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

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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), trade-offs 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-

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 anthro-

pogenic 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
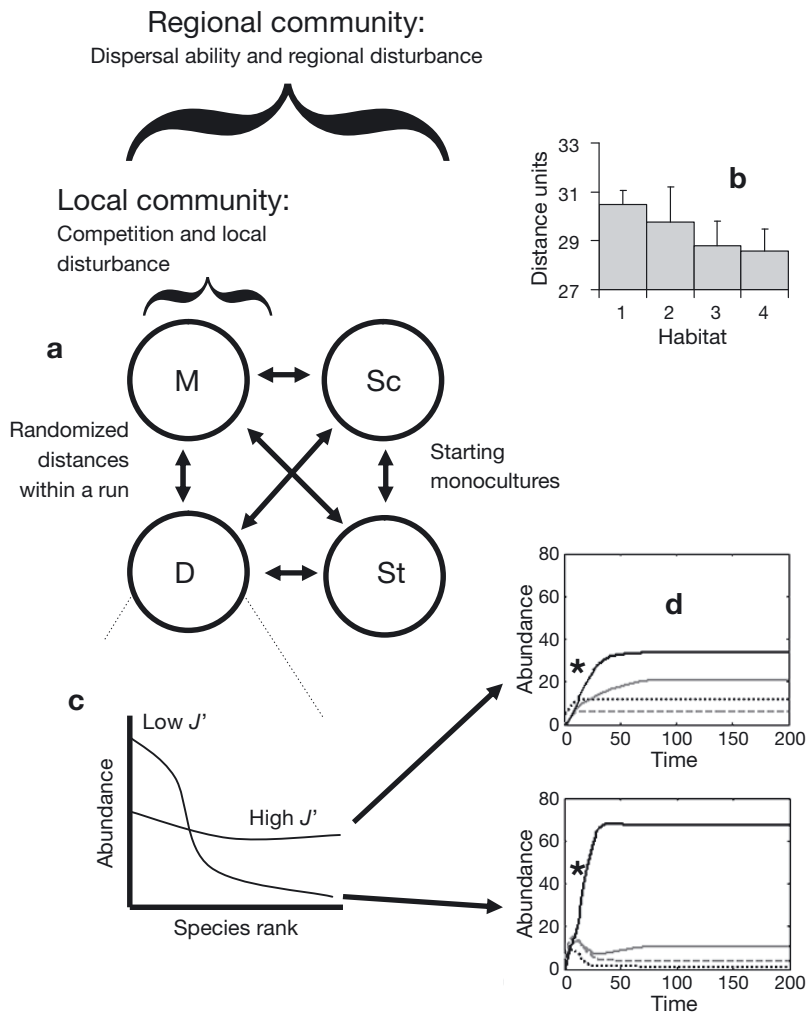
Fig. 1. Diagram of the simulation model. (a) Within each local community (large circle), a single species started as a monoculture (M: *Mytilus edulis*, Sc: *Schizoporella errata*, St: *Styela clava*, D: *Diplosoma listerianum*). These monocultures were allowed to grow and disperse to other sites, affecting 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:

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

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:

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

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-
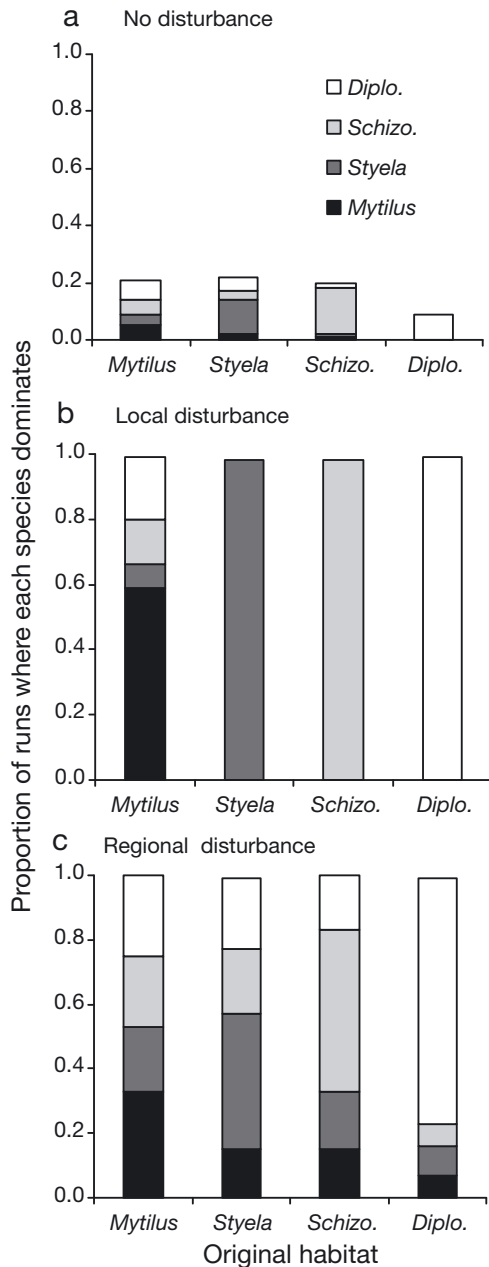
Fig. 2. Frequency of dominance events (>50% abundance) for each of the 4 simulated species partitioned by habitat. Simulations started with a monoculture at low abundance in each of the 4 habitats (original habitat, *x*-axis). A bar represents the proportion of runs that had a dominance event for each 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
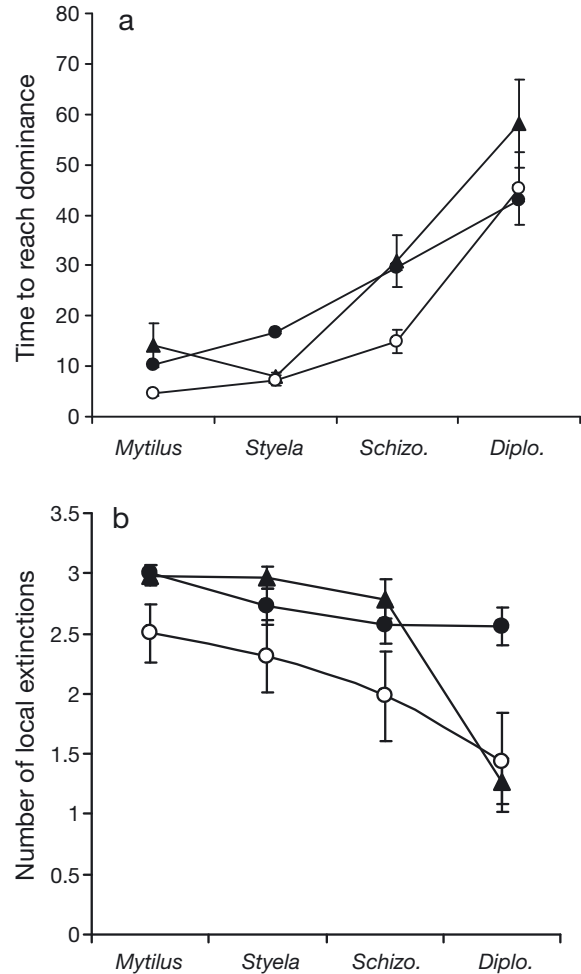

Fig. 3. (a) Average number of time steps to reach dominance, and (b) average number of local extinctions shown by each of the 4 species, under different disturbance scenarios: no disturbance (▲), regional disturbance (○), and local disturbance (●). Values are means of 1000 runs, and error bars represent ±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.
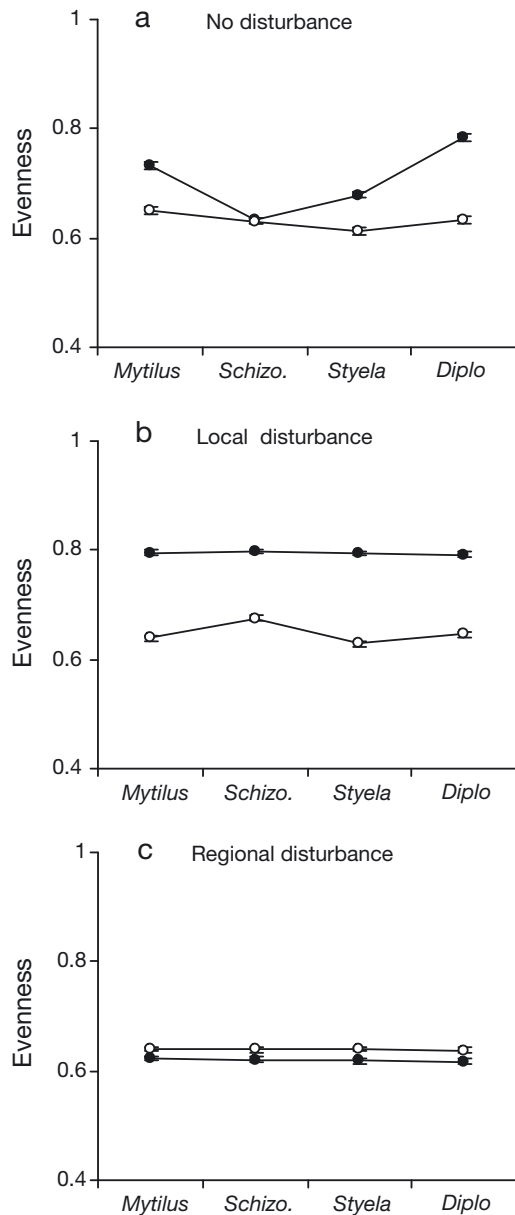
Fig. 4. Community structure (represented as evenness) at the time when a species started becoming dominant (●) or started becoming extinct (○) in the 3 scenarios. Values are means of 1000 runs. See Fig. 1 for full species names

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; how-

ever, 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

Retracted

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

$$T \qquad\qquad N$$

16 x 16 matrix   **16 x 1 vector**

```
a1  a2  a3 a4  0...                                  A1   Species 1 Community 1
b1  b2  b3 b4  0...                                  A2        .
c1  c2  c3 c4  0...                                  A3        .
d1  d2  d3 d4  0...                                  A4        .
 0   0   0  0  a1  a2  a3 a4  0...                   B1        .
 .   .   .  .  b1  b2  b3 b4  0...                   B2        .
 .   .   .  .  c1  c2  c3 c4  0...                   B3        .
 .   .   .  .  d1  d2  d3 d4  0...                   B4        .
                a1  a2  a3 a4  0...                  C1        .
                b1  b2  b3 b4  0...                  C2        .
                c1  c2  c3 c4  0...                  C3        .
                d1  d2  d3 d4  0...                  C4        .
                            a1 a2  a3  a4            D1        .
                            b1 b2  b3  b4            D2        .
                            c1 c2  c3  c4            D3
                            d1 d2  d3  d4            D4   Species 4 Community 4
```

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