

Invasion success: does size really matter?

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Abstract

The recent paper by Roy *et al.* (2001) presents a compelling relationship between range limit shifts, climatic fluctuations, and body size for marine bivalves in the fossil record. However, their extension of body size as a correlate for contemporary marine bivalve introductions is problematic and requires further scrutiny. Unlike their analysis of the fossil assemblage, the approach used for contemporary invasions does not adequately control for dispersal mechanism (vector) or source region. First, their analysis included mariculture species, intentionally introduced because of their large size, creating a vector-specific bias. Second, successful invaders from multiple source regions (Northern Hemisphere) were compared with potential invaders from a single source region (north-eastern Pacific), leaving both source and vector as uncontrolled variables. We present an analysis of body size for bivalve introductions from a single vector and source region, indicating no correlation between body size and invasion success when eliminating intentional introduction, source region and transport vector as confounding factors.

Keywords

Body size, marine bivalves, invasion success, non-indigenous species, oyster transport.

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INTRODUCTION

We read with interest the report by Roy *et al.* (2001) on the relationship between body size and range limit shifts associated with climatic fluctuations in the California marine bivalve fauna. We agree that understanding community and species responses to changing climates is of fundamental relevance to biogeographical forcing functions, as is elegantly documented by their analyses of the palaeontological record. However, we have reservations about the approach used to examine size-related patterns for contemporary invasions, and the resulting inferences appear premature.

In our view, the assemblages used by Roy *et al.* (2001) were not appropriate to test for body size as a predictor or correlate of contemporary invasion success. There are two fundamental problems. First, the assemblage of invaders does not control for mechanism of introduction (vector). Contemporary invasions result from a wide variety of human-mediated vectors (Carlton 1989; Ruiz *et al.* 2000), which may be selective for particular character traits. Roy *et al.* (2001) selected 25 species of successful bivalve invaders for their analysis, including five species that were introduced intentionally for mariculture (see below). Mariculture species are selected for introduction and cultivation partly on the basis of their large body sizes. Importantly,

great effort is often made to enhance the invasion success of mariculture species, including frequent and dense inoculations to suitable habitats with appropriate environmental conditions (based upon prior knowledge of biology and ecology). Invasion success should, but does not always, increase with increasing propagule pressure, especially when intentionally directed at appropriate habitats (Williamson 1996; Miller 2000; Ruiz *et al.* 2000). Thus, inclusion of mariculture species may greatly weight the assemblage of successful invaders in favour of large-bodied species, resulting in conclusions that are not relevant to invasions with other vectors (e.g. ballast water or hulls of ships); although other vectors may select for large body size, this has not been demonstrated.

Second, their comparison of bivalve invaders originating in the Northern Hemisphere (and invading anywhere in the world) with the bivalve fauna of the north-eastern Pacific appears arbitrary and did not control adequately for source region. Source regions can differ substantially in the taxonomic representation and biological attributes of resident species, both of which may influence invasion success (Vermeij 1991, 1996). Source regions can also differ in the operation (types and characteristics) of vectors, and this too should influence invasion opportunities among regions (Carlton 1996). Thus, to understand factors that may influence invasion success, comparison should be made

between successful vs. unsuccessful invaders from a *single* source pool and transport vector to avoid many confounding effects that can result from differences by source pool composition and transport vector (e.g. Carlton 1996; Vermeij 1996). Furthermore, this approach would be analogous to that used for evaluation of the fossil record by the authors.

To illustrate both issues, we provide two analyses. We test for a disproportionate contribution from mariculture species using shell size data compiled by Roy *et al.* (2001) for introduced Northern Hemisphere bivalves. In a second analysis we compare maximum sizes of bivalve species that successfully invaded the north-eastern Pacific to maximum sizes of all potential bivalve invaders delivered by the same vector and originating from the same source pool in the western Atlantic. The latter analysis controls for source region and vector, as well as recipient region that may also influence invasion success (Carlton 1996; Vermeij 1996; Ruiz *et al.* 2000).

METHODS

Size bias associated with mariculture species?

Five (20%) of the invading species listed by Roy *et al.* (2001) have been intentionally introduced outside their native ranges for mariculture purposes: *Argopecten irradians* (Lamarck, 1819); *Crassostrea virginica* (Gmelin, 1791); *C. gigas* (Thunberg, 1793); *Mercenaria mercenaria* (Linné, 1758); and *Ostrea edulis* (Linné, 1758). Although the Japanese littleneck clam, *Venerupis philippinarum* (Adams & Reeve, 1850) was introduced into the Mediterranean for mariculture (CIESM 2001), it successfully invaded the west coast of the United States accidentally in association with introduced Japanese oysters (*Crassostrea gigas*; Carlton 1979). As such, *V. philippinarum* was not treated as a mariculture introduction here (but see Results for this species' effects on analyses.)

To test for size bias associated with mariculture species introductions, we employed a bootstrap resampling method comparing mean shell size of the five mariculture species with the expected outcome when five species were chosen randomly from the full complement of 25 invaders. Resampling statistics provide a powerful approach to compare small, unbalanced samples for which parametric and nonparametric statistics are limited by assumptions of normality and statistical power (Efron 1979; Potvin & Roff 1993). We selected five-species combinations randomly from the original data using 10 000 iterations to construct a bootstrap sample frequency distribution (Manly 1992). The mean maximum body size of the five successful mariculture invaders was compared to the upper 5% of the bootstrap distribution to determine significance (one-tailed test,

$\alpha = 0.05$). Shell sizes were calculated as the geometric mean of maximum length and width and \log_2 transformed (Roy *et al.* 2001).

Size differences between successful vs. failed invaders?

To test the effect of size on invasion success, we used the assemblage of marine bivalves associated with the commercial transfer of the eastern oyster, *Crassostrea virginica*, from eastern to western North America. Although *C. virginica* grew well along the western coast of North America, it failed to become established there (except perhaps at Boundary Bay, British Columbia; Miller 2000). As a result, oysters were introduced repeatedly over a 60-year period in large volumes (exceeding 125 rail carloads in many years; Barrett 1963), creating a vector for the unintentional introduction of many Atlantic species transferred unwittingly along with oysters as larvae, juveniles, and adults (Carlton 1992, 1999; Miller 2000). The bivalve species associated with *C. virginica* on the east coast were compiled, and maximum shell lengths for each species were derived from the literature (Miller 2000). Some variation in the species composition and magnitude of transfers no doubt existed across oyster shipments. However, by confining the source pool of bivalves to only those from the geographical location where oysters were dredged and by integrating over the 60-year period, this approach generates a reliable source pool as a basis for the analysis. We then compared the size of successful bivalve invaders against the entire pool of associated bivalve species. (Note: *Crassostrea virginica* was not included in the size analysis, but was treated simply as the vector by which other bivalves were introduced to the west coast.)

The entire assemblage consisted of 38 bivalve species, including five successful and 33 failed invasions. We consider all species in this assemblage to have been introduced at some frequency by this vector, thus we use failed and unsuccessful interchangeably. The five successful invaders via this vector are: *Gemma gemma* (Totten, 1834); *Geukensia demissa* (Dillwyn 1817); *Macoma balthica* (Linné, 1758); *Mya arenaria* Linné, 1758; *Petricolaria pholadiformis* (Lamarck, 1818). Although *Mercenaria mercenaria* has successfully invaded two locations on the west coast of the United States as a mariculture species, this species did not become established there as an accidental associate of the oyster industry (Carlton 1979, 1992) and is therefore not considered a successful oyster-associate invader in this analysis.

We then compared the maximum mean shell length of successful invaders to the bootstrap distribution from the 38 species pool of potential invaders (one-tailed test, $\alpha = 0.05$, 10 000 iterations). This comparison allowed us to control simultaneously for the effects of vector, source region, and recipient region. Shell lengths were \log_2 transformed prior to analysis.

RESULTS AND DISCUSSION

The size frequency distribution of introduced bivalves derived from Northern Hemisphere source regions is heavily influenced by mariculture species (Fig. 1a). This is not surprising since species selected for human consumption are typically larger than the surrounding non-cultured species. In addition, mariculture bivalves probably have a

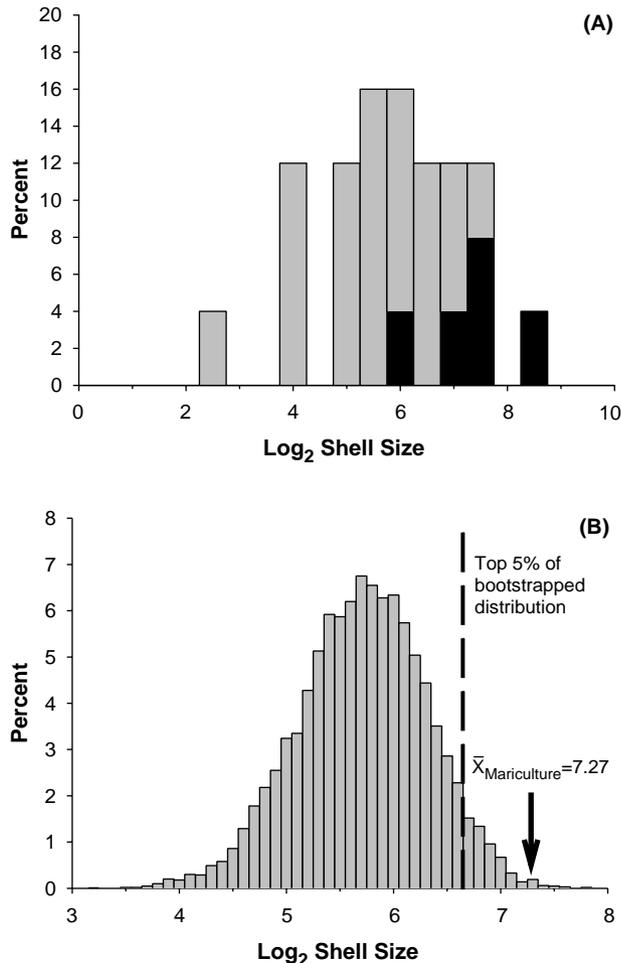


Figure 1 (A) Shell size frequency distribution of 25 successful marine bivalve invaders of the Northern Hemisphere, as reported by Roy *et al.* (2001). Black bars indicate five mariculture species. (B) Mean shell size frequency distribution generated by bootstrapping the shell size data of Fig. 1(A). Groups of five species were re-sampled with replacement and means reported from 10 000 iterations. Mariculture species are significantly larger than expected by chance alone. The arrow indicates the mean \log_2 shell size of recognized mariculture species (mean = 7.27, $P = 0.0022$, one-tailed test, $\alpha = 0.05$) and the dashed line marks the upper 5% range of the distribution.

greater invasion success than accidentally transported species because of the frequency and size of inoculations (Carlton 1992, 1999).

The group of five mariculture species has a significantly larger geometric mean size than that of the bootstrapped sample distribution generated from the 25 introduced species presented by Roy *et al.* (2001) (Fig. 1b). This result indicates that the mariculture species included are indeed statistically larger than what is expected by chance alone (inclusion of *Venerupis philippinarum* in the analysis made no difference to the statistical outcome of the test). Kolmogorov–Smirnov tests (performed on data extracted from figure 2 of Roy *et al.* 2001) indicate that removal of mariculture species results in no statistical difference between distributions ($P > 0.05$), whether or not *Venerupis philippinarum* is excluded. Consequently, the bias introduced into the original data set by inclusion of mariculture species undermines the general conclusions by Roy *et al.* (2001) about size and invasion success for contemporary bivalve invasions. However, we believe the approach of Roy *et al.* (2001) is flawed, as it does not control for vector or source region.

In a more robust analysis of size-specific pattern in contemporary invasions, we found no effect of shell length on invasion success (Fig. 2a). The mean length of eastern oyster associates that are successful invaders is not significantly different from the mean of the bootstrapped sample distribution drawn from the complete pool of 38 potential eastern oyster associates (Fig. 2b). Thus, for this vector, the outcome clearly demonstrates that invasion success was not significantly correlated with greater body size.

For modern introductions of marine bivalves, our re-evaluation of the data from Roy *et al.* (2001) and inclusion of new data do not support the hypothesis that larger body size conveys better invasion success. Although body size was associated with range extensions in response to climatic forcing (Roy *et al.* 2001), we can find no evidence that introductions are more likely to succeed as the result of body size once confounding factors (e.g. human preselection, source region, vector) have been controlled. Our analyses add to the growing literature that indicates body size either is not associated with invasion success (Veltman *et al.* 1996; Forsy & Allen 1999) or is negatively related to invasion success, i.e. small taxa are more successful (e.g. Bazzaz 1986; Rejmánek 1996, 1999).

Human-mediated transport and introductions of species are not identical to natural range expansions. As such, the methods used to evaluate and compare similarities among these phenomena must be carefully designed to control for important invasion parameters such as source region, recipient region, and invasion vector.

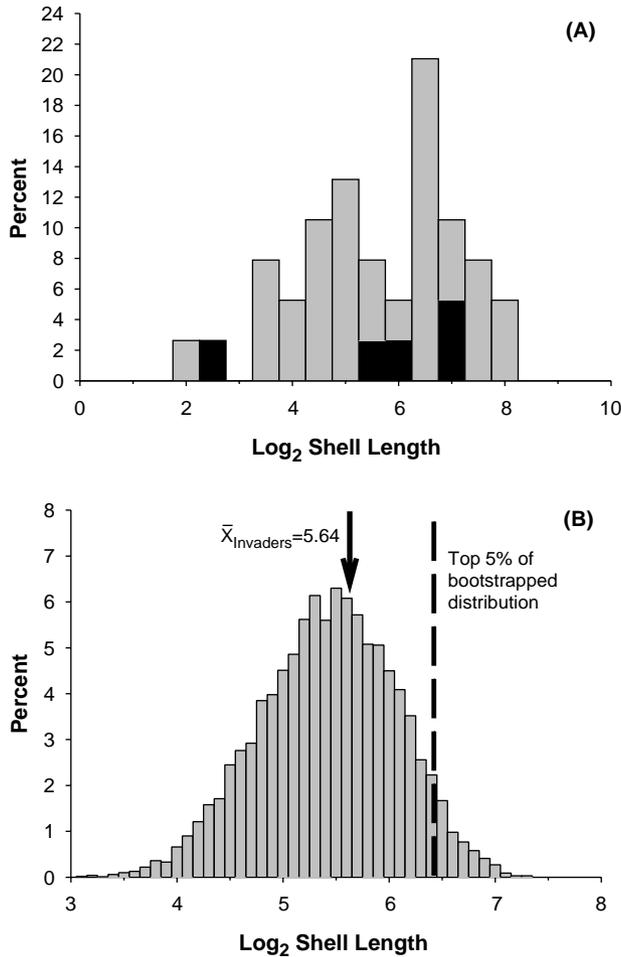


Figure 2 (A) Shell length frequency distribution of 38 western Atlantic marine and estuarine bivalves probably introduced to the west coast of North America with commercially planted oysters (*Crassostrea virginica*), as reported by Miller (2000). Black bars indicate five successful invaders of the west coast and grey bars indicate failed bivalve invaders. (B) Mean shell length frequency distribution generated by bootstrapping the shell length data of Fig. 2(A). Groups of five species were resampled with replacement and means reported from 10 000 iterations. Successful bivalve invaders are not significantly larger than what might be expected by chance alone from the entire species pool. The arrow indicates the mean \log_2 shell length of successful invaders (mean = 5.64, $P = 0.353$, one-tailed test, $\alpha = 0.05$) and the dashed line marks the upper 5% range of the distribution.

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