

Physiological Adaptation and Invasion Success: A Comparison of Native and Invasive Bay Mussels in the Central California Hybrid Zone

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Background

Invasive aquatic species can pose serious ecological and economic threats to coastal habitats. Although the mechanisms by which invasive species are introduced are generally well understood, and frequently caused by discharging ballast water, less is known about the physiological characteristics that allow an invasive species to proliferate so successfully.

What characteristics of an invader enable it to out-compete and replace a closely related native species? George Somero, director of Stanford's Hopkins Marine Station and Sea Grant Trainee Caren Braby studied two bay mussels found in Central California—*Mytilus trossulus*, a native whose range once spanned from Mexico to Canada and *M. galloprovincialis*, a Mediterranean species introduced to Southern California sometime in the early to mid decades of the last century.

This nonnative bivalve has replaced the native species from the Mexican border to the approximate latitude of Monterey Bay. Between Monterey Bay and areas just north of San Francisco Bay, the two species coexist in what is termed a "mosaic hybrid zone," an area in which one can find the native and invasive species and their hybrids.

The project's goal was to determine environmental factors important in governing the relative success of the two species. By understanding how each species is differentially affected by its environment, it may be possible to predict the invader's further spread.



Mytilus spp. Photos this story courtesy George Somero

Temperature and Salinity Studies

Two environmental factors stand out as being particularly important in understanding biogeographic patterning of bay mussels: ambient water temperature and salinity. The Mediterranean mussel would be expected to exhibit higher tolerance of warm water and lower tolerance of reduced salinities than the native, in keeping with differences in their original environments. Because the native mussel survives pulses of fresh-water inputs associated with winter rains, it is also reasonable to expect that salinity influences the distribution patterns of the species.

To test hypotheses about the roles of temperature and salinity, the scientists performed several types of field and laboratory experiments. They characterized temperatures and salinities at eight sites in Mon-

terey Bay and San Francisco Bay for over a year. Some of these sites were in estuarine environments, others were sites where waters were similar to oceanic water. In parallel with these habitat characterizations, they collected adult and juvenile mussels to determine (i) the relative abundance of native, invasive and hybrid adult mussels, and (ii) larval recruitment patterns.

The scientists reported finding significant correlations between temperature, salinity and species abundance. Contrary to their initial hypothesis, at the warmest sites the abundance of the native species actually exceeded that of the invasive. The expected relationship between ambient salinity and distribution patterns, however, was observed: the Mediterranean native was significantly more abundant at high-salinity sites. Thus, to a first approximation, salinity is the single greatest predictor of inter-site variation in species abundance—not temperature. Abundances of hybrids of the two species, it should be noted, did not exhibit significant relationships with either temperature or salinity.

Temperature and salinity also showed a significant relationship: sites with the lowest salinity had the highest temperatures, as these were sites in estuaries where there was little mixing with the open ocean (hence the relatively high temperatures) and significant fresh-water inputs from runoff and rain.

Another interesting discovery was the discrepancy in the species' maximum shell length. The non-native mussel reached a maximum of about 90 mm, compared to about

50 mm for the native. Since reproductive output is often correlated with body size, the invader likely is more fecund than the native.

Thermal Physiology and Heart Function

To gain further insights into the mechanisms responsible for their distributions, researchers studied the animals' thermal physiology. Studies of the temperatures at which the heat-shock response is activated showed that, as expected, heat shock was triggered at lower temperatures in the native (23°C) than in the invasive (25°C). Differences in heart function were also consistent with the hypothesis that the native is a cold-water species tolerant to low salinities; the invasive, a warm-water species, less intolerant to low salinities.

Larval Recruitment

To monitor larval recruitment by the native and invasive mussels at the field sites, the biologists developed a "DNA fingerprint." That is, they identified a single change within a gene that is diagnostic for the two species, which cannot be distinguished morphologically. This allowed them to accurately determine the species of large numbers of larvae.

The two species recruited with widely different success. Recruitment patterns were influenced by temperature and salinity, by the species compositions of adults already present at the sites, and by current-driven supplies of larvae from outside sites. A significant positive correlation was found between the abundance of the invader and maximal salinity and a negative correlation with maximal temperature,

trends consistent with the distribution patterns of adults noted above.

There also were positive correlations between the percent abundance of adults and of the larval population represented by the species. However, adult populations in general tended to differ more than larval populations, suggesting post-settlement selection. The more dilute, upper-estuarine sites where the native is strongly favored may be a good example of post-settlement effects of salinity-temperature combinations, the scientists said. It remains unclear how the larval stages of the two species respond to variations in temperature and salinity, but the recruitment data suggested that pre-settlement effects of the environment on larvae also could contribute to the observed variations in settlement among different sites. Currents appear to play a complex role in larval supply, with differences noted between northern sites in San Francisco Bay and more southern sites.

Summary

These studies showed that the native and invasive bay mussels differ markedly in their adult distribution patterns along gradients in temperature and salinity. Recruitment success, too, is governed in part by these two important environmental factors. The two species have distinct physiologies. The invader attains a larger size, which may contribute to a higher fecundity. That species also is more tolerant of high temperatures, yet less tolerant of low temperatures than the closely related native. The native has a significantly higher heart rate, which may reflect a temperature-compensated metabolic rate. Because of the invader's higher optimal tempera-



George Somero, director, Hopkins Marine Station

ture, global warming could facilitate its future northward spread. Its intolerance to low salinity, however, could hamper its spread to areas that receive a lot of rain or river discharges.

"The message is that by using physiological and genetic approaches, one can get an understanding of why an invasive species succeeds," Somero said. "Once one characterizes the environmental conditions that favor a species' survival or enable it to out-compete a related species, one can begin predicting how or if the invader will spread."

Trainee

Caren Braby

Awards

Arthur C. Giese Award to Caren Braby 2003.

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July 2005

This work is sponsored in part by a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, under grant number NA04OAR4170038, Project number A/P-1. The views expressed herein are those of the author and do not necessarily reflect the views of NOAA or any of its subagencies. The U.S. Government is authorized to reproduce and distribute for governmental purposes.

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