

LETTER

Biological invasions drive size increases in marine and estuarine invertebrates

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Abstract

Ecologists have long been fascinated by the morphological changes that species frequently undergo when introduced into new regions. In this study an unusual pattern of size change associated with the invasion of 19 species of marine and estuarine invertebrates is reported. The results show that the majority of species are significantly larger in the introduced range compared with the native range with little evidence for any decrease in size following invasion. This invasion-driven increase in body size sharply contrasts with the pattern observed in many other taxa including plants, mammals and lizards, where invaders frequently exhibit post-invasion decreases and increases in size. These size changes were not influenced by differences in latitude, sample size or length of time since invasion. Although several mechanisms, may explain the results, none have been demonstrated.

Keywords

Biological invasions, body size, climate change, extinction, fossil record, introduced species, marine invertebrates, range expansion.

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INTRODUCTION

The impacts of biological invasions upon native ecosystems and human economies are now widely appreciated (Chapin *et al.* 2000; Sala *et al.* 2000). However, much less is known about the consequences of biological invasions for the invading species itself (Ruiz *et al.* 1997, 1999; Grosholz 2002). Species introduced into a new region frequently undergo changes in size and shape relative to their native range, which can strongly influence the magnitude of the impacts of the invader. Size changes that have occurred as the result of recent human-mediated introductions have been best described for plants. In a study of European plants introduced into California, Crawley (1987) found that many (43%) species were larger in California compared with their native European range – a substantial number of species (28%) got smaller, while the rest remained unchanged. A recent re-analysis using more extensive data found that 35% of European plants got larger in California and 29% got smaller (Thébaud & Simberloff 2001). These comparative studies have been accompanied by several common garden experiments, whose aim was to determine if size changes in invading plants had a genetic basis, but whose conclusions were notably conflicting (Blossey & Nötzold 1995; Willis *et al.* 2000; Maron & Vila 2001;

Siemann & Rogers 2001; Thébaud & Simberloff 2001; Leger & Rice 2003).

For other taxa, there are no similarly comprehensive summaries, although there are many examples of invading species getting both larger and smaller in the introduced range. These include studies of lizards (Losos *et al.* 1997), mammals (Dayan & Simberloff 1994; Simbloff *et al.* 2000) and birds (Johnston & Selander 1973), and also studies that have demonstrated strong latitudinal clines in size that have occurred since the initial invasion (Weber & Schmid 1998; Yom-Tov *et al.* 1999; Huey *et al.* 2000). The overall conclusion from these studies is that size responds variably to introduction: some species get larger, some get smaller and some remain unchanged. These patterns seen in modern invasions are similar to patterns of size change witnessed in historical colonization of islands by species from mainland sources. There have been comprehensive studies of the patterns of size change for lizards, birds and mammals showing that species colonizing islands are frequently either smaller or larger than their mainland ancestors (Foster 1964; Schoener 1969; Van Valen 1973; Lomolino 1985).

In contrast to these results for other taxa, in this study we demonstrate that introduced marine (including estuarine) invertebrates show a significant directional pattern,

becoming larger in the introduced range compared with the native range. Using the existing literature to include a broad range of invertebrate taxa from several phyla, it was found that the majority of species (63%) are larger in the introduced range relative to the native range with little evidence for any species getting smaller in association with invasion.

MATERIALS AND METHODS

We examined patterns of body size change in introduced marine invertebrates by compiling available records from the primary literature together with unpublished data. Using a set of restrictive criteria (see 'Criteria for analysis' below), we found sufficient data for 19 introduced species representing four classes in three phyla (Table 1). We investigated whether there were differences in body size between the invaded and native ranges for introduced marine and estuarine invertebrates at two different levels. The first level involved comparisons across all 19 species for which sufficient data were available for both native and introduced ranges. Species were assigned to either one of the three categories: (1) larger in the introduced range, (2) smaller in

the introduced range or (3) unchanged in the introduced range relative to the native range. If the difference between native and introduced populations was 5% or less, it was scored as unchanged (see Lomolino 1985). For each species, the maximum size reported for each population was used to calculate mean maximum size (MMS) for both native and introduced ranges. There were compelling reasons for this choice of metric (see 'Metrics for analysis' below).

We conducted the analysis at the species level by comparing MMS separately for native and introduced populations for each species. Thus, the power of the analysis is a function of the number of species and not the number of populations used to calculate a particular mean. The results are not dependent on the use of means and similar results would have been produced using median maximum size. Recent studies have also used this approach for statistically comparing native and introduced populations for multiple species, in some cases using only a single summary statistic for either native or introduced populations (Mitchell & Power 2003; Torchin *et al.* 2003).

For a subset of species where we were able to gather sufficient data, both simple and multiple regression analyses

Table 1 Description of regions, latitude range, sample size and date of introduction for species used in analyses. Range abbreviations refer to geographical regions as follows: north-west Pacific Ocean (NWP), north-east Pacific Ocean (NEP), south-west Pacific Ocean (SWP), north-east Atlantic Ocean (NEA), south-east Atlantic Ocean (SEA), south-west Atlantic Ocean (SWA), northern Gulf of Mexico (NGM)

Taxon	Native range	Introduced range	Native/introduced latitude range	Native/introduced sample size (No. of populations)	Date of introduction
Asteroids (seastars)					
<i>Asterias amurensis</i>	NWP	SWP	35–41°N/42°S	>50 (5)/>50 (1)	1986
Decapod crustaceans (crabs)					
<i>Carcinus maenas</i>	NEA	NWA, NEP, NWP, SEA	39–60°N/38–46°N	100–8461 (17)/219–21 000 (7)	1945–1998
<i>Eriocheir sinensis</i>	NWP	NEA, NEP	35°N/39–52°N	>50 (1)/>50–200 (5)	1935–1992
<i>Hemigrapsus sanguineus</i>	NWP	NWA	33–40°N/39–41°N	>50 (3)/>50–325 (4)	1987–1994
<i>Rhithropanopeus harrisi</i>	NWA	NEP	38°N/38–54°N	>50 (2)/>50–1192 (3)	1937–1971
Bivalve molluscs (clams and mussels)					
<i>Gemma gemma</i>	NWA	NEP	39–41°N/38°N	>50 (2)/>50–75 (2)	1893–1930
<i>Geukensia demissa</i>	NWA	NEP	34–37°N/35°N	>50 (4)/>50 (1)	1955
<i>Macoma petalum</i>	NWA	NEP	33–47°N/38°N	>50–2504 (7)/>50 (1)	1870
<i>Mercenaria mercenaria</i>	NWA	NEA	33–46°N/51°N	150–465 (2)/1243 (1)	1925
<i>Musculista senhousia</i>	NWP	NEP	35°N/34°N	>50–465 (1)/1243–3379 (2)	1976
<i>Mya arenaria</i>	NWA	NEP	43–44°N/38–59°N	>50 (3)/>50 (6)	1874–1888
<i>Mytilus galloprovincialis</i>	NEA	NEP	41°N/30–39°N	28 485 (1)/>50–140 (5)	1920–1984
<i>Perna perna</i>	SWA, SEA	NGM	28–35°S/26–27°N	>50 (2)/>50 (2)	1990
<i>Venerupis philippinarum</i>	NWP	NEP	35–42°N/21–52°N	>50–3103 (2)/>50 (2)	1950–1977
Gastropod molluscs (snails)					
<i>Batillaria attrimentaria</i>	NWP	NEP	33°N/38°N	378 (1)/>50–116 (2)	1941–1955
<i>Ilyanassa obsoleta</i>	NWA	NEP	38–41°N/38°N	>50–593 (2)/>50 (1)	1907
<i>Littorina saxatilis</i>	NWA	NEP	41°N/38°N	>50 (2)/404 (2)	1993
<i>Rapana venosa</i>	NWP	NWA	42°N/38°N	>50 (1)/>50 (2)	1996
<i>Urosalpinx cinerea</i>	NWA	NEA, NEP	37–39°N/38–51°N	>50–30 000 (11)/1700 (2)	1900–1927

were used to quantify the relationship of the difference in MMS between native and introduced populations and three independent variables: (1) difference in latitude between the native and introduced populations, (2) sample size for native and introduced populations, and (3) the invasion period for introduced populations. We expressed difference in latitude as the mean latitude for introduced populations of a certain species minus the mean latitude for native populations for that species. Therefore, a positive latitude increase means that the introduced populations are resident at higher latitudes than native populations. Differences in sample size are expressed as the percentage difference of native populations minus introduced populations of the same species and invasion period as the number of years from the time the invasion had first been reported to the time when the data were collected. This latter variable could only be used in simple regressions, because there are no values for native species.

The second level of analysis involved comparisons of native and introduced populations of the European green crab (*Carcinus maenas*) using data from 17 native populations (north-western Europe) and seven introduced populations (eastern and western North America, southern Australia). The MMS between native and introduced regions were compared by using simple and multiple regression of MMS for native or introduced populations against latitude, sample size and invasion period.

Criteria for analysis

For a species to be included in this analysis, the following criteria must be fulfilled: (1) a clear description of how body size was measured (e.g. carapace width, shell length); (2) some estimate of size distribution for more than one population in either the introduced and native ranges; (3) a minimum sample size of 50 individuals, and (4) certainty of the non-native status and the approximate date of introduction. Unpublished data must be verifiable by the authors.

Metrics for analysis

There were several compelling reasons for choosing MMS to analyse body size: (1) means, medians, upper quartiles and other metrics could not be obtained for many species because many size frequency plots had no sample size information, (2) seasonal juveniles recruitment could substantially skew mean and median values (although not quartiles), (3) although MMS varies with sample size, for species where we had substantial data, we found that the largest individual was closely correlated with the mean for that population (e.g. $r = 0.54$, $P = 0.0015$ for 17 populations of green crabs), (4) we explicitly addressed sample size for a subset of species in our analyses and found that large sample size did not statistically influence the results,

(5) maximum size has been frequently used in palaeontological studies of the effects of body size in marine invertebrates (Roy *et al.* 1996, 2001). To examine a possible asymptotic relationship between sample size and MMS, several models were fit to these data with $y = y_0 + a(1 - b^x)$ providing the best fit. Statistical analyses for all the above tests were performed with SAS 8.0 (SAS Institute, Inc., Cary, NC, USA) or with Systat 9.0 (SPSS, Inc.).

RESULTS

From the analysis of all 19 invertebrate species, it was found that 12 species (63%) had significantly greater MMS in the introduced range relative to the native range (G -test = 10.12, $P < 0.01$; Fig. 1). There was no evidence for a significant decrease in MMS with the exception of the smallest species in the data set, the gem clam *Gemma gemma* (4.6 mm introduced range, 5.0 mm native range). This difference of 0.4 mm is less than the unit of measurement (mm) for all other species suggesting that the difference is within the range (and a possible artefact) of measurement error. We also found no significant effects of latitude, invasion period, and sample size on differences in MMS between native and introduced ranges for the 19 species (latitude $y = 0.401x + 13.68$, $R^2 = 0.024$, $P = 0.55$, $n = 17$; invasion period $y = -0.0735x - 129.95$, $R^2 = 0.028$, $P = 0.49$, $n = 19$; sample size $y = 0.0036x + 8.74$, $R^2 = 0.252$, $P = 0.14$, $n = 10$). The multiple regression of latitude and sample size on differences in MMS yielded similar results (for latitude: partial correlation = 0.29, $F = 0.071$, $P = 0.79$; for sample size: partial correlation = -0.002, $F = 0.001$, $P = 0.97$). We found no significant differences in latitude (Wilcoxon $Z = -0.59$, $P = 0.55$) and sample size ($Z = -0.50$, $P = 0.61$) for populations in the native vs. introduced range.

For the European green crab, there was a highly significant difference between the MMS of introduced populations (92.1 ± 7.98 mm) and native populations (77.8 ± 7.33 mm) (Student's $t = -4.07$, d.f. = 21, $P = 0.0005$; Fig. 2). We did find a significant effect of latitude on MMS with introduced populations at lower latitude than native populations (Fig. 2) (latitude $y = -0.683x + 116.7$, $R^2 = 0.202$, $P = 0.028$; latitude of introduced vs. native populations, Mann-Whitney $U = 113.0$, $P = 0.001$). However, there were no significant effects of sample size on MMS for either native or introduced populations of green crabs or when native and introduced populations were pooled ($R^2 = 0.08$, $P = 0.16$). In the multiple regression, the influence of latitude and sample size yielded similar results with respect to MMS for green crabs (for latitude: partial correlation = -0.42, $F = 6.69$, $P = 0.01$; for sample size: partial correlation = -0.01, $F = 0.56$, $P = 0.46$). For European green crabs, there were no significant differences in sample sizes used to calculate

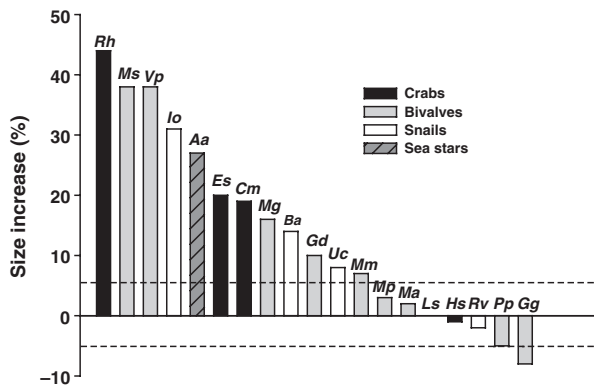


Figure 1 The magnitude of size differences between introduced and native populations of 19 introduced marine and estuarine species. Dashed lines indicate the 5% level for determining if size changes were 'significant'. Taxonomic species grouping with species are listed alphabetically by abbreviation within taxon: Crabs (Crustacea: Decapoda: Brachyura): *Cm*, *Carcinus maenas*; *Es*, *Eriocheir sinensis*; *Hs*, *Hemigrapsus sanguineus*; *Rb*, *Rhithropanopeus harrisi*; Bivalves (Mollusca: Bivalvia): *Gd*, *Geukensia demissa*; *Gg*, *Gemma gemma*; *Ma*, *Mya arenaria*; *Mg*, *Mytilus galloprovincialis*; *Mm*, *Mercenaria mercenaria*; *Mp*, *Macoma petalum*; *Ms*, *Musculista senhousia*; *Vp*, *Venerupis philippinarum*; Snails (Mollusca: Gastropoda): *Ba*, *Batillaria attramentaria*; *Io*, *Ilyanassa obsoleta*; *Pp*, *Perna perna*; *Rv*, *Repana venosa*; *Uc*, *Urosalpinx cinerea*; Sea Stars (Echinodermata: Asteroidea): *Aa*, *Asterias amurensis*.

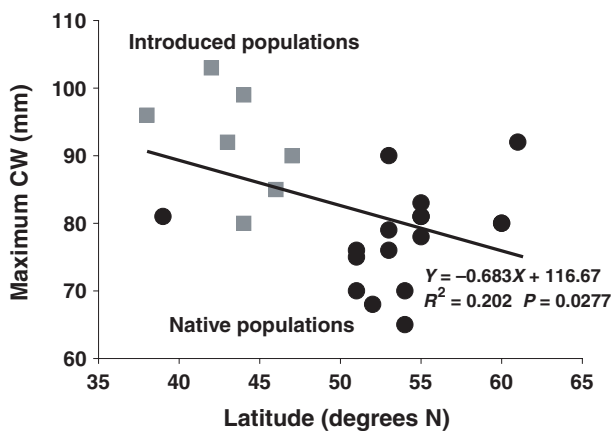


Figure 2 The body size (maximum carapace width in millimetre) of European green crabs from both native and introduced populations vs. latitude of population. Each point represents a single population in the native range (black circles) or the introduced populations (grey squares). Regression statistics include all points (native and introduced) and are based on an ordinary least squares (OLS) model.

MMS for native (3861 ± 4990 , range 219–21 000) vs. introduced populations (3874 ± 3291 , range 100–8461) of European green crabs (Mann–Whitney $U = 67.0$, $P = 0.634$). We also found no significant effect of invasion

period ($y = -0.049x - 2.02$, $P = 0.11$) for the introduced populations and this relationship was not improved by adding either sample size or latitude as additional independent variables.

DISCUSSION

We found a consistent pattern of increased body size in the introduced range for invading marine invertebrates with the majority of species getting larger (63%) and the rest remaining unchanged with little evidence of size decrease. This pattern contrasts that for other taxa where both decreases and increases in size following invasion have been demonstrated. For instance, the data for plants European plants invading California suggest that nearly 30% of invading species got smaller in the introduced range. As our data include multiple phyla covering a range of morphologies, life histories, trophic positions, and geographical source and recipient regions, we suggest that our results are likely to be robust for marine invertebrates. However, the conclusions should be viewed with some caution, because the analyses are limited to the data available for 19 species, and in some cases there is data for only one population in either the native or introduced ranges. The analysis will inspire future investigations of size change in marine invertebrates including experimental investigations of underlying mechanisms.

No significant influence of latitude, sample size or invasion period on size differences were found between populations in the native range relative to the introduced range. Latitude and invasion period explain <5% of the variance and are highly non-significant. However, for the European green crab, a significant relationship was found between latitude and MMS (Fig. 2). The results of the present study are contrary to Bergmann's rule for ectotherms (Atkinson 1994; Atkinson & Sibly 1997): introduced populations of *Carcinus* generally and systematically occurred at lower latitudes and had larger MMS.

Several mechanisms, operating alone or in combination, may explain the observed size increases. First, greater resources in the introduced range relative to the native range could translate into faster growth and larger body size. Second, the absence of predators or parasites in the introduced range could also result in larger body size (Torchin *et al.* 2001, 2003; Mitchell & Power 2003). Third, size increases or shifts could result from sampling effects. Within a species, both the sampling associated with transfers and founder effects may result in substantively different genetic structure between invading and native populations. Although this is a viable explanation for individual species, sampling effects could not readily explain the overall directional pattern, because such within-species sampling appears equally probable to produce size decreases and size increases.

Simons (2003) suggested that the invasion process itself may be selective across species, whereby those species that would exhibit 'increased vigour' in a new territory are more likely to colonize than those that would exhibit 'reduced vigour'. It is unclear whether such sampling bias has occurred across species, selecting for species with 'increased vigour', or whether this is a general phenomenon associated with invasions. In either case, such explanation does not provide insight into the underlying biological mechanism(s) for increased vigour and the traits in which this is manifest.

More broadly, our results also address recent studies of historical range expansions of marine invertebrates in the fossil record, occurring in response to climate change and extinctions (Roy *et al.* 1996; Jablonski 1998; Roy *et al.* 2000; Hellberg *et al.* 2001). These studies have found significant morphological change, including size increases, associated with range expansions by molluscs (Roy *et al.* 2000; Hellberg *et al.* 2001). Our findings from modern invasions support the idea that size increase may often follow range expansions of marine invertebrates and can result from rapid phenotypic change during the early stages of colonization. Our results also provide an alternative to suggestions by authors studying post-Pleistocene range expansions (Roy *et al.* 2001, 2002) that larger species were more likely to successfully colonize new regions. Rather than larger species being more successful colonists, which is not evident in some modern marine assemblages (Miller *et al.* 2002), species may increase in size after colonization. In summary, processes underlying size changes in modern invasions may also contribute to the patterns witnessed in historical range expansions following major extinction and climatic events.

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