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

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"Aquatic Nuisance Species: Physiological Adaptation and Invasion Success: A Comparison of Native and Invasive Species of Bay Mussels in the Central California Hybrid Zone."

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Marine species invasions pose serious ecological and economic threats to coastal areas throughout the world. The mechanisms by which invasive species are introduced to a new habitat are generally well understood, and frequently involve release of invasive larvae or adults in ballast water. However, we currently have little knowledge concerning the physiological characteristics of an invasive species that allow it to succeed, following its introduction. What characteristics of an invader enable it to succeed and, in some cases, to out-compete and replace a closely related native species? We examined the physiological basis of invasive success by comparing two congeneric bay mussels found along the coast of Central California. *Mytilus trossulus* is a native bay mussel that formerly occurred along the Pacific Coast of the United States from Mexico to Canada. At some point in the early to middle decades of the past century, a second species of bay mussel, *M. galloprovincialis*, was introduced into Southern California waters. Since its introduction, this invasive species has replaced the native species from the Mexican border to the approximate latitude of Monterey Bay. Between Monterey Bay and areas just to the north of San Francisco Bay, the two species coexist in what is termed a "mosaic hybrid zone." In this zone, one can find the native and the invasive species and their hybrids.

Our studies sought to determine what environmental factors are important in governing the relative success of the native and invasive species. By understanding how the species are affected by their environment, it may be possible better to predict the further spread of the invasive species to sites at higher latitude. Two environmental factors stand out as being particularly important in governing biogeographic patterning of bay mussels: ambient water temperature and salinity. The invasive species originated in the Mediterranean Sea, so it has been conjectured that this species will exhibit higher tolerance of elevated temperatures and lower tolerance of reduced salinities than *M. trossulus*, in keeping with the differences in environmental conditions between the Mediterranean Sea and temperate Eastern Pacific Ocean. *Mytilus trossulus* encounters greatly reduced salinities during periods of winter rainfall, so salinity could be the most critical determinant of how effectively the invasive species can replace the native at sites to the north of the current hybrid zone.

To test hypotheses about the roles of temperature and salinity in influencing distribution patterns, we performed several types of field and laboratory experiments. We characterized habitat temperatures and salinities on a year-round basis at environmentally eight diverse sites in Monterey Bay and San Francisco Bay where bay mussels are abundant. In parallel with the habitat characterizations, we collected adult and juvenile mussels to determine (i) the relative abundance of native, invasive and hybrid adult mussels and (ii) larval recruitment patterns at these ecologically diverse sites. We observed significant correlations between habitat temperature, habitat salinity, and species abundance. Contrary to our initial hypothesis, at the warmest field sites the abundance of the native species exceeded that of the invasive. However, the expected relationship between ambient salinity and distribution patterns was observed: *M. galloprovincialis* was significantly more abundant at high salinity sites [the regression equation relating average salinity (2001-2003) and percentage contribution of the invasive species has an R^2 value of 0.76.]. Thus, to a first approximation, salinity appears to explain a significant fraction of the inter-site variation in abundance of the adults of the two species. Abundance of hybrids between the two species did not exhibit significant relationships with either temperature or salinity. Temperature and salinity also showed a significant relationship: sites with the lowest salinities had the highest temperatures [R^2 of the relationship between average salinity and maximal temperature was 0.72]. We also made an unexpected finding when the size distributions of the native and invasive species were compared. The native species attained a maximal size (valve length) of approximately 50 mm, whereas the invasive species reached much larger sizes, up to approximately 90 mm. These differences in adult size could translate into differences in reproductive output, because fecundity is likely to correlate strongly with body size.

To gain further insights into the mechanisms responsible for the observed adult distributions, we studied the thermal physiology of the two species. We characterized the temperatures at which the native and invasive species activate the heat-shock response. The heat-shock response comprises the temperature-induced synthesis of several classes of molecular chaperones that assist in refolding proteins that have been denatured by heat. Synthesis of heat-shock proteins was triggered at lower temperatures in *M. trossulus* (approx. 23°C) than in *M. galloprovincialis* (approx. 25°C). The latter species also was able to continue synthesizing proteins at a higher temperature than the native species (36°C *versus* 33°C, respectively). Therefore, at the physiological and biochemical level, clear differences in thermal tolerance were found between the two species.

Heart function also showed a significantly different response to temperature between the two species. The rate of heart beat showed the expected increase with rising body temperature, but at a particular high temperature, termed the “critical temperature” heart beat rapidly decreased. The critical temperature was significantly lower in *M. trossulus*. Conversely, *M. trossulus* was able to sustain heart function at lower temperatures than *M. galloprovincialis*. Another difference noted in heart function between the two species was the intrinsic rate of heart beat: *M. trossulus* showed a significantly higher rate of heart beat under all conditions. This difference is consistent with a high degree of temperature compensation of physiological activity in the more cold-adapted native by mussel. Thermal acclimation experiments (14°C and 21°C) showed that the sensitivity of heart function to temperature could be varied during exposure to different temperatures. Both species manifested abilities to increase heat tolerance of heart function during warm acclimation, but *M. galloprovincialis* always had the greater tolerance of high temperatures. All of the differences in heart function observed in these experiments are consistent with the hypothesis that *M. trossulus* is a more cold-adapted species than the Mediterranean invasive, *M. galloprovincialis*.

We also studied the effects of ambient salinity on the rate of heart beat. As salinity was reduced, heart rate dropped rapidly below a certain salinity ("critical salinity"). The decrease occurred at a higher salinity in *M. trossulus* than in *M. galloprovincialis*. Because sharp reductions in the rate of heart beat were accompanied by valve closure, the native species may be responding more effectively to reductions in salinity than the invasive species, by closing down contact with seawater before osmotic stress reaches strongly perturbing levels.

Another striking difference between the two species that was noted throughout this three-year study was in mortality: the invasive species survived much better under all treatment conditions than the native species.

To monitor larval recruitment by the native and invasive mussels at the 8 field sites, it was necessary to develop a molecular technique that allowed accurate identification of large numbers of individuals. A single nucleotide polymorphism (SNP) detection system involving real-time polymerase chain reaction (rt-PCR) technology was developed for this purpose. The two species recruited with widely different success at the 8 field sites. Recruitment patterns were influenced by the physical characteristics of the study site (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 percent abundance of *M. galloprovincialis* and maximal salinity, and a negative correlation between percent abundance of the invader and maximal temperature was observed. These trends are consistent with the distribution patterns of adults noted above. There also were positive correlations between the percent abundance of adults and percent 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 *M. trossulus* is strongly favored may be a good example of post-settlement effects of salinity-temperature combinations. It remains unclear how the larval stages of the two species respond to variations in temperature and salinity, but the recruitment data suggest that pre-settlement effects of the environment on larvae also could contribute to the observed variations in settlement among different sites. Current patterns appear to play a complex role in larval supply, with differences noted between northern sites in San Francisco Bay and more southern sites.

In summary, these studies showed that native and invasive congeners of 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 physiological differences. The invader, *M. galloprovincialis*, attains a larger size, which may contribute to a higher fecundity. The species also is more tolerant of high temperatures, yet less tolerant of low temperatures than its native congener, *M. trossulus*. The latter species has a significantly higher heart rate, which may reflect a temperature-compensated metabolic rate. Because of *M. galloprovincialis*' higher optimal temperature, its future northward spread could be facilitated by global warming.