

24. V. I. Morgan, I. D. Goodwin, D. M. Etheridge, C. W. Wooley, *Nature* **354**, 58 (1991).
25. E. Mosley-Thompson *et al.*, *Ann. Glaciol.* **21**, 131 (1995).
26. Special issue on State of the Climate in 2004, *Bull. Am. Meteorol. Soc.* **86** (suppl.) (2005).
27. R. Thomas *et al.*, *Science* **306**, 255 (2004); published online 23 September 2004 (10.1126/science.1099650).
28. I. Velicogna, J. Wahr, *Science* **311**, 1754 (2006); published online 1 March 2006 (10.1126/science.1123785).
29. Intergovernmental Panel on Climate Change, *IPCC Third Assessment Report, Climate Change 2001: The Scientific Basis* (Cambridge Univ. Press, Cambridge, 2001).
30. This research was funded by the NSF Office of Polar Programs Glaciology Program, the Australian Government's Cooperative Research Centres Programme through the Antarctic Climate and Ecosystems Cooperative Research Center, the Italian National Antarctic Research Program (PNRA), and several other international scientific research programs. Sincere gratitude is owed to all of those who contributed to the planning, extraction, and analysis of the

ice core, snow stake, and snow pit data. The ERA-40 data were obtained from the University Corporation for Atmospheric Research Data Support Section ([www.dss.ucar.edu](http://www.dss.ucar.edu)). This is contribution 1338 of the Byrd Polar Research Center.

#### Supporting Online Material

[www.sciencemag.org/cgi/content/full/313/5788/827/DC1](http://www.sciencemag.org/cgi/content/full/313/5788/827/DC1)  
Materials and Methods  
References

13 April 2006; accepted 22 June 2006  
10.1126/science.1128243

# Divergent Induced Responses to an Invasive Predator in Marine Mussel Populations

Aaren S. Freeman\* and James E. Byers

Invasive species may precipitate evolutionary change in invaded communities. In southern New England (USA) the invasive Asian shore crab, *Hemigrapsus sanguineus*, preys on mussels (*Mytilus edulis*), but the crab has not yet invaded northern New England. We show that southern New England mussels express inducible shell thickening when exposed to waterborne cues from *Hemigrapsus*, whereas naïve northern mussel populations do not respond. Yet, both populations thicken their shells in response to a long-established crab, *Carcinus maenas*. Our findings are consistent with the rapid evolution of an inducible morphological response to *Hemigrapsus* within 15 years of its introduction.

Anthropogenic introductions increasingly bring organisms into contact that have no shared evolutionary history, which results in novel interactions between non-native and native competitors, prey, and predators (1). These novel species combinations create potentially strong selection pressure that can drive evolutionary change of heritable traits (1–3). Although several studies have shown that invaders can evolve rapidly in a novel, invaded environment (1), examples of invader-driven rapid evolutionary change in native species are rarer (1, 3, 4). Rapid evolutionary change may particularly influence the ability of native prey to recognize and respond to novel invasive predators with inducible morphological defenses.

Inducible defenses are the expression of alternative forms (phenotypic plasticity) by organisms in response to cues from a predator or competitor. Some commonly noted inducible defenses include shape changes in barnacles, spines on bryozoans and cladocerans, thickened shells of mollusks, defensive chemicals in plants, and morphological and behavioral characters in anuran tadpoles (5, 6). Although selection may act on inducible defenses (5), in terms of both the degree of plasticity (7) and the prey's capacity to recognize cues from predators (8, 9), to date there have been no examples of an invasive species driving the rapid evolution and

emergence of an inducible morphological response. To test for the evolution of predator recognition and expression of inducible morphological defenses in a marine mussel (*Mytilus edulis*), we juxtaposed the induced defenses of two mussel populations having different historical contact with two invasive crab predators.

The Asian shore crab, *Hemigrapsus sanguineus*, was first reported in North America in New Jersey in 1988 and currently ranges from North Carolina to the midcoast of Maine, U.S.A. (10, 11). *M. edulis* is a large component of *H. sanguineus*' diet (12), but perhaps because this is a novel predator in the North Atlantic Ocean, nothing is known about inducible defenses in mussels to this crab. A longer term resident of New England, the green crab, *Carcinus maenas*, was introduced from Europe to the Mid-Atlantic United States in 1817 and currently ranges from New Jersey, U.S.A., to Prince Edward Island, Canada (13). *C. maenas* has had substantial impacts on native communities throughout its introduced range (13–15) and is known to induce defenses in *M. edulis* from several populations (14, 16, 17). Small mussels are vulnerable to both crab species (12), show high relative growth amenable to detecting induced defenses, and represent a crucial, prereproductive stage under strong selection.

Given the invasion history of these two crabs, *M. edulis* in northern New England (specifically northeastern Maine) has never experienced predation by *H. sanguineus*. Because the genus *Hemigrapsus* is not native to the Atlantic, neither have they been exposed to any *Hemi-*

*grapsus* congeners. However, they have experienced predation by *C. maenas* for more than 50 years. In contrast, mussels in southern New England have experienced predation by *C. maenas* and *H. sanguineus* for 100+ and ~15 years, respectively. To determine whether natural selection has altered the mussels' capacity to respond to these two crabs, we quantified the responses of mussels from these northern and southern populations to these two crab predators. If predator cues are species-specific, and if selection has altered the capacity of mussels to recognize and respond to these invasive predators, we expected that mussels from southern New England would respond to cues from both crabs, whereas northern mussels would respond to cues from *C. maenas* but not *H. sanguineus*.

To compare the inducible defenses of mussels from northern and southern New England in response to *C. maenas* and *H. sanguineus*, we collected mussels (13- to 20-mm shell length) from floating docks at six sites each in northern Maine and southern New England and brought them to Northeastern University's Marine Science Center at Nahant, MA (Fig. 1) (18). These mussels were then raised with nonlethal, waterborne cues from *C. maenas*, *H. sanguineus*, or no predator (control). Using the final measurements of each mussel's shell thickness index (STI), adjusted to its initial STI, we assessed the development of inducible defenses (19). After 3 months, mussels had grown, and mussels from northern and southern New England had thickened their shells differently in response to waterborne cues from the two invasive crab predators (i.e., there was a significant population by predator treatment interaction) (20). Mussels from southern sites thickened their shells in response to waterborne cues from *H. sanguineus* relative to controls ( $P = 0.011$ ), and mussels appeared to thicken their shells in response to *C. maenas*, although the trend was not significant ( $P = 0.145$ ) (Fig. 2). In contrast, although mussels from northern sites developed significantly thicker shells in response to cues from *C. maenas* ( $P = 0.001$ ), they did not respond to cues from *H. sanguineus* ( $P = 0.573$ ) (Fig. 2). In addition, there were clear population differences in the temperature-sensitive process of shell accretion, with mussels from northern populations thickening their shells more than mussels from southern populations (Fig. 2). These findings suggest that northern and southern mussel populations are

Zoology Department, Rudman Hall, University of New Hampshire, Durham, NH 03824, USA.

\*To whom correspondence should be addressed. E-mail: [afreeman@cisunix.unh.edu](mailto:afreeman@cisunix.unh.edu)

genetically distinct. This pattern of warm water-adapted mollusks secreting shell more slowly than northern conspecifics is consistent with countergradient variation, a pattern seen in the New England snail *Littorina obtusata* (21).

To determine whether the previous results were robust or influenced by a laboratory setting more similar to northern collection sites (e.g., water temperature and concentration of background cues from *H. sanguineus*), we ran an additional induction experiment under field conditions more similar to southern sites. We collected another generation of small *M. edulis* from similar northern and southern floating docks (Fig. 1) and raised them for 3 months while exposed to nonlethal, waterborne cues from unfed *C. maenas*, unfed *H. sanguineus*, or no predator (control). In this in situ experiment, mussels and predators were housed in steel mesh cages suspended from a floating dock in Woods Hole, Massachusetts. Mussels were separated from the cue crabs by steel mesh but could also experience any background cues due to ambient crabs in this environment (19). These mussels responded to the cue crabs nearly identically to the previous laboratory experiment, with only northern mussels not responding to *H. sanguineus* (Fig. 3) (22).

Our results clearly indicate that mussels from populations in northern and southern New England respond differently to waterborne cues from *H. sanguineus*. Yet, mussels in both regions express similar induced shell thickening in response to *C. maenas*, a resident throughout this coast for more than 50 years. Although brief, we believe the historical contact with and predation by *H. sanguineus* accounts for the divergent mussel responses. The mussel's inducible

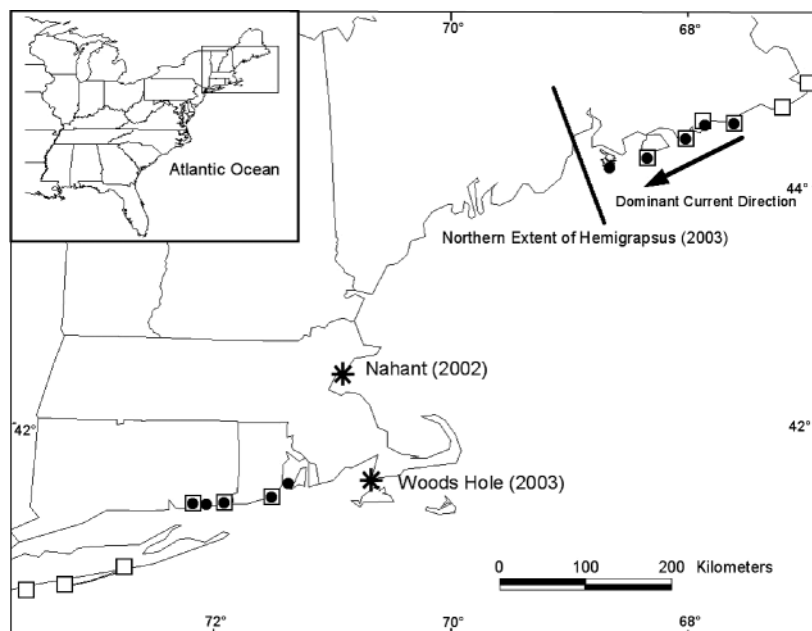
response to *H. sanguineus* reflects natural selection favoring the recognition of this novel predator through rapid evolution of cue specificity or thresholds (23). In addition, this response may be brought about by a novel mechanism of shell thickening; however, it more likely relies on mechanisms for induced defenses to other crabs (8). Despite the mussel's planktonic larvae, the response to *H. sanguineus* manifested by southern *M. edulis* has not spread to northern mussels. This suggests strong local adaptation and/or mostly unidirectional gene flow due to dispersal barriers such as the predominantly southwestward currents in northern New England (24).

Although invasive predatory crabs can induce defenses in native mollusks (5, 14, 16), these previous examples did not establish that predator recognition and an inducible morphological defense emerged as a result of selection from the invasive predator. Inducible morphological defenses are distinct from other prey defenses (i.e., behavioral responses and fixed traits) because they are often irreversible and they may require a sizeable time lag to develop after predator cues are detected (25, 26). The few examples of natural selection by invasive predators deal with the alteration of existing predator-specific responses, fixed traits, and adaptive behavioral responses (1, 3, 4, 7).

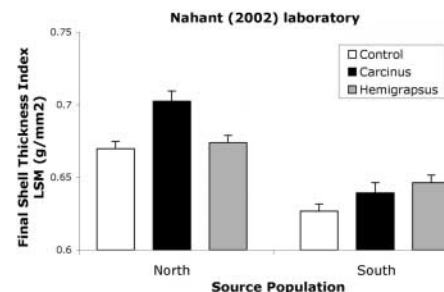
Although recent historical contact with *H. sanguineus* appears to have selected for predator recognition in *M. edulis*, we cannot rule out nonheritable processes in individual mussels, such as learning by native prey (27) or conditioned predator recognition. However, there are no examples of inducible morphological defenses resulting strictly from learning. In

addition, in situ background cues necessary for learning (28) appeared to have a negligible effect in our system. At the time of the experiments, *H. sanguineus* was only recently established in Nahant and thus much less abundant compared with southern New England where the crab had been established for several years. If background cues were influential in our system, southern control mussels in the in situ experiment would have thickened their shells, diminishing the difference between control and *H. sanguineus*-exposed mussels in our Woods Hole field experiment relative to the Nahant laboratory experiment. However, this difference was greater in the in situ field experiment than in the Nahant lab experiment, suggesting that ambient background cues were not sufficient to influence our experiments or learning in southern mussels before their collection.

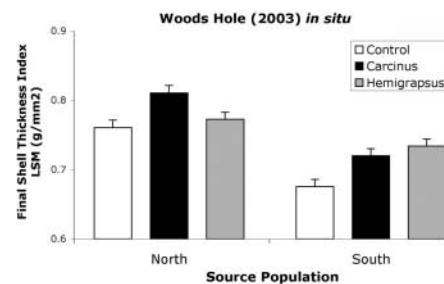
Alternatively, the differing mussel responses to the two crabs may be related to heritable population differences in recognition of *H. sanguineus* unrelated to the introduction of *H. sanguineus*. However, because the genus *Hemigrapsus* is novel to the Atlantic Ocean, there is



**Fig. 1.** Sites of the induction experiments at Nahant in 2002 and Woods Hole in 2003 (asterisks). Also indicated are collection sites for mussels used in the Nahant laboratory experiment (open squares) and the Woods Hole field induction experiment (filled circles).



**Fig. 2.** Adjusted final STI of mussels raised in a laboratory induction experiment at Nahant, Massachusetts, Gulf of Maine. Mussels from northern and southern populations were raised as controls or in the presence of cues from *C. maenas* or *H. sanguineus*. Values are adjusted least square means (LSM) from an analysis of covariance with initial STI as a covariate. Error bars, 1 SEM.



**Fig. 3.** Adjusted final STI of mussels raised in situ in cages suspended from a floating dock in Woods Hole, MA, in 2003. Mussels from northern and southern populations were raised as controls or in the presence of cues from *C. maenas* or *H. sanguineus*. Values are adjusted least square means (LSM) from an analysis of covariance with initial STI as a covariate. Error bars, 1 SEM.

little reason to believe that any Atlantic mussels recognized it before its invasion. Thus, even if the extremely limited gene flow of *M. edulis* between Europe and North America (29) disproportionately influenced northern or southern New England mussels, this effect would not help to explain a population's predisposition to recognize *Hemigrapsus*. Moreover, even if *M. edulis* recognized *H. sanguineus* before its invasion, it is doubtful that the trait would be lost only in northern New England mussels, given the capacity of mussels to maintain cue recognition in the absence of reinforcing predation (17). Alternatively, northern New England mollusks may generally experience lower predation than southern conspecifics (30). Thus, although previous recognition of *H. sanguineus* per se seems unlikely, southern New England mussels may more readily express inducible defenses to many predator species by responding to a lower threshold of cues or with decreased specificity to predators (28). In fact, this potential gradient in cue thresholds and sensitivities may promote the rapid evolution of recognition of a novel, invasive predator in southern New England mussels.

Species interactions can differ on various geographic scales because of local selection and other processes (31, 32). Similarly, there is considerable potential for the evolutionary history of invasive and native species interactions to vary spatially and temporally. Although we have only a nascent understanding of the role of inducible defenses in marine systems (15, 33), this phenomenon is likely highly influenced by the evolutionary history of the interacting species. The confluence of evolutionary and ecological interactions represents an essential field of inquiry to understand fully the impacts of invasive species.

#### References and Notes

- G. W. Cox, *Alien Species and Evolution* (Island Press, Washington, DC, 2004).
- D. Reznick, J. A. Endler, *Evolution Int. J. Org. Evolution* **36**, 160 (1982).
- S. Y. Strauss, J. A. Lau, S. P. Carroll, *Ecol. Lett.* **9**, 357 (2006).
- B. L. Phillips, R. Shine, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 17150 (2004).
- G. C. Trussell, L. D. Smith, *Proc. Nat. Acad. Sci. U.S.A.* **97**, 2123 (2000).
- R. Tollrian, C. D. Harvell, *The Ecology and Evolution of Inducible Defenses* (Princeton University Press, Princeton, NJ, 1998).
- G. C. Trussell, M. O. Nicklin, *Ecology* **83**, 1635 (2002).
- C. D. Schlichting, M. Pigliucci, *Phenotypic Evolution* (Sinauer Associates, Sunderland, MA, 1998).
- J. M. Kiesecker, A. R. Blaustein, *Ecology* **78**, 1752 (1997).
- J. J. McDermott, *ICES J. Mar. Sci.* **55**, 289 (1998).
- R. Seeley, personal communication.
- A. M. Lohrer, R. B. Whitlatch, *Mar. Ecol. Prog. Ser.* **227**, 135 (2002).
- J. T. Carlton, A. N. Cohen, *J. Biogeogr.* **30**, 1809 (2003).
- G. H. Leonard, M. D. Bertness, P. O. Yund, *Ecology* **80**, 1 (1999).
- G. C. Trussell, P. J. Ewanchuk, M. D. Bertness, *Ecol. Lett.* **5**, 241 (2002).
- L. D. Smith, J. A. Jennings, *Mar. Biol.* **136**, 461 (2000).
- O. Reimer, S. Harms-Ringdahl, *Mar. Biol.* **139**, 959 (2001).
- Details are available in table S1 as supporting material on Science Online.
- Details are available in Materials and Methods as supporting material on Science Online.
- Analysis of covariance (ANCOVA) of final STI in laboratory experiment at Nahant, MA (2002): Site(Population)  $P < 0.0001$ ; Predator  $P = 0.0033$ ; Population  $P = 0.0207$ ; Predator  $\times$  Population  $P = 0.0249$ ; Predator  $\times$  Site(Population)  $P = 0.3378$ ; Initial STI  $P < 0.0001$ . See table S2 in supporting material on Science Online.
- G. C. Trussell, *Evolution Int. J. Org. Evolution* **54**, 151 (2000).
- ANCOVA of final STI of mussels raised as controls or with cues from *C. maenas* or *H. sanguineus* in cages suspended from a floating dock in Woods Hole, MA (2003): Site(Population)  $P = 0.0135$ ; Predator  $P = 0.0006$ ; Population  $P = 0.0018$ ; Predator  $\times$  Population  $P = 0.0292$ ; Predator  $\times$  Site(Population)  $P = 0.7647$ ; Initial STI  $P < 0.0001$ ; Initial STI  $\times$  Population  $P = 0.0692$ . A priori linear contrasts: *Carcinus*(North) versus Control(North)  $P = 0.0031$ ; *Carcinus*(South) versus Control(South)  $P = 0.0049$ ; *Hemigrapsus*(North) versus Control(North)  $P = 0.3996$ ; *Hemigrapsus*(South) versus Control(South)  $P = 0.0006$ . (See table S3.)
- C. M. Payne, C. V. Tillberg, A. V. Suarez, *Ann. Zool. Fenn.* **41**, 843 (2004).
- J. E. Byers, J. M. Pringle, *Mar. Ecol. Prog. Ser.* **313**, 27 (2006).
- D. K. Padilla, S. C. Adolph, *Evol. Ecol.* **10**, 105 (1996).
- A. Sih, in *Phenotypic Plasticity*, T. J. DeWitt, S. M. Scheiner, Eds. (Oxford Univ. Press, New York, 2004), vol. 1, pp. 112–126.
- R. F. Maloney, I. G. Mclean, *Mar. Biol.* **50**, 1193 (1995).
- G. E. Brown, D. P. Chivers, in *Ecology of Predator-Prey Interactions*, P. Barbosa, I. Castellanos, Eds. (Oxford Univ. Press, New York, NY, 2005).
- C. Riginos, M. J. Hickerson, C. M. Henzler, C. W. Cunningham, *Evolution Int. J. Org. Evolution* **58**, 2438 (2004).
- M. D. Bertness, S. D. Garrity, S. C. Levings, *Evolution Int. J. Org. Evolution* **35**, 995 (1981).
- M. N. Dethier, D. O. Duggins, *Mar. Ecol. Prog. Ser.* **50**, 97 (1988).
- E. Sanford et al., *Science* **300**, 1135 (2003).
- P. T. Raimondi, S. E. Forde, L. F. Delph, C. M. Lively, *Oikos* **91**, 353 (2000).
- We thank the following: E. Enos, S. Genovese, E. Maney, C. Neefus, G. Trussell, Marine Biological Laboratory (Woods Hole), Great Bay National Estuarine Research Reserve Graduate Research Fellowship, University of New Hampshire (UNH) Graduate School, UNH Marine Program, and UNH Zoology Department. This manuscript was improved by comments from I. Altman, M. Bertness, A. Blakeslee, J. Dijkstra, B. Griffen, M. Lesser, J. Meyer, M. Scott, G. Trussell, and three anonymous reviewers.

#### Supporting Online Material

www.sciencemag.org/cgi/content/full/313/5788/831/DC1

Materials and Methods

Tables S1 to S5

References

27 January 2006; accepted 13 June 2006

10.1126/science.1125485

## Loss of a Harvested Fish Species Disrupts Carbon Flow in a Diverse Tropical River

Brad W. Taylor,<sup>1\*</sup> Alexander S. Flecker,<sup>2</sup> Robert O. Hall Jr.<sup>1</sup>

Harvesting threatens many vertebrate species, yet few whole-system manipulations have been conducted to predict the consequences of vertebrate losses on ecosystem function. Here, we show that a harvested migratory detrital-feeding fish (Prochilodontidae: *Prochilodus mariae*) modulates carbon flow and ecosystem metabolism. Natural declines in and experimental removal of *Prochilodus* decreased downstream transport of organic carbon and increased primary production and respiration. Thus, besides its economic value, *Prochilodus* is a critical ecological component of South American rivers. Lack of functional redundancy for this species highlights the importance of individual species and, contrary to theory, suggests that losing one species from lower trophic levels can affect ecosystem functioning even in species-rich ecosystems.

Widespread interest in the importance of species to ecosystem functioning stems from concerns that the rapid

rate of human-induced species losses could affect ecosystem properties and services negatively (1). Freshwater ecosystems provide es-

sential ecosystem services and contain a large fraction of species diversity that may be declining faster than the diversity in marine or terrestrial ecosystems (2). Humans have overharvested many of the large, long-lived predatory fishes and are now shifting fishing efforts to the abundant, higher-yielding species at lower trophic levels, such as detritivores (3). Detritus is the major pathway of energy and material flow in most ecosystems, supports higher trophic levels, and is a major source of inorganic nutrient regeneration and uptake; losses of detritivores could disrupt ecosystem functioning (4). Both greater abundance and higher species richness at lower trophic levels

<sup>1</sup>Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA. <sup>2</sup>Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA.

\*Present address: Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA.

†To whom correspondence should be addressed. E-mail: brad.taylor@dartmouth.edu