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Response to Comment on “Divergent Induced Responses to an Invasive Predator in Marine Mussel Populations”

Aaren S. Freeman* and James E. Byers

Preliminary DNA analysis indicates that only a few *Mytilus trossulus* mussels were present in our study of *M. edulis*. Excluding these *M. trossulus* did not influence the outcome of our analyses. Our study provides essential evidence that populations of *M. edulis* respond differently to the two crab predators, and the adaptive significance of shell thickening in mollusks is well established.

On the basis of the published findings of Rawson *et al.* (1), we had already presumed that some *Mytilus trossulus* may have been present at our two northern Maine sites (Lubec and Cutler), as the comment from Rawson and colleagues now reiterates (2). Nevertheless, an analysis of our data excluding these two sites had no effect on our results [see Supporting Online Material in (3)]. Still, an appreciable frequency of *M. trossulus* in the remainder of Maine would be cause for concern, because our experiments intended to focus only on *M. edulis*. We therefore instigated genotyping of dried tissues of the mussels used in our original study. To ensure complete independence of genetic results, samples were processed with a blinded procedure by Rawson and an independent third party (E. Boyle at University of Massachusetts, Boston). To date, we have processed all 144 of the mussels used in the 2002 experiment from the six sites in northeastern Maine. Of these 144, 26 were *M. trossulus*. However, as we had originally presumed on the basis of available published data, these *M. trossulus* were almost entirely from the Lubec and Cutler sites (10 *M. trossulus* out of 22 mussels and 8 out of 22, respectively). Removing all *M. trossulus* from analysis of this experiment did not influence our result.

Because we have not yet genotyped mussels from our second experiment, to further explore the robustness of our results we reexamined our 2003 data as if *M. trossulus* were solely responsible for the lack of a response to the Asian shore crab *Hemigrapsus sanguineus* in northeastern Maine. In 2003, we avoided sampling the Cutler and Lubec sites. However, if we eliminate 19% of mussels showing the least response to *H. sanguineus* in that year, we find the same pattern of significance as that previously published (3). This analysis assumes that the rate of *M. trossulus* contamination

outside Lubec and Cutler was twice what we found in 2002. It also very conservatively assumes that only *M. trossulus* are not responding to *H. sanguineus* and therefore may be masking an actual response by northern *M. edulis*. This strict assumption is unlikely to hold because natural variability is often present in all populations (making it very unlikely that all *M. trossulus* consistently show the least response to *H. sanguineus*). Moreover, because *M. trossulus* co-occurs with *H. sanguineus* in other parts of its range (1, 4), this mussel would be more likely to recognize a sympatric predator than would any other mussel in New England, because no other mussels in the northwest Atlantic share an evolutionary history with this crab genus. Thus, even without considering our genotypic evidence that *M. trossulus* was rare outside of Lubec and Cutler, contamination levels of *M. trossulus* as high as those suggested by the data presented in (2) do not alter the interpretation of our study (3).

Our statement that the mussel's response to *H. sanguineus* “reflects natural selection favoring the recognition of this novel predator through rapid evolution of cue specificity or thresholds” is taken somewhat out of context, but we should have been clearer that we were hypothesizing about the mechanism by which this response could evolve quickly in mussels. We did not attempt to document graded responses to these predators in our study. We believe it is more parsimonious to infer that natural selection has modified thresholds or specificities of existing responses to native crabs to include *H. sanguineus*, rather than to infer the appearance of a novel induced defense. In addition, the issue of crushed conspecifics is more complicated than Rawson *et al.* (2) suggest. Separately, we have documented that behavioral responses to predators differ from behavioral responses to crushed conspecifics (feeding is reduced in the presence of crushed conspecifics). This suggests that looking at the mussel's response to feeding predators would further confound morphological and behavioral responses. Although it would be interesting to examine how mussels respond to

damaged mussels or crabs consuming mussels, we isolated an essential aspect of the mussel's response—that the response to crabs per se differs between populations. We also discussed the possibility of nonheritable processes such as learning and conditioned predator recognition (5) (i.e., the type of learning Rawson *et al.* describe) and the role of background cues in our report (3). However, we collected all of our mussels from floating docks in an attempt to minimize predation the young mussels may have experienced and background cues that would be necessary for conditioned predator recognition (crabs are far less abundant on the undersides of floating docks than other substrates). Furthermore, a primary purpose for repeating our experiments in a second year in an in situ field environment similar to the collection sites of southern mussels was to expose all treatments (including the controls) to any background cues. Cues present in sufficient amounts in these environments to stimulate learning also would have triggered induction in the control mussels, thus eliminating differences from crab-cue treatments.

Finally, Rawson *et al.* (2) argue that thicker-shelled mussels may or may not be better defended from crab predators. This contention is surprising in light of solid evidence of greater crushing resistance in thickened shells (6–8). As the comment authors acknowledge, such evidence is a “standard feature of shell-thickening studies in other mollusks” (including *M. edulis*), and thus if included in our study would be viewed by many as redundant. Although, strictly speaking, Rawson *et al.* are correct that we did not experimentally establish the adaptive significance of shell thickening with *H. sanguineus* as a predator, mussels induced to increase their shell thickness index by 10% have a 48% increase in handling time by *Carcinus maenas* (9). Ultimately, by using the same metric to document induced responses to both crabs, we believe that we have made a valid comparison of an adaptive trait.

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