ICES CM 2007/A:02

Dominance and community thresholds in Long Island Sound benthic communities.

Pablo Munguia and Rick Osman

Smithsonian Environmental Research Center
647 Contees Wharf Rd.,
Edgewater, Maryland, 21037-0028
United States
tel: +443.482.2267
e-mail:munguiap@si.edu

ABSTRACT

Community structure tends to change through succession generating changes in species dominance. This has lead to studies claiming that different states can occur within the same system. A state can be defined as either the shift in species dominance or the actual change in community structure (the change in the identity of the species present). However, less emphasis has been placed on the changes in the mechanism that drives successional patterns, or thresholds. The main obstacle behind the understanding of community thresholds is the fact that coexisting species have varying life history traits creating both spatial and temporal overlaps in their population dynamics, and thus in community structure. The present study is aimed at understanding community thresholds that may alter the benthic community of Long Island Sound in the northwestern Atlantic. This benthic community is comprised of a large number of sessile benthic species, including bryozoans, ascidians and mussels. The community tends to change over patches as a "shifting mosaic;" altering species dominance that may span different temporal and spatial scales. Here, we use a series of modeling techniques to understand the threshold dynamics of the community. Species with different life history traits, ranging from broadcast spawning to brooding species, were simulated and their population dynamics followed over time. We induced small changes in the mechanisms that may alter dominance, such as dispersal and competitive abilities, in order to determine the relative importance of these mechanisms in inducing thresholds and how it affects the duration and fluctuations in species dominance.

KEYWORDS: sessile species, global warming, community structure, invasive species

INTRODUCTION

A major goal in ecology focuses on understanding the maintenance of diversity and the dynamics of community structure. The group of species comprising a community tend to vary both spatially (i.e. similar habitats with different species composition) as well as temporally (i.e. through succession; e.g. Schmida and Wilson 1985). This variation stems from two main sources, (1) the range of life histories present in a community and (2) the mechanisms that affect communities as a whole. Life history traits tend to be responsible for a species' abundance and distribution patterns (Munguia et al. 2007). For example, long-living propagules can disperse longer distances, and increase the distribution of a species; high reproductive rate may reflect high densities at local habitats. Mechanisms that are responsible for affecting whole communities, such as disturbance or habitat heterogeneity, can vary across spatial scales (Cornell and Karlson 1996). The number of localities affected by such mechanism may vary, thus creating variation in community structure across sites.

The variation in community structure will reflect different extinction and dominance patterns. The turning point where a species can become locally dominant or extinct is referred to as a community threshold. Therefore, thresholds can be responsible for changes in community structure, and they can lead to either stable states or transitional states in the dynamics of a community (Law and Morton 1993). Thresholds become particularly important in spatially structured habitats, where local communities are connected to one another via species dispersal and these localities share a species pool that defines a region (Shurin et al. 2004).

In marine systems, species tend to have two or more life history stages that vary in their spatial range. In some species, individuals are able to disperse over large distances at the larval stage, but are relatively sedentary as adults. Other species may present sedentary larvae or juveniles, while adult stages are relatively motile. Coupled with this, species differ in their mating strategies, competitive and dispersal abilities. In this fashion, the spatial area that would be considered a "community" for one species could in fact be only a part of a larger habitat for another species. The spatial scale at which species function combined with the physical structure of communities needs to be considered in order to understand diversity patterns (Munguia 2007). Marine habitats can vary in their "patchiness"; in some systems such as coral reefs, habitat could be very patchy interspersed by areas where the inhabiting species cannot colonize. Other habitats such as sea grass beds could offer a continuum that becomes patchy only at very large spatial scales.

This presentation is part of a larger study that attempts to incorporate different models (population, hydrodynamic, and ecosystem models) to understand the role of global warming, invasive species and human alterations of the ecosystem on the native benthic communities of Long Island Sound in the northwestern Atlantic (Figure 1). Long Island Sound is populated by a large number of sessile species such as bryozoans, sponges, bivalves and ascidians. Over the last 15 years it has been noted that the distribution and abundance of species varies, giving rise to different community structures. We can identify four distinct subtidal epifaunal invertebrate communities that are easily distinguished by the taxa that dominate them: 1) a diverse bryozoan-dominated community 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 mussel/algae community that can 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. Further, the duration of the states tends to vary as well, suggesting that community thresholds are responsible for the stability of the different community states. Warm winter temperatures and anthropogenic pressure (e.g. boat traffic, land modifications) seem to occur more frequently, suggesting that alterations at the regional level are taking place.

The objectives of this presentation were a first approximation at understanding the relationship between different life histories and disturbance operating at different spatial scales, and how community thresholds may vary – affecting species diversity. By using a simulation model, we studied the effects of disturbance on community thresholds at two different spatial scales: a local scale representing changes in predator pressure, and a regional scale representing global warming which would affect the region as a whole (Figure 2). This approach allowed us to explore the thresholds exerted on four species that differed in their life history stages (representing the range of life history stages present in Long Island Sound). In particular we asked (1) if regional and local disturbance generate species dominance patterns and (2) whether particular life history traits can counter the effects of disturbance (or if both broadcast spawners and brooders show similar dominance patterns).

METHODS

Simulation model

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 a range of life history stages of sessile invertebrates of Long Island Sound. Each species represented the dominant species in each of the four states that have been observed in the region (Osman unpubl. data). Species had a tradeoff between dispersal ability and local population growth rate. For example, mussels (*Mytilus edulis*) were the best dispersers given that it produces a large number of larvae that can remain in the water column for a long period of time, but their local population growth was the lowest of the four species. The next two species were a bryozoan (*Microporella sciliata*) that has planktonic larvae, and the brooding solitary ascidian *Styela clava*. Finally, the colonial brooding ascidian *Botrylloides violaceous* was represented as the poor disperser with the highest local population growth rate.

The model used modified Lotka-Volterra equations, were species suffered density dependence 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, a transition matrix T_{ij} was created where each cell is defined as the birth rate of species i minus the dispersal rate 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 the used to model the population dynamics:

$$N_{ij(t+1)} = N_{ij(t)} + T_{ij} * N_{ij(t)} ((K_j - N_{j(t)}) / K_j) \qquad (1)$$

where N_{ij} is the abundance of species i in community j, and N_j is the sum of species abundances in community j. Each run of the model started with abundances set at 5 individuals per species in each local community (Figure 3a). There was a mortality factor set at 10% to simulate natural deaths. Simulations were followed for 100 time steps, which was enough time to observe changes in community composition and for any single species to achieve dominance.

The local disturbance scenario was simulated by reducing all of the populations within a locality to 30% abundance every 4 time steps. The community affected was randomly selected every time, therefore mimicking the effects of a motile predator on these sessile communities. The regional disturbance also occurred at the same rate – every four time steps, however all of the populations within each of the four communities were reduced to 30% abundance. Each scenario, normal conditions, local disturbance and regional disturbance, was iterated 1000 times.

Output analysis

The model kept track of the abundance of each species in each habitat; therefore we could calculate in any given run the community structure of each local community. With this information we kept track of the dominant species in each locality (we defined dominance as the most abundant species in a given local community at the end of the 100 time steps). We then calculated the proportion of runs that each species dominated in each of the four localities. We compared the results from simulations under normal conditions (i.e. no local or regional disturbance), local, and regional disturbance.

RESULTS & DISCUSSION

Under normal conditions, the model showed typical Lotka-Volterra population dynamics for all four species in each of the localities (Figure 3b). In this scenario, there were few dominance events; however, each species had a higher number of dominance events in their original habitat relative to the other three habitats. For example, *Styela* tended to dominate its original habitat more often than the other three habitats were it had the potential to invade. The low number of dominance events suggests that species are constantly fluctuating within the region and coexisting at relatively equal abundance levels. Sessile benthic species tend to show similar patterns if there are no large disturbance events, or if none of the species is competitively superior to the rest. These patterns have been observed in a number of systems, leading to the concept of priority effects: the species that first arrives to a habitat will tend to dominate (Almany 2003, Shurin et al. 2004, Munguia 2007).

When disturbance events were incorporated into the model, community structure changed dramatically. Regional disturbance affected all species in each of the four local habitats equally; by opening up space, it created a larger number of dominance events (Figure 3c). Most of the runs had a dominant species in each habitat, and it seemed that brooders showed a larger number of dominance events relative to broadcast spawning mussels. However, each habitat had a large number of dominance events by species other than the original inhabitant, suggesting that the system was relatively chaotic. When a disturbance event took place in the whole region, abundance levels would drop low enough that priority effects would determine the dominant species as with the normal scenario. This disturbance occurred relatively frequently, as simulating seasonal changes, which would explain the shifts in dominance patterns.

Local disturbance tended to fix dominant species in each habitat (Figure 3d). Here the priority effects were most apparent, where the original inhabitant dominated its locality with no other species dominating. The only exception were the broadcast spawning mussels, which even though they dominated their original habitat in 60% of the model runs, had the other species dominate their habitat. The remaining three species, the barnacles, *Styela* and *Botrylloides* did show dominance events within the mussel habitat. This suggests that broadcast spawning species may be more susceptible to localized random disturbances relative to brooding species because there is fewer localized retention of propagules.

With this modeling example, we have shown that disturbance can interact with life history traits to determine dominance patterns. The scale at which disturbance is operating can be considered a threshold for benthic communities and can help determine species dominance. This could help determine the variability and duration of the dominant species in a given habitat within Long Island Sound. Further, community structure does not seem to affect dominance patterns, rather, it seems that for sessile species, the order of establishment helps determine dominance. Given that the role of thresholds may be useful in determining the fate of community structure, we would like to propose that thresholds can be used instead of diversity levels as a metric to gauge management strategies.

REFERENCES

Almany, G. R. 2003. Priority effects in coral reef fish communities. Ecology **84**:1920-1935.

Cornell, H. V., and R. H. Karlson. 1996. Species richness of reef-building corals determined by local and regional processes. Journal of Animal Ecology **65**:233-241.

Law, R., and R. D. Morton. 1993. Alternative permanent states of ecological communities. Ecology **74**:1347-1361.

Munguia, P. 2007. Spatial structure of communities on dead pen shells (*Atrina rigida*) in sea grass beds. Marine Biology, *in press*.

Munguia, P., C. Mackie, and D.R. Levitan. 2007. The influence of stage-dependent dispersal on the population dynamics of three amphipod species. Oecologia, *in press*.

Schmida, A. & M.V. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography, **12**, 1-20.

Shurin, J. B., P. Amarasekare, J. M. Chase, R. D. Holt, M. F. Hoopes, and M. A. Leibold. 2004. Alternative stable states and regional community structure. Journal of theoretical Biology **227**:359-368.

FIGURES

Figure 1. Map of Long Island Sound in the Northwestern Atlantic. Inset shows the area where surveys and experiments have been carried out for the last 20 years by Osman and collaborators.

Figure 2. Potential effects of disturbance on community structure at different spatial scales. (a) typical rank-abundance curve expected for any community, the curve represents all the species that could be found in a system, and it shows a small proportion of species that are highly abundant, and a large proportion that are rare. (b) if disturbance takes place at a local scale, the dominant species could be the ones that are affected the most, just by chance. Rare species, if affected may not go extinct from the system due to rescue effects from other local populations. (c) When disturbance occurs across all habitats within a region, all of the species suffer proportionately, and species extinctions can be expected.

Figure 3. Species setup and results from the simulation model testing the interaction between disturbance and life history traits and their effects on dominance patterns. (a) Model setup prior to the run of the simulations. Each of the four habitats was seeded with one of the four species. Original habitat and species are color-coded for clarity. (b) proportion of runs (of 1000 iterations) where a species dominated a particular habitat. The shaded area in each bar represents the habitats that each species dominated, e.g. most of *Styela*-dominated habitats occurred in localities originally seeded with *Styela*. Low proportion of dominance events means that there were a large number of runs where species coexisted with relatively equal numbers. (c) In the regional disturbance scenario, dominance occurred frequently, but with no clear pattern. (d) In the local disturbance

scenario, species tended to dominate their original habitat and did not dominate other habitats, with the exception of the mussel habitat that was dominated by the bryozoans and ascidians.

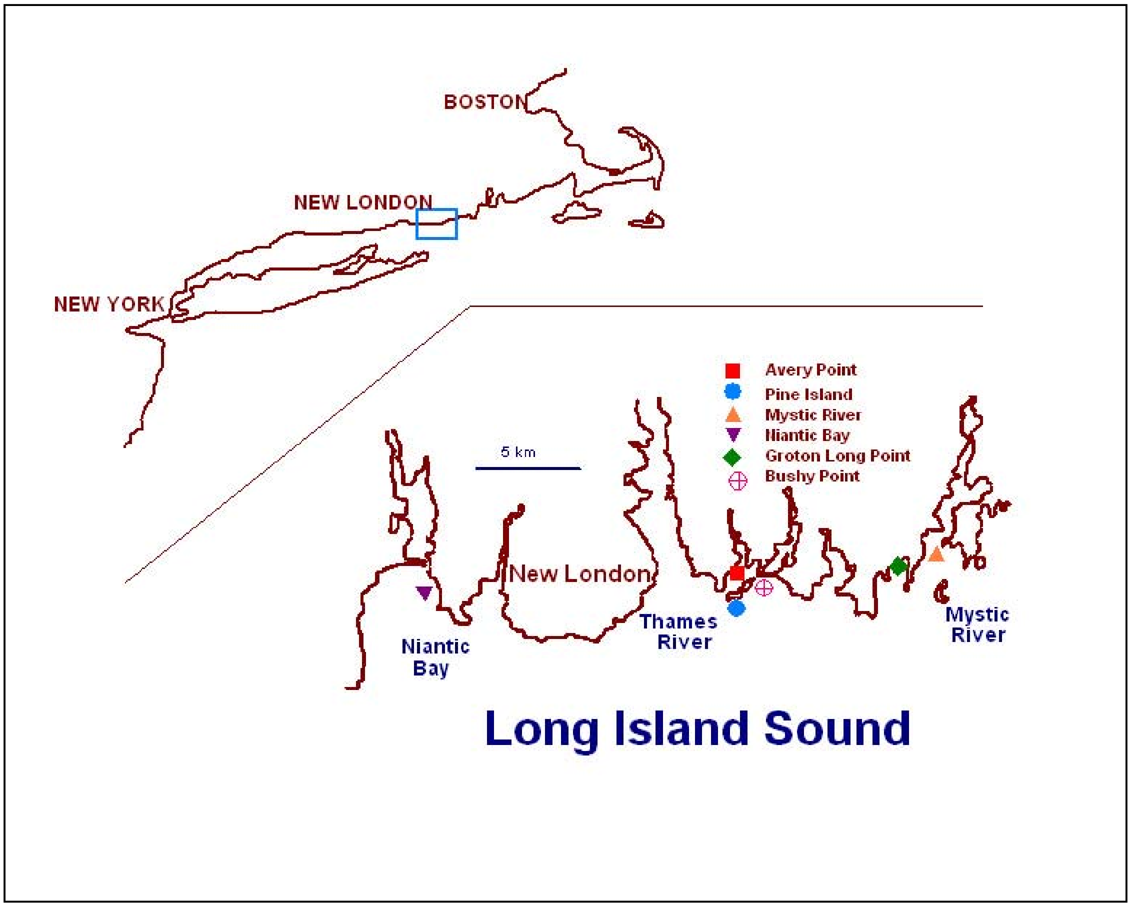

BOSTON
NEW LONDON
NEW YORK
■ Avery Point
● Pine Island
▲ Mystic River
▼ Niantic Bay
◆ Groton Long Point
⊕ Bushy Point
5 km
New London
Thames River
Mystic River
Niantic Bay
Long Island Sound

Figure 1

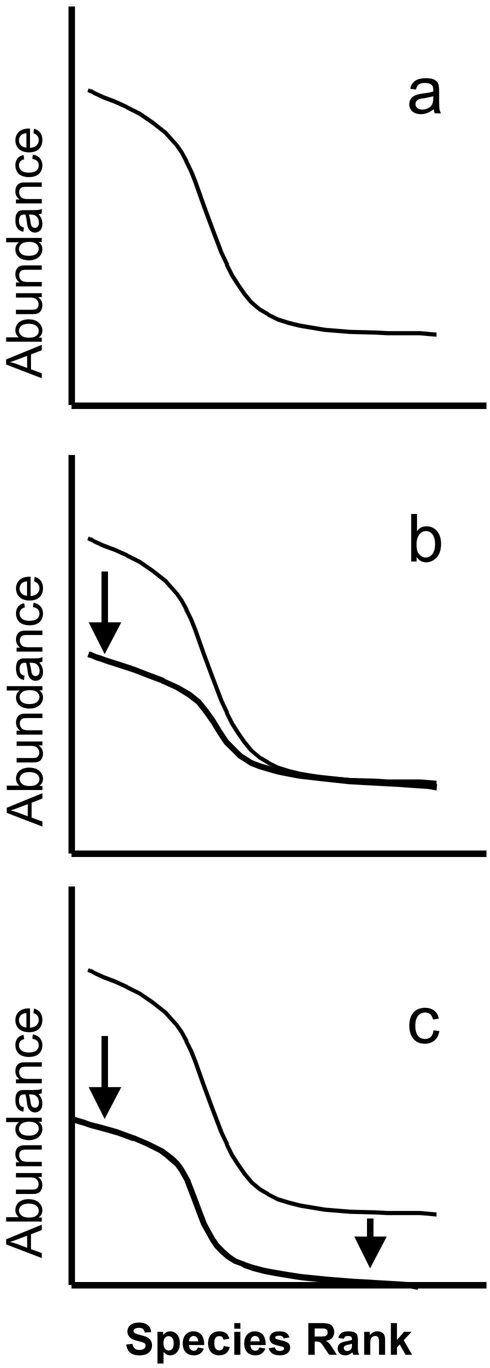
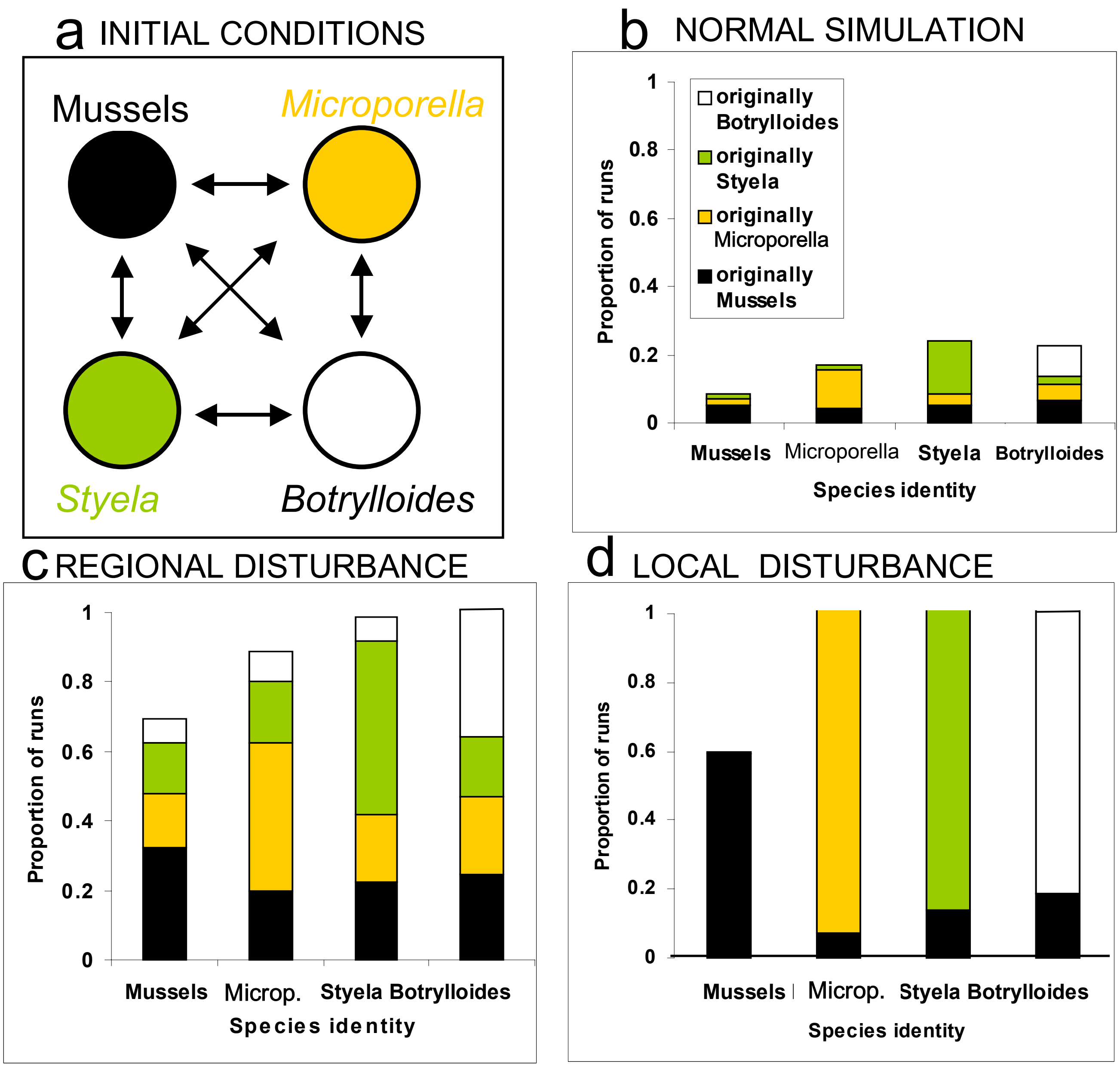


Figure 2.



a INITIAL CONDITIONS
Mussels
Microporella
Styela
Botrylloides
b NORMAL SIMULATION
Proportion of runs
1
0.8
0.6
0.4
0.2
0
□ originally Botrylloides
🟩 originally Styela
🟨 originally Microporella
■ originally Mussels
Mussels
Microporella
Styela
Botrylloides
Species identity
c REGIONAL DISTURBANCE
Proportion of runs
1
0.8
0.6
0.4
0.2
0
Mussels
Microp.
Styela
Botrylloides
Species identity
d LOCAL DISTURBANCE
Proportion of runs
1
0.8
0.6
0.4
0.2
0
Mussels
Microp.
Styela
Botrylloides
Species identity

Figure 3.