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DO ALTERNATE STABLE COMMUNITY STATES EXIST IN THE GULF OF MAINE ROCKY INTERTIDAL ZONE? REPLY

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We appreciate the opportunity to reply to Petraitis and Dudgeon (2004)'s comments on our recent paper examining the hypothesis that mussel beds and seaweed canopies on Gulf of Maine rocky shores represent stochastic alternative community states. While they have made some constructive comments, we remain highly confident that in the systems we have studied community recovery from disturbance is highly deterministic and strongly driven by consumer control. In our study, we have asked if mussel bed/seaweed canopy alternative states currently exist in the Gulf of Maine (Bertness et al. 2002, Bertness et al. 2003), while they have simply asked if they are possible (Petraitis and Latham 1999, Petraitis and Dudgeon 1999). These are very different questions, and their criticism of our work fails to recognize this difference. Our experiments have utilized multiple sites (>30 sites) in two different rocky shore environments (open coast and tidal rivers), and the consistency in community recovery in relation to consumer pressure has been unambiguous. Given the robustness of our results, we will be relatively brief in our response

Petraitis and Dudgeon (hereafter P&D) object to the design of our experiments on the Damariscotta River because physical conditions varied between our mussel bed and algal-canopy sites. However, we attempted to choose mussel bed and algal-canopy sites that were as similar as we could find in terms of physical conditions. We tried to avoid sites with extreme physical conditions to maximize detecting the presence of stochastic alternative states. The mussel bed and algal-canopy sites we chose, however, did indeed differ in abiotic parameters (i.e., flow rates) and that is part of the problem. In the vast majority of habitat in the Damariscotta River, one observes a tight correlation between these two community types and flow rate, and it is this correlation that seems to be the major arbiter of the determinism we have found. We have been unable to find shoreline habitat having strictly identical flow conditions yet with a different community type. Although such places may exist in the Gulf of Maine, we have not observed them. If they do exist, they seem to be remarkably rare.

P&D also argue that we did not use large enough clearings to trigger a state change. It is true that we did not use the largest patch sizes used by P&D, but we did feel that we used a large enough patch size to detect stochasticity in the system. The 9-m^2 patches we used were at the threshold they have previously suggested would lead to stochastic changes. How big is big enough? or perhaps more importantly, How common are 9-m^2 patches (or larger) in the Gulf of Maine? Although ice scour may be important in the northern Gulf of Maine, and more so in the Saint Lawrence seaway and the Canadian Maritimes, its role in central Maine on the open coast seems negligible. Indeed, none of us have observed such large patch formation by any disturbance agent in the more than 20 years that we have been working in the Gulf of Maine. In tidal rivers, patch formation by ice can be important to mussel bed

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habitats because ice concentrates as it passes through the constrictions where mussel beds are found. But again patch sizes on the order of 9-m^2 or larger are very rare. The impact of ice on river algal canopies also appears rather negligible when compared to the patch sizes being discussed as part of ecological experiments. Even after the harsh winter last year when much of the northern section of the Damariscotta River was completely frozen, we observed no large patch generation. And when ice does impact algal canopies, it usually does so by giving plants a haircut, leaving the holdfast intact. So while our patches may not have been "large enough," we are left wondering what agents could create patches of such size, and, if they do exist, how important are they on ecological time scales. In the central and southern Gulf of Maine it seems that disturbances of such magnitude are exceedingly uncommon.

Despite the poor dispersal ability of *Ascophyllum*, colonization of large disturbances is not impossible, but can take time. On the Damariscotta River we have documented *Ascophyllum* recruitment to the perimeter of large bare patches and over time (4–5 years) to the center of large disturbances. Even in extremely large disturbances (however rare) such as those used by P&D, we suspect that *Ascophyllum* will eventually colonize them. If this were not the case, it would be difficult to explain why dense *Ascophyllum* canopies dominate low-flow environments in tidal rivers. If large-scale ice scour is important, and *Ascophyllum* was not able to recolonize these disturbances, then these habitats should be mosaics of seaweed canopy, barnacles, and mussels.

P&D argue that our usage of press experiments (caging) in addition to pulse experiments (patch formation) is inappropriate to test for stochastic alternative community states. While this may violate some strict interpretations of theory, we suggest that theory may warrant some reconsideration. By not experimentally examining the role of consumers in these systems, one ignores a fundamental aspect of their natural history. Such criticisms also have rightly been made of experiments examining the link between species diversity and ecosystem function without considering the role of consumers (see Duffy 2002, Paine 2002). That consumers impact community structure in numerous habitat types cannot be disputed, particularly on rocky shores, and to ignore their role in community dynamics during recovery from disturbance will not provide any meaningful insights into how these dynamics unfold.

Our experiments cleared large plots of all space holders and followed recovery in these patches just as P&D have done. In addition to following natural recovery, we followed caged, cage-control, and control plots to assess the impact of consumers on recovery. Our caged plots accurately forecasted how recovery has progressed in uncaged areas associated with crack-and-crevice refuges from consumers. We acknowledge that cage artifacts can be problematic in some habitats, but strongly defend the prudent use of consumer-exclusion cages as a method to understand the role of consumers in community recovery.

P&D also criticize the statistical analysis of our experiments, stating that we should have used a split-plot or partially nested design. In particular, they suggest that sites should be nested within habitat types and that caging treatments should be grouped within the patch-size treatment. These are fair points, especially concerning the nesting of sites, but we disagree that issues regarding our caging treatments are as black and white as they state. When analyzing the experiment, we reasoned that caging treatments within patch treatments could be viewed as independent because we observed nothing to suggest that there were correlated responses among caging treatments. When placing our cages, we did our best to do so randomly while at the same time trying to make sure that they were not too close to one another or the edge of our patches. In addition, recovery within our plots not associated with our caging treatments was quite heterogeneous, especially in areas having lots of cracks and crevices. Hence, the amount of heterogeneity in recovery outside of caging treatments was much greater and seemed to have little to do with what was occurring inside our caging treatments and open control plots. For these reasons, we considered the caging treatments to be orthogonal.

P&D suggest a split-plot analysis for our experiment and point out that this analysis can also be confounded by autocorrelation problems. Nevertheless, we have reanalyzed our data with the analysis (option 2 in Petraitis and Dudgeon 2004) they suggest. The results of this analysis, despite being more conservative compared to our original analysis, produced remarkably similar results except that patch-size effects and interactions with patch size became more significant for mussel percent cover. Regardless of the analysis used, our results were unambiguous; removing consumers resulted in the rapid recovery of the original community (both mussel beds and algal canopies) within 2–3 years regardless of patch size. We believe in the importance of proper statistics, which is why we have explored P&D's suggestions, but we also think that a sound understanding of the natural history of one's study system is just as important. We will let readers judge our results for themselves.

Perhaps the most important issue in this debate is the question being asked. We have asked explicitly, "Do alternative community states exist in these systems?" This is different than asking "Can they exist?" We suspect that they can, but if they do, they exist in a very narrow subset of the environments that are typical of rocky shores in the Gulf of Maine. In our numerous collective years of work on tidal rivers and the open coast of the Gulf of Maine, we have failed to observe the presence of mussel beds or *Ascophyllum* canopies that were not tightly correlated with high and low water movement, respectively (Bertness et al. 2002, 2003). Although mussel bed/algal canopy alternative community states are theoretically possible, evidence indicating that they currently exist under the same environmental conditions is entirely lacking. We challenge P&D to provide credible evidence that mussel bed/algal canopy alternative community states are not only theoretically possible, but that they currently exist in the Gulf of Maine under the same environmental conditions. Reference to John Lewis' work is misleading. Lewis (1964) was talking about British shores, not North American shores. On British shores *Ascophyllum* is not the habitat-dominating seaweed it is in New England.

We suggest that a better approach to understanding the *relative* importance of stochastically determined alternative community states is not to demonstrate that they are possible, but to identify the conditions when and where they can occur and *how common they are.* To date, our work suggests that *Ascophyllum*-canopy and mussel bed communities in the Gulf of Maine are generally deterministic, consumer-driven states, rather than stochastic alternative community states. We suspect that if stochastically determined *Ascophyllum* canopy/mussel bed alternative states exist, they are exceedingly rare.

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