

HOT TOPICS IN MARINE BIOLOGY 17.1



The Molecular Sleuth Returns: Where Did the Invaders Come From?

Invasions from distant waters seem to be more and more frequent in recent years. Sometimes the source of an invasion is obvious. Some species are introduced purposefully, usually because they are useful food species and cultured easily. Until recently such introductions were rather frequent, with no attention paid to the possible disastrous side effects. The most dramatic of such changes in terrestrial faunas have occurred on oceanic islands, where introductions of pigs (done on purpose) and rats (by accident) have caused extinctions of many endemic species of snails, birds, small reptiles, and others on islands all over the world.

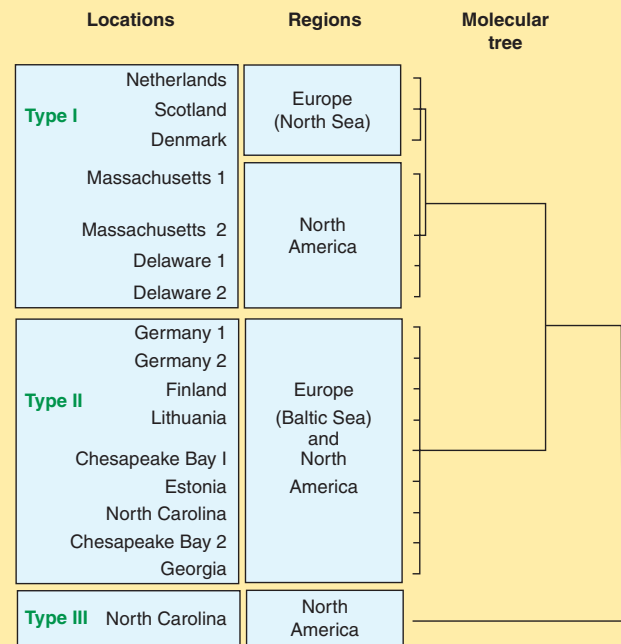
When an invasion occurs, the source of the new population may not be evident. This is of great interest from the points of view of both population biology and management. If a species invaded Europe from eastern North American waters, has a single shipping source been the invasion route, or are propagules coming from the entire eastern coast? From the point of view of management, a single source might suggest some decisions about regulating shipping.

Even if you arrive at a site within weeks of an invasion, you are probably unlikely to witness the vector, such as a shipload of larvae. More often, your objective will be to trace the invasion to its source, sometimes months or years after the new species has arrived. But what is the source? Populations of the green crab *Carcinus maenas* are found throughout the world and spread in the 1990s up from California to the Pacific Northwest, all the way to British Columbia. If a crab appears suddenly in Japan, for example, how will we know whether it came by shipping from South Africa, California, Europe, or Australia? Or could a few individuals have arrived on some floating material? Management decisions to reduce invasions depend on an understanding of the sources.

Morphological features are usually not very informative in tracing an invasion to its source. However, some DNA sequences have substantial genetic variation in populations, so it is possible to find markers that might connect one geographic region to another. The question is: To what degree can these differences be used to trace invasion routes?

Toward the end of the twentieth century, a small polychaete, *Marenzelleria viridis*, appeared in the North Sea (1979) and Baltic Sea (1985). This species has exerted negative effects on some native soft-bottom benthic species.\* *M. viridis* came from somewhere in eastern North American waters, but several alternative hypotheses can explain the observations. Perhaps the invasion of the North and Baltic seas happened from one source simultaneously, but the Baltic invasion was not noticed for a few years. Or did worms invade the North Sea and then spread to the Baltic? Or, finally, were there at least two different invasions from eastern North America into the North Sea and the Baltic, respectively? The salinity of the Baltic is typically only a few parts per thousand, whereas the North Sea has full open-ocean salinity. It is, therefore, of great interest that two such different bodies of water could be invaded by a single species, which apparently is very broadly adapted to salinity change.

\* See Kotta and others, 2001, and Neideman and others, 2003, in Further Reading, Hot Topics in Marine Biology.



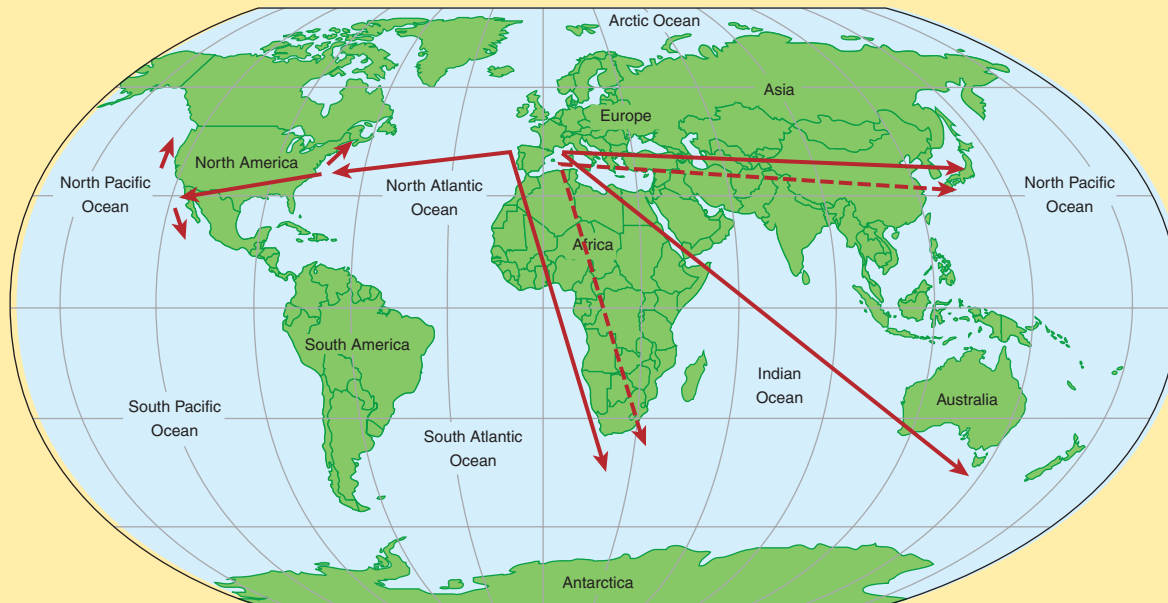
**BOX FIGURE 17.1** Genetic relationships among samples of the polychaete *Marenzelleria viridis* from eastern North American and European localities. Note that the North Sea samples cluster with Delaware and Massachusetts sites, but Baltic Sea samples cluster with more southern sites, many with low salinity. The clustering suggests separate invasions into the North Sea and Baltic Sea from two different source populations. (After Bastrop et al., 1998.)

Ralf Bastrop, Karl Jürs, and Christian Sturmbauer† attempted to solve the invasion problem by finding a molecular marker for source populations. They took samples from a number of localities along the east coast of North America and also from the North Sea and the Baltic Sea, and sequenced 16S rDNA, a sequence found in animal mitochondrial genomes. The results were striking and supported the separate invasion hypothesis (Box Figure 17.1). North Sea samples could be clustered with American samples taken in Delaware and northward. Baltic samples, however, clustered with American worms taken from Chesapeake Bay and nearby localities. The Baltic affinities were quite interesting because Chesapeake Bay has very low salinities and could have been the source of a population of immigrants that were adapted to low salinity and could better invade the Baltic.

The complications of invasions today make genetic markers essential in tracing the many sources and targets of invasion. The green crab (also known as the shore crab) is an excellent example (Box Figure 17.2). First of all, there are two closely related source species that contributed to the invasions: *Carcinus maenas* from the North Atlantic and *C. aestuarii* from the Mediterranean Sea. Both species apparently have invaded

† See Bastrop and others, 1998, in Further Reading, Hot Topics in Marine Biology. ▶

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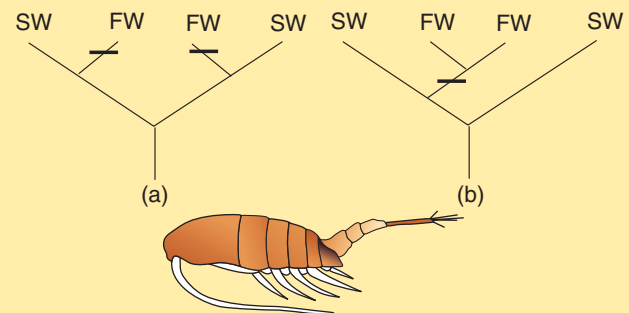
**BOX FIGURE 17.2** Presumed invasion routes of the crabs *Carcinus maenas* and *Carcinus aestuarii*. (Information for map mainly from Geller et al., 1997, and Grosholz and Ruiz, 1996.)

South Africa and Japan, but only *C. maenas* has made it to Australia and North America.<sup>‡</sup>

While invasions facilitated by human transport are now commonplace, one must remember that before people accelerated the process, larval and adult chance transport were still major sources of long-distance colonization. Populations of coastal benthic species could hopscotch from continent to continent if their larval life was long enough or if they could travel on floating materials. Now, fast-traveling ships bring larvae in ballast water. The colonizing populations are very small, however. Small populations tend to not have the genetic diversity of the large source populations, and DNA sequencing demonstrated that genetic variability was strongly reduced in the population of *C. maenas* that colonized eastern North America from northern Europe.

Once a population has arrived on a coast, it is far easier to spread along that coast than to cross an ocean. The crab appeared in San Francisco Bay in 1989 or 1990. Genetic variability in this population resembled the east coast of North America, which was the likely source population. As we discussed in Chapter 14, San Francisco Bay is probably the most highly invaded coastal water body in North America. By 1993, it had spread 80 km northward to Bodega Bay, California. In 1997 the crab had been spotted in Coos Bay, Oregon, and in the summer of 1999 it was spotted off southern Vancouver Island in Canada. It also has spread south from San Francisco. So rapid a spread is likely due only to dispersal via planktotrophic larvae. During the 1997–1998 El Niño, coastal water flow was northward along the Pacific coast of North America, which probably transported crab larvae to the outer coast of Vancouver Island.

<sup>‡</sup>See Geller and others, 1997, in Further Reading, Hot Topics in Marine Biology.



**BOX FIGURE 17.3** Two hypotheses of invasion of freshwater (FW) and marine (SW) populations of the copepod *Eurytemora affinis*. (a) A marine ancestor gave rise to two lineages, and the freshwater populations arose independently. (b) All freshwater lineages derive from one evolutionary event, with a marine lineage as an ancestor. Subsequently, the freshwater lineage invaded many widespread freshwater localities directly, resulting in divergence. Molecular evidence supports alternative (a).

The *Marezzellaria viridis* invasion example raises an interesting question that can be applied directly to a natural distribution problem. The copepod *Eurytemora affinis* is found widely distributed throughout the world in open marine coastal and freshwater populations. Two alternative hypotheses might explain the distributions (Box Figure 17.3). First, the same freshwater species might have invaded throughout the world, along with an independent invasion of an open marine species. Alternatively, invasions of open marine species onto a number of coasts might have been followed by subsequent local invasions of nearby freshwater rivers. The latter

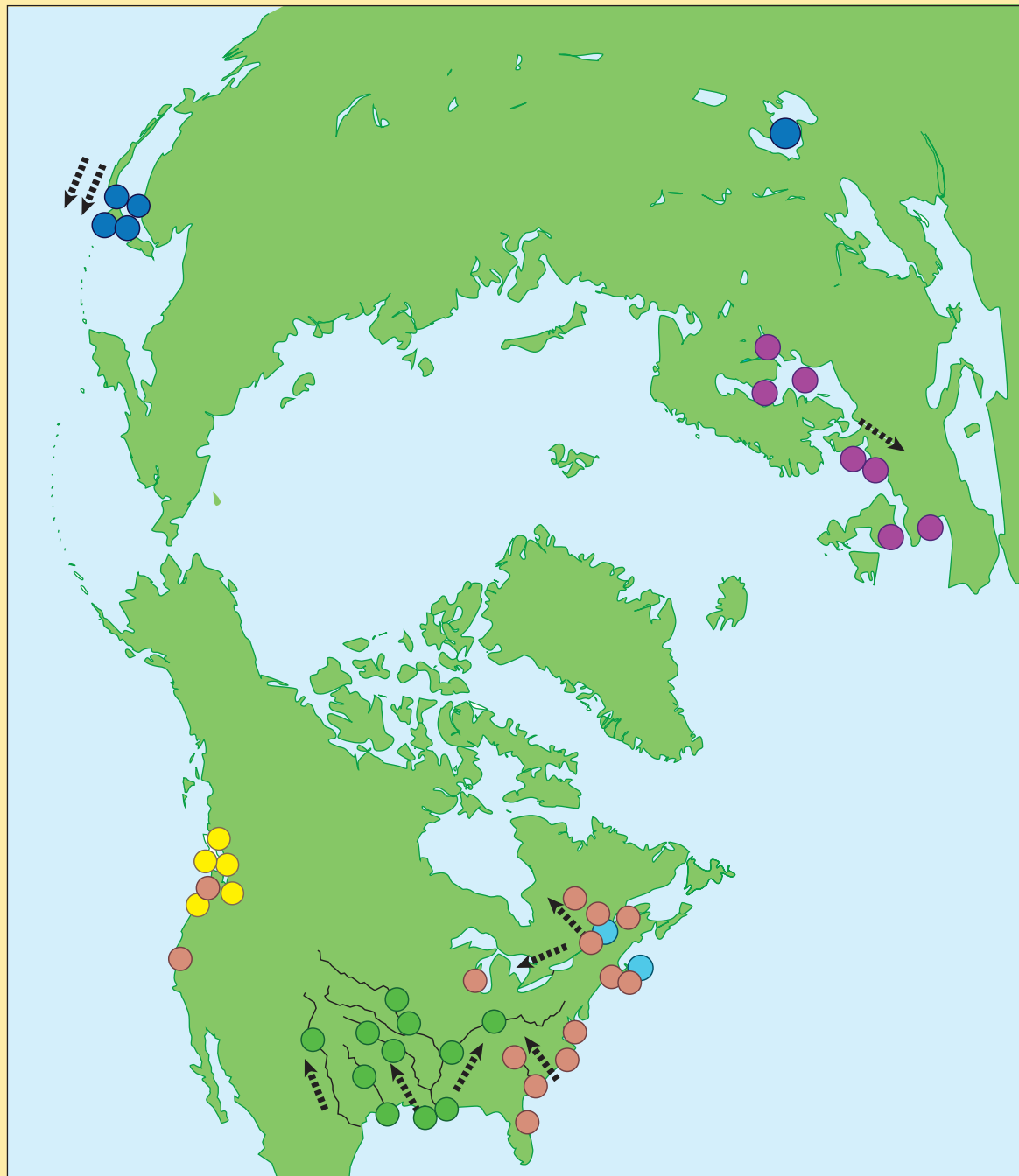
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hypothesis implies multiple origins of the freshwater populations and, therefore, multiple instances of adaptation to fresh water by marine populations. Carol Lee<sup>5</sup> used sequences of the mitochondrial gene for *Cytochrome oxidase 1*, and obtained evidence for at least

eight invasions of coastal waters throughout the world. At least five of these freshwater invasions most likely arose independently in different river drainages, but the colonization of each river drainage was derived from saltwater sources nearby on the coast (Box Figure 17.4). Colonization and adaptation to freshwater is therefore frequent.

<sup>5</sup>See Lee, 1999, in Further Reading, Hot Topics in Marine Biology.



**BOX FIGURE 17.4** Invasions and spread of the copepod *Eurytemora affinis*. Color coding indicates populations that can be closely grouped on the basis of molecular sequence similarity. (Courtesy of Carol E. Lee.)