that each transition occurred), using the values that these physico-chemical variables took immediately prior to and following each transition. Binomial general linear models were fitted using the bias-correction algorithm for maximum likelihood estimates developed by Firth (1993). This was done using the 'brglm' package developed for R (Kosmidis 2007).

Zones of transition: Another method for exploring the width of the transition zone is to explicitly investigate the range of values that variables take immediately before and after a transition. Again, this could potentially assist in identifying a window within which transition is likely, where driving variables falling within the range could prompt management intervention. Again, this window would need to be sufficiently narrow to be of value for management. Maxima and minima were identified both before and after each threshold was crossed in each year in which it was crossed and the extremes of these were used to derive a zone of transition. This zone of transition comprised the minimum value of the parameter of interest in the year that threshold was exceeded and the maximum value of the same parameter the year after (and vice versa for falling below a threshold). As such, it gave the maximum range of values observed on either side of a threshold crossing. For each site, and for the Coorong as a whole, the proportion of time in which predicted parameter values fell within this zone of transition was calculated.

Developing a predictive model for future degraded ecosystem states: *Identifying an appropriate time lag:* An attempt was made to predict future degradation by comparing the ecosystem state in any year to physicochemical conditions several years prior. Thus choice of the time lags to include was a key step. Cross-correlation analyses were used to identify significant time lags between pairs of flow, hydrodynamic and biological variables. These analyses were conducted using the cross-correlation plotting function in the time series module of SYSTAT v.11 (SYSTAT 2004). Based on these cross-correlations, tables were compiled to summarise the significant time lags identified.

A subset of the 230! (factorial, thus effectively infinite) possible combinations of cross-correlations were undertaken (with 230 being the total number of environmental variables used in the original model development; refer to the ‘Ecosystem state model’ section above). This subset was chosen based on our understanding of the likely causal relationships within the system, as well as relationships that were identified in previous analyses (e.g. see Lester & Fairweather 2009a). We focused upon 4 types of correlations: correlations among flow variables (pertaining directly to the amount of flow passing over the barrages, e.g. total flow volume); correlations between flow and hydrodynamic variables (variables that were outputs from the hydrodynamic model, e.g. water levels and salinities); correlations between flow or hydrodynamic and biological variables; and correlations among biological variables.

For flow, total flow volume per annum and average daily flow volume were identified as the parameters likely to be correlated with the hydrodynamic variables for the Coorong. The specific hydrodynamic variables investigated included the average, maximum, minimum and variance of water levels and salinity for each of the North and South Lagoons. These were selected because they are easily measured, interpretable and likely to be of significance to the biotic assemblages in the region.

Biological variables investigated were chosen as a representative subset of the assemblage present, from the data used in the construction of the ecosystem state model. The species selected were chosen either because of identified ecological significance (e.g. *Ruppia tuberosa* has been previously identified as an ecosystem engineer in the region; Rogers & Paton 2009), or because they had previously been identified as typical of one or more ecosystem states (Lester & Fairweather 2009a). Biological variables included the proportion of sediment cores containing *R. tuberosa* (as a measure of the coverage of that macrophyte); abundances of a selection of bird species, including 2 wader species (red-necked stint and banded stilt), 2 piscivorous species (little pied cormorant *Phalacrocorax melanoleucos* and Australian pelican) and 2 waterfowl (grey teal and Australasian shelduck); catch per unit effort for 3 commercial fish species (Australian salmon *Arripis truttaceus*, black bream *Acanthopagrus butcheri* and yellow-eyed mullet *Aldrichetta forsteri*); and abundances of 3 benthic macroinvertebrate groups (chironomid larvae and the polychaetes *Australonereis ehlersi* and *Capitella* sp.).

The year with the single strongest correlation (whether positive or negative) was identified for each cross-correlation comparison, separating flow correlated with hydrodynamic variables from flow or hydrodynamic variables correlated with biological variables. From this analysis, those years that had the strongest correlations most often were identified as time lags to be used in the predictive modelling step.

Modelling future degraded ecosystem states for chosen time lags: The most significant time lags identified with cross-correlations were retained for use in predicting future degraded ecosystem states. Where several years had very similar numbers of significant cross-correlations (Table 2), time lags were chosen in order to allow sufficient time for management intervention (i.e. a 3 yr time lag) and to investigate how the predictors of future degraded ecosystem states changed over shorter times (i.e. a 1 yr lag).

Ecosystem states were modelled for 12 sites along the length of the Coorong (see Lester & Fairweather 2009b for details) for the period of 1999 to 2007 using

Table 2. Numbers of significant time lags among flow, hydrodynamic and biological cross-correlations. **Bold** numbers indicate the highest number of statistically significant correlations for each column. For flow versus hydrodynamic variables, n = 19. For biological versus flow, hydrodynamic or biological variables, n = 82. Biological variables were cross-correlated against a combination of flow and hydrodynamic variables, as well as among biological variables. Refer to ‘Methods: Identifying an appropriate time lag’ for additional information on the variables used

Time lag (yr)	Flow vs. hydrodynamic variables			Biological vs. flow, hydrodynamic or biological variables		
	Positive	Negative	Total	Positive	Negative	Total
1	9	**9**	**18**	**5**	2	**7**
2	7	7	14	4	**4**	**8**
3	8	6	14	3	3	6
4	**10**	4	14	3	3	6
5	8	0	8	4	3	**7**
6	2	6	8	4	3	**7**
7	0	3	3	**5**	1	6
8	0	**9**	9	**5**	2	**7**
9	8	7	15	2	2	4

the model described in Lester & Fairweather (2009a,b, 2010), with each site for each year referred to as a site-year. These predicted ecosystem states were offset from the accompanying physico-chemical data set by each of the identified significant lag periods (i.e. either 1 or 3 yr). The physico-chemical data set used was similar to that described above and in Lester & Fairweather (2009a,b, 2010), and so included a range of flows, water levels, depths, salinities, meteorological variables and water quality variables described by means, maxima, minima and variances. In addition, variables averaging the hydrodynamic conditions across all sites in each of the 2 lagoons were added to the list. Averaged variables were included to represent what is already in use by managers. These included maxima, minima, means and variances of water levels and salinities for each of the North and South Lagoons.

The ecosystem states were then classified as either degraded or healthy (i.e. not-degraded) based on whether there had been freshwater input from the River Murray in the previous 339 d (as described above). CART analyses were used to identify specific physico-chemical variables associated with the presence of future degraded ecosystem states. The analyses were conducted in CART v6.0 (Steinberg & Golovnya 2007) using a twoing-splitting algorithm and 10-fold cross-validation. The minimum size of a parent node was set to 5, with the minimum size of a child node at 2. The best tree was selected using the 1-standard error rule (Breiman et al. 1984), and variables were penalised for missing values using a value of $\beta = 0.60$ (Steinberg & Golovnya 2007). Pearson correlations between variables identified as significant predictors of future degraded ecosystem states were analysed using linear regression and, where significant correlations ($\alpha = 0.05$) among predictor variables existed, the variable with the lower level of importance for the model was excluded and the model then re-run. This approach was consistent with that used originally to construct the ecosystem state model.

RESULTS

Threshold characteristics

Within the model simulation, the system crossed the different thresholds with uneven frequencies and crossing events were not distributed equally across all sites (Table 3). The return interval and duration of exceedance of thresholds were not equal amongst the 3 regions within the Coorong (Table 3), but were inversely related. The thresholds involving salinity, tidal range and water level A were most commonly observed to be crossed (Table 3), whereas the other thresholds were crossed either uncommonly (maximum number of days since flow, depth) or only once (water level B). Water level A and tidal-range thresholds were crossed more commonly at the northern end of the Coorong (i.e. the Murray Mouth or North Lagoon regions), while the salinity threshold was crossed more frequently in the South Lagoon.

There was no obvious relationship between threshold crossings and the ENSO index. All variables were crossed most frequently in years that were not designated as either El Niño or La Niña years

Table 3. Summary of threshold characteristics. These values are based on a simulation of historical conditions within the Coorong over 114 yr. The coincidence with El Niño Southern Oscillation (ENSO) columns illustrate which threshold crossings coincided with El Niño years, La Niña years or neither. The return interval and exceedance durations show the average number of years between threshold crossings and the average length of time that a site remained over a threshold, respectively, for each of the 3 regions (Murray Mouth [MM], North Lagoon [NL] and South Lagoon [SL]). Depth is from the previous year, consistent with the predictive variable identified in the ecosystem state model (refer 'Methods: Ecosystem state model' for additional information). The depth threshold was only crossed at North Lagoon sites. The number of days since flow occurred over the barrages is not spatially variable, so the return intervals and exceedance durations presented under the MM column are representative of the whole Coorong. The water level B threshold was only crossed in the final year of simulation for the 3 southernmost sites (SL), so it was not possible to calculate return intervals or exceedance duration. na: no value possible; m AHD: metres above the Australian Height Datum, which approximates sea level

Threshold	Threshold value	No. years crossed	Coincidence ENSO (yr)			Return interval (yr)			Exceedance duration (yr)		
			El Niño	La Niña	Neither	MM	NL	SL	MM	NL	SL
Tidal range	0.05 m	18	6	2	10	na	2.6	20.5	na	13.8	4.6
Maximum no. days since flow	339 d	4	3	0	1	34.3	na	na	1.8	na	na
Salinity	64.5 g l^{-1}	24	9	2	13	na	10.3	5.6	na	7.3	9.1
Depth	1.99 m	6	0	3	3	na	15.0	na	na	1.7	na
Water level A	0.37 m AHD	11	2	3	6	8.2	5.0	10.2	1.8	1.6	1.6
Water level B	−0.09 m AHD	1	0	0	1	na	na	na	na	na	na

(including when the relative proportion of ENSO years was taken into account), so we identified no direct link between thresholds and ENSO in the present study.

Determining rates of change

The rate of change in predictive variables increased as a threshold was approached for those thresholds where analysis was possible. This included salinity, water level A, tidal range and depth. Analysis of a rate of change is nonsensical for a count variable such as the number of days since flow, so that was not attempted. The threshold for water level B was only crossed in a single year, so it had an insufficient sample size for analysis. Differences in the scale of variables somewhat masked the increasing rate of change for the tidal range, water level A and depth thresholds (Fig. 1a vs. Fig. 1b), but all tended to increase within 1 mo of the transition, or 1 yr for the salinity threshold (and depth to a lesser extent; see Fig. 1b). The patterns illustrated in Fig. 1 are for mean rates of change, but minimum and maximum rates of change also exhibited the same pattern. In addition to increasing rates of change near a transition, the bootstrapped variability of the rate of change also increased as a transition approached (Fig. 1), again becoming apparent approximately 1 mo before the transition occurred.

Characterising transitions

Transitions between ecosystem states occurred less frequently than threshold crossings (as defined above). Transitions between marine states and hypersaline states occurred 61 times over the 114 yr model run. Transitions over the maximum number of days since flow threshold for marine states occurred 51 times (i.e. from Estuarine/Marine to Marine, Unhealthy Marine or Degraded Marine states; see Table 1), while transitions over the same threshold occurred 23 times for hypersaline states (i.e. from Healthy Hypersaline or Average Hypersaline to Unhealthy Hypersaline or Degraded Hypersaline; see Table 1). There were only 3 transitions observed between the Unhealthy Marine and Degraded Marine states (salinity threshold), 3 between Unhealthy Hypersaline and Degraded Hypersaline states (water level B threshold) and none between the Marine and either the Unhealthy or Degraded Marine states (depth threshold). The remaining results will relate to transitions between states, rather than the crossing of individual thresholds (which may or may not result in a shift in ecosystem state).

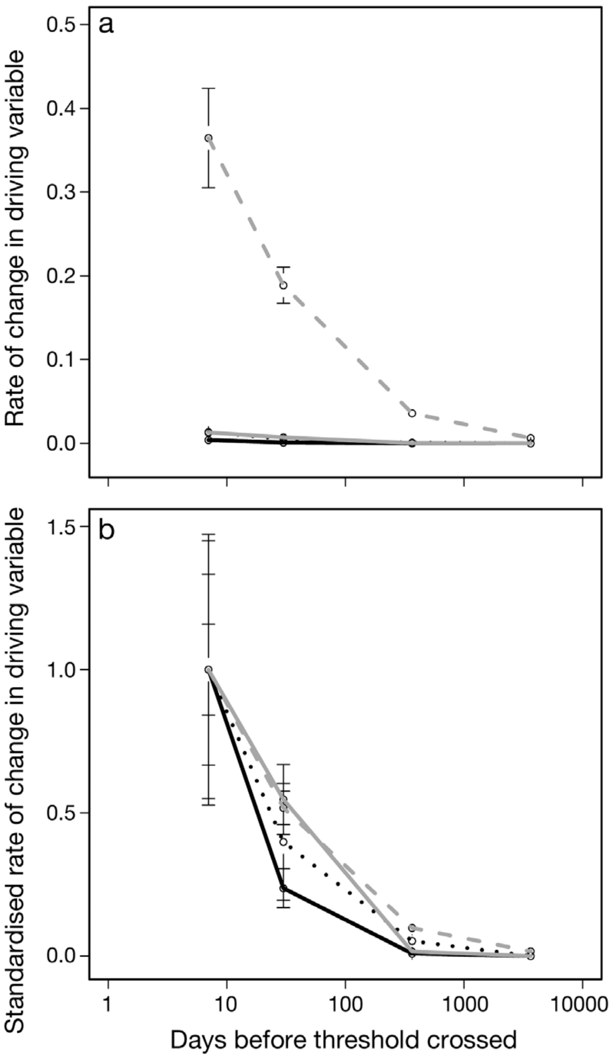

Fig. 1. Evidence of increasing rates of change in days preceding a threshold crossing for 4 variables (note log scale on the *x*-axis): tidal range (m d^{-1}; black solid line), salinity (g l^{-1} d^{-1}; grey dashed line), depth (m d^{-1}; black dotted line) and water level A (m AHD d^{-1}; grey solid line), given as (a) raw values and (b) scaled to the maximum value in each variable. Error bars are SE

Logistic regression

Logistic regression of the predictive variables to determine the shape of the transition was done for the tidal range, water level A and maximum number of days since flow thresholds. Regression analysis was not undertaken for the water level B, depth or salinity thresholds. The resultant regression equations showed very sharp transitions. The regression for the water level A threshold (Fig. 2) is presented here as an example of the typical behaviour observed, with other variables (i.e. tidal range and maximum number of days since flow) showing similar and consistent patterns.

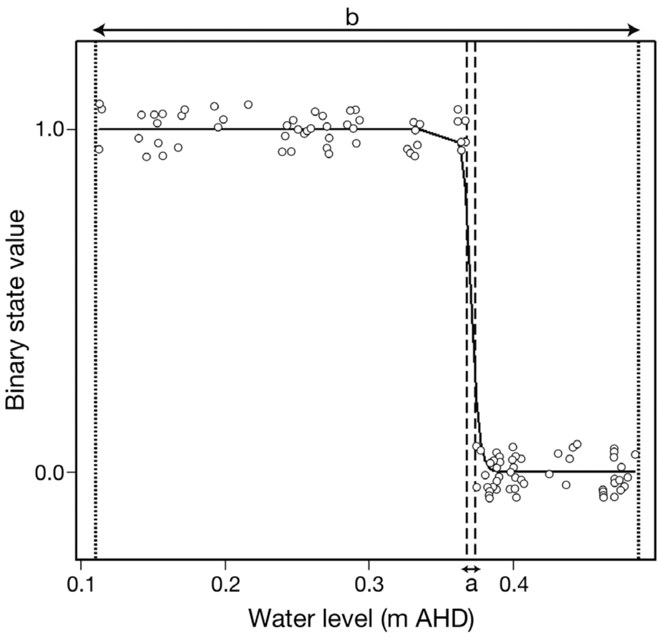

Fig. 2. Logistic regression of threshold crossings for water level A resulting in transitions in ecosystem state. Circles are the data points from the hydrodynamic modelling and have been jittered to assist in visualisation and interpretation (thus the position of identical points has been varied slightly so that all points are visible). The solid line is the line fitted to predicted values from the logistic regression. Domains ‘a’ (between the dashed vertical lines) and ‘b’ (between the dotted vertical lines) correspond to values given in Table 4 and show the smallest and largest distance across a threshold, respectively. m AHD: metres above the Australian Height Datum, which approximates sea level

The spread of values for each variable around the threshold tended to be quite continuous (i.e. there was no jump in values on either side of the threshold, suggesting a gradual change in the variable of interest), consistent with the notion that small changes in physical variables can result in large changes in biological communities. Ratios comparing the largest and smallest differences across a threshold were large for all variables, indicating inconsistencies in the size of shifts across each threshold (Table 4).

Zones of transition

In contrast to the sharp transitions identified using logistic regression, exploration of any zone of transition showed extremely wide zones around each threshold (where sufficient numbers of transitions occurred for analysis). Again, the water level A threshold has been used as an example (Fig. 3), but other thresholds showed similar behaviour. For this water level threshold, 94% of all cases fell within the bounds of values that occurred in the year immediately prior to or following a transition (illustrated by domain ‘b’ in Fig. 2), suggesting that using presence within this wide zone of transition would not be a useful predictor of impending transition because only the most extreme cases fell outside this zone of transition and many false positives would be returned. For other thresholds, the proportion of cases falling within the zone of transition was 51% for tidal range and 68% for the maximum number of days without flow. Again, no zones were computed for the other thresholds due to the small number of transitions observed across each.

A predictive model for future degraded ecosystem states

Identifying an appropriate time lag

The strongest cross-correlations were observed between flow and hydrodynamic variables in the Coorong. All cross-correlations undertaken comparing flow and hydrodynamic variables had at least one significant time lag (Table 2). One year time lags were the strongest most commonly for flow and hydrodynamic variables (Fig. 4), indicating a close relationship between flow, water levels and salinity within the Coorong. Periodicity was also evident in the pattern of significant lags, so that 2, 3 and 4 yr lags were also statistically significant for a high proportion of the cross-correlations investigated (Table 2).

Table 4. Width of the minimum and maximum zones of transition for each threshold. Thresholds for water level B, salinity and depth were not crossed enough times to justify logistic regression (i.e. <3 in each case). m AHD: metres above the Australian Height Datum, which approximates sea level

Threshold	Smallest distance across a transition (‘a’ in Fig. 2)	Largest distance across a transition (‘b’ in Fig. 2)	Ratio b:a
Tidal range (m)	0.00[a]	0.09	300.67[b]
Maximum no. days since flow			
Hypersaline (southern) basin	74	577	7.80
Marine (northern) basin	74	421	5.69
Water level A (m AHD)	0.01	0.37	44.83

[a] Size of the difference in tidal range was below the precision of the hydrodynamic model, so it is presented as 0.00

[b] Value of ‘a’ was below the precision of the hydrodynamic model, so this value should be interpreted with caution, but is presented to demonstrate the size of the difference in zones of transition for tidal range

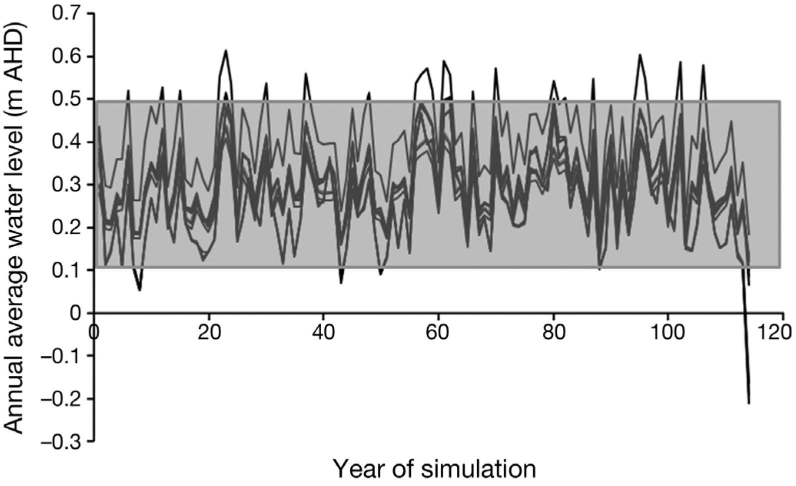

Fig. 3. Extent of the zone of transition for the water level A threshold. Each line predicts a trajectory of predicted average annual water levels for one site, based on a simulation of historical conditions within the Coorong over 114 yr for each of 12 focal sites in the Coorong. The shaded area indicates the extent of the zone of transition that encompasses the highest water level in the year prior to the threshold being crossed and the lowest water level in the year following the threshold crossing (or vice versa). m AHD: metres above the Australian Height Datum, which approximates sea level. Note that water levels below 0 m AHD occurred for 3 sites at the end of the simulation

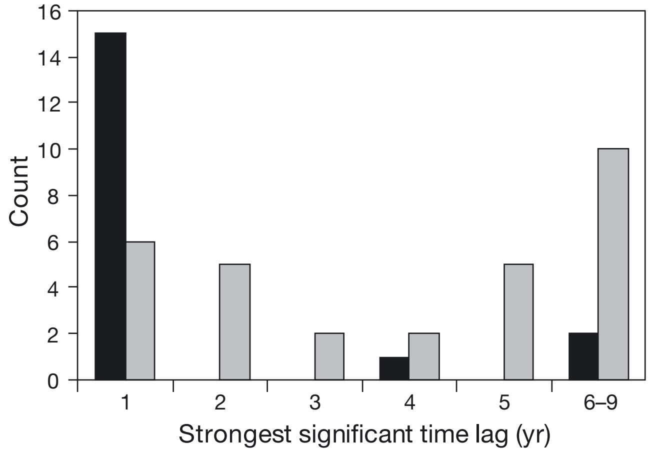

Fig. 4. Cross-correlation histograms showing the frequency of the strongest significant correlations for flow versus hydrodynamic variables (black bars), and biological versus flow, hydrodynamic and biological variables (grey bars). Refer to 'Methods: Identifying an appropriate time lag' for additional information on the variables used

Relationships amongst flow, hydrodynamic and biological variables were weaker. There were fewer significant cross-correlations observed (Table 2) and there was less consistency in the lags that tended to be significantly correlated among variables (Fig. 4). Interestingly, biological variables were generally more strongly cross-correlated with other biological variables than with either flow or hydrodynamic variables. A 2 yr time lag was marginally the most common significant cross-correlation (Table 2), but all lags between 1 and 8 yr showed similar numbers of significant correlations. The strongest correlations occurred for longer time lags, with lags of more than 5 yr being most commonly the strongest (Fig. 4).

Modelling future degraded ecosystem states

The 1 and 3 yr intervals were used as the time lags over which to model future degraded ecosystem states in the Coorong. Both models were relatively simple, with only 1 or 2 predictive variables needed (Fig. 5).

The 1 yr model correctly predicted all degraded site-years (Fig. 5a), but also predicted that 15 % of healthy site-years would be degraded, to give an overall misclassification rate of 14 %. Significant predictive variables were the average daily flow volume over the barrages (adjusted for the distance of the relevant site along the Coorong) and the maximum depth of water reached for the year. Thus we conclude that degradation next year could be predicted by monitoring daily flow and water depth.

For the 3 yr model (Fig. 5b), there was a single predictive variable, average annual South Lagoon salinity. Again, all degraded site-years were correctly classified. Here, 21 % of healthy site-years were predicted to be degraded, for an overall misclassification rate of 15 %. Thus we conclude that degradation 3 yr hence could be predicted by monitoring South Lagoon salinity now.

DISCUSSION

Several different approaches were used here to explore the behaviour of physico-chemical variables around thresholds with a view to identifying any mechanism for predicting upcoming ecological transitions. These methods included investigating how rates of change varied as thresholds approached, identification of a zone of transition around each threshold, and comparison with trends in environmental forcing factors. Rates of change and variability in rates of change increased near transitions but not within a time frame to assist managers. The increase happened late during the time series (see Fig. 1, note the log scale for time) and thus there was not much early-warning capacity. It

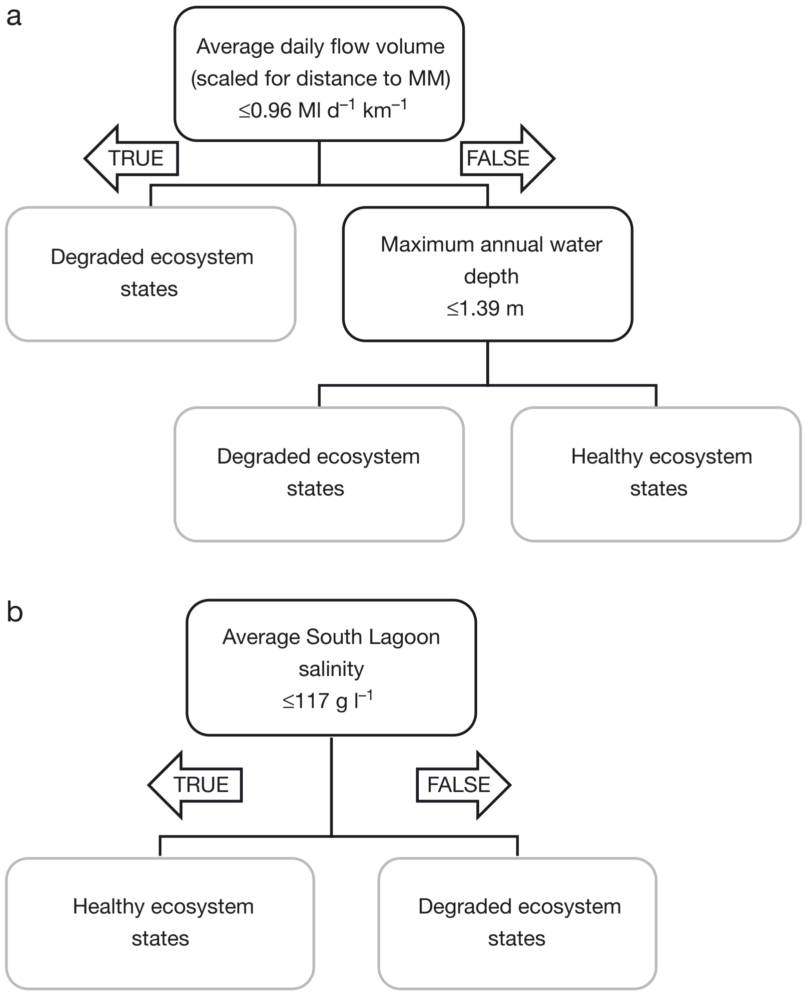

Fig. 5. Classification and regression tree models to predict future degraded ecosystem states for (a) 1 yr in advance and (b) 3 yr in advance. Each is presented as a logic tree, which can be followed to identify whether degraded ecosystem states are likely in either 1 or 3 yr time. Each decision box (black outline) contains a splitting parameter and its threshold value. The arrows indicate the direction the tree should be followed when the statement is true versus false. When a terminal node box (grey outline) is reached, the future presence of either degraded or healthy ecosystem states has been identified. Degraded ecosystem states (5 of 8) are defined as those that occur when no freshwater barrage flows have occurred in 339 d; healthy ecosystem states (3 of 8) are all others. MM: Murray Mouth

is likely that by the time managers were aware that rates of change were increasing, the threshold would have been crossed and thus intervention would no longer be possible.

Attempts to identify a zone of transition were also of limited value in predicting upcoming ecological transitions. Logistic regression did not give a realistic idea of the fuzziness of thresholds, which were extremely sharp, thus giving rise to an impression of (false) precision. The crispness of these transitions is likely to be an artefact of the CART methodology used to produce the model, and such apparent precision may not be biologically meaningful. In an attempt to remedy this artificial crispness, we investigated the range of values that fell within a past observed zone of transition. This approach had the other problem: that zone was too broad to be of use. In our case, 51 to 94 % of occasions fell within the zone in which transitions were possible in the scenario investigated, yet obviously did not always result in transitions (see Table 3).

Thus the question remains of how to 'fuzzify' the artificially sharp transitions arising from the CART methodology without producing zones too broad to be of use. Fuzzy logic techniques have been applied in some ecological systems (Prato 2005) in a manner that may be of use for this application. Field experiments focused on how ecosystems respond in practice are also likely to be necessary to define real ranges of transition. These experiments should be based on specific hypotheses regarding the mechanisms by which components of the ecosystem respond. For example, the levels of treatments used should be set as a range-finding exercise to determine whether the thresholds are crisp or fuzzy. Such an experiment would use the observed distribution of values around the analytically-derived threshold (e.g. from CART analyses) to set the upper and lower bounds of treatment levels (Petraitis 1998). Thus the results of such an experiment would directly relate to the crispness of thresholds in practice.

In the past, efforts to predict approaching ecological transitions using thresholds have focused upon characteristics such as changes in variances, critical slowing down, changes in return rates or skewness (Carpenter & Brock 2006, Carpenter et al. 2008, Dakos et al. 2008, Guttal & Jayaprakash 2008). These have largely been detected using deterministic models describing system behaviour in various response variables. The utility of these characteristics for guiding management of complex ecosystems has, in most cases, yet to be determined. The detection of some of these characteristics requires significant data resources, for example complete and lengthy time series, and not all of the leading indicators seem to become apparent in a time frame that would allow management intervention (e.g. see simulations in Carpenter et al. 2008). Our alternative approach used thresholds derived from a statistical model, and focused on the behaviour of thresholds derived from predictive variables (as there is no time series of values associated with ecosystem states; they are either present or absent). Here we used descriptions of the past to infer the future and so focused on a nested set of rates of change, logistic regression, environmental forcing and zones of transition. However, these approaches also proved of limited use for management with the results either too precise or not precise enough to be useful, or where the early warning comes too late.

Instead, more value was seen in using lagged environmental variables to identify changes toward degraded states. It is theoretically possible to construct models of these leading indicators using different lengths of lag. Models were developed at both 1 and 3 yr lags to investigate differences in the drivers of degraded ecosystem states at different points in time, as well as to provide managers with ongoing predictions of the likely future condition of the region. Both resulted in quite good levels of prediction, given the inherent variability of the system and the time lags involved (particularly for 3 yr in advance). A 3 yr advance model, in particular, would give sufficient warning to managers to intervene in the system to prevent future degradation (see below).

The choice of time lag based on cross-correlations for these predictive models was not clear-cut. Particularly for relationships involving biological variables, many lags had numerous significant correlations. Therefore, we based our choice of 1 and 3 yr lags on the practicality of using the resultant models for management of the system. Three years gives good opportunity for managers to act. In a large system like the Murray-Darling Basin, it would realistically take at least 1 yr to deliver additional environmental water by the time the need for that water had been established, politically sanctioned and then the water sourced and actually diverted to the estuary. Three years would give managers at least 1 yr to source the water and 1 yr for the effects of that water to begin to be apparent. This would then allow managers to use the 1 yr model to see if the intervention had been successful. There would be much less opportunity to intervene with only a 1 yr lag, but this model could highlight any imminent need for emergency actions. Time frames longer than 3 yr are outside (Australian) political time frames and many management planning cycles, so are not likely to be practical for informing the management of the site, because it is unlikely that water could be reliably secured that far in advance. In addition, weather within the Murray-Darling Basin is so variable that we expect the predictive capacity of the models would diminish as the lag involved increased, and it would be more difficult to justify that the water be required in the long run. The wisdom of allowing ecological modelling to be driven by political time periods is debatable, and it could be argued that management, in particular, should be driven by ecological time frames, rather than vice versa. We do not pretend to have a solution for this philosophical question, but better understanding the significant time lags within an ecological system should contribute to future debate on the issue.

Thus the 2 models were derived quite deliberately. We wanted to investigate the consistency of the predictors of future degraded ecosystem states over time. The 2 models we derived for the different time lags gave different thresholds and had different predictors (i.e. the physico-chemical variables involved) to focus upon. Thus the choice of indicator of future degradation is specific to the time frame involved. Managers should not expect modelling (or any other approach to natural resource management) to provide a 'silver bullet' that will cover all situations. Instead they need to look at a range of threshold values to fit specific purposes and then use them appropriately. It would also be possible to combine the use of the different models in clever ways to allow for different decisions to be made. For example, the 3 yr model could be used to predict future degraded states, the system could be managed accordingly and then the 1 yr model (with its different thresholds) implemented to test whether the intervention that was imposed had indeed succeeded in avoiding those conditions associated with a high likelihood of future degraded states, before they occurred.

Both the 1 and 3 yr models tended to err on the side of conservatism, with all observed misclassifications consisting of site-years that supported healthy ecosystem states being predicted to be degraded (Type I error). A moderate bias for such conservatism is almost certainly preferable to failing to predict degradation when it does occur (Type II error), because it allows managers the opportunity to intervene so as to prevent irreparable harm to the ecosystem (Fairweather 1991). Unnecessary intervention in up to 15% of cases is not likely to be unreasonable, given the inherent climatic and flow variability within the system and the time frame of up to 3 yr in advance.

Thus modelling specifically for upcoming degradation did identify useful trigger levels in a suitable time frame, so this approach could be used to inform future management (e.g. by using the leading indicator of average South Lagoon salinity for degradation 3 yr hence as a trigger for environmental flows or for other restoration/rehabilitation actions), but it does not provide clues about as yet unknown thresholds in the system (e.g. transition to a novel but overly degraded state) as the threshold dynamics options were looking to explore. Thus we can never know when we are approaching a new threshold using this method.

There is another caveat to this approach. In many cases, we have not yet tested the predictions from the models (Lester & Fairweather 2009a). The outcomes that are predicted should be contrasted against what observations occur over the fullness of time, but we also feel that targeted experiments might be possible to speed up our understanding of how these models translate in practice. Experiments could attempt to force specific predictive variables over thresholds and then observe whether the predicted state changes occurred. This could be actively done on a small scale, or could be undertaken more passively: following the development of a stated hypothesis, a wait-and-see approach could be adopted and the behaviour of the system then observed. Additional water will either be available for the system or not, and in either case specific hypotheses could be developed based on both the 1 and 3 yr models and compared with observations. We would also suggest the use of time-series analysis to routinely explore possible lags for both auto-correlation (within an environmental variable) and cross-correlations (amongst sets of variables) as a means to better understand the overall system behaviour for predictive purposes, as done here.

The present study illustrates the nature of threshold dynamics for one Australian estuary. It does, however, raise several points of interest for other estuarine and marine ecosystems, should these patterns prove applicable more broadly. Different estuaries will show other characteristics and different behaviour, and so need to be modelled by our general approach to identify ecosystem states in terms of biota and the environmental transitions between them. Here the ecological response model we developed was built at 2 distinct time frames (i.e. seasonally and annually) with 12 sites distributed along the Coorong. The modelling approach, however, is not constrained to these, and spatio-temporal scales can be changed to reflect the available data. Despite the spatio-temporal resolution included here, there was a general lack of portents identified for changes in ecosystem states in the estuary based on threshold dynamics. This suggests that focus should be placed on those aspects of threshold dynamics that have been shown to be able to potentially predict changes in ecosystem state (e.g. identified via direct modelling); these should be tested with monitoring and then management should be directed accordingly.

It is clear that concern about climate change will put more pressure upon water resources into the future, particularly for semi-arid estuaries. An essentially synthetic approach can be seen being actively developed in a few studies to date from across the globe (e.g. see Anderson et al. 2006, Powell 2008, Kim & Montagna 2009, Lester et al. 2009, Zweig & Kitchens 2009) to fulfil a need that water resource managers shall feel keenly over the years to come. This synthesis entails an ability to realistically infer what the future climate is likely to be in specific locations, translate how that might diminish water flows but increase demands for irrigation and other extractive uses, and then foresee the ecological consequences of such changes. Given this growing need, models that are able to predict future ecological degradation in a suitable time frame, with reasonable predictive accuracy, will be a significant and useful resource for estuarine management.

In conclusion, our main recommendations are that exploring threshold dynamics may not be the best method for predicting upcoming changes in ecosystem states with a view to preventing ecological degradation through active management. Instead we may need to identify leading indicators of likely future change by specifically modelling for known degraded states in the future and thus identifying usable thresholds to trigger management action in the region. However, a mechanism for predicting unknown transitions in the future remains a key knowledge gap.

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