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 &

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 km². 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 Feeding	Larval Period	Recruitment Range	Recruitment Peak	Adult Feeding	Adult 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	<1 d	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
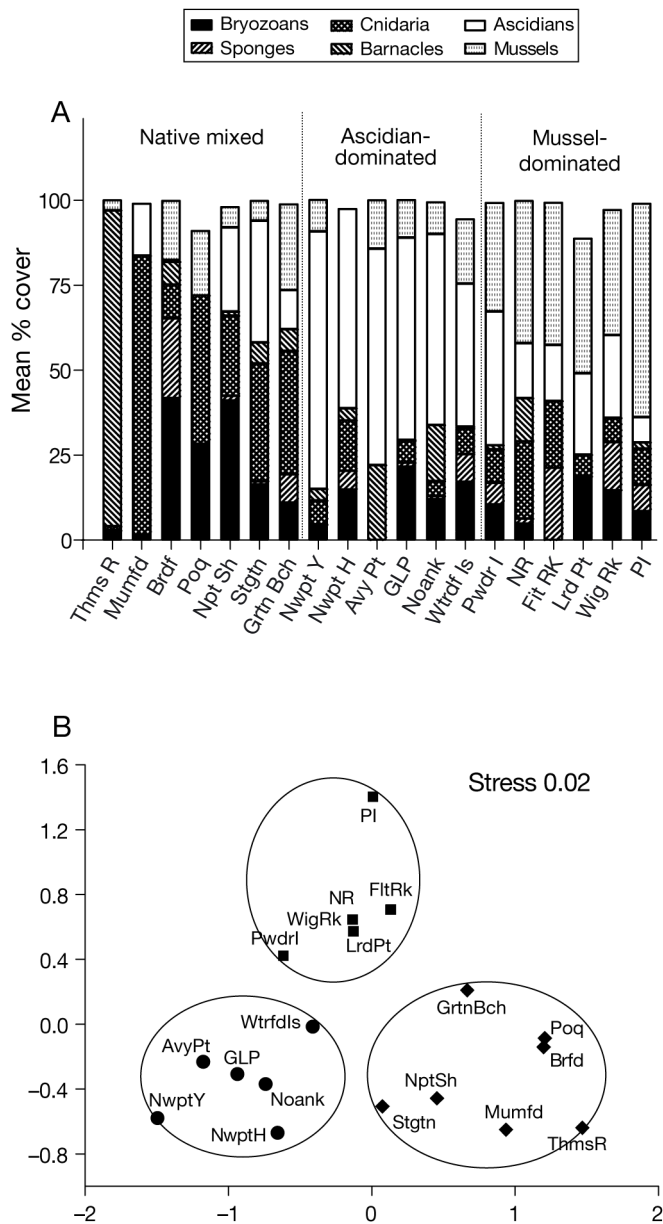
Fig. 1. Dominance variability of benthic sessile invertebrates among 19 sites surveyed in eastern Long Island Sound and Narragansett Bay in 2004. (A) Each bar shows the mean % cover for each taxa at the site. Means are based on analyses of a minimum of 20 random photos of 140 cm^2 of the substrates at 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').

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
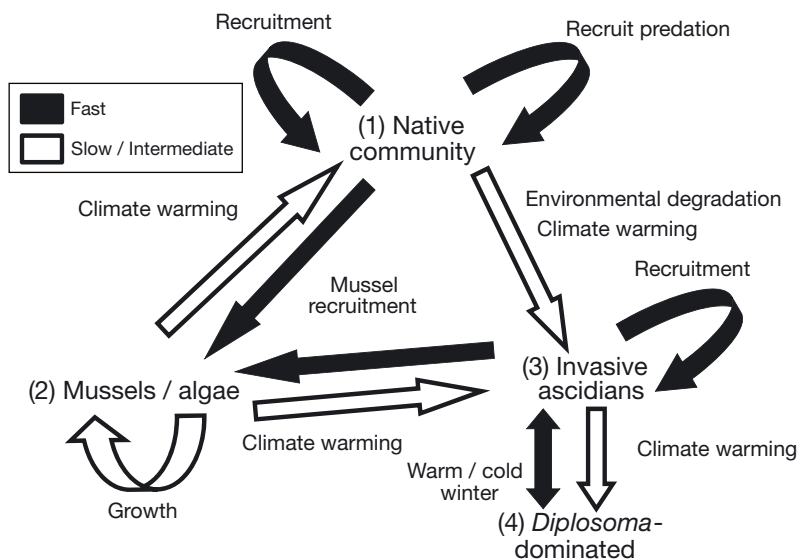

Fig. 2. The 4 different community states: (1) the native community, (2) mussels/algae, (3) invasive ascidians (4) a state dominated by *Diplosoma listerianum*. Arrows represent the changes from one community state to another with the hypothesized processes labeled. The speed at which transitions may 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

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)
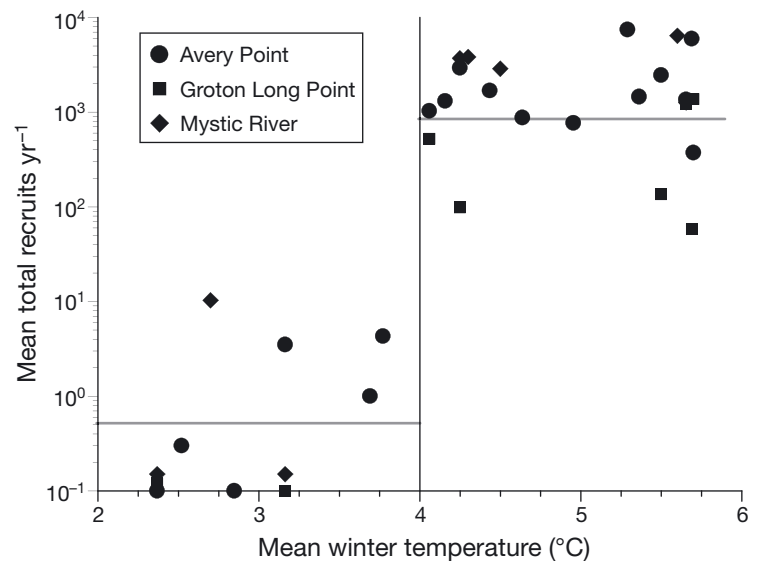

Fig. 3. *Diplosoma listerianum*. Mean total annual recruitment of *D. listerianum* on panels at 3 different field sites as a function of mean winter temperature. Horizontal grey lines = means above and below the 4°C temperature threshold. Recruitment was generally lower at Groton Long Point, but recruitment 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

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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.
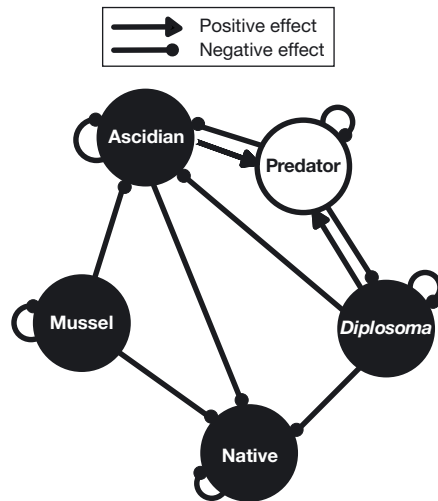

Fig. 4. Simple loop model representing the local dynamics comprised of the 4 alternate states shown in Fig. 2. The nodes and connectors between the different states represent simplified models used to test for stability with loop analysis. The local community structure is represented by the 4 community 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_suppl.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 sup-

port 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
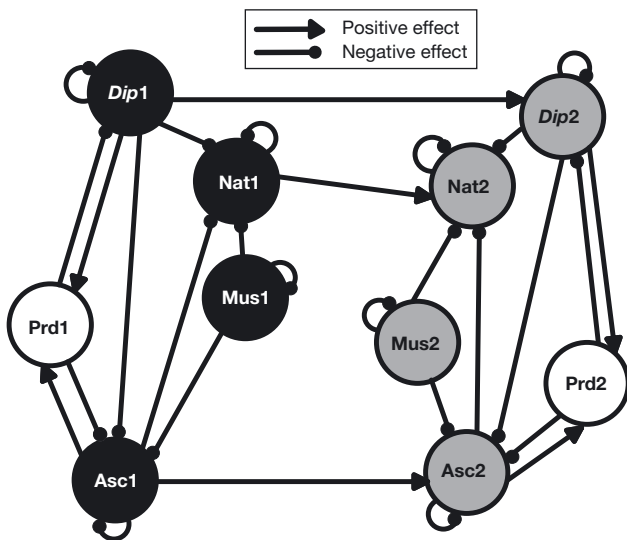

Fig. 5. Simplest loop model representing regional dynamics comprised of the 4 alternate states shown in Fig. 2, where the interactions observed at the local scale are expanded to 2 sites. The 2 sites have the same internal dynamics as represented in Fig. 4. Site 1 (black circles) represents an external 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

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.

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 com-

munities. 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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