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Changes in habitat heterogeneity alter marine sessile benthic communities

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Abstract. Habitat heterogeneity is considered an important mechanism influencing diversity patterns in spatially structured habitats. However, spatial heterogeneity is not static and it can change along temporal scales. These changes, whether gradual or rapid, have the potential of forcing species extinctions or facilitating the introduction of nonnative species. Here, we present modeling results that show how changes in spatial heterogeneity over several generations can produce strong changes in benthic species composition residing in eastern Long Island Sound, USA. For many benthic species, hard substrate is a limiting resource which can vary in availability among different coastal areas. We modeled gradual changes from a heterogeneous landscape (mimicking patches of natural hard and soft substrate) to a homogenous one (analogous to a fully developed coast with hard, manmade substrate) and followed the abundance and distribution patterns of species possessing four different life histories. We also modeled changes from homogeneous to heterogeneous landscapes. We found that as regions become more homogeneous, species extinctions become more frequent and poor dispersers dominate locally. In contrast, as habitats become more heterogeneous, species distributing across localities leads to regional species coexistence and fewer extinctions. These results suggest that focusing on changing habitat heterogeneity can be a useful management strategy to prevent poor dispersing species, such as invasive ascidians, from driving communities to monocultures.

Key words: community ecology; diversity; homogeneity; management; metacommunity; model.

INTRODUCTION

Habitat heterogeneity is an important contributor to species diversity patterns (e.g., Western 2001, Cottenie 2005, Holyoak et al. 2005). It is thought that spatial and temporal variations in resources, disturbances, and abiotic conditions give rise to heterogeneous patches in a landscape. Lack of variation in these parameters tends to result in more homogeneous habitats. Therefore, species distribution and coexistence can be heavily influenced by the degree of variation in niche space (Connell 1978, Leibold et al. 2004), and understanding such variation is important in conservation and management of species and habitats (Callaway and Aschehoug 2000, Fahrig 2003, Byers 2005). In particular, habitat heterogeneity can have relevance when considering refugia and reserve networks (e.g., Roberts et al. 2003).

Species benefit from habitat heterogeneity because it can promote coexistence at large regional scales by partitioning habitats among species; therefore, differences in local conditions can result in higher diversity

levels within a region (Mouquet and Loreau 2003, Amarasekare et al. 2004). Furthermore, for species with multiple life history stages such as marine organisms, heterogeneous environments can also provide unique habitats necessary for each life-stage and thus maintain populations within a regional landscape (Amarasekare 2003). However, in heterogeneous habitats, the patchy distribution of resources may be more susceptible to disturbance leading to the extinction of local populations and a decrease in diversity (Thrush et al. 2006).

In contrast, in homogeneous habitats species interactions may have a much more important role in determining species abundance levels, and may drive diversity down (Hubbell 2001). Habitat homogeneity refers to habitats with similar abiotic conditions, quality or quantity of resources (Leibold et al. 2004). In a region with homogeneous habitats the maintenance of diversity is typically achieved by trade-offs in species' colonizing and competitive abilities (Simberloff 1978, Yu and Wilson 2001, Mouquet et al. 2002). Diversity levels can also be modified by other mechanisms such as predation, especially when predators are selective (Menge and Sutherland 1987).

While the effects of habitat homogeneity and heterogeneity have been well explored theoretically (e.g., Amarasekare et al. 2004, Shurin et al. 2004, Holyoak

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et al. 2005), in nature, identifying the states and their effects on diversity can be difficult. Habitats may undergo transitions from one state to another or have different degrees of heterogeneity resulting from the interplay of different processes (Seabloom et al. 2002, Thrush et al. 2006). Transitions can result in species extinction or facilitate the establishment of invasive species. Alternatively, maintaining habitat heterogeneity can give rise to species sorting across a landscape allowing for coexistence and an increase in the species pool (Leibold et al. 2004).

Habitat heterogeneity is thought to fluctuate over long time periods and can influence species' evolution (e.g., Kawecki and Ebert 2004). The degree of habitat heterogeneity (whether close to homogeneous or fully heterogeneous) is generally considered to be a regional trait, with localities differing in one or more abiotic conditions that allow species to thrive only in some areas, thus producing patchy distributions (Leibold et al. 2004). Most theoretical work assumes that the degree of habitat heterogeneity within a system is static over ecological time scales (e.g., Holyoak et al. 2005). In a changing environment where rates of species introductions and extinction are increasing, the dynamic nature of habitat heterogeneity needs to be incorporated in ecological theory given the rapid habitat changes occurring at the landscape level.

One obvious cause of change in spatial habitat heterogeneity is disturbance, which can change resource levels and produce gaps in existing habitat that allow colonization of different species (Connell 1978, Sousa 1980). Variation in successional stages among patches following a disturbance can also contribute to increased heterogeneity (Connell and Slatyer 1977). These different stages, coupled with a species' ability to reproduce and spread into new habitats, gives rise to population sources and sinks. In homogeneous habitats, a population source depends on the frequency of disturbances that affect successional stages (Miller 1982), whereas in heterogeneous habitats sources depend more on habitat quality (i.e., habitat with high resource levels can allow for high population growth and production of exported propagules). Habitats that are changing in the degree of heterogeneity through disturbance are therefore altering the effect that population sources and sinks have on the region.

Marine benthic communities are characteristically associated with habitat heterogeneity across a variety of scales. First, many species are associated with particular substrate types (e.g., rocks vs. sediments) which can vary across local to regional scales (e.g., Levin et al. 2001). Second, many benthic species have distinct life stages, usually consisting of a larval or juvenile dispersing stage that colonizes new habitats and a sedentary adult stage (e.g., Osman 1977, Munguia et al. 2007). Third, broad environmental differences, such as tides and currents, can create additional heterogeneity within substrate types (e.g., Thrush et al. 2006). Fourth,

the species themselves can produce distinct habitat types such as reefs, grass beds, or algal forests that increase habitat heterogeneity (e.g., Munguia 2004). Finally, the quality of each habitat can vary as a function of size, substrate type (e.g., rock vs. piling), previous species that have colonized it, presence of particular guilds of predators, (e.g., Osman and Whitlatch 2004), or frequency and magnitude of disturbance (e.g., Sousa 1980). Most coastal areas not only exhibit this heterogeneity across multiple scales, but they are also undergoing rapid transformation as a consequence of coastal development which can alter habitat heterogeneity through increased levels of disturbance and shoreline modification.

The objective of this study was to explore how gradual changes in habitat heterogeneity can affect the distributions of representative benthic species and influence local and regional diversity patterns. We were particularly interested assessing the effects of increasing coastal man-made structures on benthic communities and how the restoration of habitats and increasing habitat heterogeneity might help maintain diversity.

METHODS

Basic approach

We started by generating in a model environment two different baseline habitat conditions for the Long Island Sound (Fig. 1) benthic community: homogeneous and heterogeneous. Heterogeneous habitat represents current conditions and homogeneous habitat represents an extreme condition in which all shoreline is converted to hard substrate by increases in man-made structures. Populations of four species with different life histories were used to represent the observed range of life histories found in this habitat type. Changes were simulated first in an individual-based model (IBM) in which currents transporting larval stages were generated by a hydrodynamic tidal model of Long Island Sound (Bogden and O'Donnell 1998). In a second approach, we used a simulation model in which habitat conditions changed gradually over time, and followed the effect of these changes on different life histories. Habitat changed from a heterogeneous state to a homogeneous state and vice versa, to understand how changes from one state to another could affect distribution of species with different life histories and consequently diversity of the Long Island Sound.

Benthic system

Within Long Island Sound we have identified four distinct subtidal epifaunal invertebrate communities that are easily distinguished by the taxa that dominate them (Osman and Whitlatch 1998, 2004, 2007, Osman et al. 2010): (1) a diverse native community often dominated by bryozoans that is most 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

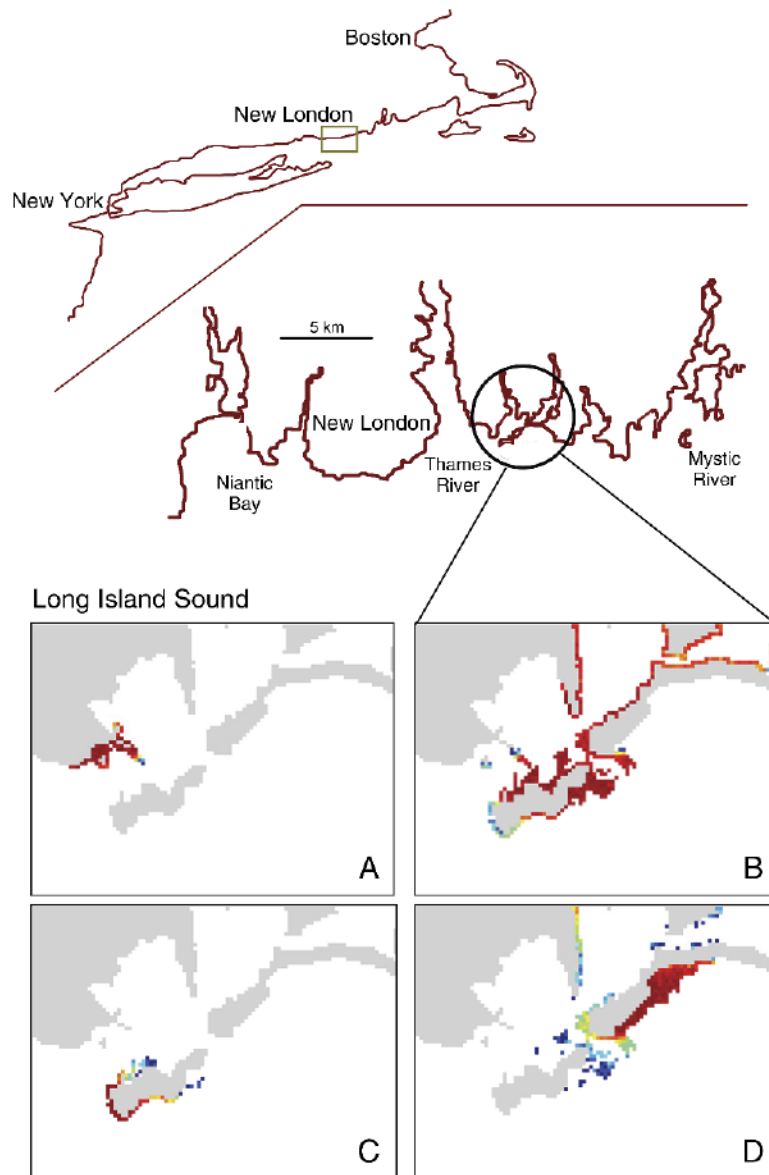


FIG. 1. Map of Long Island Sound (LIS) and the area on the eastern LIS where the individual-based model (IBM) was set up with a hydrodynamics model (circle). Bottom panels (A–D) represent the landscape that the IBM produces: the shaded area represents land, and marine species distributions are shown in a color spectrum (red, high density; blue, low density). Each of the four panels shows the distribution and density of individual species at the end of a simulation where species are coexisting in a heterogeneous environment: (A) *Mytilus* (bivalve), (B) *Schyzoporella* (bryozoan), (C) *Styela* (ascidian), (D) *Diplosoma* (ascidian).

mussel/algae community that periodically replaces the bryozoan or ascidian communities; and (4) an ascidian community dominated by the invasive colonial ascidian *Diplosoma listerianum* that is restricted to years with abnormally warm winters. All four community types require hard substrate to colonize, often offered by pilings and other man-made structures. These four states share a regional species pool of approximately 200 species. The native and ascidian communities have between 22 and 24 species, while the *Diplosoma* and *Mytilus* dominated community have fewer than 10 species (R. Osman, *unpublished data*).

Observations and experiments over the past 15 years have shown that these four states all exhibit a level of resilience that allows them to be maintained for years, if not indefinitely, by interacting physical and biological processes (e.g., Osman and Whitlatch 1998, 2004, 2007). However, switches between states occur over time periods of months to years over equally variable spatial scales (R. Osman and R. Whitlatch, *unpublished data*). These switches appear to require unique sets of environmental changes or stresses. These stresses (Osman et al. 2010) vary from those that are local and operate fast (e.g., predation by different predator guilds)

TABLE 1. Life history parameters of the four species used in the both the individual-based model (IBM; bold) and simulation model (parentheses).

Parameter	<i>Mytilus</i>	<i>Schizoporella</i>	<i>Styela</i>	<i>Diplosoma</i>
Birth	100	50	5	1
Dispersal	875 min (0.8)	583 min (0.5)	175 min (0.3)	60 min (0.1)
Affinity	NA (0.2)	NA (0.2)	NA (0.6)	NA (0.8)
Death	0.01 per day (0.5)	0.01 per day (0.5)	0.01 per day (0.5)	0.01 per day (0.5)

Notes: 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 *Diplosoma*. Dispersal represents the probability that any individual may be able to reach a new habitat within the next time step. In the IBM model, dispersal ability was modeled as the half life of each individual larva in minutes. Affinity is the competitive ability of each species to maintain or displace individuals from a particular local habitat. Death is the per capita mortality rate of each individual in the absence of predators, disturbance, or competitors. "NA" indicates that, in the IBM model, adult competitive ability was preemptive where individuals, once settled, would occupy space and would not be removed until they died.

to those that are regional and operate much more slowly (e.g., climate change). Local stresses can result in the different threshold communities co-existing at sites near one another. More regional stresses operating at variable rates can produce broader regional switches in threshold conditions, but of potentially variable duration. Therefore this system has interacting effects of stresses with fast, intermediate, and slow rates of action on the switching among threshold communities over local to regional scales.

Contrasting heterogeneity and homogeneity

We first used a model that integrated Long Island Sound hydrodynamics with an individual-based model (IBM) with the ability to manipulate life history traits (Hamilton 2005). This model has a very high level of detail relative to a simulation model; however, it is more difficult to make generalized predictions as it is specific to Long Island Sound (Fig. 1). We utilize this model to show how different marine life histories and hydrodynamics give rise to diversity patterns in simplified versions of heterogeneity and homogeneity. Briefly, the model consists of a map with a 20×20 m grid that outlines the northeastern region of Long Island Sound where the bathymetry and temporal hydrodynamics of the Sound are modeled (see Hamilton 2005 for more details). The model allows for the incorporation of species which can have different life history traits, such as per capita propagule output, growth rate, and death rate at different life stages. In this particular simulation, we created four different species that spanned the range of life histories observed (Table 1), each one representing one of the four different states (see also Osman et al. 2010): (1) the blue mussel *Mytilus edulis* with long-lived larvae that allow it to disperse well but with a low probability of being retained in the local population producing the larvae. This species has long-lived adults but is dependent on recruitment from outside to sustain local populations. (2) The native bryozoan *Schizoporella errata* which has very short-lived larvae that enable recruitment back into the local population. This species

is usually outcompeted by ascidians. (3) The solitary ascidian *Styela clava* which has a larval period of ~ 1 d with some probability of local recruitment but is likely to disperse farther than the bryozoan. Adults of this stalked species generally avoid competition for space but newly recruited individuals are subject to fairly intense predation. (4) The invasive colonial ascidian *Diplosoma listerianum* has short-lived larvae that disperse locally but as an adult can overgrow other species and outcompete them for space (Osman and Whitlatch 2007). Two scenarios were modeled: a heterogeneous scenario which contained habitable patches of seagrass and hard substrate and uninhabitable soft substrate and an homogeneous scenario where in addition to the patches above, the whole coastline had a 20 m zone of hard substrate simulating the addition of man-made structures as a consequence of coastal development. This second scenario, while extreme, is not unrealistic given the rate at which the coastline is being developed (currently, coastline development in different counties ranges from 16% to 58%, Titus et al. 2009). However, even though 60% of coastal communities have implemented harbor management plans, there is also an increase in managed shellfish beds which also provide hard substrate to these benthic species (2000 acres of hard substrate added every year, with an estimated current area of 77 800 acres; Connecticut Progress Council 1995). In both cases we kept track of the density of individuals in a 20×20 m area throughout the model for a year-long run. Differences in the total amount of suitable area was kept at a minimum in both scenarios to avoid area limiting effects and to highlight the importance of dispersal ability.

The model runs three different iterations within each setup; this low iteration size produces enough variation to represent stochastic processes given that the fate of each individual is tracked (Hamilton 2005). At the beginning of the simulation, a single adult population for each species was seeded in a 40×40 m area of hard substrate selected at random (the initial location varied among iterations). These sources were monocultures

(i.e., only one species populated a particular source) and there was a minimum distance of 300 m between sources. Adults were allowed to reproduce throughout each simulation, taking advantage of the tidal cycle within the hydrodynamics module: larvae would remain for different periods of time in the water column according to their life history characteristics and then settle on suitable locations. Each time step of the model determined the survival, direction and distance traveled for each larva, as well as the fate of each adult. If no suitable settlement location was found, then the larvae would die in the water column. When an individual settled on suitable habitat (e.g., hard substrate), it would grow and reproduce unless affected by stochastic death (probability set at 0.05 per day). These time steps occurred every three hours, and the simulation was performed for the growth and dispersal season (20 weeks), which is most relevant for this study. We chose to model a single season to reflect how contrasting scenarios in terms of heterogeneity would affect population dynamics. At the end of the simulation, data were collected in the form of species density (number of individuals per occupied cell).

Gradual changes in heterogeneity

A simulation model was used to generate community patterns during succession. A network of four local communities was colonized by four species in the species pool and the model tracked all sixteen local populations. The four species simulated the same range of life histories as the IBM (Table 1). Each species represented the dominant species in each of the four states that have been observed in the region. Species had a trade-off between dispersal ability and local population growth rate (e.g., Mouquet et al. 2003, Amarasekare et al. 2004).

The model used modified Lotka-Volterra equations, in which species were affected by density dependence and shared a local carrying capacity K (set at 100 individuals). The system was spatially explicit with distances between habitats defined at the start of each simulation. For each species i in community j , we estimated the relative contribution of other sites weighted by the dispersal ability:

$$T_{ij} = b_i - \left(b_i \times d_i \times \sum [1/\text{distances to } j] \right) \quad (1)$$

where each cell was defined as the birth rate of species i minus the dispersal rate d_i weighted by the distance between community j and every other community (e.g., distance between j and $j=1$). Therefore, dispersal ability is spatially explicit and the distance to the source population defines the arrival of propagules to a novel habitat. These T_{ij} were then used to model the population dynamics:

$$N_{ij(t+1)} = N_{ij(t)} + T_{ij} \times N_{ij(t)} \left([K_j - N_{ij(t)} \times C_{ij}] / K_j \right) \quad (2)$$

where N_{ij} is the abundance of species i in community j , and N_j is the sum of species abundances in community j . In order to generate a species affinity to a particular habitat and reflect heterogeneity levels, C_{ij} , each habitat had a particular quality H_j and each species a particular preference A_i (see Mouquet et al. 2003 for more details); both variables had values bounded by 0 and 1:

$$C_{ij} = 1 - |H_j - A_i|. \quad (3)$$

The difference between H_j and A_i would determine the affinity of a species to a particular habitat, and this affinity would influence local population growth rate. In a heterogeneous environment, each habitat was best suited for a particular species, while in a homogeneous habitat, there wasn't a particular species that benefited the most: species had to rely on their life histories (dispersal and growth rate) in order to outcompete other species present. A_i remained fixed through the simulations, not allowing species to "adapt" to the environment; however H_j would gradually change and increase or decrease in variance depending on the scenario. H_j for all habitats started near 0.4 (i.e., average H_j value for all habitats equaled 0.4) with a deviation of 0.02 for homogeneous habitats. For heterogeneous habitats, the mean of H_j equaled 0.4, however, the standard deviation was 0.28. In both cases, every 30 time steps H_j would become more similar among habitats (i.e., becoming homogeneous) or dissimilar (i.e., becoming heterogeneous), until the end of the run, where H_j values would approximate the starting values of the opposite scenario.

Each run of the model started with monocultures set at five individuals per species in each local community (starting at 5% of the local carrying capacity). At the end of each time step, each individual had a density-independent probability of dying (Table 1). 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 localities. Each run in turn was carried out for 1000 iterations. Simulations were performed in MATLAB (The Mathworks, Inc., Natick, Massachusetts, USA).

RESULTS

Contrasting homogeneity and heterogeneity

The individual-based model showed an increase in abundance over time for all species after an initial decline (Fig. 2). This initial decline in density was produced by a simple demographic shift in each species, reflecting the lag between propagule production and establishment; however such lag could be due to model simplifications. In homogeneous environments *Diplosoma* had the highest density while in heterogeneous environments *Mytilus* had the highest density. The species abundance ranking also shifted between the two scenarios. For example, *Styela* was relatively common in homogeneous environments but was the species with the lowest density in heterogeneous environments (Fig. 2). Finally, overall density also

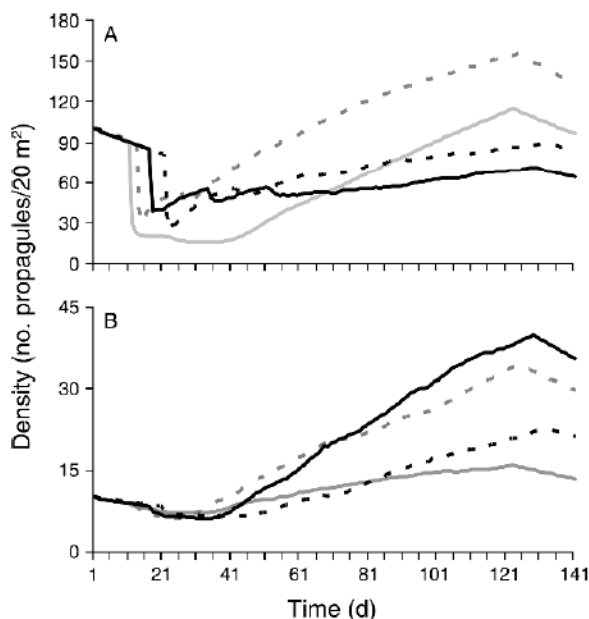


FIG. 2. Population dynamics of four species with a range of life histories using an individual-based model of the Long Island Sound benthic ecosystem. Densities are calculated only considering those cells where individuals occurred. (A) Scenario depicting a homogeneous state, where the coastland presents a complete 20 m wide cover of hard substrate suitable for colonization by all species. (B) Scenario depicting a heterogeneous state where the coastland is intermixed by hard substrate, unsuitable soft substrate and seasonally changing substrate such as sea grass beds. Lines represent the life history in order of dispersal ability: a broadcast spawning with low retention ability species (*Mytilus*, solid black line), a broadcasting native bryozoan (*Schizoporella*, black dotted line), a solitary brooding ascidian (*Styela*, solid gray line), and an invasive colonial brooding ascidian such as *Diplosoma listeri-anum* (gray dotted line). Note difference in scales on the y-axes.

differed in the two scenarios; populations reached greater numbers in homogeneous environments. Differences in density between scenarios reflect greater suitable habitat available, however life histories still determine success and show trade-offs between colonizing and competing abilities.

Gradual changes in heterogeneity

Our simulation model shows how changes in heterogeneity will affect local populations, and how habitat connectivity can affect these changes. When a heterogeneous habitat shifts to a homogeneous landscape, the solitary brooding species dominates at each locality (Fig. 3A), and all the communities show the same rank abundance distribution. The broadcast spawning species tends to disappear from the system, reducing diversity. When a homogeneous habitat shifts to a heterogeneous habitat, all four species are able to coexist locally and there were no signs of localized extinctions (Fig. 3B).

Local populations responded to changes in heterogeneity (Fig. 4), however changes were life-history

dependent. *Mytilus* showed increasing variability when habitats became homogeneous (Fig. 4A) than when they became heterogeneous (Fig. 4B). *Schizoporella* maintained similar variability when habitats became homogeneous (Fig. 4A), but had a major reduction in population variability when habitats became heterogeneous (Fig. 4B). Finally both *Styela* and *Diplosoma* showed a reduction in population variability in both heterogeneity scenarios with a greater change in transitions to homogeneity.

Habitat connectivity affected population variability when the scenario transitioned from heterogeneous to homogeneous (Fig. 4C). In late stages of community formation, population variance increased as connectivity decreased. However, when habitats transitioned from homogeneous to heterogeneous (Fig. 4D), there was a switch in population variability. In habitats with high connectivity variance was reduced from early to late stages of community formation. In habitats with low connectivity, the pattern was reversed: variability increased with community age.

DISCUSSION

The individual-based model contrasts population changes of four representative life histories in heterogeneous or homogeneous landscapes. In heterogeneous landscapes, the best disperser has the highest density of individuals after a year of simulation (Fig. 2). In homogeneous landscapes, the brooding species has the highest density. These two extremes reflect theoretical outcomes for homogeneous and heterogeneous landscapes (Amarasekare 2003, Shurin et al. 2004).

A colonial ascidian such as *Diplosoma* has the potential to dominate a particular area given its rapid somatic growth and strong competitive ability (Osman and Whitlatch 2007). Its production of short-lived larvae that can settle immediately gives this species a high probability of adding new propagules within existing populations. A species such as *Diplosoma* will have a high probability of dominating homogeneous habitats where population spread is not limited by dispersal ability (Mouquet and Loreau 2003). *Styela* has the lowest density in the heterogeneous scenario and second highest in the homogeneous model, a function of its intermediate dispersal ability and competitive rank. Conversely, a species such as *Mytilus* with long-lived larvae and high dispersal ability has a high colonization potential in habitats far from the propagule source but is also unlikely to spread by the addition of propagules to source populations (e.g., McQuaid and Phillips 2000). *Schizoporella* is representative of some of the native species, and it shows intermediate densities in both scenarios, having short-lived larvae and poor competitive ability which restricts the species to local habitats without ascidians or mussels. These habitat requirements result in patchy distributions in Long Island Sound and highlights conservation concern for native populations with limited dispersal ability.

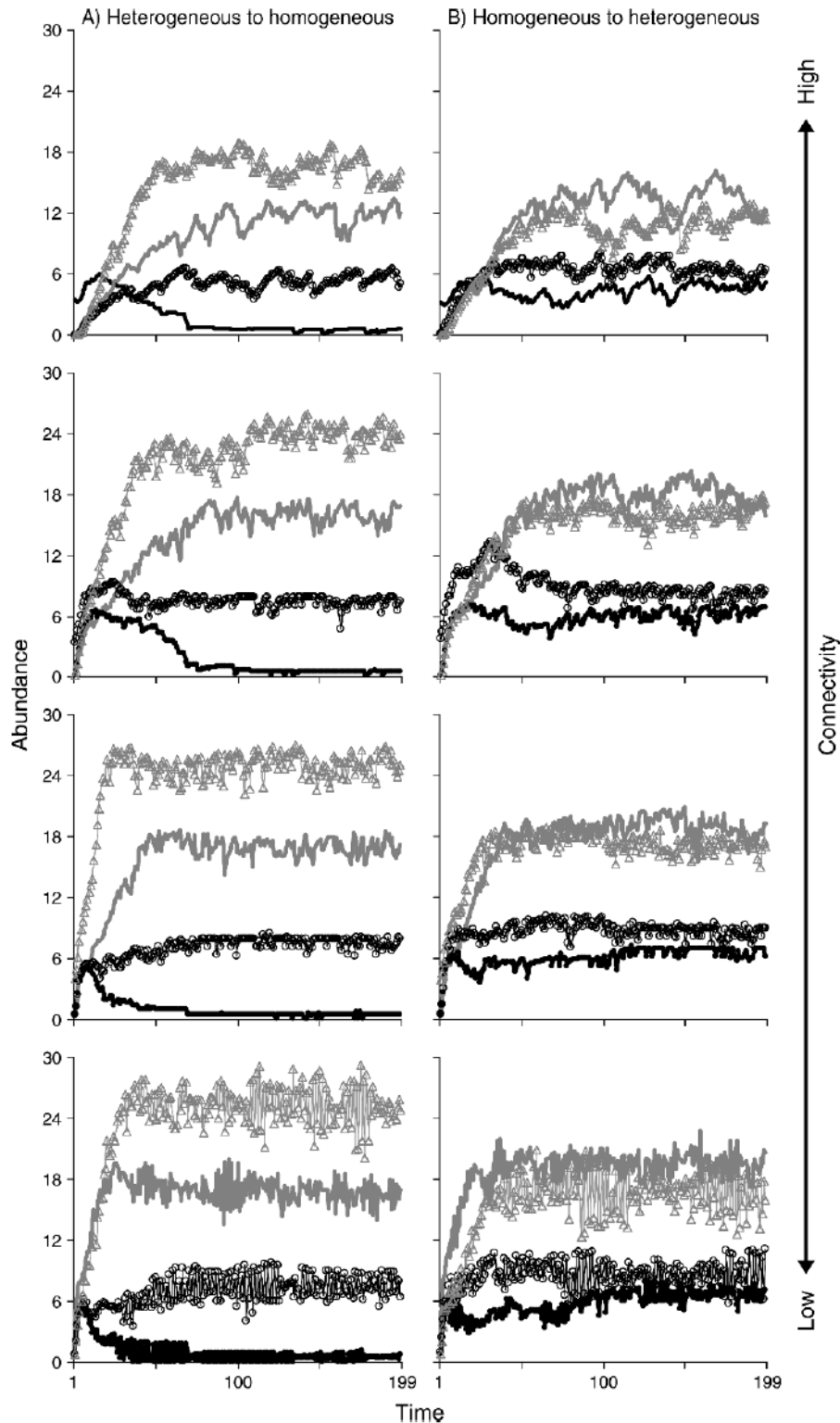


FIG. 3. Population dynamics of four different species in habitats undergoing changes in habitat heterogeneity. Each panel represents a local community with different levels of connectivity to the rest, from high connectivity (top) to low connectivity (bottom). Left column, habitats undergoing changes from heterogeneous to homogeneous. Right column, habitats undergoing changes from homogeneous to heterogeneous. Each curve represents the life history in order of dispersal ability: a broadcast spawning with low-retention-ability species (black line, *Mytilus*), a broadcasting native bryozoan (black line with open circles, *Schizoporella*), a solitary brooding ascidian (gray line with open triangles, *Styela*), and an invasive colonial brooding ascidian such as *Diplosoma* sp. (solid gray line).

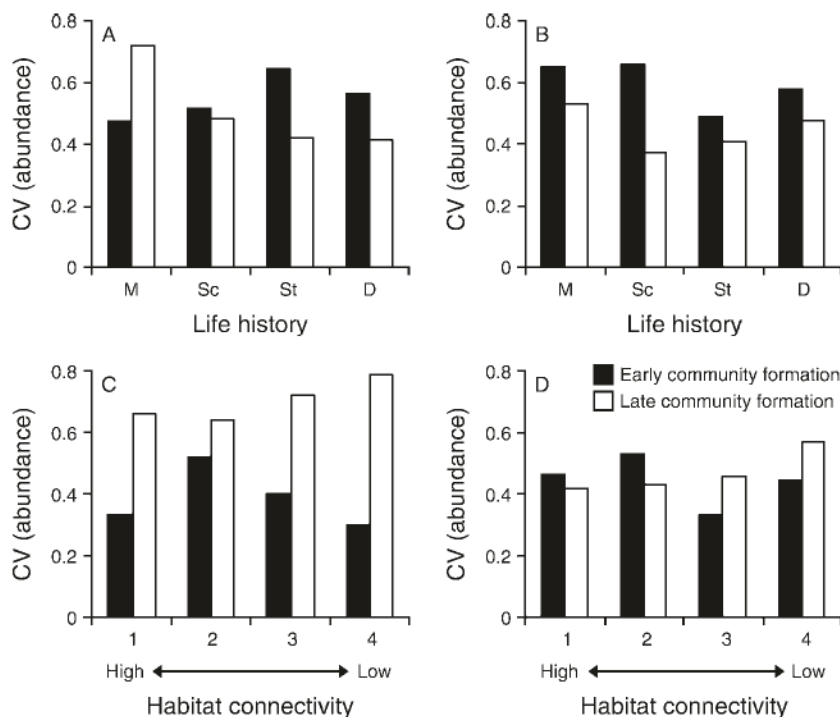


FIG. 4. Variation of population abundances of (A,B) each species or (C,D) within each habitat for habitats undergoing changes from heterogeneous to homogeneous (A,C) or habitats undergoing changes from homogeneous to heterogeneous (B,D). Black bars represent the coefficient of variation during early (first 60 time steps) stages of community formation, and open bars represent the variation during late (last 60 time steps) stages of community formation. Pairs of bars represent the life history in order of dispersal ability: a broadcast spawning with low retention ability species (M, *Mytilus*), a broadcasting native bryozoan (Sc, *Schizoporella*), a solitary brooding ascidian (St, *Styela*), and an invasive colonial brooding ascidian (D, *Diplosoma*). Habitat connectivity for each habitat is ranked from high to low in the bottom panels.

Mytilus was the only species that did equally well in terms of abundance in both scenarios, while the rest of the species had much lower abundances in the heterogeneity simulation. The density reduction is due to the increased importance of dispersal ability to reach habitats that are not adjacent. Species with high dispersal potential will thrive in heterogeneous habitats (Fig. 2) because the patchiness of suitable habitats will enhance regional abundance levels. Witman et al. (2003) found that broadcasting species such as *Mytilus* showed massive recruitment events, but predators responded quickly to areas with recruits and eliminated them at most within six months of the recruitment event. We observed a similar local extinction when a summer storm dislodged and removed a dominant *Mytilus* population at our Pine Island site. Clearly, these broadcasting species can survive as long as patchy heterogeneous habitats are present, and disturbance events either due to storms or predators occur at low frequency, allowing propagules to seek refugia in other habitats.

The contrast between homogeneous and heterogeneous landscapes seems clear: in homogeneous habitats competitive ability can determine species abundance levels, while in heterogeneous habitats dispersal ability and differences in species resource requirements will

determine abundance levels. However, when habitats are shifting in the degree of heterogeneity, it is harder to predict the effect of these mechanisms (Table 2). In our model, populations responded to changes in heterogeneity differently depending on the direction of change between heterogeneity and homogeneity (Fig. 4A, B). When simulations started with heterogeneous habitats, poor dispersers (*Styela* and *Diplosoma*) showed greater variability than good dispersers (*Mytilus*). However, by the time habitats had become homogeneous, *Mytilus* showed greater variability due to more and more frequent localized extinctions. In the reverse process, where simulations started with homogeneous habitats, all species showed a reduction in population variability, with *Schizoporella* showing the greatest decrease over time (Fig. 4B). In this scenario, abundance levels tended to vary more as dispersal ability became more limited during early stages of community development. This is analogous to observed patterns of successional dynamics and community formation in hard substrate habitats (e.g., Osman 1977, Munguia 2004).

Habitat connectivity (Fig. 3) affects local population dynamics in a similar way to previous models (e.g., Loreau and Mouquet 1999). It is important to note two points that arise with our model: (1) transitory dynamics

TABLE 2. Potential effects of changes in habitat heterogeneity and homogeneity.

Trait	Heterogeneity to homogeneity	Homogeneity to heterogeneity
Poor dispersal ability	Increased survival, region becomes one large locality.	Local populations are more susceptible to local disturbance.
Good dispersal ability	Increased extinction probability due to competitive displacement.	Dispersal ability enhances distribution of populations.
Isolated	Colonizing ability becomes very important.	Increased diversity due to species sorting.
Connected	Competitive displacement becomes important.	Habitats perceived as isolated due to differences in quality.

differ between the two habitat scenarios and (2) changes in heterogeneity produce expectations that differ from a static view of habitat quality. While the static view of homogeneous and heterogeneous scenarios seems clear cut (e.g., Amarasekare 2003, Leibold et al. 2004), the species discussed above can persist and coexist suggesting the endpoints in habitat quality may not be as important as the transition from one end point to the next.

Spatial distribution of heterogeneous localities

A dynamic view of habitat heterogeneity also highlights the importance of the landscape within a region. For example, as a region becomes more homogeneous, gradual changes in habitat quality will alter not only heterogeneity, but also the spatial coverage of each habitat type. The rate of change in heterogeneity can be as important as changes in habitat spatial distribution. Disturbance events can induce random changes in habitat quality; however management strategies, such as formation of rock walls or limiting boat traffic could control the location of such disturbances. The different species are likely to respond differently to changes in heterogeneity or homogeneity (Table 2). For example, as homogeneous habitats become more common, diversity could decrease due to extinction of poor competitors (Mouquet and Loreau 2003). Alternatively, if heterogeneous habitats become common, diversity could increase if disturbance rates are low and do not lead to localized extinctions.

In our model, habitat connectivity was very influential on the variation in abundance levels during late succession when simulations started with heterogeneous habitats (Fig. 4C). However, in simulations that started with homogeneous habitats, connectivity did not have such influence (Fig. 4D). In highly connected localities (habitats 1 and 2 in Fig. 4C and D), variation in abundance differs between early and late stages of community development. This pattern suggests that highly connected systems will show the greatest effects of changes in heterogeneity; regions that show high connectivity such as bays and estuaries may be more affected by changes in habitat heterogeneity (e.g., Thrush et al. 2006). Conversely, more isolated habitats (habitats 3 and 4 in Fig. 4C and D) show similar variability during early and late successional stages. This

variability is due to different species dispersal and recruiting abilities.

Changes in heterogeneity and management

Constant change in environmental conditions affects species fitness, population dynamics and eventually geographic distributions (Brown and Lomolino 1998). However, when changes occur at rates faster than previously experienced, species invasions as well as population extinctions may arise, with the potential to fundamentally change regional diversity and ecosystem function (e.g., Solan et al. 2004, 2006, Byers 2005). Within changing coastlines, whether because of heterogeneous systems as the size of developed coastline increases homogeneity or in areas where restoration efforts increase heterogeneity, management efforts need to consider whether such changes should be static (a single event) or whether these changes should occur periodically.

Management strategies tend to consider habitats as a static concept (but see Hobbs and Huenneke 1992), which may not be a good approach given rapid changes in habitat heterogeneity (Roberts et al. 2003). Preservation of a particular habitat may not necessarily mean managing for native species directly. In the San Juan Island archipelago for example, marine reserves increase the abundance of nonnative bivalves (Byers 2005). Previous studies suggest that heterogeneous landscapes created through disturbance can favor species invasions of weedy and fast growing plant species (e.g., Hobbs and Huenneke 1992). In marine systems, homogeneous landscapes can favor species that can aggressively expand in area through localized dispersal and colony formation such as *Diplosoma*. In the Long Island Sound, current management of the coastal habitat could still allow for invasive ascidians to dominate over native sessile species. Hard substrate cover is increasing in the Long Island Sound, either as a management strategy to increase shellfish fisheries or as a consequence of development (Connecticut Progress Council 1995, State of Connecticut Department of Environmental Protection 2000). Both state and municipal agencies are working in concert to maintain and regulate coastal development (State of Connecticut Department of Environmental Protection 2000, Titus et al. 2009). However, if a different management approach is taken where the distance and level of

heterogeneity are incorporated then natives may be able to maintain healthy populations. Our results highlight the importance of incorporating life history information in management strategies.

Results from this model show that changes in heterogeneity are not straightforward with linear predictions. It is important to consider the degree of heterogeneity present, and the direction that changes are required to take place (either to a more homogeneous or heterogeneous state). Changes in heterogeneity may not have reversible effects, and may lead to extinction of local populations, depending on the context of habitat changes (Table 2). Further, given the level of connectivity among local habitats required to maintain populations, management strategies should identify source populations; by managing heterogeneity levels habitat connectivity can be manipulated indirectly and establish successful sink populations.

Results from the modeling efforts highlight the interaction between life histories, habitat connectivity and the habitat dynamics affecting heterogeneity. Habitat heterogeneity can change over ecological timescales from such processes as habitat fragmentation and destruction, and changes in climate and land use (Levin et al. 2001, Western 2001, Fahrig 2003, Munguia and Miller 2008). All these processes have the potential to drive local species extinctions either as a direct effect of changes in habitat, or indirectly as a consequence of the removal of population sources (Tilman et al. 1994). When treating heterogeneity as a dynamic characteristic of a region instead of the traditional static parameter, different community dynamics arise highlighting the importance of life histories and habitat connectivity in the maintenance of populations. An important direction of this work would be to assess how restoration efforts would work when considering taking a system from a homogeneous to a heterogeneous series of habitats. This approach could be crucial in the maintenance of native species in light of increasing invasion of nonnative species. It would also be important when considering the creation of reserves, in particular the location, degree of heterogeneity, and the types of life histories that are meant to be preserved (Roberts et al. 2003).

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