HOT TOPICS IN MARINE BIOLOGY 14.1

The Powerful Interaction of Invasion and Climate Change

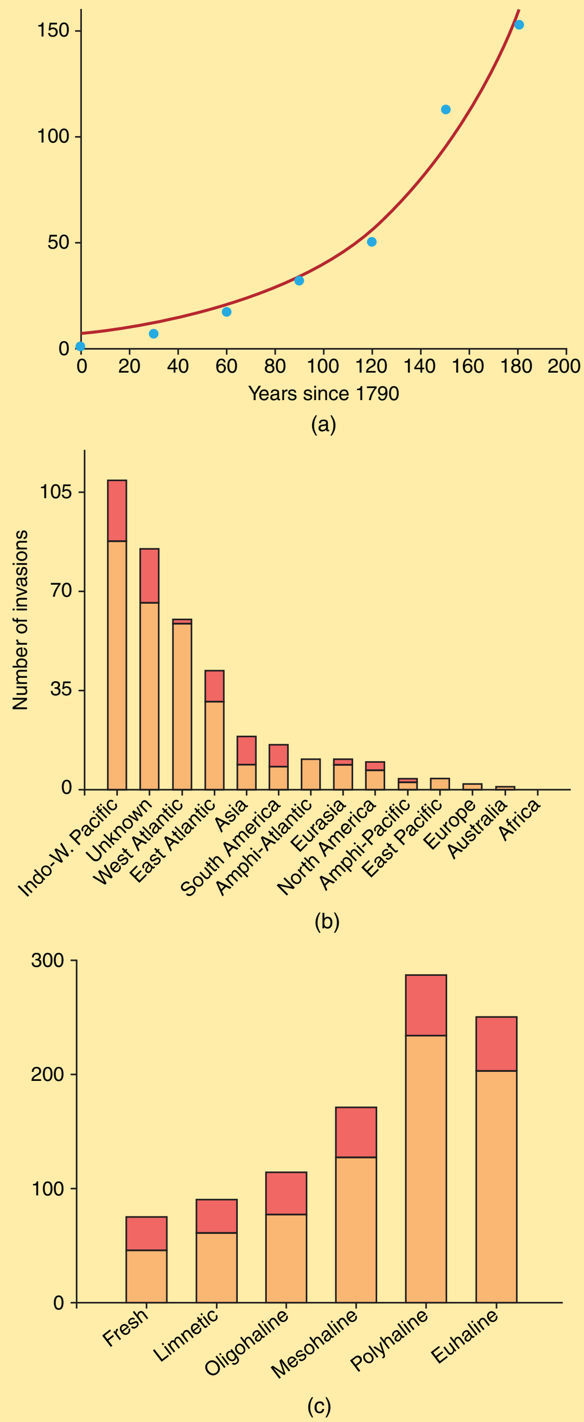
While some species may have been overlooked, we can state with a fair amount of confidence that alien species are appearing throughout the world and some are increasing in abundance to the point that they have strong effects on local biotas. These effects are sufficiently notable that we cannot have overlooked such a barrage of new invaders in the past. The work of a number of investigators has recently established a scenario involving the *interaction* of factors that is likely to completely reorganize the ecological structure of rocky-shore habitats throughout the world.

Briefly stated, here is the working hypothesis: (1) Invasion frequency is on the rise. Transport of larvae and adults by fast-moving shipping throughout the world greatly increases the rate of arrival of potential invaders. (2) Global warming is changing climate conditions throughout the marine world. This is encouraging the successful spread of species that are better adapted to warm water than local resident species. (3) As local environmental disturbance increases, biological diversity decreases. This decreases the extent of exploitation of resources by local species, which makes invasion more likely. Other warm-tolerant invaders, such as diseases and harmful phytoplankton species, may also be more on the rise.

INVASION FREQUENCY

Scientists have identified about 300 marine and estuarine species that invaded the United States by the year 2000 (Ruiz et al., 2000). It is not always trivial to exactly define what an invasive species really is. After all, nearly all of the hard-substrate-dwelling invertebrates living today on the east coast of the United States invaded the Atlantic from the Pacific nearly 3 million years ago, by an Arctic seaway connection. The snail *Littorina littorea* exploded in abundance in the northeastern states in the nineteenth century, but it is not exactly clear when this species first arrived from Europe. It has been found in shell middens dating back a few thousand years and even in a Viking settlement on the northern shore of Newfoundland, reckoned to be about 1,000 years old. Molecular evidence supports the idea that it was in the Americas for several thousand years, but accounts from local naturalists show clearly that *L. littorea* was not south of Nova Scotia until the end of the nineteenth century. Many other species that have suddenly appeared are believed to be **cryptogenic**, which means that they were here all along, but were too rare to have been noticed. The bivalve mollusk *Rangia cuneata* has increased in scattered east coast estuaries in recent years, but we are not sure whether it was continuously present all along, or managed to disperse from remote estuaries along the Gulf of Mexico. As a result it is not so easy to answer a simple question: Which places have been invaded the most? Chesapeake Bay has fewer listed invasive species than San Francisco Bay; but it is possible that many species that are thought to be native simply arrived early on, even in colonial days, but were not noticed to be invasives.

Despite all of these uncertainties, Greg Ruiz and colleagues accumulated records of first appearances, water body of origin, and likely means of dispersal. They demonstrated that invasion frequency has been steadily increasing (**Box Figure 14.1**). Most species have come by means of ships, and most are adapted to open



BOX FIG. 14.1 A profile of marine invasions. (a) Frequency of invasions over time; (b) number of invasions as a function of region; and (c) number of invasions as a function of salinity of the water body. Red part of bars indicates repeated invasions. (After Ruiz et al., 2000)

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marine or near-marine salinities. Purposeful introductions of alien species to enhance fisheries and even accidental releases of imported pets are also major vectors. Most invasions of invertebrates and algae came from the Indo-Pacific region and invaded the west coast of the United States.

CLIMATE CHANGE

In Chapter 2, we documented the steady increase in sea-surface temperature in shallow-water localities on both coasts of North America, and most of the ocean. The increase is likely to impose physiological stress on some species, but will also shift reproductive cycles, migration routes, and larval success. Because of a history of millions of years of seafloor spreading and continental drift, most of our world's coastlines extend north and south over many degrees of latitude. In any one location, we usually have a mix of species, some which are better adapted to warmer temperatures, some to colder temperatures. Temperature change, therefore, will shift the advantage toward some species that perform better at higher temperatures.

How will invasive species enter the picture? Imagine a group of native species, all living in a location where temperatures are increasing. Imagine that these species are in the typical sort of coastal environment where local environmental fluctuations are strong and human disturbance is fairly common. Robert Whitlatch's research group at the University of Connecticut (see Stachowicz et al., 2002) have been monitoring rocky shores of eastern Connecticut for many years, and water temperatures have been steadily increasing. Sea squirts tend to dominate rocky surfaces on the lower shore, but their dominance is quite ephemeral. Most colonies tend to senesce in late fall, so dominance the next spring and summer arises from the timing and magnitude of recruitment of larvae from the few colonies that survive the winter. Sea squirt larvae are planktonic but larvae live for only a few hours, so recruitment derives from nearby sources. Stachowicz and others (2002) found that native sea squirts recruited more in colder years, and that the timing of recruitment of natives was uncorrelated with sea-surface temperature. (Incidentally, one of the so-called natives really was an invasive, but arrived over 100 years ago!) In contrast, the dominant invasive species recruited earlier in years when sea-surface temperature was above average: Warmer winters seemed to be the key to the success of invaders. This gave them priority, and they tended to dominate the rocks. As climate gets warmer, this trend will only increase. Ironically, another invasive species has invaded deeper waters, and this species tends to be successful in colder periods. It has blanketed the bottom of much of eastern Long Island Sound. In the long run, however, the warm-adapted species will win.

RESISTANCE TO INVASION BY DIVERSE LOCAL BIOTAS

As temperature increases, invasion occurs against a backdrop of local variation in population size and diversity. Species come and go. The important question is whether environmental disturbance and reduction of local diversity increases the success of invasions. With a large number of resident species, it is probable that more and more will exist that will occur in the different microhabitats. The net result will be an occupation of all available food and space resources. The complete occupation of resources leads to an obvious prediction: Invasive species should have trouble invading high-diversity communities. A stable, high-diversity community will consist of species that, in total, consume a large fraction of the available resources, suggesting that the possibility for successful invasion is lower in high-diversity communities. At any one time, a given species might be declining in population density, but if there are many species, then some other species will take its place on the resource occupied by the first species. Thus the total resource use will remain high, making it hard for additional species to invade from without.

John Stachowicz, Robert Whitlatch, and Richard Osman (1999) completed a study focusing on the native and invasive sea squirts we

BOX FIG. 14.2 The colonial sea squirt *Botrylloides diegensis* has invaded rocks of southern New England and displaced colder-water-adapted native species. Here, colonies of *B. diegensis* are overgrowing native *Ciona* sea squirts, colored white. (Courtesy of Robert Whitlatch)

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have discussed. In southern New England, the Pacific Ocean ascidian *Botrylloides diegensis* has invaded and spread in recent years (Box Figure 14.2). The native community in any one small area of rock usually consists of three or four different sessile species, and the question is whether they can resist invasion by virtue of their diversity.

They hit upon an ingenious and simple experimental design. They allowed species of native sessile suspension-feeding invertebrates to settle and dominate small 232 cm^2 tiles, which were then combined into assemblages of one, two, three, and four species. The "community" consisted of 25 tiles with the different species combinations and 5 tiles covered by the potential invader *Botrylloides diegensis*. The results were impressive: *Botrylloides* mortality was higher in the tile assemblages with higher species diversity.

The mechanism for resistance to invasion by more sessile species may lie in the compensating effect of having more species that can utilize a resource. Stachowicz and others found that if the tiles had only one or two species, population fluctuations often resulted in large areas of empty space. But with more species, one species might increase in numbers and take the space given up by species in decline. Under these circumstances, an assemblage with low species richness might be more likely to have available resources for an invading population, whereas higher diversity might result in more complete and continuous resource use, which would repel invasions. It is possible for one species to dominate space and repel invasions, but the seasonal nature of the environment and the eventual occurrences of disturbances will kill off some of the species and open space for invasion.

Does disturbance facilitate invasion? Altman and Whitlatch (2007) simulated disturbances on hard surfaces and found that native sea squirt species suffered, relative to nonindigenous species. As might be expected, colonial species invaded disturbed surfaces more readily than solitary species, probably because of the ability of colonials to spread by vegetative growth on surfaces.

Overall, warming alone is not the key to successful invasions. It is the interaction between factors that matters. Invasive species are warm adapted, but their success is facilitated by an interaction with local diversity, which is influenced by disturbance frequency. These scenarios are probably common and make invasion biology a series of complex interactions that often may be understood only retrospectively. ■

FIG. 14.31 The salt marsh at Herring Creek, near Harwich, on Cape Cod, Massachusetts. Tall form of *Spartina alterniflora* in foreground; short form behind. In the distance is the common reed *Phragmites australis* fringing the marsh. (Photograph by Jeffrey Levinton)

Spartina Salt Marshes

Ecosystem Engineers, Geographic Extent, and Setting

- ***Spartina* salt marshes are dominated by cordgrasses, which function as ecosystem engineers by binding fine sediment and causing the buildup of meadows above low water.**

Spartina salt marshes (**Figure 14.31**) develop in tidal areas of quiet water, where a variety of salt-tolerant grasses colonize the sediment and then trap fine sediment. A study of *Spartina* salt marshes on the Atlantic and Gulf coast of North America found a range of vertical sediment accretion rate of 0.09 to 1.78 cm per year (Turner et al., 2002). Characteristic of these grasses is an extensive **rhizome system** beneath the sediment surface, which is crucial in maintaining the structure of the marsh sediment and the entire salt marsh.

Spartina alterniflora, the dominant eastern and Gulf coast American species found lowest in the intertidal