

From Europe to America: Pliocene to Recent trans-Atlantic expansion of cold-water North Atlantic molluscs

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Data on the geographical distribution, phylogeny and fossil record of cool-temperate North Atlantic shell-bearing molluscs that live in waters shallower than 100 m depth belong to two biogeographic provinces, one in eastern North America north of Cape Cod, the other in northern Europe. Amphi-Atlantic species, which are found in both provinces, comprise 30.8% of the 402 species in the northeastern Atlantic and 47.3% of the 262 species in the northwestern Atlantic. Some 54.8% of these amphi-Atlantic species have phylogenetic origins in the North Pacific. Comparisons among fossil Atlantic faunas show that amphi-Atlantic distributions became established in the Middle Pliocene (about 3.5 million years ago), and that all represent westward expansions of European taxa to North America. No American taxa spread eastward to Europe without human assistance. These results are in accord with previous phylogeographic studies among populations within several amphi-Atlantic species. Explanations for the unidirectional expansion of species across the Atlantic remain uncertain, but may include smaller size and greater prior extinction of the North American as compared to the European fauna and biased transport mechanisms. Destruction of the European source fauna may jeopardize faunas on both sides of the Atlantic.

Keywords: invasion; Atlantic; molluscs; biogeography

1. INTRODUCTION

An important emerging issue in biogeography and conservation biology is the degree of connection among the biotas of different regions. Protecting and managing geographically widespread species requires knowledge not only of where species occur, but where self-sustaining populations are found. If source populations are endangered, the species as a whole becomes vulnerable to precipitous decline and perhaps extinction. Policies in effect in one region therefore have repercussions in other regions as well. It is therefore important to identify where source areas exist, or have existed in the past, and to ascertain what makes some regions more likely to act as sources of immigrants than others.

An effective but under-used approach to answering these questions is to analyse patterns of spread in species for which reliable data on past distributions are available. It is well known that the limits of range of species have changed over the roughly 250 years during which living species have received scientific study. Reid (1996), for example, documents the northerly shift in the southern range limits of the gastropod *Littorina littorea* (Linnaeus) in Europe. Over longer time intervals of thousands to millions of years, the dynamic nature of range limits becomes even more apparent, as chronicled by discoveries of fossil representatives in areas where members of the same species do not occur today. Some parts of a species's range are vacated, only to be colonized again from populations elsewhere. Information about past distributions can therefore be used to identify source regions for recolonizing species or for species that expand into areas never previously occupied by them.

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Earlier studies have shown that movements of species across barriers between neighbouring regions are surprisingly unidirectional, with one region acting as the source or donor and the other acting mainly as the recipient region (Vermeij 1991a, 2005). These highly asymmetrical patterns of spread can arise for one or more of the following four reasons: (i) the donor biota is home to competitively, defensively, or reproductively more vigorous species; (ii) the donor biota is larger or more productive than the recipient biota and therefore 'exports' larger numbers of individuals; (iii) currents and organisms that carry potential colonists largely travel from the donor to the recipient region and (iv) prior extinction eliminated more species, and therefore provided greater opportunity for the establishment of newly arrived species in the absence of well adapted incumbents, in the recipient biota than in the donor biota.

This paper explores how, when and to what extent biogeographic connections between the northeastern and northwestern shallow-water Atlantic marine molluscan faunas were established. With a combination of taxonomic, phylogenetic and stratigraphic data, I show that species achieved distributions on both sides of the cool-temperate North Atlantic beginning in Middle Pliocene time, some 3.5 million years ago; and that the chief donor regions for these species are the northeastern Atlantic and the North Pacific. Cool-temperate eastern North America therefore served as the recipient region for those species that are or were found on both sides of the North Atlantic.

2. BACKGROUND

The present study concerns shell-bearing molluscs in shallow water (from shore to a depth of 100 m) in the

cool-temperate North Atlantic. The cool-temperate fauna occurs in two distinct, separated regions: the northeastern Atlantic (extending from the Lofoten Islands of Norway to northern Scotland and to about 60° N latitude in Norway) and the northwestern Atlantic (extending from the Straits of Belle Isle in Newfoundland in the north to Cape Cod, Massachusetts, in the south). Many cool-temperate species extend south of these limits as well as northward into the Arctic. Many also extend to deeper water. I exclude exclusively polar, deep-water and warm-water species from the present analysis, but I do include species that are occasionally found in shallow water even if their chief distribution is in waters greater than 100 m in depth. This latter category includes many species that in the western Atlantic occur only at bathyal depths, but that can be found in shallow waters locally in the northeastern Atlantic.

Although a substantial oceanic barrier separates eastern Atlantic from western Atlantic faunas at all latitudes, many species nonetheless occur on both sides of the Atlantic. [Fernandes & Rolán \(1994\)](#) published a provisional check-list of molluscan species known from both the eastern and western Atlantic, but they did not analyse their list, and made no distinctions among species from different climatic zones. Earlier work already revealed that the biogeographic history of tropical Atlantic molluscs found in both the American and West African sides of the Atlantic differs strikingly from that of species at north-temperate latitudes ([Vermeij 1991b](#); [Vermeij & Rosenberg 1993](#)). It therefore makes sense to analyse species from different climatic zones separately.

From the perspective of historical biogeography, the shallow-water cool-temperate North Atlantic biota is a mixture of species whose lineages have occurred in the Atlantic for millions of years (typically back to Early Oligocene time, about 33 million years ago) and species whose lineages extended from the North Pacific into the Atlantic via the Arctic beginning some 4.7 million years ago in the Early Pliocene ([Vermeij 1991b, 2001](#)). In the former category, some subgenus- or genus-level clades have existed exclusively in the eastern Atlantic, others only on the western Atlantic side and still others on both sides.

3. METHODS

Using the primary taxonomic literature, extensively updated from earlier analyses ([Vermeij 1991b](#); [Fernandes & Rolán 1994](#); [Vermeij 2001](#)), I compiled a complete list of shallow-water (less than 100 m depth), cool-temperate, shell-bearing molluscan species in the North Atlantic. Species were divided into three biogeographic categories: (i) northeastern Atlantic (European) endemics, (ii) northwestern Atlantic (eastern North American) endemics and (iii) amphi-Atlantic species (found on both sides of the North Atlantic). Species introduced by humans were not included except in their 'natural' range.

For each taxon, I determined its historical status. Relevant categories are: (i) species (or the higher-level taxa to which they belong) known as fossils only in the eastern Atlantic, including coasts of Europe and Africa outside the study area; (ii) species known as fossils only in the western Atlantic, including parts of eastern North America outside the study area; (iii) amphi-Atlantic taxa, those with a fossil record on both sides of the Atlantic but not known outside the basin;

and (iv) taxa known during or after Pliocene time from either or both sides of the Atlantic but confined to the North Pacific before Middle Pliocene time (trans-Arctic invaders). The third category includes species that have become extinct on one or the other side of the Atlantic and that are therefore restricted in the living fauna to either the eastern or the western Atlantic within the temperate zone. The fourth category includes species known from both the Atlantic and North Pacific, as well as Atlantic endemic species that are demonstrably derived from North Pacific ancestors. To determine a taxon's historical status, I relied on phylogenetic and stratigraphic data, again extensively updated and expanded from earlier analyses.

4. RESULTS AND DISCUSSION

In line with previous findings on molluscs and other groups ([Briggs 1970, 1974](#); [South 1987](#); [Vermeij 1991b](#)), the shell-bearing Mollusca are substantially more diverse in the cool-temperate northeastern Atlantic (402 species) than in the cool-temperate northwestern Atlantic (262 species). The 124 amphi-Atlantic species comprise 30.8% of the northeastern Atlantic and 47.3% of the northwestern Atlantic fauna.

Amphi-Atlantic taxa contributed at most a tiny fraction of Pliocene and earlier Atlantic faunas, implying that there was almost no connection between the two faunas before the Pliocene as there is now. Although available fossil faunas of the Atlantic lived in warmer waters than do the Recent faunas discussed here, it is remarkable that no Miocene or Early Pliocene fauna on either side of the Atlantic contained amphi-Atlantic species. In the Middle Pliocene (3.1–3.7 Myr) Zone 2 Yorktown fauna of Virginia, with 444 shell-bearing molluscan species ([Campbell 1993](#)), only two species (*Mytilus edulis* Linnaeus and *Buccinum undatum* Linnaeus) are today amphi-Atlantic. None of the 115 gastropods of the Oorderen Sands Member of the Lillo Formation of Belgium (approximately contemporaneous with Zone 2 of the Yorktown fauna; see [Louwye et al. 2004](#)) occurred on both sides of the Atlantic ([Vermeij 2001](#)).

Two circumstances caused taxonomic connections between the northeastern and northwestern Atlantic molluscan faunas to increase after the Middle Pliocene. One was the arrival of invaders from the North Pacific via the Arctic. In the living northeastern Atlantic fauna, at least 84 species (20.9%) are of Pacific origin, whereas in the northwestern Atlantic this number is 118 (45.0%). At least 68 of these species with Pacific origins have a current amphi-Atlantic distribution (54.8% of amphi-Atlantic species). An additional seven species of Pacific origin, which today occur only in the northwestern part of the Atlantic, are recorded as fossils in Europe, making the total amphi-Atlantic component at least 75 species. These formerly amphi-Atlantic species are the bivalves *Megalythia thraciaeformis* (Storer; [Jansse et al. 2003](#)), *Macromeris polynyma* (Stimpson; [Moerdijk 2003](#)), *Mya arenaria* Linnaeus ([Petersen et al. 1992](#); [Strasser 1999](#)) and the gastropods *Buccinum elatior* (Middendorff), *Nodotoma impressa* (Mörch), *Propebela rugulata* (Möller in Troschel) and *Solariella varicosa* (Mighels & Adams; see [Harmer 1914–25](#)). All of these species are known from the Early Pleistocene of the North Sea Basin. *Mya arenaria* was reintroduced to Europe by humans, possibly in the late

Middle Ages or the sixteenth century (Petersen *et al.* 1992; Strasser 1999).

The second circumstance is the apparent westward spread of species that before Pliocene time seem to have been confined to the European side of the Atlantic. In the living fauna, this element comprises 55 species, which is 44.4% of the amphi-Atlantic component, 13.7% of the eastern Atlantic fauna and 20.5% of the western Atlantic fauna. There is no evidence of any western Atlantic lineage becoming established on the European coast without human assistance.

One possible explanation for the apparent absence of pre-Pliocene amphi-Atlantic species and for the westward spread of endemic eastern Atlantic lineages to North America is the absence of appropriate North American fossil faunas. Large, well studied fossil faunas of Oligocene, Miocene and Pliocene age in the northwestern Atlantic are available only from New Jersey southward, well within the mild-temperate zone. Any pre-Pleistocene taxon with an amphi-Atlantic distribution and whose North American range did not extend south to New Jersey would therefore not be recognizable as amphi-Atlantic.

An argument against this possibility is that the warm- and cool-temperate fossil faunas of North America contain many species belonging to genera that today either extend north of Cape Cod or are characteristic of the cold North Atlantic. These genera include the gastropods *Crepidula*, *Disputaea*, *Euspira*, *Urosalpinx* and *Ilyanassa*; and the bivalves *Nucula*, *Placopecten*, *Lucinoma*, *Astarte*, *Ceronia*, *Mysella*, *Ensis*, *Mulinia*, *Gemma*, *Mercenaria*, *Petricolaria*, *Clidiophora*, *Cochlodesma*, *Periploma* and *Crassithracia*. These taxa are either not known from the eastern Atlantic at all (e.g. *Urosalpinx*, *Ilyanassa*, *Ceronia*, *Cochlodesma* and *Periploma*) or the fossil western Atlantic species are distinct from their eastern Atlantic counterparts.

Some European genera may have been represented in North America either as amphi-Atlantic species or as pairs of closely related eastern and western Atlantic species during the Oligocene and Miocene, but there is no definitive evidence for the existence of amphi-Atlantic species from those times. Fossil American Arctic faunas contain at least four genera of Atlantic molluscs that are unknown from the western Atlantic fossil record but do occur in Europe. One of these, the pectinid bivalve *Arctinula*, occurs in the Nuwok Formation (Oligocene) of northern Alaska (MacNeil 1957; for age see McNeil & Miller 1990) and the Late Pliocene Kap København Formation of North Greenland (Simonarsson *et al.* 1998). It also occurs in the living fauna south to Massachusetts (Lubinsky 1980). The thyasirid lucinoidean bivalve *Thyasira alaskana* (Kauffman), a species closely related to the living amphi-Atlantic *Thyasira gouldii* (Philippi), is known from the Nuwok Formation (Kauffman 1969). The arcticid bivalve *Arctica*, represented in the Nuwok Formation by *Arctica carteriana* (Dall; MacNeil 1957), is today present throughout the cool-temperate North Atlantic as *Arctica islandica* (Linnaeus 1758). All fossil Oligocene and later occurrences of *Arctica* other than *A. carteriana* are from Europe. Finally, the hiatellid bivalve *Cyrtodaria* has been present in the Arctic basin since at least the Oligocene (MacNeil 1957; Simonarsson *et al.* 1998) and perhaps since the Early Paleocene (Marincovich & Zinsmeister 1991; Marincovich 1993;

but see Gordillo 2001, who considers the Early Paleocene records to refer to *Hiatella*). In Europe, the genus occurs from the Eocene to the Late Pliocene (Nesis 1965; Janssen *et al.* 1984). Today, *Cyrtodaria* occurs only in the Arctic, as *Cyrtodaria kurriana* (Dunker), and in the northwestern Atlantic, as *Cyrtodaria siliqua* (Spengler; Nesis 1965). If any of these genera extended to temperate eastern North America during the Oligocene or Miocene, there is no record of them there. Given that the species of *Thyasira*, *Arctica* and *Cyrtodaria* from pre-Pliocene Arctic North America differ from contemporaneous European congeners at the species level, there is no evidence for amphi-Atlantic cool-temperate species before the Middle Pliocene.

Several genera in addition to those discussed above have an amphi-Atlantic distribution, but their histories on the two sides of the Atlantic seem to have been entirely separate. The bivalve genus *Glossus*, known in the modern fauna only from Europe as *Glossus humanus* (Linnaeus 1758), has an Oligocene to Late Pliocene record in eastern North America and an Oligocene to Recent record in Europe (Janssen *et al.* 1984; Ward 1992). My examination of species in this genus shows that the western Atlantic lineage, characterized by a keel extending from the umbo to the posteroventral margin of the valve, differs consistently from the European lineage, which lacks this feature. Other native Atlantic genera known as fossils from both sides of the Atlantic, but with independent histories in North America and Europe, include the gastropods *Euspira* (Paleocene or earlier to Recent on both coasts: Janssen *et al.* 1984; Petuch 1988, 1993; Marquet 1997; Petuch 2004), *Ecphora* (Early Oligocene to Late Pliocene in the western Atlantic, Early Oligocene to Late Miocene in Europe: Vermeij 1995 and references therein) and *Atractodon* (Late Pleistocene of North America, Late Miocene to Middle Pliocene in Europe: Clarke *et al.* 1972; Marquet 1997); and the bivalves *Nucula* (throughout Cenozoic on both sides of the Atlantic), *Astarte* (Early Miocene to Recent in the western Atlantic, throughout the Cenozoic in Europe), *Mysella* (Early Pliocene to Recent in North America, Middle Miocene to Recent in Europe), *Abra* (Early Pliocene to Recent in North America, Early Oligocene to Recent in Europe), *Ensis* (Early Miocene to Recent in North America, Late Oligocene to Recent in Europe: van Urk 1971, 1972; Ward 1998) and *Crassithracia* (Early Pliocene to Recent in North America, Oligocene to Recent in Europe: for scope of genus, see Marshall 2002). These examples demonstrate that, if amphi-Atlantic connections existed before the Pliocene in the cool-temperate North Atlantic, they were brief and ancient, probably dating to the Early Oligocene.

Phylogeographic studies using molecular markers in living populations strongly support the hypothesis that American populations of amphi-Atlantic species are derived, and largely isolated, from European populations. Haplotypes present in the northwestern Atlantic typically comprise a subset of those present in Europe, although some species show unique North American haplotypes as well (see Wares 2001; Wares & Cunningham 2001; Wares *et al.* 2002; Reginos *et al.* 2004 for studies of *Semibalanus*, *Asterias*, *Idotea*, *Littorina* and *Mytilus*). A purported exception is the bivalve *A. islandica* (Dahlgren *et al.* 2000), but Wares (2001) has used the same data to argue that *Arctica* falls in line with the other species studied.

It is noteworthy that Iceland appears to be a geographical stepping-stone for European taxa to reach North America, but not for North American taxa to reach Europe. A few taxa from the northwestern Atlantic reach Iceland but not Europe; examples include the rissoid gastropods *Onoba leptalea* (Verrill), *Onoba exarata* (Stimpson), *Onoba mighelsi* (Stimpson) and *Alvania pseudoareolata* (Warén) (see Warén 1996). The Pliocene Tjörnes beds of Iceland further contain the American carditid bivalve *Cyclocardia borealis* (Conrad), a species never recorded from fossil or living faunas in Europe (Gladenkov *et al.* 1980). The rissoids almost certainly reached Iceland from the north in the Arctic rather than directly from North America.

Just how the east-to-west movement of species in the North Atlantic is accomplished remains a mystery. In the North Atlantic, the predominant circulation is clockwise, meaning that water flows from the subtropical and warm-temperate western Atlantic via the Gulf Stream eastward to Europe. The source areas of the Gulf Stream are too warm to carry recruits of northwestern Atlantic cool-temperate species eastward, perhaps accounting for the absence of west-to-east invaders in the cold North Atlantic; but return flow from east to west in the North Atlantic is at best indirect. The East Greenland Current flows south from Denmark Strait between Iceland and Greenland and eventually merges with the southward-flowing Labrador Current in the Northwestern Atlantic (Ottersen *et al.* 2004), but this transport is long and circuitous.

As is true in other cases of markedly asymmetrical interchange between neighbouring biotas, the donor biota (Europe in this case) is richer in species than the recipient biota (North America in this case), but the difference in richness (a factor of 1.4) is far exceeded by the apparently completely one-sided invasion from Europe to North America. There are no data on the relative competitive performance levels of European and American species or populations, so that the contribution of competitive superiority of the European biota relative to the American one cannot be evaluated. Whether the larger size of the cool-temperate European biota reflects a larger region and a larger potential number of colonizing individuals than the eastern North American biota also remains an open question. It is difficult to obtain credible estimates of the areas or linear extents of the regions in which temperate biotas occur, because many species on both coasts extend north and/or south of the limits defining the cool-temperate zone.

An important and unanswered question is whether the pattern of ocean circulation in the Atlantic was different at those times in the last 3.5 million years when east-to-west transport of species was more common than it appears to be today. As noted above, the molecular studies of amphi-Atlantic species all point to genetic differences between eastern and western populations, and therefore imply substantial genetic isolation between populations of the two sides of the Atlantic. The observed patterns of movement of species may have required oceanographic conditions quite different from those today. These different conditions could well have been ephemeral and infrequent. It is possible, for example, that brief, warm interglacial episodes were particularly favourable to trans-Atlantic expansion of European species, because potential

stepping-stones, which are now largely too cold for temperate species, could have become temporarily habitable. The occurrence of several European molluscan species in the Middle to Late Pliocene Kap København Formation of North Greenland (Simonarsson *et al.* 1998) further implies that a relatively warm Arctic Ocean during the Pliocene could have facilitated westward expansion of some eastern Atlantic taxa.

Evidence from warm- to mild-temperate North Atlantic faunas (Vermeij 1989, 2001) indicates that the magnitude of Pliocene extinction in the western Atlantic (75% of standing Pliocene diversity) is higher than that in Europe (40–50%). No comparable data are known from the two cool-temperate faunas, but some 47% of Pliocene molluscan species in the Pliocene of Iceland are now extinct (Vermeij 2001), a figure in line with other European faunas. The Kap København Formation of the Late Pliocene of Greenland contains species that are all still living (Simonarsson *et al.* 1998). The role of greater prior extinction and of greater opportunity for colonization in the northwestern Atlantic remains a plausible explanation for the one-sided expansion of European species across the Atlantic, but data on extinction in cool-temperate North America are needed to settle this matter.

Several previously amphi-Atlantic genera and species have become restricted to one side of the Atlantic or the other. As noted above, restriction to North America characterizes at least seven taxa that during the Early Pleistocene occurred on both sides of the Atlantic, as well as the genus *Cyrtodaria*. *Atractodon* would have fit this pattern as well had it not been for the Late Pleistocene extinction of this genus in North America. *Glossus* is the only formerly amphi-Atlantic genus to have become restricted to Europe (see above).

The fact that some taxa survived longer in the western Atlantic than in the eastern Atlantic during the Pleistocene may mean that the role of Europe as a refuge shifted to eastern North America after the Pliocene, and therefore that the donor status may also be shifting to the American side. However, as noted above, phylogeographic studies are unanimous in showing that the predominant direction of expansion continues to be from east to west, even in cases where, as in *Littorina* and some other examples, such expansions are geologically very recent.

5. CONCLUSIONS

One of the great lessons of history, and one of the important contributions of paleobiology, is the finding that geographical ranges of species are dynamic. Modern distributions are a poor guide to the locations of evolutionary origins of species. Although comparative genetic analyses of living populations by phylogeographic methods provide clues about patterns of dispersal, only the long-term data provided by the fossil record can indicate whether and where species occurred in the past outside their present range limits. This information is vital for understanding patterns of connection among populations, among species and among biotas.

My analysis of the history of the North Atlantic cool-temperate molluscan fauna in waters less than 100 m deep shows that the North American coast from Cape Cod northward has served as recipient region for species expanding westward from Europe and for other species

entering through Bering Strait to the Arctic from the North Pacific. Europe received newcomers from the North Pacific but not from North America. Its biota therefore serves as both recipient and donor, whereas that of cool-temperate North America acts only as recipient.

A majority of ampho-Atlantic species have a North Pacific origin. It remains an open question how the ampho-Atlantic distribution of these species was achieved. Did these species first colonize Europe and then expand westward, as did ampho-Atlantic species with pre-Pliocene European roots, or did colonists from the North Pacific reach Europe and eastern North America separately? Phylogeographic evidence favours the first of these alternatives, but more work is needed to sort explicitly between these two scenarios.

For a biota as well characterized as that of the North Atlantic, it is surprising how little we know about routes of dispersal and locations of source populations. The data summarized here imply that Europe provides recruits for all ampho-Atlantic populations, and that failure to conserve populations in the eastern Atlantic would therefore jeopardize populations throughout the North Atlantic basin.

Together with the phylogeographic evidence cited earlier, the historical data cited here also imply that trans-Atlantic connections within species may be infrequent and brief. As the world warms, especially at high latitudes, this situation may change. Greater interchange between the two biotas of the North Atlantic and between the North Atlantic biotas and those of the North Pacific, may result from a warming of the Arctic Ocean and of such potential stepping stones as Greenland.

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