

REPORT

Climate change, species range limits and body size in marine bivalves

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Abstract

We use data on the Pleistocene and modern range limits of Californian marine bivalves to show that species that shifted their geographical ranges in response to Pleistocene climatic fluctuations were preferentially drawn from the large end of the regional body size–frequency distributions. This difference is not due to phylogenetic effects (i.e. dominance of extralimital species by a few large-bodied clades), differences among major ecological categories (burrowing *versus* surface-dwelling, or suspension feeding *versus* non-suspension feeding), or differences in modes of reproduction and larval development. In addition, we show that successful invasive species of bivalves in present-day marine habitats also tend to be large-bodied, despite the difference in mechanisms between present-day and Pleistocene range expansions. These results indicate that range limits of large-bodied bivalve species are more unstable than small-bodied ones, and that body size and its correlates need to be considered when attempting to predict the responses of marine communities to climate change, biotic interchanges and human-mediated invasions.

Keywords

Body size, range limit, marine bivalves, California, Pleistocene, invasive species.

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INTRODUCTION

Understanding how species and communities respond to changing climates is essential for predicting the biological consequences of regional and global environmental change (Davis *et al.* 1998). One potential approach to this problem draws on the fossil record of range extensions and local extinctions in response to Pleistocene glacial-interglacial cycles, well-documented in groups ranging from terrestrial plants, mammals and insects to marine mollusks and fishes (Valentine & Jablonski 1993; Elias 1994; FAUNMAP 1996; Roy *et al.* 1996; Jackson *et al.* 2000). This record can be used to pinpoint ecological or life history traits that impose or permit greater variability in geographical ranges of some species relative to others in the same community, an important consideration for the stability of ecologically and economically important species associations.

Body size influences almost every aspect of the biology of a species, from physiology to life history (Peters 1983; Calder 1984; Brown 1995), but relatively little is known about how this trait affects species' responses to climate change, particularly in marine organisms. Here we compare

Pleistocene and Recent bivalve faunas of the Californian region to show that species exhibiting climate-driven changes in their range limits represent a nonrandom sample of the Pleistocene assemblage in terms of body size: large-bodied bivalve species are significantly over-represented among those that shifted their geographical ranges in response to glacial-interglacial cycles. Similar size-selectivity is also seen for present-day invasive species, suggesting that Pleistocene range dynamics can provide insights and perhaps predictions for human-mediated biotic interchanges as well.

METHODS

The bivalve fauna of California is one of the best-studied in the world (Coan *et al.* 2000) and this region also contains extensive fossiliferous marine Pleistocene terrace deposits that preserve over 80% of the living bivalve species (Valentine 1989). These assemblages thus provide an excellent system for quantifying the biogeographical behaviour of marine invertebrate species during past climatic fluctuations (Roy *et al.* 1996). We compiled a database of middle and late Pleistocene occurrences of 216 living bivalve

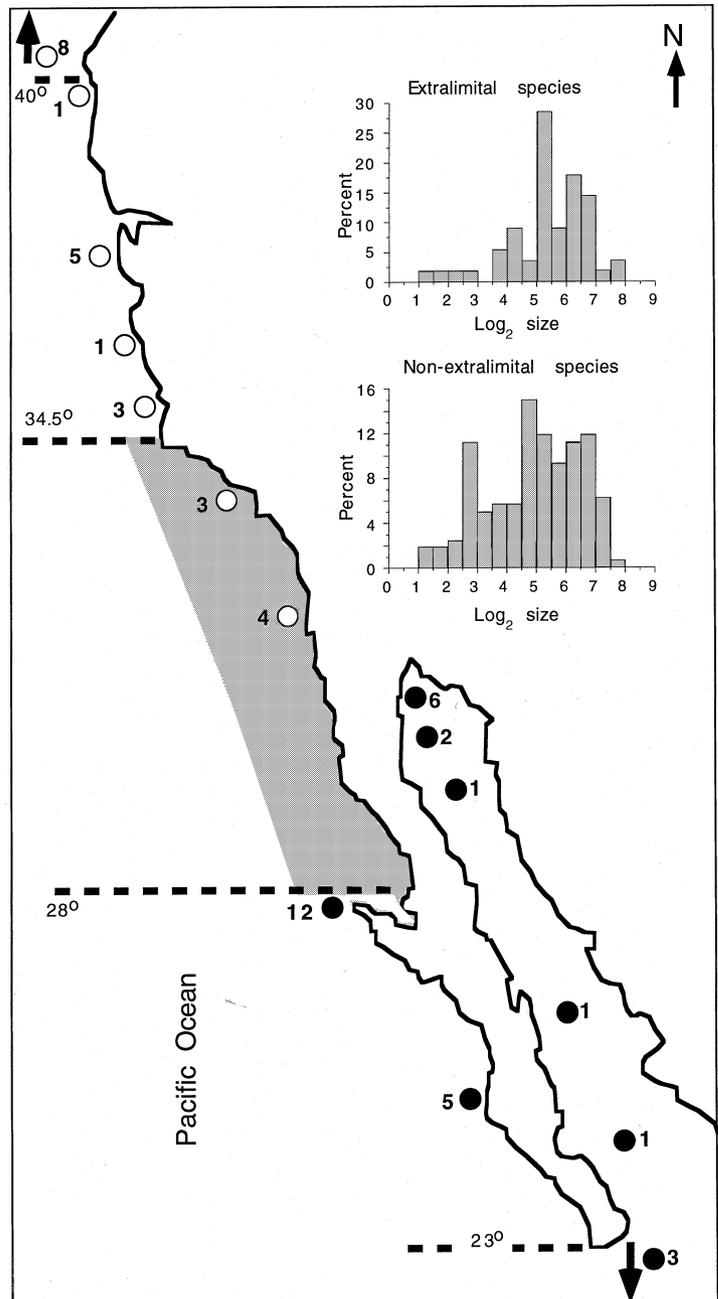
species within this region, and compared the Pleistocene occurrences of each species to its present distribution using the database described in Roy *et al.* (2000a). A species was categorized as extralimital if its Pleistocene occurrence fell outside its present-day range limit by at least one degree of latitude (Fig. 1). This definition provides only a minimum estimate of the number of species that exhibited range shifts involving local extinctions, but is robust to sampling and preservational biases since it is based on Pleistocene

co-occurrences of species whose ranges are disjunct today (Roy *et al.* 1995).

RESULTS AND DISCUSSION

While all 216 species in our Pleistocene dataset still live somewhere along the north-eastern Pacific shelf, 56 (26%) are extralimital (i.e. locally extinct) in the Californian region (Fig. 1). Because our data are from both glacial and

Figure 1 Approximate positions of present-day range limits of the extralimital bivalve species. Extralimital species are those whose Pleistocene occurrences within the California region (shaded area) fall at least 1° of latitude outside of their present-day range limits. The open circles represent the present-day southern range limit of northern extralimital species while the filled circles mark the present-day northern range limit for southern extralimitals. The number beside each circle represents the number of species whose ranges end near that point. The inset shows the size–frequency distributions of the extralimital *versus* nonextralimital bivalve species. Body size is defined as the geometric mean of the length and height (in mm) of the largest reported specimen for each species, following Jablonski (1996). The size data were log₂-transformed following Brown (1995) and Roy *et al.* (2000b). The distributions are significantly different ($P = 0.01$, Kolmogorov-Smirnov test).



interglacial deposits, both northern and southern extralimital species are represented, although the record is biased in favour of interglacials (Valentine & Meade 1961). The size–frequency distribution of the extralimital species differs significantly from the rest of the Pleistocene species pool, with extralimital species drawn preferentially from the larger sizes ($P = 0.01$, Kolmogorov–Smirnov test, Fig. 1). These results are not due to over-representation of a few large-bodied clades among the extralimitals. The extralimital species belong to 27 families, which coincides with the random expectation of 27 ± 4 families (95% confidence interval based on 1000 iterations) when 56 species are drawn without replacement from the total pool of Pleistocene species. Neither do the larger body sizes of extralimitals reflect any differences in general life habit. For the two broad ecological categories that typify most marine bivalves, those that live on the sediment surface (epifaunal) and those that burrow (infaunal), the infaunal–epifaunal ratio among the extralimital species is not significantly different from that of the nonextralimital species ($P > 0.1$, G -test; Sokal & Rohlf 1995). Similarly, in terms of feeding mode, suspension feeding bivalves make up 75% of the extralimital species and 83% of the nonextralimital species, a difference that is not significant ($P > 0.1$, G -test).

The discordance between Pleistocene and Recent range limits can result from two fundamentally different biogeographic processes, vicariance or dispersal, and the relative role of each of these processes is debated. In the vicariant model, local extinction in response to environmental changes leads to the shrinkage of a formerly more extensive range (Lindberg & Lipps 1996). The alternative is that these local extinctions do not record secular shifts in distributions but reflect climatically driven oscillations in species range limits (Roy *et al.* 1995) similar to changes in abundance recorded on shorter timescales (Sagarin *et al.* 1999). If range fluctuations rather than secular changes in range limits are the norm in the Pleistocene then our data suggest that on a spatial matrix of shifting environmental conditions, large marine bivalves are better at exploiting favourable habitats. Time series for the occupation of particular sites during repeated glacial/interglacial cycles remain too sparsely sampled to test this directly, but this hypothesis can be tested using data from modern ecosystems since it implies that size should also play an important role in the success of invasive species in marine habitats.

To test the general relationship between body size and range changes in marine bivalves, we compiled body-size data for the 25 invasive species of northern hemisphere marine bivalves that are known to have become well established outside their native ranges (Carlton 1992, 1999; Table 1). A comparison of the size–frequency distribution of these introduced species with that of the native marine bivalves of the north-eastern Pacific shelf suggests that

Table 1 Introduced species of bivalves and their respective body sizes (in mm) used in this study. List of taxa compiled from Carlton (1992, 1999). Size data compiled from the literature (sources available from the authors)

Taxon	Length	Height
<i>Mytilus galloprovincialis</i>	150	80
<i>Ostrea edulis</i>	170	141
<i>Corbula gibba</i>	15	12.5
<i>Geukensia demissa</i>	100	39
<i>Mytilopsis leucophaeata</i>	20	8
<i>Crassostrea virginica</i>	200	139
<i>Argopecten irradians</i>	70	70
<i>Mya arenaria</i>	150	84
<i>Ensis directus</i>	150	30
<i>Macoma balthica</i>	45	37
<i>Petricolaria pholadiformis</i>	71	25
<i>Mercenaria mercenaria</i>	150	138
<i>Gemma gemma</i>	5	4.7
<i>Mytilus edulis</i>	115	56
<i>Musculista senhousia</i>	35	18
<i>Crassostrea gigas</i>	450	260
<i>Potamocorbula amurensis</i>	28	19
<i>Nuttallia obscurata</i>	57	44
<i>Theora lubrica</i>	20	12
<i>Venerupis philippinarum</i>	70	54
<i>Neotrapezium liratum</i>	53	25
<i>Laternula marilina</i>	40	22
<i>Perna perna</i>	170	85
<i>Mytella charruana</i>	50	22
<i>Rangia cuneata</i>	63	44

successful bivalve invaders in present-day marine habitats are also predominantly large-bodied (Fig. 2), despite the very different dispersal mechanisms behind these human-mediated range expansions. Whether the subsequent spread and establishment of introduced species in present-day and ancient communities represent similar processes in the two systems is an intriguing question for which data are presently unavailable.

Data on both fossil and living bivalves do not suggest any direct role for the mode of reproduction and larval development in the size-related pattern reported here. In marine mollusks, brooding is associated with small body size, although exceptions are well known and no absolute size threshold exists across taxa (see Sellmer 1967; Strathmann & Strathmann 1982; Jablonski & Lutz 1983; Strathmann 1985; Levin & Bridges 1995; Pechenik 1999). This absence or reduction in larval dispersal might in principle curtail the colonization potential of small-bodied bivalves. However, such brooders tend to fall well below the modal size in the frequency distributions shown in Figs 1 and 2, so that our analyses are heavily dominated by comparisons within the single broad category of relatively

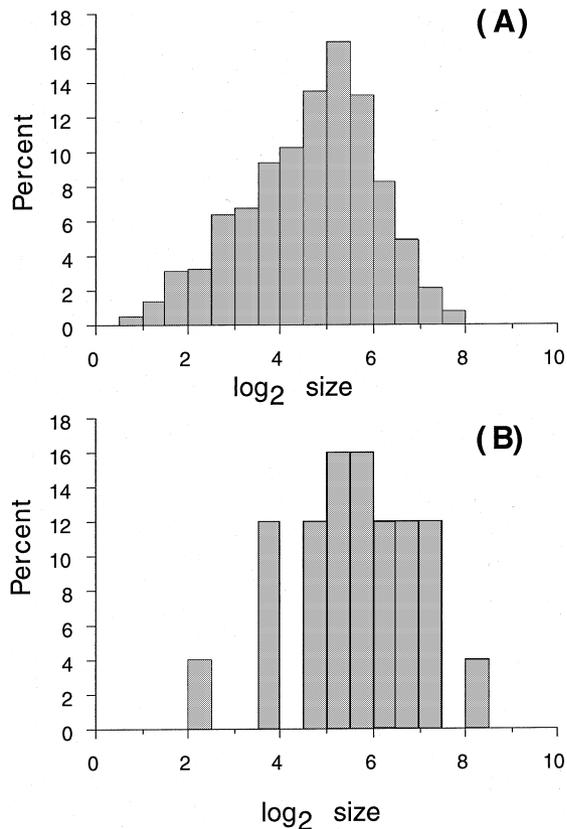


Figure 2 Comparison of the size–frequency distributions of 914 species of native north-eastern Pacific marine bivalves (A) and 25 species of introduced marine bivalves that have become successfully established in the northern hemisphere (B). The distributions are significantly different ($P = 0.013$, Kolmogorov–Smirnov test) with the introduced species being larger (median \log_2 size for native species is 4.8 units while that for the introduced species is 5.7 units). Data for (A) are from Roy *et al.* (2000b) and those for (B) were compiled through a literature search (sources available from the authors).

high-dispersal, planktotrophic development. Furthermore, very small brooding bivalve species are also capable of long-distance colonization, arguably because the small adult size facilitates rafting, and the brooding habit promotes retention of offspring in favourable habitats and successful fertilization of gametes in subsequent generations of colonists. Examples include *Gemma gemma* (Sellmer 1967), *Gaimardia trapetina* (Helmuth *et al.* 1994) and *Lasaea* spp. (O Foighil & Jozefowicz 1999). Our analyses included the first of these species, but suggest that these brooders and small-bodied larval broadcasters play a lesser role than large-bodied forms when statistical analyses of entire faunas are performed.

Thus our combined results for living and fossil biotas show that for marine bivalves, range limits of large-bodied species are less stable than the limits of small-bodied

species, irrespective of clade membership or general life habit. While body size can change locally in response to climate change (Smith *et al.* 1995; Chiba 1998; Hadly *et al.* 1998), ours is the first demonstration that it can also determine the tendency for marine species to invade and/or become locally extinct. The processes underlying this unexpected role for body size remain unclear. Species range limits are determined by complex interactions between environmental gradients and biotic factors such as population size and dispersal rates (Davis *et al.* 1998; Case & Taper, 2000) many of which correlate with body size (Peters 1983; Brown 1995). The sign or strength of the correlations may differ between marine and terrestrial clades, however; for example, fecundity is a positive function of body size in marine bivalves (Jablonski 1996) in contrast to terrestrial mammals and birds (Peters 1983). Whatever the causal mechanism, our results suggest that body size and its life-history correlates need to be incorporated into models attempting to predict the responses of marine ecosystems, reserves and fisheries to global warming, as well as in studies of invasion biology.

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BIOSKETCH

Kaustuv Roy's research interests include macroecology, biogeography, palaeoecology and marine conservation biology.

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