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LETTER

Body size and invasion success in marine bivalves

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Abstract

The role of body size in marine bivalve invasions has been the subject of debate. Roy *et al.* found that large-bodied species of marine bivalves were more likely to be successful invaders, consistent with patterns seen during Pleistocene climatic change, but Miller *et al.* argued that such selectivity was largely driven by the inclusion of mariculture species in the analysis and that size-selectivity was absent outside of mariculture introductions. Here we use data on non-mariculture species from the north-eastern Pacific coast and from a global species pool to test the original hypothesis of Roy *et al.* that range limits of larger bivalves are more fluid than those of smaller species. First, we test the hypothesis that larger bivalve species are more successful than small species in expanding their geographical ranges following introduction into new regions. Second, we compare body sizes of indigenous and non-indigenous species for 299 of the 303 known intertidal and shelf species within the marine bivalve clade that contains the greater number of non-mariculture invaders, the Mytilidae. The results from both tests provide additional support for the view that body size plays an important role in mediating invasion success in marine bivalves, in contrast to Miller *et al.* Thus range expansions in Recent bivalves are consistent with patterns seen in Pleistocene faunas despite the many differences in the mechanisms.

Keywords

Body size, marine bivalves, introduced species, range expansion.

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INTRODUCTION

The correlation of body size with many important aspects of species' life histories suggests that size should be significantly related to the colonization success of introduced species. Roy *et al.* (2001) showed that geographical range limits of large marine bivalve species underwent more fluctuations in response to late Pleistocene climatic changes than smaller species, and they found a similar size-selectivity in a preliminary analysis of human-mediated invasions involving marine bivalves. Miller *et al.* (2002) raise two useful issues regarding that analysis of human-mediated invasions: (1) controlling for the mechanism of introduction and (2) controlling for the source species pool in the comparisons of size frequency distributions of introduced and native species. Miller *et al.* (2002) separated bivalve species introduced through mariculture from non-mariculture species and showed that successfully introduced mariculture species are indeed significantly larger. However, their analysis of non-mariculture species did not support the hypothesis that larger bivalves are more successful invaders. They accordingly conclude that body size plays no role in the invasion success of marine bivalves. Miller *et al.* (2002) thus raise important issues regarding strategies for analysing the role of body size in human-mediated invasions as well as the actual patterns involved. Here we take those concerns into account and re-evaluate the role of body size in marine bivalve invasions.

The human-mediated invasion process can be viewed as having three distinct phases: the initial successful introduction of a species outside its native range, the establishment of a local self-sustaining population, and finally the spread of a species in its introduced range (Sakai *et al.* 2001). Traits such as body size and correlated life history characteristics could be associated with any of these phases and such traits could even differ among phases (Sakai *et al.* 2001) or at different taxonomic ranks (Cassey 2001). For example, large body size is associated with successful introduction of birds in Australia but among the introduced species, small-bodied taxa have attained more extensive ranges in their new regions (Duncan *et al.* 2001).

For invertebrates, the role of size or other traits in the invasion process is difficult to analyse due to a general lack of data on failed introductions (Vázquez & Simberloff 2001), and the problem is particularly acute for marine invertebrates. Thus for bivalve introductions, the definition of a native source pool (*sensu* Miller *et al.* 2002) poses a significant challenge. More importantly, the choice of a native source pool could influence the results of the tests for trait selectivity as evidenced by the very broad comparison presented in Roy *et al.* (2001), where the size-frequency distributions of bivalves of the north-eastern Pacific marine shelf were used as a representation of most marine bivalve faunas, versus a more restricted comparison presented by Miller *et al.* (2002). Similar uncertainties also exist for the introduction vectors for many marine invertebrate introductions.

Given the problems of defining source pools and the lack of information on introduction vectors, here we use a more direct approach to test for the role of body size in invasions. We focus on the role of body size in post-establishment range expansion within a given region, thereby circumventing the source problem altogether. We use data from a single region, the north-eastern Pacific coast, and again only for non-mariculture species, to test the original hypothesis of Roy *et al.* (2001) that range limits of larger introduced bivalves are more fluid than those of smaller species. In particular, we test the hypothesis that larger bivalve species are better at colonizing new habitats in the introduced part of their range compared with small ones.

In addition to analysing post-establishment range expansion patterns, we compare body sizes of indigenous and non-indigenous species within a single clade. Following Kolar & Lodge (2001) we define indigenous species as those that are restricted to their native ranges and non-indigenous species as those introduced by humans, intentionally or otherwise, to areas beyond their native distributions. As closely related species share many ecological and life history traits, the use of such a phylogenetically restricted analysis can be useful in determining the importance of particular attributes, such as body size, in the invasion process. In addition, by including all living species of a clade one can unambiguously define the global source pool and evaluate the invaders relative to that pool. This approach is different from that of Miller *et al.* (2002) where the source pool is defined relative to an invasion vector. The lack of data on failed invasions is, however, a problem in interpreting the processes underlying the results of the phylogenetically restricted analyses as well as those of Miller *et al.* (2002). The implications of such biases are further discussed below.

The results from both tests provide strong support for the view that body size does indeed play an important role in mediating invasion success in marine bivalves, in contrast to Miller *et al.* (2002). Thus these results are consistent with patterns seen in Pleistocene faunas despite the many differences in the mechanisms.

METHODS

To test the relationship between body size and post-invasion geographical distribution we used 13 species of bivalves introduced to the north-eastern Pacific coast. This species pool excludes species introduced to this region for mariculture (Miller *et al.* 2002). For each introduced species we compiled body size, defined as the geometric mean of length and height (Roy *et al.* 2001), and the estimated year of first introduction along the north-eastern Pacific coast. For some species there is considerable uncertainty regarding the date of introduction, largely due to difficulties associated with species identifications. For example, estimates for *Mytilus galloprovincialis* vary between the late 1800s (Carlton 1992) and 1985 (Ruiz *et al.* 2000). For these species we ran separate analyses using the minimum and maximum estimated dates of introduction to test for the effects of such uncertainty. As the geographical distribution of introduced bivalves along the north-eastern Pacific coast is quite disjunct and often locally clumped, continuous measures of geographical range (such as latitudinal range) are not appropriate. We therefore categorized each introduced species as either widespread or narrow following Carlton (1992). We used multiple logistic regression to explore the effect of body size and date of introduction on the post-invasion geographical spread of these bivalve species. All size data were $\log_2$ transformed. A logistic likelihood ratio test was used to evaluate the significance of the relationships.

For the clade-based test we analysed the clade containing the largest number of non-indigenous species not intentionally introduced outside their native ranges for mariculture purposes (as defined by Miller *et al.* 2002), the family Mytilidae, to test for size-selectivity in present-day invasions. By our count there are 303 living shallow-water species, and we have been able to obtain size data for 299 of these (in addition to the database described in Roy *et al.* 2001 the data are from Barnard 1964; Oliver 1992, 1995; Poppe & Goto 1993; Rios 1994; Lamprell & Healy 1998; Okutani 2000; and many local records). Owing to limited information in the literature we used only shell length (maximum dimension in mm) but have found this to be an effective proxy for size comparisons within this taxon. We compared shell lengths of the indigenous mytilid species ($n = 292$) with the shell lengths of the non-indigenous mytilid species ($n = 7$), measured in their home ranges, i.e. prior to arrival in the new habitat, as listed in Roy *et al.* (2001) with the addition of *Perna viridis* (Ingrao *et al.* 2001; L = 120 mm, Lee & Morton 1985).

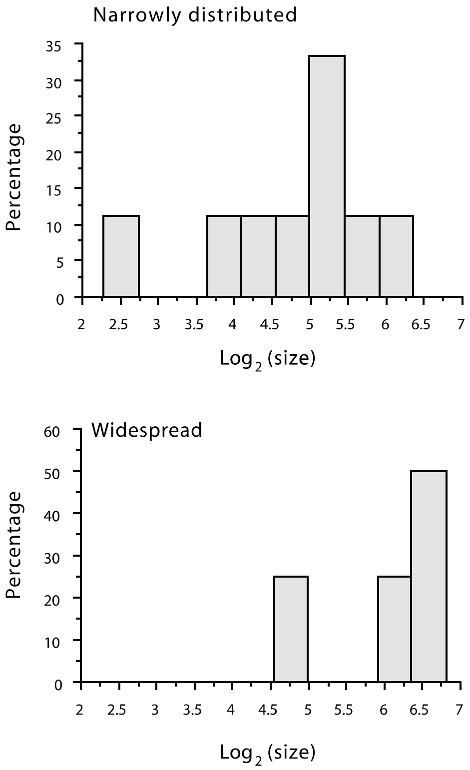

Figure 1 Frequency distributions of body sizes of north-eastern Pacific invasive marine bivalve species. The upper histogram represents species that are geographically restricted along the north-east Pacific coast, ($n = 9$) while the lower histogram represents species more widely distributed in their introduced range ($n = 4$) (see text for details).

Table 1 Results of logistic likelihood ratio tests. Full model is based on a multiple logistic regression with date of introduction and size as independent variables and distribution along the NE Pacific coast as dependent variable. Numbers in parenthesis represent results of analysis using the date of introduction from Ruiz *et al.* (2000) (see text for details)

	d.f.	Chi-Square	*P*-value
Full Model			
Date of introduction	1	0.053 (0.635)	0.81 (0.42)
Log_2 (size)	1	2.81 (4.0)	0.09 (0.04)
Only size			
Log_2 (size)	1	4.5	0.03

RESULTS AND DISCUSSION

The size-frequency distributions of narrow and widespread species of introduced bivalves in the north-eastern Pacific are shown in Fig. 1. This figure shows that widespread species are larger compared with narrowly distributed ones. This pattern is supported by a logistic likelihood ratio test based on the full model that shows that the date of introduction is not a significant predictor of geographical distribution but that body size is (Table 1). In fact, once the variable with no significant effect (i.e. date of introduction) is removed from the model, body size is a highly significant predictor of post-invasion spread of these species (Table 1).

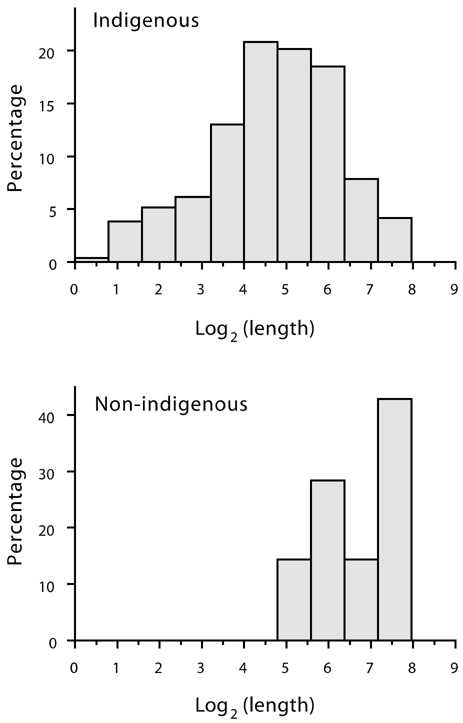

Figure 2 Frequency distributions of body sizes for non-mariculture, indigenous and non-indigenous species in the bivalve family Mytilidae. Above, species that are not found outside their native ranges ($n = 292$); below, species that have been introduced outside their native ranges through human activity ($n = 7$). The distributions are significantly different ($P = 0.001$, Mann–Whitney *U*-test); median $\log_2$ size for indigenous species is 4.8 units (28.5 mm) while that for non-indigenous species is 6.9 units (120 mm). These differences become even more pronounced if the ecologically specialized Lithophaginae are excluded (see text).

For the clade-level test the size-frequency distribution of the non-indigenous species of mytilids differs significantly from the rest of the living mytilid species (Mann–Whitney *U*-test, $P = 0.001$) (Fig. 2). The difference between the two size-frequency distributions is even more pronounced when members of the subfamily Lithophaginae, an ecologically specialized group of mytilids, are excluded from the analysis ($P = 0.0006$, Mann–Whitney *U*-test; median for indigenous species is 23.5 mm, 4.6 $\log_2$ units, $n = 251$; that for non-indigenous species is 120 mm, 6.9 units, $n = 7$). In fact, even if the most intensively cultured species that occur on our non-indigenous list, *Mytilus edulis* and *Perna perna*, actually did owe their expansion to intentional introductions, the differences are still significant when those species are omitted from the analysis ($P = 0.02$ with lithophagines, 0.01 without them). These results show that for mytilid bivalves, unintentional human introductions are preferentially expanding the geographical distributions of the larger species.

The lack of data on failed introductions makes it impossible to test whether (1) large-bodied mytilids are better at getting established outside their ranges or (2) the human introduction process is biased towards the larger species and small species are not associated with vectors such as ballast water. However, regardless of the actual process involved, these results, as well as those from the previous analysis, have important implications for the consequences of human introductions. In particular, biotic homogenization of the global biota resulting from human activities is a matter of increasing concern and such spatial homogenization can potentially be enhanced if the winning species are selective with respect to traits such as body size that can mediate susceptibility to extinction (Lockwood *et al.* 2000; McKinney & Lockwood 2001). Based on the above results we stand by our comment that the strikingly similar role of body size in both natural and human-mediated range shifts suggests that some of the same processes underlie the dynamics of the two systems, despite some very obvious differences in the mechanisms of introduction.

Body size has long been proposed as a trait potentially associated with colonization success, largely because life-history features that lead to faster population growth (e.g. fecundity, incubation time) tend to correlate with body size (Ehrlich 1989; Duncan *et al.* 2001). However, relatively few studies have statistically examined this relationship. For animal introductions, existing studies relating body size and invasion success are almost exclusively from terrestrial vertebrates and have produced mixed results. In part the different conclusions reflect differences in methodology. For example, some studies have compared the sizes of invasive species with the native species pool in the invaded region (e.g. Forys & Allen 1999), while others have compared body sizes of successful invaders with those that failed (Veltman *et al.* 1996; Duncan *et al.* 2001). In general, for terrestrial vertebrates size is either not a strong predictor of invasion success (Veltman *et al.* 1996 for bird introductions in New Zealand) or larger bodied species have a higher probability of introduction success (Duncan *et al.* 2001 for bird introductions in Australia). Duncan *et al.* (2001) also showed that for successful introductions smaller body size is related to larger geographical range in the introduced region, presumably due to the correlation between smaller body size and traits leading to faster population growth.

If parameters such as population growth rates are indeed important in determining invasion success, then a very important expectation is that small size would be associated with invasion success in terrestrial birds and mammals, but large size would be beneficial in the case of marine invertebrates. This important contrast stems from fundamental differences in life histories of vertebrates and marine invertebrates; fecundity and body size are positively related in marine bivalves (Jablonski 1996) but negatively so in birds and mammals (Peters 1983). In addition, a large native range is often considered to be a good predictor of invasion success (e.g. Lodge 1993) and in many marine bivalve lineages body size and latitudinal range are positively correlated (Roy, Jablonski & Valentine, unpublished observation). Thus, our results fit the pattern expected for marine bivalves and it is not surprising that data from birds or other terrestrial vertebrates may show a different trend.

Although our results reveal an important role of body size in mediating invasion success in marine bivalves, we do not claim that other factors are unimportant. A number of studies involving terrestrial animals have shown that factors such as introduction effort as well as climatic and habitat similarities between native and introduced ranges play important roles in determining invasion success (Veltman *et al.* 1996; Williamson 1996). We suspect that some of these factors are also important in marine invasions (see Ruiz *et al.* 2000; Miller *et al.* 2002). However, the lack of data on introduction efforts, as well as instances of failed invasions in marine and estuarine habitats, makes it difficult to evaluate their relative importance. Furthermore, while our results suggest that larger bivalves are better at colonizing new habitats in their introduced range, how they achieve these distributions remains an open question. Coastal oceanographic processes, as well as larval durations, may be important determinants of the post-invasion spread of marine invertebrate species but explicit tests of such hypotheses are currently lacking (Grosholz 1996).

Thus while we agree with Miller *et al.* (2002) that natural range expansions of species and human-mediated introductions are analogous but not identical, our further analyses reinforce our suggestion that traits associated with larger body sizes have conferred advantages on invaders in both cases. Large-bodied bivalve species had more fluid ranges during Pleistocene climate changes and, among non-mariculture introductions, larger-bodied invasive species achieve wider distributions than smaller species. In terms of long-term consequences, geographically widespread species tend to resist extinction better than narrowly ranging forms (Jablonski 1987), hence over the long-term the larger-bodied bivalves, introduced accidentally as well as through mariculture, may also be better able to persist in their introduced ranges compared with smaller native species.

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