Beyond area relationships: Extinction and recolonization in molecular marine biogeography

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Summary

In vicariance biogeography, the traditional focus on solely determining area relationships can obscure biologically interesting complexity. Even in the case of neighboring sister areas, the rise and fall of barriers to dispersal can yield a complex pattern of vicariance and interchange. Vicariance biogeographers view incongruent historical patterns as noise that must be filtered out. Here, we sharpen the focus of vicariance biogeography, and attempt to identify organismal characteristics that unite sets of taxa with congruent histories. Emphasizing examples from coastal marine invertebrates, we apply this perspective to two well-studied model systems: the southeastern United States, and the trans-Arctic interchange through the Bering Strait.

In both systems, populations from neighboring areas tend to show either great genetic similarity, usually inferred to result from continuing gene flow, or reciprocal monophyly accompanied by deep genetic divergence. Because dispersal ability is a poor predictor of which taxa fall in either category, we consider the possibility that genetic similarities often attributed to continuing gene flow may result instead from extinction in one area followed by recolonization from the other. Similarly, reciprocal monophyly between neighboring areas suggests that taxa in those areas have resisted recent local extinction. Our perspective shifts focus away from larval dispersal ability, which has long dominated molecular marine biogeography. Instead, we can focus on extinction itself, asking why taxa showing reciprocal monophyly have resisted local extinction.

A focus on extinction and recolonization is especially fruitful for understanding the trans-Arctic interchange. In group after group, researchers have found genetic evidence consistent with local extinction in the NW Atlantic followed by recolonization either from the NE Atlantic or from the North Pacific. In general, taxa which are restricted to rocky substrata appear to have been more prone to local extinction. The ability to recolonize the NW Atlantic from neighboring areas does not appear to depend on dispersal ability, although present-day geographical distribution does seem to be important. We conclude by reviewing some of the reasons why biogeographers have failed to find a consistent relationship between larval dispersal ability and patterns of geographical subdivision.
**Introduction**

It is widely recognized that historical information is essential to fully appreciate the evolutionary context of species interactions (Vermeij, 1978; Brooks, 1985; Brooks and McLennan, 1991; Futuyma and McCafferty, 1990). In many cases, placing this historical information in a geographical context may also be important. Is a strong interaction between two or more species in a particular area the result of a long shared history, or did one or more of the species arrive only recently? Did a particular character state evolve *in situ*, or does it also appear in related species that diverged long ago? Establishing the geographical and historical context for the members of a community is known as historical biogeography. The only direct evidence for the composition of past communities comes from the fossil record (Valentine and Jablonski, 1993), but because of the paucity of fossil evidence for many taxa, and because of developments in phylogenetic methods, phylogenetic information has become increasingly important.

The first systematic attempt to infer biotic history from phylogenetic and geographic information was vicariance biogeography (Croizat et al., 1974; Nelson and Platnick, 1981; Nelson and Rosen, 1981; Humphries and Parenti, 1986). Vicariance biogeographers recognized that the current distributions of extant organisms may, in some cases, reflect the fragmentation (vicariance) of widespread ancestral ranges. Moreover, they recognized that in the absence of extinction or dispersal, the order in which these areas became fragmented will be reflected in the phylogenies of taxa taken from those areas (Fig. 1). The development of methods for recovering this sequence of fragmentation, or area relationships, has been the subject of much discussion (Rosen, 1976; Nelson and Platnick, 1981; Brooks, 1985; Humphries and

![Figure 1. Geographic subdivision of a contiguous area by a sequence of vicariance events. If no postvicariance dispersal or extinction has taken place, the phylogenies of taxa taken from the subdivided areas will be perfectly congruent. In this case, the consensus area cladogram reflects the sequence of vicariant subdivision of the ancestral biota.](image-url)
Parenti, 1986; Wiley, 1988; Page, 1988, 1991). All of these methods rely on finding congruence between phylogenies of unrelated species collected from the same areas (Fig. 1).

Even when area relationships can be readily determined, focusing only on area relationships obscures biologically interesting complexity. Consider the simplest possible case – neighboring sister areas. These areas share many pairs of closely related taxa and are currently divided by a barrier to dispersal. As is often the case, the barrier between these sister areas is transitory, driven by cyclical processes such as climate change (Briggs, 1974; Vermeij, 1978, 1989, 1991b). Even when barriers to migration are in place, they affect some taxa more strongly than others (Vermeij, 1978, 1989, 1991a, b). For these reasons, we would not expect all taxa in these neighboring areas to have experienced the same history. In the following section, we discuss two sets of taxa in these neighboring areas that have experienced distinct histories.

Vicariance, extinction and recolonization

Assume that one set of taxa in these neighboring sister areas has experienced little or no genetic connection (effective gene flow or recent recolonization) since the barrier first arose. As predicted by population genetic models, isolation has led to complete lineage sorting (Neigel and Avise, 1986; Avise, 1994), resulting in reciprocal monophyly and deep genetic divergence on either side of the barrier (Fig. 2A). Assume that a second set of taxa has experienced local extinction on one side of the barrier followed by recolonization across the barrier (Fig. 2B). Because of this recent recolonization event, there is little genetic divergence between these populations. Although considering either set of taxa would lead one to identify these as sister areas, the histories of the two sets of taxa differ in important ways. For example, every member of the second group of taxa experienced recent dispersal across the barrier. Does this mean that these taxa share characteristics making them better at dispersal than members of the first group?

A more subtle alternative scenario is that both sets of taxa share the same capability for dispersal and experienced approximately the same degree of intermittent dispersal across the barrier. In the first set of taxa, however, the genetic impact of dispersal was swamped by large standing populations on both sides of the barrier. In the second set of taxa, the genetic impact of the same level of dispersal was magnified because local extinction allowed the dispersers to found an entirely new population (e.g. Slatkin, 1977, 1985, 1987; but see Wade and McCauley, 1988). Therefore, an absence of genetic differentiation between neighboring populations may have as much to do with ecological opportunity created by local extinction as with dispersal ability.

A focus on extinction and recolonization shifts attention away from dispersal ability, and toward the conditions that underlie local extinction. Are taxa that show
Figure 2. Two distinct histories experienced by taxa divided by the same vicariant event. (A) Cessation of gene flow resulting in reciprocal monophyly. (B) Local extinction on one side of the barrier followed by recolonization from the other side.

reciprocal monophyly between neighboring areas more resistant to extreme conditions? Is ability to disperse related to the probability of local extinction (Jablonski, 1986)? As Vermeij (1989) has argued, studying the factors that cause local extinction – or range restriction in his terminology – can help illuminate the factors that cause a species to become globally extinct.
Sharpening the focus of vicariance biogeography: searching for sets of congruent histories

Vicariance biogeographers attempt to identify a single set of area relationships from congruent elements in the phylogenies of taxa from those areas. If more than one set of congruent histories exists, these multiple histories are considered noise. In the preceding example, however, considering those multiple histories was more illuminating than simply identifying area relationships.

In this chapter, we argue that it is fruitful to focus and extend the goals of vicariance biogeography. Rather than focusing exclusively on identifying area relationships, we attempt to identify sets of taxa with congruent histories. This approach recognizes that regional biotas may have complex histories, and seeks to identify sets of taxa that have responded to the rise and fall of barriers to dispersal in similar ways. There are two advantages to this approach. First, it can help ecologists determine which interacting species may have had a long shared history (Brooks, 1985; Brooks and MacLennan, 1991). Second, and most important, it holds the promise of finding general lessons in biogeography. We may be able to learn if taxa with congruent histories share characteristics that can explain this congruence.

To explore characteristics that may underlie congruent histories, and to explore the implications of extinction and recolonization on geographic subdivision, we focus on genetic studies of coastal, benthic marine invertebrates. This is because they are reasonably well studied, have simple, largely one-dimensional ranges up and down coastlines, and often have excellent fossil records. The larvae of benthic marine invertebrates can be classified as planktotrophic (with pelagic, feeding larvae) or nonplanktotrophic [including pelagic nonfeeding, brooded or benthic crawling; Jablonski and Lutz (1983)]. Planktotrophic larvae are generally considered to have the greatest potential for dispersal (Scheltema, 1979, 1986). Although the population genetics and biogeography of marine invertebrates have been studied for nearly 30 years, much remains to be learned about the basic factors controlling the distribution of taxa in time and space. Even the organismal characteristic that has received the most attention, larval dispersal ability, is not consistently associated with patterns of geographical subdivision (Burton, 1983; Hedgecock, 1986; Ó Foighil, 1989; Palumbi, 1994, 1995).

We apply our perspective to two model biogeographic systems. The first system, the coast of the SE United States, represents the simplest possible case of two neighboring sister areas: the Gulf of Mexico and the western Atlantic. The second model system involves taxa that took part in the trans-Arctic interchange between the North Pacific and North Atlantic Oceans following the opening of the Bering Strait ca. 3.5 Ma. For both of these systems, we identify sets of taxa with congruent patterns of geographic subdivision. We find that neither an organism's geographic range nor its presumed larval dispersal ability, as predicted by larval type, can consistently explain patterns of geographic subdivision. We argue that in both model
systems, local extinction and recolonization may be more important in explaining marine biogeographic patterns than has been previously thought.

**Extinction and recolonization in the southeastern United States**

Due largely to the efforts of John Avise and his colleagues, the coast of the SE United States has become one of the most intensively studied marine biogeographic systems (reviewed in Avise, 1992). The Gulf of Mexico and the Atlantic coast of the SE United States share many closely related species and subspecies, making them obvious sister areas (Fig. 3). This simple designation of sister areas, however, obscures a complex history between the Gulf of Mexico and the Atlantic. This complex history likely represents repeated episodes of vicariance and dispersal in response to climatically driven changes in sea temperature and sea level (reviewed in Felder and Staton, 1994). Two general patterns have emerged from studies of taxa collected from the SE United States – they either show reciprocal monophyly between the

![Figure 3](image_url) *Figure 3. The first model system considered, the coast of the SE United States. Taxa found in both the Gulf and the Western Atlantic fall into two general categories: tropical species that are continuously distributed, and temperate species that are disjunct across southern Florida.*
Gulf of Mexico and the Atlantic coast (Fig. 2A), or show clear evidence of recent genetic connection (Fig. 2B).

Are there organismal characteristics consistently associated with each of these biogeographic patterns? One easily defined characteristic is present-day geographic distribution. Some coastal taxa in the SE United States are continuously distributed, whereas other species found in both the Gulf of Mexico and the Carolinas are not found in the tropical waters of southern Florida (Fig. 3, Frey, 1965; Briggs, 1974; Cunningham et al., 1991; Felder and Staton, 1994). Have the same characteristics that prevent disjunct taxa from living in southern Florida increased the probability of vicariance during warmer periods? Probably not. Species with continuous distributions appear to be just as likely to show reciprocal monophyly between the Gulf of Mexico and the Atlantic as disjunct taxa (Tab. 1; Avise, 1992). Similarly, dispersal ability does not consistently predict patterns of geographical subdivision in the SE United States. Taxa with good dispersal ability are as likely to show reciprocal monophyly as they are to show evidence of recent genetic connection (Tab. 1).

Why is it difficult to explain these patterns of geographic subdivision? One obvious possibility is that a major vicariant event may have divided populations of taxa that now show reciprocal monophyly. Such an event is expected to affect all species regardless of their life history characteristics (Avise, 1992). However, this an-

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution pattern</th>
<th>Dispersal ability</th>
<th>Reciprocal monophyly</th>
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<tr>
<td>Hydroid (Hydractinia)</td>
<td>disjunct</td>
<td>poor</td>
<td>yes</td>
</tr>
<tr>
<td>Fish (toadfish)</td>
<td>disjunct</td>
<td>good</td>
<td>yes</td>
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<tr>
<td>Fish (black sea bass)</td>
<td>disjunct</td>
<td>good</td>
<td>yes</td>
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<tr>
<td>Hermit crab (P. poll.)</td>
<td>disjunct</td>
<td>good</td>
<td>yes</td>
</tr>
<tr>
<td>Crab (Sesarma)</td>
<td>disjunct</td>
<td>good</td>
<td>yes</td>
</tr>
<tr>
<td>Crab (Uca)</td>
<td>disjunct</td>
<td>good</td>
<td>yes*</td>
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<tr>
<td>Hermit crab (P. long.)</td>
<td>disjunct</td>
<td>good</td>
<td>no</td>
</tr>
<tr>
<td>Fish (sturgeon)</td>
<td>disjunct</td>
<td>good</td>
<td>no</td>
</tr>
<tr>
<td>Fish (menhaden)</td>
<td>disjunct</td>
<td>good</td>
<td>no</td>
</tr>
<tr>
<td>Horseshoe crab (Limulus)</td>
<td>continuous</td>
<td>good</td>
<td>yes</td>
</tr>
<tr>
<td>Oyster (Crassostrea)</td>
<td>continuous</td>
<td>good</td>
<td>yes</td>
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<tr>
<td>Mussel (Geukensia)</td>
<td>continuous</td>
<td>good</td>
<td>yes</td>
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<tr>
<td>Clam (Mercenaria)</td>
<td>continuous</td>
<td>good</td>
<td>yes</td>
</tr>
<tr>
<td>Eel</td>
<td>continuous</td>
<td>good</td>
<td>no</td>
</tr>
<tr>
<td>Fish (catfish)</td>
<td>continuous</td>
<td>good</td>
<td>no</td>
</tr>
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swer does not explain why some taxa show evidence of recent genetic connection. In some cases, continuing gene flow may account for the lack of genetic differentiation. In others it may have been caused by local extinction in one area followed by recolonization from another (Slatkin, 1977, 1985, 1987; but see Wade and McCauley, 1988). Whereas continuing gene flow may be enhanced by plank-trophic larvae, rare dispersal events in nonplanktrophic species may be sufficient to colonize an area where the species is not currently found (Johannesson, 1988). If recolonization following local extinction occurs commonly in the SE United States, then vulnerability to local extinction may be as important as dispersal ability in determining which taxa show reciprocal monophyly.

For example, it is well known that isotherms become greatly compressed along the Atlantic coast of the SE United States during glaciation (e.g. Cronin, 1988). Such compression of isotherms may increase the probability of local extinction of temperate taxa in the Atlantic, followed by recolonization from the Gulf of Mexico. Using intraspecific allelic phylogenies, it may be possible to identify sets of taxa that were eradicated locally during the last glacial maximum and were later recolonized from the Gulf of Mexico. A newly colonized area is not only expected to show relatively low genetic diversity, but an intraspecific phylogeny is expected to show that alleles from the source population are paraphyletic with respect to alleles from the newly colonized area (Fig. 2B; Ortí et al., 1994; Templeton, 1993, 1994; Hellberg, 1994; Hewitt, 1996).

Just as taxa with little genetic differentiation may have experienced local extinction and recolonization, taxa with reciprocal monophyly on either side of a barrier must have resisted local extinction in the recent past. Genetic evidence for continuous residence is particularly important, because even a good fossil record may not provide unambiguous evidence for continuous residence. For example, if the population on the Atlantic side of the barrier repeatedly becomes extinct, but is always recoloned rapidly by the population on the other side of the barrier (relative to the rate of sedimentation or fossilization), the fossil record might appear continuous.

The preceding discussion suggests that genetic evidence might be an important source of information about whether local extinction has occurred in the recent past. If populations in neighboring sister areas have a genetic signature consistent with a recent range expansion (Ortí et al., 1994; Templeton, 1993, 1994; Hellberg, 1994), they may have undergone a local extinction followed by recolonization. This is especially likely if there was a long fossil history in the newly colonized area (e.g. Palumbi and Kessing, 1991; Ortí et al., 1994). On the other hand, taxa showing reciprocal monophyly are likely to have resisted extinction in the recent past.
The trans-Arctic interchange: a model system for marine biogeographic studies

The SE United States represents the simplest possible case – two neighboring sister areas. In this section, we consider a more complicated and interesting model system involving three neighboring areas: the North Pacific, the NW Atlantic and the NE Atlantic (Fig. 4). Before discussing biogeographic patterns, it is important to briefly sketch the geological background of a pivotal event in the marine northern hemisphere, the trans-Arctic interchange.

For most of the Cenozoic Era, the region that is now the Bering Strait between North America and Asia was a land bridge and was closed to marine migration. The isolation of the cold-water faunas of the North Pacific and North Atlantic was end-

![Image of the Earth with arrows indicating the Bering Strait and connections to the North Pacific and NE Atlantic.]
ed abruptly by the opening of the Bering Strait approximately 3.5 Ma. The exchange of taxa was asymmetric, with most invaders moving from the Pacific to the Atlantic (Fig. 4; Durham and MacNeil, 1967; Vermeij, 1989, 1991a,b). Because the opening of the Bering Strait during the late Pliocene took place when the earth's temperatures were considerably warmer than at any time during the Pleistocene (Herman and Hopkins, 1980; Shackleton et al., 1984; Carter et al., 1986; Andrews, 1988), many temperate and Arctic species took part in the interchange. The initial opening of the Bering Strait was soon followed by the onset of Northern Hemisphere glaciations between 2.5 Ma. and 3.1 Ma. (Shackleton et al., 1984). Pleistocene fluctuations of temperature and sea level have undoubtedly affected the likelihood of biotic interchange between the North Pacific and the North Atlantic.

Because the North Pacific and North Atlantic share many closely related taxa, they might be considered sister areas (Fig. 4). As with the SE United States, the simple designation of sister areas may obscure more interesting patterns. First, the major cause of this close area relationship is the dispersal associated with the trans-Arctic interchange rather than the vicariance of a widely distributed ancestral biota. Second, the repeated opportunities for vicariance and dispersal caused by glacial episodes have generated a complex history that is obscured by the designation of simple area relationships.

We consider the biogeography of the trans-Arctic interchange from two perspectives. We begin by considering the large-scale problem of determining which taxa took part in the exchange and in which direction they went. Although the identity of trans-Arctic invaders has been traditionally inferred from the fossil record, it is also possible to infer dispersal from phylogenetic information (Brundin, 1981; Bremer, 1992). We consider two gastropod genera with good fossil records and ask whether fossils and phylogenies give the same answers about their dispersal. Then we ask whether organismal characteristics can predict which species took part in the exchange. Like Vermeij (1991a), we conclude that the most important factor in determining which species took part in the interchange was ecological opportunity opened up by extinction in the North Atlantic.

Next, we consider at a finer scale the histories of species that invaded the North Atlantic. We identify four patterns that have emerged from genetic studies of the Northern Hemisphere marine fauna. These patterns are distinguished by the degree of genetic divergence between three areas – the North Pacific, the NW Atlantic and the NE Atlantic (Fig. 4). Finally, as before, we ask whether there are organismal characteristics that might explain the observed patterns.

Inferring dispersal from phylogenies and fossils: two case studies

Whether dispersal events can be inferred from the fossil record and from phylogenetic information is controversial (Croizat et al., 1974; Platnick and Nelson, 1978;
Platnick, 1981; Brundin, 1981; Patterson, 1981; Humphries and Parenti, 1986; Bremer, 1992). In the case of the trans-Arctic interchange, however, the simultaneous appearance of Pacific taxa in the North Atlantic (and vice versa) at the same time as the Bering Strait opened is strong evidence that a major biotic exchange took place. The marked asymmetry of the trans-Arctic interchange appears to be typical of invasions that follow the disappearance of major barriers (Webb, 1985; Vermeij, 1991a, b). In the following case studies, we ask whether the occurrence and directionality of dispersal events, as inferred from phylogenetic and fossil information, coincide.

The genus Littorina comprises 19 living species of marine rocky-intertidal herbivorous gastropods that are widely distributed through the Northern Hemisphere. Like many other genera that are thought to have participated in the trans-Arctic interchange, Littorina has a long history in the North Pacific but was not found in the North Atlantic fossil record until after the opening of the Bering Strait 3.5 Ma (Vermeij, 1991a; Reid, 1996). The fossil record indicates that two lineages of Littorina independently invaded the North Atlantic (Reid, 1996). A morphological cladogram of Littorina species is also consistent with two independent invasions of the North Atlantic and no dispersal in the opposite direction (Fig. 5A; Vermeij, 1991a; Reid, 1996). As with the morphological evidence, phylogenies derived from allozymes and mitochondrial DNA (mtDNA) both support the fossil-based hypothesis of two independent invasions of the North Atlantic (Zaslavskaya et al., 1992; Reid et al., 1996).

The genus Nucella is another group of marine rocky-shore gastropods. The fossil record suggests that there has been a single invasion of the Atlantic from the Pacific (Durham and MacNeil, 1967; Vermeij, 1991a). A mtDNA phylogeny also supports a single Pacific-to-Atlantic invasion (Fig. 5B; Collins et al., 1996). For Nucella and Littorina, fossil and phylogenetic information strongly support hypotheses of recent invasion of the North Atlantic from the Pacific. This agreement supports the assertion that phylogenetic information can illuminate the biogeographic histories of invaders that have no fossil record.

Why did only a subset of taxa take part in the trans-Arctic interchange?

Because so many taxa have recently invaded the North Atlantic, it is reasonable to ask if these invaders share organismal characteristics in common. In a statistical analysis of trans-Arctic invaders, Vermeij (1978, 1989, 1991a) found that the identity of invading species could not be predicted by larval dispersal ability. This is illustrated by Littorina, where one invading lineage has planktotrophic larvae, while the other, like Nucella, has nonplanktotrophic larvae.

On the other hand, Vermeij notes that invading species dominate rocky shore communities in the North Atlantic. This is evident in the shallow rocky shore of the
Figure 5. (A) Morphological cladogram of the gastropod genus Littorina, after Reid (1990). This cladogram supports the fossil-based hypothesis of independent invasions of the Atlantic by two independent Littorina lineages. One of these invading lineages has planktotrophic larvae, while the other has non-planktotrophic larvae. (B) The mtDNA cladogram for the gastropod genus Nucella, based on the 740-bp mitochondrial cytochrome b gene (after Collins et al., 1996).

NW Atlantic, where almost every major species is a recent invader from the North Pacific. The list of invaders includes 11 of 12 molluscan species, barnacles, hermit crabs, seastars, sea urchins and kelps (Vermeij, 1991a). Invading species compose much lower proportions of soft-bottom communities.
Does this mean that rocky-shore species in the North Pacific were more likely to have invaded the Atlantic than soft-bottom species? Apparently not. Close relatives of species that invaded the Atlantic make up similar proportions of present-day rocky-shore and soft-bottom communities of the North Pacific (Vermeij, 1991a). As discussed in the following section, the reason so many Pacific invaders are found on North Atlantic rocky shores appears to have more to do with ecological opportunity caused by extinction than dispersal ability (Vermeij, 1991a).

Glaciation and extinction in the NW Atlantic

The onset of Northern Hemispheric glaciation between 2.5 Ma and 3.1 Ma is believed to be responsible for large-scale extinction, especially in the North Atlantic (Raffi et al., 1985; Stanley, 1986). In the NW Atlantic, where the compression of isotherms was especially severe, cold-temperate species currently found north of Cape Cod appear to have been forced to the south of Cape Cod during the last glacial maximum (Vermeij, 1978, 1991a; Cronin, 1988). As a result, rocky-shore animals would have been especially likely to become extinct because there is virtually no hard substratum south of Cape Cod (Vermeij, 1978, 1991; Wethey, 1985; Ingólfsson, 1992). In an important paper, Ingólfsson (1992) has gone so far as to suggest that virtually the entire NW Atlantic rocky-shore fauna was exterminated during the most recent glacial maximum, and has subsequently been recolonized from elsewhere. If glaciations caused an especially high rate of extinction along the rocky shore, there would have been more ecological opportunities for invading species than for soft-bottom species.

A closer look at the histories of invading species

Because the Bering Strait opened before the onset of Northern Hemisphere glaciation, many temperate species were able to invade the Atlantic. Repeated opportunities for vicariant speciation during glacial maxima, combined with the continuing possibility of reinvasion from the Pacific, may have made the histories of invading taxa complex. In the following section, we consider only marine taxa that have invaded from the Pacific and that are currently found on both coasts of the North Atlantic. For these taxa, four broad classes of biogeographic histories can be defined according to the relative amount of trans-Arctic genetic divergence and trans-Atlantic genetic divergence (Fig. 6).
Large Pacific-Atlantic divergence: classes I and II

Taxa in classes I and II show clear reciprocal monophyly and deep genetic divergence between the Atlantic and Pacific (Fig. 6). Class I taxa are further defined by reciprocal monophyly between the NW and NE Atlantic, although the genetic divergence within the Atlantic is less than between the Atlantic and the Pacific (Fig. 6). This pattern is consistent not only with little or no recent genetic connection across the Atlantic, but also with a period of continuous residence on both sides of the Atlantic. By contrast, class II taxa also show deep Pacific-Atlantic divergence but

Figure 6. Four classes of biogeographic histories of Northern Hemisphere marine taxa. These classes are defined by the degree of genetic divergence across the Arctic and the across the Atlantic. See text for details.
very little differentiation between the NW and NE Atlantic (Fig. 6). The class II pattern is consistent with either continuing gene flow, or with a recent colonization event from one side of the Atlantic to the other (as in Fig. 2B).

As described above, in some cases it might be possible to distinguish between these alternatives (e.g. Templeton, 1993, 1994; Hellberg, 1994).

The class I pattern can be illustrated by a lineage of North Pacific hermit crabs that invaded the Atlantic during the trans-Arctic interchange. After their arrival in the Atlantic, these hermit crabs speciated on either side of the North Atlantic to become Pagurus acadianus (NW Atlantic) and P. bernhardus (NE Atlantic). The Atlantic species are monophyletic relative to the Pacific species (Cunningham et al., 1992; Cunningham, unpublished data). The Pacific-Atlantic divergence in a fragment of the mitochondrial 16S gene is about 3.2% across the Arctic and about 1% across the Atlantic (Cunningham et al., 1992; distances calculated according to Kimura, 1980). As a point of comparison, the same fragment was calculated to have diverged at a rate of about 1% per million years in several pairs of fiddler crabs now divided by the Isthmus of Panama (Sturmbauer et al., 1996). The degree of divergence observed in these hermit crabs is consistent not only with cessation of gene flow between the Pacific and Atlantic soon after the initial opening of the Bering Strait, but also with continuous residence on both sides of the Atlantic through abrupt climatic fluctuations over the past several hundred thousand years (Dansgaard et al., 1993).

The class II pattern can be illustrated by the gastropod genus Nucella discussed previously. As with Pagurus, an independent calibration of the rate of mitochondrial cytochrome b evolution in Nucella suggests a cessation of gene flow between the Pacific and Atlantic soon after the initial opening of the Bering Strait (Collins et al., 1996). Unlike Pagurus, however, there is virtually no divergence between populations of N. lapillus in the NW and NE Atlantic. European and North American populations share some identical mitochondrial haplotypes, and the average sequence divergence between the NW and NE Atlantic populations sampled over a 720-base pair region of cytochrome b is 0.05% (Collins, unpublished data). Another likely example of the class II pattern is of the barnacle Semibalanus balanoides. In a study of the AT-rich region of mitochondrial genome, S. balanoides exhibits a deep divergence between the North Pacific and the Atlantic, although the degree of divergence suggests a vicariance event in the past million or so years (Brown, 1995) Although there is considerable genetic diversity in the North Atlantic, there is no pattern of reciprocal monophyly between the NW and NE Atlantic (Brown, 1995; D. Rand, personal communication). This is consistent with a recent genetic connection across the Atlantic.

The class II pattern was also apparent in a study of the nuclear ribosomal intergenic spacer of the seaweed Acrosiphonia arcta (van Oppen et al., 1994). Like other class II species, there is deep divergence between Pacific and Atlantic populations and little divergence across the Atlantic. Unlike other class II species, however, high
Arctic populations of *A. arcta* in Greenland show great divergence from Pacific populations and from other Atlantic populations. Van Oppen et al. (1994) interpreted the high Arctic and temperate populations as having resulted from independent invasions from the Pacific.

What organismal characteristics might we expect to be associated with these patterns? Because both classes I and II show little or no genetic connection across the Arctic, they are likely to be largely absent from Arctic regions. Also, because class I taxa show deep genetic divergence across the North Atlantic, they are likely to have resisted local extinction through at least the most recent glacial episode.

By contrast, Atlantic members of class II taxa have diverged from Pacific taxa, but appear to have had a recent genetic connection across the Atlantic. Although this pattern can result from continuing gene flow, this is unlikely to be the only cause since at least one of the class II taxa, the gastropod *Nucella lapillus*, has non-planktotrophic larvae (Collins et al., 1996). A more likely possibility is that non-planktotrophic taxa went locally extinct on one coast or the other, only to be recolonized from the other coast, most likely by rafting of adults (Johannesson, 1988; Ingólfsson, 1992, 1995). As discussed previously, taxa found on the rocky shore of the NW Atlantic are especially likely candidates for local extinction. The absence of rocky shore south of Cape Cod may be fatal for *N. lapillus*, which is restricted to rocky shores, but not necessarily for *Pagurus*, which is more flexible in its habitat requirements (Ingólfsson, 1992).

Although habitat requirements and geographic range for these taxa seem consistent with expected class I and class II patterns, larval dispersal ability is clearly not a reliable predictor. It is *Pagurus*, with larvae that can spend 2–3 weeks in the plankton that shows deep trans-Atlantic divergence, whereas *Nucella*, with non-planktotrophic larvae, shows evidence of recent genetic connection.

**Low Pacific-Atlantic divergence: classes III and IV**

Taxa in classes III and IV show evidence of very recent genetic connection between the North Pacific and the North Atlantic (Fig. 6). The class III pattern is further characterized by a deep genetic divergence between the NW and NE Atlantic. This intriguing pattern is consistent with successive invasions of the Atlantic from the Pacific. The class III pattern has been observed in three taxa: the sea urchin *Strongylocentrotus droebachiensis* (Palumbi and Wilson, 1990; C. Biermann, personal communication), the red alga *Phycodrys rubens* (van Oppen et al., 1995) and the clam *Macoma balthica* (Meehan, 1985; Meehan et al., 1989). All three taxa show less divergence between the NW Atlantic and the North Pacific than either does with the NE Atlantic. The pattern is somewhat more complicated in *Macoma balthica* because a small population of NE Atlantic genotypes has recently been introduced into the San Francisco Bay. Introductions into the San Francisco Bay are
relatively common, and are presumably caused by ballast water discharge (Meehan et al., 1989; Carlton and Geller, 1993).

Likewise, populations of the smelt Osmerus from the NW Atlantic show evidence of more recent genetic connection with the Pacific than with the NE Atlantic (Taylor and Dodson, 1994). Although Osmerus shows reciprocal monophyly among all three areas, the degree of genetic divergence between the NW Atlantic and the North Pacific is substantially lower than the degree of divergence across the Atlantic (6.6 vs. 15% in the cytochrome b gene).

Interestingly, all class III taxa only show evidence of recent genetic connection between the Pacific and the NW Atlantic, but not with the NE Atlantic. This is consistent with the hypothesis that class III taxa have been in continuous residence in the NE Atlantic for some time, but that the NW Atlantic has been recently colonized from the Pacific. In the case of the sea urchin S. droebachiensis, the presence of identical haplotypes in the Pacific and Western Atlantic indicates a recolonization within the last 100,000 years (Palumbi and Kessing, 1991). Although NW Atlantic populations of the smelt Osmerus may have experienced relatively recent gene flow with populations from the Pacific, this connection appears to predate other class III taxa (Taylor and Dodson, 1994).

As with class II taxa, the class III pattern is consistent with local extinction in the NW Atlantic followed by recolonization from elsewhere. It may be that in some cases the only difference between class II and class III taxa is the location of the source population for recolonization, with a NE Atlantic source producing the class II pattern, and a Pacific source producing the class III pattern.

Class IV taxa show little genetic divergence either between the Pacific and the Atlantic, or across the Atlantic (Fig. 6). This pattern is seen in the sea urchin S. pallidus in which Pacific and Atlantic populations share identical mitochondrial haplotypes (Palumbi and Kessing, 1991; C. Biermann, personal communication). This pattern may result from recent, homogenizing gene flow, but is also consistent with a local extinction in the North Atlantic followed by recolonization from the Pacific. Palumbi and Kessing (1991) cite two factors supporting extinction followed by recolonization. First, the fossil record of S. pallidus, like S. droebachiensis, indicates that this taxon arrived soon after the initial opening of the Bering Strait ca. 3.5 Ma. Second, as with its congeneric S. droebachiensis, the genetic diversity of S. pallidus is extremely low, consistent with a recent and very extreme bottleneck (Palumbi and Kessing, 1991). Palumbi and Kessing argue that populations in both oceans were founded from a single refugium.

Another taxon showing the class IV pattern is the stickleback fish Gasterosteus aculeatus (Haglund et al., 1992; Ortí et al., 1995). The pattern of incomplete lineage sorting observed between the Pacific and the Atlantic strongly suggests a recent Pacific-Atlantic colonization event. Because Atlantic stickleback fossils go back 1.9 Ma, Ortí et al. (1995) have argued persuasively that the present pattern has resulted from a local extinction in the entire Atlantic followed by a recolonization from
the Pacific. As predicted by a recent range expansion, not only is genetic diversity in
the Atlantic lower than in the Pacific, but Pacific haplotypes are paraphyletic with
respect to Atlantic haplotypes (Orti et al., 1995).

Perhaps the best-studied taxon showing the class IV pattern is the mussel *Mytilus
trossulus*, which shows little divergence across either the Atlantic or the Arctic (e.g.
Varvio et al., 1988; McDonald et al., 1991; Rawson and Hilbish, 1995). Other *Mytilus*
species in the North Atlantic appear to have arrived during an earlier inva-
sion from the North Pacific. This earlier invasion gave rise to the endemic North
Atlantic species *M. edulis* and *M. galloprovincialis*. Of these, only *M. edulis* is cur-
rently found on both coasts of the Atlantic, and it shows very little differentiation
between the NW and NE Atlantic. This would place *M. edulis* in the class II cate-
gory.

*Summary of the histories of invading taxa*

When we consider genetic patterns of invading Pacific taxa now found on both
coasts of the Atlantic, complex patterns emerge. Some taxa appear to have had lit-
tle or no genetic connection between the North Atlantic and the North Pacific since
soon after the onset of Northern Hemisphere glaciation (class I and class II taxa,
Fig. 6). Other taxa appear to have undergone multiple invasions of the North
Atlantic (class III and some class IV taxa, Fig. 6). Interestingly, both class II and class
III patterns are consistent with recent local extinction in the NW Atlantic followed
by recolonization of the NW Atlantic from either the NE Atlantic (class II) or the
North Pacific (class III). Class II and class III patterns are consistent with the hy-
pothesis that the rocky-shore taxa of the NW Atlantic were especially hard hit dur-
ing the last glacial maximum (Vermeij, 1978, 1991a; Wethey, 1985; Ingólfssson,

Several questions and concerns remain. Chief among these is the correct identifi-
cation of taxa that have been introduced in historical times (e.g. Carlton and
Geller, 1993). The identification of introduced taxa is somewhat easier in the
Northern Hemisphere, due to relatively good historical records for macroinverte-
brates. One promising approach is to document the genetic pattern observed in spe-
cies known to have been introduced by human activity, and to treat with caution
any taxa displaying similar patterns. The other outstanding question is whether
taxa that show reciprocal monophyly across the same barrier were divided at the
same time (true congruence) or at different times (pseudocongruence). This issue is
beyond the scope of this chapter, but was considered in detail by Cunningham and
Collins (1994). Suffice it to say that for some taxa in the trans-Arctic interchange,
it should be possible to calibrate the rate of molecular evolution using fossil evi-
dence (e.g. Cunningham and Collins, 1994; Collins et al., 1996; Reid et al., 1996).
Are there generalities in molecular marine biogeography? Or has the focus on larval type been a red herring?

Using examples from the SE United States and the trans-Arctic interchange, we argued that there is no consistent relationship between larval type, usually considered a proxy for dispersal ability, and geographic subdivision. This lack of consistency is not new and was noted in some of the earliest reviews of marine population genetics and biogeography (Burton and Feldman, 1982; Burton, 1983). Yet despite these troubling observations, the relationship between larval type and geographical subdivision has continued to draw more attention than any other pattern. As with the examples we considered here, some studies in other parts of the world have found the predicted relationship (e.g. McMillan et al., 1992; Kohn and Perron, 1994; Hellberg, 1996), while others have not (e.g. Hedgecock, 1986; Edmands and Potts, 1997).

In this chapter, we argued that in many cases, patterns of local extinction and recolonization may be as important as larval dispersal ability and may help to explain anomalous observations. We conclude this chapter by reviewing how larval type may influence the ability of dispersing organisms to colonize new habitats.

The paradox of Rockall and the efficacy of larval dispersal

Rockall is a tiny rocky island in the North Atlantic, 400 km west of the Outer Hebrides. The paradox of Rockall is that this tiny, remote island has 17 species of invertebrates, all of which have nonplanktotrophic larvae (Johannesson, 1988). If planktotrophic larvae are better at dispersal, why are there no planktonic species? Furthermore, how have these nonplanktotrophic species colonized this remote open ocean island? The pattern found on Rockall is not unique. Cobb seamount, 510 km west of the coast of Oregon in the NE Pacific, has a benthic community of 117 species that contains mainly species with nonplanktotrophic larvae (Parker and Tunnicliffe, 1994). South Georgia, a much larger but even more isolated island in the South Atlantic, is also dominated by nonplanktotrophic species (Davenport et al., 1997). These cases indicate that in certain circumstances, species with nonplanktotrophic larvae are able to disperse great distances and colonize habitats where planktotrophic larval species are unable to establish viable populations.

Most of these nonplanktotrophic species appear to raft, or arrive on floating debris. There is direct evidence that the brooding bivalve Gaimardia trapesina has rafted on kelp as far as 1300–2000 km (Helmuth et al., 1994). In one study of 41 floating clumps of seaweed around Iceland, 39 taxa were found (Ingólfsson, 1995), including hundreds of representatives of gastropods and bivalves. Other benthic invertebrates, such as corals, may disperse as adults on floating pumice (Jokiel, 1989, 1990). In the ascidian Botrylloides, adults rafting on eelgrass dispersed about 200
times farther than planktotrophic larvae of the same species, and had comparable success at recruitment (Worcestor, 1994).

These results indicate that dispersal by rafting may be effective for colonizing new and distant habitats. Planktotrophic larvae may more commonly disperse great distances, but rafting of adults in nonplanktotrophic species, while perhaps less common, may more often result in the establishment of viable populations. A single female that has brooding larvae, is impregnated, or is storing sperm may establish a new population [in some gastropod species females may store viable sperm for over 1 year (Giese and Pearse, 1977)]. In new habitats the poor dispersal ability of nonplanktotrophic larvae may enhance the likelihood of establishment and survival of the population.

Therefore, it seems that the relationship between larval type and dispersal ability may be complex. In short, when local extinction takes place, recolonization from a neighboring area may be just as likely to take place by rafting as by dispersal of planktotrophic larvae. If this is true, then vulnerability to local extinction may be as important as dispersal ability in explaining patterns of geographic subdivision.

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