3

Invasive Animals in Marshes

BIOLOGICAL AGENTS OF CHANGE

James E. Byers

Relative to other marine systems, salt marshes and estuaries are highly susceptible to invasion, and impacts by exotic species in these systems seem particularly pronounced. These impacts range from purely trophic and competitive effects that can lead to replacement of native species by exotics, to physical transformation by exotic species that engineer habitat and alter large-scale abiotic and hydrographic properties of the marsh environment. I discuss several examples of each of these, as well as three mechanisms that promote high establishment rates and strong competitive effects of nonnative species in marshes.

Although the problem of exotic species in marsh systems is substantial, marshes' tractable, discrete boundaries make intervention more successful than in other marine systems, such as the open coast. However, protocols and policies (ideally standardized at a national or international level) need to be in place for eradication or containment of incipient invasions, which often require fast action to be effective. Protocols and monitoring efforts should aim not only to detect newly introduced species but also to quantify the dynamics and impacts of established invaders to enable prioritization of intervention efforts. Estuaries and associated marshes are a heavily invaded habitat that must be well managed to mitigate the increasing ecological impacts of exotic species on native species and the valuable ecosystems services they provide.

Salt marshes are one of the most anthropogenically impacted marine ecosystems (Cairnes 1993; Kennish 2001; Nicholls 2004). Historically, physical and chemical impacts to salt marshes have been the most conspicuous and influential. Physical changes include extensive habitat conversion (e.g., filling and dredging) and altered hydrography that stem, especially in recent times, from marshes occupying valuable coastal real estate. Kennish (2001) calculates that more than 50 percent of original tidal salt marsh in the United States has been lost through such physical alterations. Chemical impacts on marshes largely result from the close proximity of this marine habitat to humans and the associated pollutants they produce. That is, salt marshes are typically the outlets for watersheds where large volumes of anthropogenic pollutants are deposited (Fox et al.

1999; Sanger, Holland, and Scott 1999; Holland et al. 2004). Furthermore, as the large number of marsh Environmental Protection Agency (EPA) Superfund sites attests, marshes historically have directly received large quantities of contaminants because they were perceived as a convenient, valueless dumping ground.

While these physical and chemical impacts have affected marsh biota for decades, only relatively recently, with the surge in globalization and consequent transport of nonnative species, have biological forces themselves been recognized as major agents of change (e.g., Ruiz et al. 1999). By skewing optimal environmental conditions away from conditions to which native species are adapted, many physical and chemical impacts may have set the stage for more frequent and successful biological invasions. Biological impacts of nonnative species range from purely trophic and competitive effects that can lead to replacement of native species by exotics, to physical transformation by exotic species that engineer habitat and alter large-scale abiotic and hydrographic properties of the marsh environment. Perhaps the best-documented example of the severe biological impacts possible from invasive species is San Francisco Bay, where more than 240 nonindigenous species now reside, and 90 to 95 percent of the biomass is exotic in many areas of the bay (Cohen and Carlton 1998; Lee, Thimpson, and Lowe 2003). Clearly, to fully understand modern impacts on both the function and the taxonomic composition of estuaries and salt marshes, impacts of exotic species must be considered.

Relative to other marine systems, salt marshes and estuaries are highly susceptible to invasion, and impacts by exotic species in these systems seem particularly pronounced. I begin this chapter by discussing underlying properties of estuaries that may be important in explaining these patterns. I then highlight some prominent impacts driven by invasive animals in salt marshes, using examples of nonindigenous species that exert large engineering effects and ones whose impacts are limited to trophic or competitive effects. I briefly conclude with recommendations for how to best monitor and manage salt marshes against these threats. Although the focus of this chapter is animal invasions, most of the messages here are germane to invasions of all types.

ESTUARIES, INCLUDING THEIR ASSOCIATED MARSHES, ARE THE MOST INVADED MARINE HABITAT

Compared to open coasts, a much higher number and proportion of exotic species are found in embayments, including associated marshes (see, e.g., Ruiz et al. 1997, 2000; Reise, Gollash, and Wolff 2002; Nehring 2002). For example, in Elkhorn Slough, California, Wasson, Fenn, and Pearse (2005) documented 526 invertebrates comprised of 443 natives, 58 exotics, and 25 cryptogens (species whose geographic origin is uncertain). The surrounding rocky intertidal open coast contained 588 species, of which only 8 were exotic and 13 cryptogenic. The number and proportion of exotics were significantly higher in the estuary (11 percent) than on the adjacent coast (1 percent). Furthermore, exotic species in the estuary were not only more diverse but also more abundant and conspicuous than on the open coast (e.g., the mudsnail *Batillaria attramentaria*, the orange sponge *Hymeniacidon*, the reef-building tube worm *Ficopomatus enigmaticus*). Similarly, while more than 240 nonnative species are known from San Franscico Bay, fewer than 10 are found on the adjacent outer coast (Ruiz et al. 1997).

Perhaps even more enigmatic is the observation that in many cases, even species that are typically open coast residents in their native habitats often remain in embayments and marshes in their introduced range (Griffiths 2000; Robinson et al. 2005; Wasson et al. 2005). For example, the snail *Littorina saxatilis*, which is almost exclusively coastal in eastern North America and Europe where it is native, has not left the confines of San Francisco Bay where it has been established for more than a decade (Carlton and Cohen 1998; W. Miller, personal communication).

Clearly this pattern of a higher number of invaders in marshes and estuaries may be due in part to a sampling bias. Embayments and marshes are located nearshore in close proximity to humans, who as a result have examined these habitats more than most other marine habitats (e.g., Ruiz et al. 1997, 2000; Cohen and Carlton 1998; Hewitt et al. 1999). In addition, compared to open marine systems, salt marshes have discrete boundaries and a high proportion of benthic, tractable species.

However, three general, spatially variable factors likely contribute to a true pattern of higher numbers of introduced species in estuaries and marshes. First, bays and their associated marshes receive vast quantities of exotic propagules from ballast water. In U.S. ports alone, tens of millions of metric tons of ballast water from ports of origin all over the world are discharged yearly, with each liter containing up to ten zooplankton organisms (Verling et al. 2005). Second, bays are retention zones where larvae often are not advected away. Byers and Pringle (2006) demonstrated that advection typical of open coastlines makes retention, and thus establishment, difficult and may be largely responsible for the dearth of invasive species in those environs. Third, marsh and estuarine habitats best match the habitat from which most nonindigenous species propagules are exported. Two of the biggest vectors for nonindigenous marine species are ballast water and aquaculture, particularly shellfish imports (Ruiz et al. 2000). These sources most often originate from estuaries and bays, and the similarity of source and recipient habitats, especially in the case of intentionally introduced oysters and their associated communities (Ruesink et al. 2005), results in a high rate of successful establishment.

EXOTIC SPECIES MAY HAVE GREATER IMPACTS IN ESTUARIES AND MARSHES THAN OTHER MARINE HABITATS

Having more nonindigenous species in estuaries and marshes increases not only their cumulative impact but also the odds of having species with particularly high per capita impact. That is, having more exotic species essentially creates a sampling effect, whereby more species simply means species with greater impacts have a higher probability of being among those established.

However, even after we standardize for the number of introduced species, we may still expect marshes to experience larger impacts from exotic species for at least two additional reasons. First, as emphasized previously (and throughout this book in general), salt marshes are one of the most anthropogenically disturbed habitats. Pollutants, eutrophication, habitat filling, drainage, dredge spoils dumping, and channelization are a few of the many, often severe abiotic alterations humans have imposed on this habitat type (e.g., Kennish 1992, 2001; Valiela, Rutecki, and Fox 2004; see also chaps. 8 and 9, this volume). The novel and sustained environmental changes that anthropogenic disturbances impose may often be enough to move a species out of the parameter space that defined its evolutionary history and to which it was adapted—a process dubbed selection regime modification (SRM) (Byers 2002a). A native marsh species may therefore suddenly find itself in an environment that in key ways is just as novel as it is to a nonindigenous species (Byers 2002a). SRM can thus accentuate competitive impacts of exotics on natives by eliminating a native species' prior resident effect or "home court advantage." That is, disturbances increase invader establishment and impact not only by creating new microhabitats, introducing propagules, and decreasing populations of native species that can resist invasion, but also by potentially weakening the *per capita* ability of the native biota to resist invaders. Because marshes are usually heavily altered by humans, they are a prime environment for selection regime modification and thus large resultant impacts through competition with exotic species (Byers 2000b, 2002a).

Second, the retentive environment that contributes to increased exotic establishment in marshes also likely enhances their population-level competitive effects (Byers and Pringle 2006; Byers 2009). Within marshes, populations tend to be closed, and impacts of exotic species on natives may therefore be intensified. Specifically, because there is tight coupling of adults and successive generations, local, density-dependent impacts of exotic species may directly effect a lower population growth rate of the resident population. The separation between disparate marshes along a coast helps ensure their insulation and provides little chance that a declining native population will receive a rescue effect from an immigration pulse.

Although the closed nature of salt marsh and estuarine habitats increases the propensity for high competitive impacts, it also has positive implications. This tendency toward closed populations should make invasive species there easier to control, mitigate, or eradicate. In fact, nearly all marine eradications are done in embayments. For example, Anderson (2005) describes the successful response of various government and nonprofit agencies responding to incipient invasions of *Caulerpa taxifolia* in a small southern California lagoon. Similarly, Hutchings, Hilliard, and Coles (2002) discuss the discovery of a problematic invasive mussel, *Mytilopsis sallei*, in two harbors near Darwin, Australia. The harbors were quarantined, and large doses of sodium hypochlorite and copper sulfate were added to poison the mussel. The process successfully eliminated *Mytilopsis* despite densities of the mussel that had already reached ten thousand square meters (Kuris 2003). In contrast, few if any eradication attempts on the open coast have been reported, except for one that was successful (Culver and Kuris 2000). An established population of the African shell-boring sabellid polychaete, *Terebrasabella heterouncinata*, was eliminated from a coastal site in California by removing 1.6 million potential snail hosts in the infected area (Culver and Kuris 2000). Although eradication was successful, it was only possible due to an extremely anomalous, localized distribution of the invader.

EXAMPLES OF PROBLEMATIC ESTUARINE/MARSH ANIMAL INVADERS

Before we delve into some examples, it is worth stating that the depiction and assessment of impacts by nonindigenous species in marshes (as well as most every ecosystem) is likely conservative. Although there is a growing body of research on impacts of marine invaders (e.g., Grosholz 2002), many early invasions occurred with little notice. Presumably many of their immediate and pronounced impacts could have occurred long ago (Cohen and Carlton 1998), setting a different baseline for benchmarking modern-day changes (Dayton et al. 1998). A further issue that compounds the difficulty of assessing impact is the problem of cryptogenic species, species whose definitive native geographic distribution is unknown. For example, Ruiz et al. (2000) tallied 298 exotic invertebrate and algal species in coastal and estuarine waters of North America; however, this figure excludes cryptogenic species, hundreds of which may in fact be exotic species that just have not been identified as such. Even if impacts by such cryptogenic species are observed, the impacts cannot be definitively ascribed to an exotic species. Carlton (1996) estimates that 37 percent of the total number of known exotic and cryptogenic species in San Francisco Bay are cryptogenic; in Chesapeake Bay, this percentage is far higher. Robinson et al. (2005) report that South Africa has ten marine species that are confirmed as exotic and twenty-two as cryptogenic.

As in the ecological literature, the taxa on which my examples are focused are better studied because they are larger and economically or culturally important. The invasion history of many fish, crustaceans, and mollusks, for example, is typically well known due to their importance as a human food source (and for mollusks also their interest to early shell collectors). Ray (2005b) calculates that in the Pacific Northwest and Alaska, 47 of the 162 exotic marine and estuarine animal species are mollusks and 39 are crustaceans, thus combining for over half of the total. Similarly, Ruiz et al. (2000)

determine that half of the identified exotic invertebrate and algae species in coastal and estuarine waters North America are mollusks and crustaceans. Nonnative fish species are also a large contributor (Ruiz et al. 2000; Ray 2005a). For these species, it is not uncommon to have some background data on their invasion history and sometimes even their population dynamics. In contrast, many microorganisms, including diatoms, protozoans, and fungi, are easily transported unintentionally by humans, yet little historic record exists of these organisms because early natural historians seldom had the interest, let alone the expertise to identify them. Even today, many of these taxa are overlooked. Thus, the ease of incidental introduction and the likelihood of invasion detection are inversely correlated (Ruiz et al. 2000). Therefore, as a preface to the following examples, it is important to keep in mind that we know little about the impacts from what are likely to be the most common invaders.

The examples that follow are organized by type of impact: invasive ecosystem engineers that change the structural character of the system and other invasive species that change competitive or trophic relationships between species. While there is a growing list of problematic, conspicuous invaders of North American estuaries and marshes (e.g., Chinese mitten crab *Eriocheir sinensis*, in San Francisco Bay [Rudnick et al. 2003]; Atlantic ribbed mussel *Guekensia demissa*, in California and Baja Mexico [Torchin, Hechinger, et al. 2005]), I have selected examples to illustrate some of the best-documented, quantified impacts.

PROMINENT EXAMPLES OF EXOTIC ECOSYSTEM ENGINEERS

Organisms that create, modify, or destroy structure often disproportionately affect the communities they invade. These so-called ecosystem engineers (Jones, Lawton, and Shachak 1994) essentially alter the entire playing field on which ecological interactions take place by changing habitat structure, refuge availability, and even abiotic processes (e.g., hydrography) (Wright and Jones 2006; Crain and Bertness 2006). Especially in urban areas, where marshes are often already small fractions of their original extent, any habitat conversion by ecosystem engineers can alter a substantial proportion of remaining marsh habitat. In terrestrial realms, ecosystem engineers are predominantly plant species, whereas in marine environments, it is largely animals that fill this role (e.g., oysters, coral, tube worms) with occasional contributions from vegetation (e.g., macroalgae) (Crooks 2002). As interfaces between terrestrial and marine environments, salt marshes have a mix of plant and animal engineers. Traditionally, the focus in marshes has been on the structural changes caused by introduced angiosperms (see chapters on *Spartina* and *Phragmites* in this volume), but plenty of invasive animal species are causing structural change as well. Examples of organisms that have been shown to be important habitat engineers include oysters, the tube worm *Ficopomatus enigmaticus*, the mussel *Musculista senhousia*, the burrowing isopod *Sphaeroma quoyanum*, and nutria (*Myocastor coypus*). These species engineer habitat in their native range as well; however, in a novel environment where their habitat structure arises *de novo* or where there are few checks on their abundance and thus the scale or rate at which habitat is altered, they can strongly affect native biota that do not share a common evolutionary history with the invasive engineer (Crooks 2002).

FICOPOMATUS ENIGMATICUS

Ficopomatus enigmaticus is a cosmopolitan, reef-building serpulid polychaete introduced to many estuaries worldwide, including marshes of California and coastal lagoons of Argentina (fig. 3.1). In Mar Chiquita Lagoon, Argentina, reefs composed of thousands of calcareous tubes of this species cover roughly 80 percent of the lagoon. Reefs, which can be up to 4 meters in diameter and 0.5 meter high, increase habitat structure, modify the abundance of species that use it for shelter, and change the pattern of distribution of soft-bottom species (Schwindt and

FIGURE 3.1 *Ficopomatus enigmaticus* reefs in Argentina. Photo courtesy of Martin Bruschetti.

Iribarne 2000). The reefs built by *Ficopomatus* in Mar Chiquita also greatly affect the physical environment by altering the bedload sediment transport and water flow (Schwindt, Iribarne, and Isla 2004). In general, ecosystem engineering species, such as *F. enigmaticus*, that invade soft sediment environments and create hard substrate tend to have large impacts on community composition. This is because hard substrata are novel to most marshes, and thus they often provide exotic species equal opportunity to compete for space because native marsh species are not specifically adapted to this habitat type. Thus, transformation of soft bottom estuarine habitat into hard substratum is a prime example of selection regime modification, and it has been found to be associated with increases in invasive species (Wasson et al. 2005; Tyrrell and Byers 2007).

MUSCULISTA SENHOUSIA

Several decades ago, this Asian mytilid mussel invaded marshes and associated mudflats of Mission Bay (San Diego), San Francisco Bay, and Puget Sound among others along the Pacific coast of North America (Crooks 1998). The mussel anchors itself through byssal mats it produces that dramatically alter soft sediment habitats. Crooks (1998) noted marked changes to sedimentary properties and to the resident biota. Densities of macrofauna as well as species richness were typically higher inside than outside mussel mats. A tanaid amphipod, *Leptochelia dubia*, and the gastropod *Barleeia subtenuis* were particularly enhanced within mussel mats. In contrast, the abundance of native, filter-feeding clams declined, possibly because of competition for food (Crooks 2001). Through a series of experiments that compared community effects of live mussel mats to structural mimics, Crooks and Khim (1999), demonstrated that the physical structure of the mussels far outweighed the effects of living mussels. In fact, they determined specifically that the structure provided by the mussel mats was more influential than the mussel shells. In general, the effects of *Musculista* and *Ficopomatus* agree with observed effects of other habitat-modifying exotic ecosystem engineers, illustrating dramatic effects on biota by nonnative species capable of creating and altering physical structure.

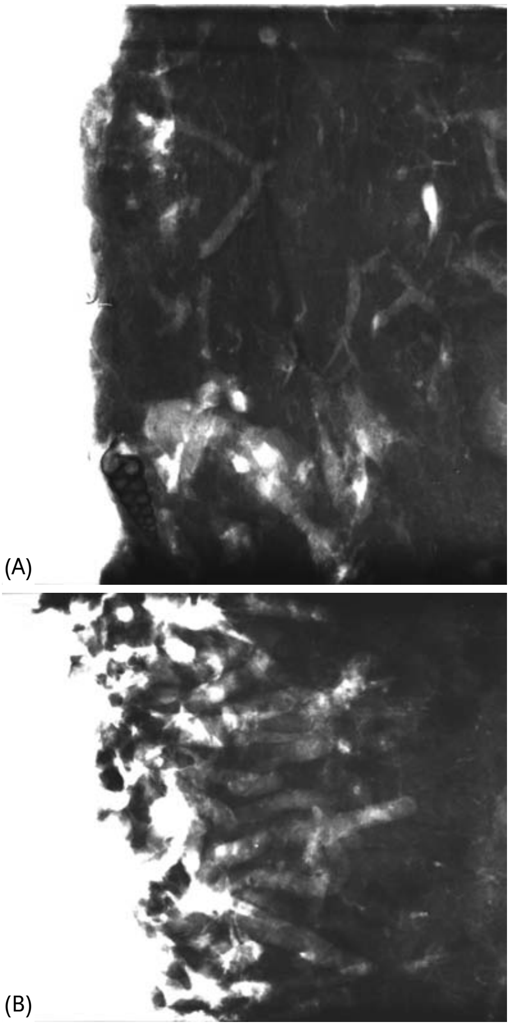

FIGURE 3.2 X-radiographs of marsh bank sediment containing (A) low and (B) high densities of *Sphaeroma quoyanum*. White areas are plant roots and rhizomes (A) or *Sphaeroma* burrows (B). Picture is from San Diego Bay, 1998. Photos courtesy of Theresa Talley and Springer.

SPHAEROMA QUOYANUM

Sphaeroma quoyanum is a burrowing Australasian isopod introduced to salt marshes of San Diego Bay and San Francisco Bay, among others. This isopod forms dense, anastomosing burrow networks (fig. 3.2). These burrows typically cut into the edges of marsh banks, reducing sediment stability and causing erosional loss in excess of one meter of marsh edge per year, dramatically reducing the extent of vegetated marsh and accelerating its conversion into mudflat (Talley, Crooks, and Levin 2001) (fig. 3.3). Carlton (1979) estimated that in infested areas of San Francisco Bay, vegetated marsh has been eroded back by dozens of meters since the introduction of *Sphaeroma* in the late 1800s. This makes *Sphaeroma* one of the largest agents of shoreline erosion in San Francisco Bay. By eroding vast tracks of marsh habitat, *Sphaeroma* not only accelerates conversion of marsh habitat into mudflat but also alters hydrography and sedimentation regimes (Talley et al. 2001). Bioeroders are a broad class of recognized ecosystem engineers (Meadows and Meadows 1991) that seemingly have potential for great impact in marshes where shallow root systems and persistent hydrological exposure can heighten their effects.

MYOCASTOR COYPUS

Coypu, also known as nutria, were introduced from South America to almost every continent to farm for their fur (Carter and Leonard 2002) (fig. 3.4). In the southeastern United States, their population size is now estimated at twenty to thirty million (Maryland Department of Natural Resources 2004). Through their burrowing and rooting activity, nutria decrease aboveground biomass, belowground production, soil elevation, and the expansion of the root zone. Collectively these effects depress soil-building processes. Marshes with low sediment deposition are particularly susceptible to nutria impacts and may be destroyed without substantial human remediation (Ford and Grace 1998). Through destruction of some of the important vegetative physical structures of the marsh, coypu exert far-reaching consequences for the marsh community.

EXAMPLES OF EXOTIC SPECIES WITH PURELY TROPHIC AND COMPETITIVE IMPACTS

In addition to structural changes, invasive estuarine and marsh species may also exert important impacts through their biotic interactions (e.g., competition, predation, parasitism, and apparent competition).

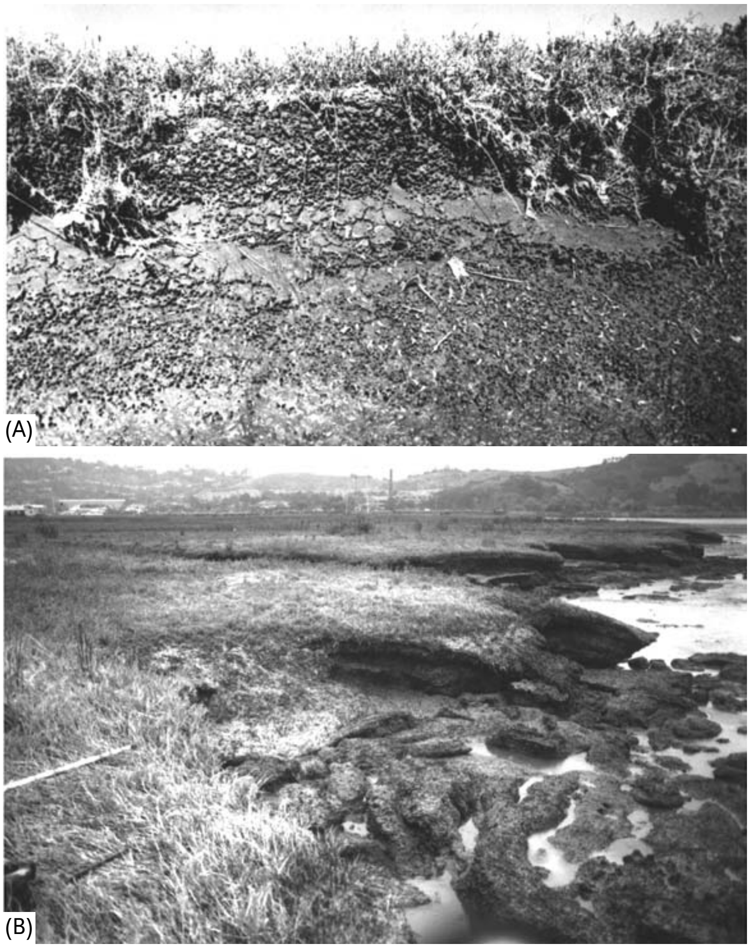

FIGURE 3.3 (A) Extensive burrowing by *Sphaeroma quoyanum* in vertical marsh banks, San Diego Bay. (B) Such burrowing loosens sediment, increasing erosion, undercutting banks, and releasing chunks of marsh surface and reducing marsh habitat. Corte Madera Marsh, San Francisco Bay. Photos courtesy of Theresa Talley and Springer.

BATILLARIA ATTRAMENTARIA

An exotic snail, *Batillaria attramentaria*, has successfully invaded several salt marshes and mud flats in northern California, Washington, and British Columbia (Byers 1999) (fig. 3.5). In California, populations of the native mud snail, *Cerithidea californica*, have declined precipitously. Experimental manipulations demonstrated that the snail species competed exploitatively for epipelic diatoms colonizing the surface of the marsh mud. Although the two species did not differ in their effect on resource levels at any experimental snail density, the introduced snail was always more efficient at converting limited resources to tissue growth. *Batillaria*'s enhanced resource conversion efficiency provides a sufficient explanation for its successful invasion and subsequent exclusion of *Cerithidea* (Byers 2000a). Byers and Goldwasser (2001) subsequently combined these detailed, quantitative field data on *Batillaria* and its interactions with *Cerithidea* in an individual-based model. In empirically parameterized simulations, the native snail was driven extinct within fifty-five to seventy years after the introduction of *Batillaria*, closely matching direct field estimates of *Cerithidea*'s time to displacement (Byers 1999).

FIGURE 3.4 Nutria (*Myocastor coypus*) in marsh. Photo courtesy of Guerry O'Holm.

FIGURE 3.5 The exotic mudsnail, *Batillaria attramentaria* (the two snails pictured on the right), has successfully invaded several salt marshes and mud flats in northern California, where it contributes to the exclusion of the native confamilial mudsnail, *Cerithidea californica* (the two snails pictured on the left). Photo by Jeb Byers and John Meyer.

Replacement of one mud snail for another might seem like a superficial biotic change. However, because of its superior resource conversion efficiency, *Batillaria* achieves higher densities than *Cerithidea*, thus suppressing the diatom standing stock to very low levels. Such resource depression is likely to dramatically affect other benthic grazers within the marsh, such as ghost shrimp and other snails. But the largest impact stemming from the replacement of native *Cerithidea* was uncovered only recently.

Both *Batillaria* and *Cerithidea* are first intermediate hosts for trematode parasites. All but one of these trematode species must obligately pass through a second intermediate host and then on to a final host during their life cycles. Depending on the trematode species, mollusks, crustaceans, or fishes may serve as second intermediate hosts for the metacercarial cysts. The trematode life cycle is completed when a second intermediate host is eaten by the final host, typically a shorebird. *Cerithidea californica* hosts at least eighteen native trematode species throughout its range in California (Martin 1972). *Batillaria*, however, hosts just a single trematode species—itself a nonnative species (*Cercaria batillariae*) (Torchin, Byers, and Huspeni 2005; fig. 3.6). In Elkhorn Slough, California, hundreds of cysts of *C. batillariae* were found in all individuals of the three fish species examined, including within physiologically sensitive regions like the pericardium.

Because trematode parasites are highly specific for the species of snail they infect, in marshes where *C. californica* becomes extirpated by *Batillaria*, *Cerithidea*'s parasites will also become locally extinct. The removal of

FIGURE 3.6 Cercaria of the multihost trematode parasite, *Cercaria batillariae*. This nonnative trematode is found in marshes along the Pacific coast of North America where it infects only a single species of first intermediate host—the nonnative mudsnail, *Batillaria attramentaria*. The cercariae are released from infected snails and penetrate into native estuarine fish as a second intermediate host. Length of cercariae is about 0.5 millimeter. Photo courtesy of Todd Huspeni.

multiple native trematode species will ultimately result in local eliminations of trematode infections in mollusks, crustaceans, and potentially several fishes that serve as second intermediate hosts for *C. californica's* parasites (Martin 1972). Although the exact manifestations are still unclear, the reduction in infections will likely alter host population dynamics (Lafferty 1992) and potentially the metabolism, foraging, and abundance of shorebirds as well (Lafferty and Morris 1996). Thus, the most far-reaching effects of *Cerithidea*'s loss on the community structure of the native marsh system seems very likely to stem from the concomitant loss of its dependent, trophically transmitted trematode species.

VENERUPIS PHILIPPINARUM

Even in typically closed marsh populations, not every species exerts competitive effects (Byers 2009). Filter (suspension) feeding species in particular have been suggested to experience reduced competition because their planktonic food source is often not a limiting factor (Levinton 1972; Peterson 1979; Byers 2009). A nonindigenous suspension-feeding species, *Venerupis philippinarum* (= *Ruditapes philippinarum*, = *Tapes japonica*), the Japanese littleneck clam, was accidentally introduced into the eastern Pacific in the 1930s with imported oyster seed from Japan and is now found in low-energy embayments and marsh-associated mudflats from British Columbia to southern California (Quayle 1941; Haderlie and Abbott 1980). It is the most prolific introduced clam species in the San Juan Islands, Washington, and accounts for 50 percent of the annual commercial landings of hard-shell clams in the state (Washington Department of Fish and Wildlife 2000).

Byers (2005) experimentally examined the effects of high *Venerupis* densities on mortality, growth, and fecundity of the confamilial clam, *Protothaca staminea*, and whether differences in predator abundance mitigate density dependent effects. Even at densities 50 percent higher than those found naturally in the field, *Venerupis* had no direct effect on itself or *Protothaca*. Rather, the variable of overwhelming influence on the clams was crab biomass, which decreased growth of both species and increased mortality of *Venerupis*. The annualized loss rate of *Venerupis* was 50 percent when exposed to excavating crab predators due to a very shallow burial depth, nearly three centimeters shallower than *Protothaca* (Byers 2005). In fact, when exposed to predators, *Venerupis* was up to seven times more likely to be taken than *Protothaca*, whose mortality did not differ significantly with crab abundance.

By taking the brunt of predator pressure, *Venerupis* seems to play a sacrificial role that at least partially protects *Protothaca* from predator mortality. However, high consumption of *Venerupis* likely has negative effects on other invertebrate species. When an exotic species is consumed by a native predator, losses to the exotic population are converted to additional predator biomass. Hence, predation on an exotic species can indirectly harm the predator's native prey via apparent competition (Rand and Louda 2004). Noonburg and Byers (2005) demonstrate conditions under which resource competition from an invasive species is less detrimental to a native consumer than increased losses to a native predator population that is boosted by the invader.

Thus, although no direct competitive effect of *Venerupis* on *Protothaca* was detected, by serving as an easy prey source for crabs, this nonindigenous prey species may be boosting regional crab abundance and productivity. Given the ubiquity of *Venerupis* throughout the West Coast of North America, this crab food subsidy could be substantial. In addition, the thin-shelled, nonindigenous *Nuttallia obscurata*, present in high abundance throughout the U.S. Northwest and British Columbia coast, is also an easy, novel prey item for crabs when it occurs in areas without appropriate physical refuges (Byers 2002b). Because *Cancer* crabs are omnivorous predators, their increase (particularly the less harvested species, *C. gracilis* and *C. productus*) potentially affects many other native prey species, including worms, fish, crustaceans, and other bivalves. Subsidies of native predators may be a largely underappreciated means by which nonindigenous species that are consumed heavily by native predators enhance apparent competition and thus escalate the impact of predators on native species (Courchamp, Langlais, and Sugihara 2000; Byers 2002b, 2005; Noonburg and Byers 2005).

CARCINUS MAENAS

Due to inadvertent human transport, the European green crab, *Carcinus maenas*, is now a cosmopolitan species (Geller et al. 1997; Hidalgo. Baron, and Orensanz 2005). Its impacts have been well studied in marshes and embayments of the western coast of North America. Due to its omnivorous diet, *Carcinus* was found to significantly decrease the abundance of several invertebrate prey species in Bodega Bay, California (Grosholz et al. 2000). Most notably, two native clams, *Nutricola tantilla* and *N. confusa*, and a native shorecrab, *Hemigrapsus oregonensis*, decreased five- to tenfold within three years of the introduction of *Carcinus*. *Carcinus* indirectly promoted several polychaete and crustacean species, which apparently were not major prey items but rather benefited from *Carcinus*'s removal of competing species (Grosholz et al. 2000). In addition, *Carcinus* predation on *Nutricola* clam species facilitated spread of an introduced competitor clam, *Gemma gemma* throughout Bodega Harbor (Grosholz 2005). *Carcinus* thus has both direct and indirect predatory effects.

Similarly, on the East Coast of North America, where it has been established for over one hundred years, *Carcinus* has been shown to have equally profound predatory impacts, particularly on clams. In Nova Scotia, Floyd and Williams (2004) measured 80 percent reductions of small *Mya arenaria* within less than four months, with consumption rates of three to twenty-two clams per crab per day. Whitlow, Rice, and Sweeney (2003) also measured high predation rates of *Carcinus* on *M. arenaria*. Although these authors demonstrated that *Mya* was able to partially mitigate the high predation rate from the excavating crabs by burrowing more deeply in the sediment, deeper burial typically decreases feeding efficiency and thus growth rates of clams (Zaklan and Ydenberg 1997). Thus, predatory effects of *Carcinus* can be both density and trait mediated.

RECOMMENDATIONS AND CONCLUSIONS

With increasing globalization, the influx of nonindigenous species to salt marshes is not likely to abate soon. The relatively retentive nature of most embayments, estuaries, and associated marshes seems to contribute both to higher invasive establishment as well as to strong competitive effects. Because nonindigenous species often originate from estuaries and bays, the similarity of source and recipient habitats also likely contributes to a high rate of successful establishment. Finally, the high rate of disturbance to marsh environments suggests that selection regimes may be sufficiently altered to promote high establishment rates and subsequent impact of introduced species.

Policies to reduce the supply rate of exotic propagules, such as new mandatory ballast water exchange during transoceanic crossings (Federal Register 2004) are extremely commendable, since preventing invasions in the first place is the most proactive policy. But because this policy alone will not eliminate future invasions or mitigate effects of invaders already present, it is important to maintain vigilance in marsh habitats. In the United States, the Environmental Protection Agency's Environmental Monitoring and Assessment Program and several National Oceanographic and Atmospheric Administration subagencies such as Sea Grant have conducted periodic regional inventories of marshes and bays for exotic species (Cohen et al. 2001; Lee et al. 2004; Pederson et al. 2005). Taking these efforts one step further to implement a standardized, national or international protocol to detect incipient invasions would strengthen our approach even more (e.g., Wasson et al. 2002). Ad hoc assessments have certainly led to some invaders being overlooked, presenting enormous problems in establishing appropriate baselines of impact assessment (Dayton et al. 1998) and slowing potential mitigation by resource managers. Protocols and policies need to be in place for eradication or containment of incipient invasions, which often require fast action to be effective (e.g., Anderson 2005).

In addition to detecting introduced species and following the dynamics of established ones, quantitative monitoring is important because it aids restoration. Specifically, it complements adaptive management, which through frequent data-driven assessments can refine intervention techniques to restore native marsh populations, habitat, and ecosystem function. Clearly restoration efforts should be prioritized based on an understanding of invaders' impact, be they engineering or trophic effects. Because impact assessment can be slow, if forthcoming at all, on first approximation such prioritization may do best to focus on invasive habitat engineers (e.g., oysters, reef-building polychaetes) because of their often far-reaching and lasting legacy effects and their ability to transform abiotic properties of a marsh and thus alter ecosystem services (Byers et al. 2006).

Because not all invasive species are detrimental to native species or systems (e.g., Bruno et al. 2005; Byers 2009), monitoring marshes for early impact detection may be crucial for proper prioritization of intervention efforts. However, it is very important to avoid false confidence in the promptness of impact detection in such monitoring programs, because exotic impact is sometimes virtually undetectable until after the exotic species is extremely abundant (Byers and Goldwasser 2001). This lag in impact may be especially pronounced if the mechanism of impact by the exotic species is to decrease births of a long-lived native species—a less conspicuous impact than increasing death of adults. In such cases, demographic lag times necessitate alternative, faster-responding metrics for impact detection than adult population densities.

As an illustration, Byers and Goldwasser (2001) sought to identify empirically measurable quantities that provide the earliest warning of impact by the invasive snail *Batillaria* on the native *Cerithidea*. Through an individual-based model parameterized with empirical data, they tracked many population- and individual-level responses of *Cerithidea* to *Batillaria*'s invasion, including population density, biomass, egg production, mean size, proportion of parasitized individuals, and individual growth rate, as well as availability of shared food resources. In model simulations, the initial number of invading *Batillaria* was set to guarantee extinction of *Cerithidea* within ninety years. Despite a rapid initial increase in the invader population, all metrics for *Cerithidea* were slow to exhibit signs of impact. Most took at least twenty-five years from invasion to exhibit detectable changes, by which time the exotic snail was established at extremely high densities. *Cerithidea* egg production was the fastest, most consistent response metric, exhibiting declines within twenty to twenty-five years after invasion in about 90 percent of simulations. Monitoring programs and risk assessment analyses must identify and concentrate on reliable, early-warning metrics.

Habitat alteration and biotic effects by exotic species now join anthropogenic physical alterations and chemical inputs as dominant impacts on estuarine and marsh environments. Dramatic modification of selection regimes in marshes suggests that synergism between these disturbance agents enhances invasion rates and impacts. Therefore, policies to protect marshes and estuaries from physical and chemical anthropogenic disturbance should simultaneously improve their resistance and resilience to biological invasions. Although the closed nature of most estuarine and marsh habitats and their populations increases the propensity for impacts by nonindigenous species, it also makes the species easier to document, track, control, and potentially eradicate. For example, the tractable, discrete boundaries of marsh systems certainly make intervention more successful than in other marine systems such as the open coast with its porous boundaries, complicating currents, and an influx of propagules from elsewhere. Marshes are a jeopardized, increasingly compromised habitat to which we must pay strong attention; otherwise, we risk losing many of the native species and valuable ecosystems services they provide.

Acknowledgments. I thank Irit Altman, Tyra Byers, John Meyer, Whitman Miller, and Ted Grosholz for helpful edits and discussions on this chapter.

REFERENCES

Anderson, L. W. J. 2005. California's reaction to *Caulerpa taxifolia*: A model for invasive species rapid response. *Biological Invasions* 7: 1003–1016.

Bruno, J. E., J. D. Fridley, K. D. Bromberg, and M. D. Bertness. 2005. Insights into biotic interactions from studies of species invasions. Pages 13–40 *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines (eds.), *Species Invasions: Insights into Ecology, Evolution, and Biogeography*. Sunderland, MA: Sinauer.

Byers, J. E. 1999. The distribution of an introduced mollusc and its role in the long-term demise of a native confamilial species. *Biological Invasions* 1: 339–353.

———. 2000a. Competition between two estuarine snails: Implications for invasions of exotic species. *Ecology* 81: 1225–1239.

———. 2000b. Differential susceptibility to hypoxia aids estuarine invasion. *Marine Ecology Progress Series* 203: 123–132.

———. 2002a. Impact of nonindigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97: 449–458.

———. 2002b. Physical habitat attribute mediates biotic resistance to nonindigenous species invasion. *Oecologia* 130: 146–156.

———. 2005. Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. *Ecology* 86: 487–500.

———. 2009. *Competition in Marine Invasions*. In: *Biological invasions in marine ecosystems: Ecological, management, and geographic perspectives*. Eds.: Gil Rilov & Jeff Crooks. Springer-Verlag. pp. 245–260.

Byers, J. E., K. Cuddington, C. G. Jones, T. S. Talley, A. Hastings, J. Lambrinos, J. A. Crooks, and W. G. Wilson. 2006. Using ecosystem engineers to restore ecological systems. *Trends in Ecology and Evolution* 21, no. 9: 493–500.

Byers, J. E., and L. Goldwasser. 2001. Exposing the mechanism and timing of impact of nonindigenous species on native species. *Ecology* 82: 1330–1343.

Byers, J. E., and J. M. Pringle. 2006. Going against the flow: Retention, range limits and invasions in advective environments. *Marine Ecology Progress Series* 313: 27–41.

Cairnes, J. 1993. Is restoration ecology practical? *Restoration Ecology* March: 3–7.

Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Unpublished PhD diss., University of California, Davis.

———. 1996. Biological invasions and cryptogenic species. *Ecology* 77: 1653–1655.

Carlton, J. T., and A. N. Cohen. 1998. Periwinkle's progress: The Atlantic snail *Littorina saxatilis* (Mollusca: Gastropoda) establishes a colony on a Pacific shore. *Veliger* 41: 333–338.

Carter, J., and B. P. Leonard. 2002. A review of the literature on the worldwide distribution, spread of, and efforts to eradicate the coypu (*Myocastor coypus*). *Wildlife Society Bulletin* 30: 162–175.

Cohen, A., H. Berry, C. Mills, D. Milne, K. Britton-Simmons, M. Wonham, D. Secord, J. Barkas, B. Bingham, B. Bookheim, J. E. Byers, J. Chapman, J. Cordell, B. Dumbauld, A. Fukuyama, L. Harris, A. Kohn, K. Li, T. Mumford, V. Radashevsky, A. Sewell, and K. Welch. 2001. Washington state exotics expedition 2000: A rapid assessment survey of exotic species in the shallow waters of Elliott Bay, Totten and Eld Inlets, and Willapa Bay. Unpublished manuscript, Nearshore Habitat Program, Washington State Department of Natural Resources, Olympia.

Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279: 555–558.

Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: Modelling the hyperpredation process. *Journal of Animal Ecology* 69: 154–164.

Crain, C. M., and M. D. Bertness. 2006. Ecosystem engineering across environmental gradients: Implications for conservation and management. *BioScience* 56: 211–218.

Crooks, J. A. 1998. Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. *Marine Ecology Progress Series* 162: 137–152.

———. 2001. Assessing invader roles within changing ecosystems: Historical and experimental perspectives on an exotic mussel in an urbanized lagoon. *Biological Invasions* 3: 23–36.

———. 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos* 97: 153–166.

Crooks, J. A., and H. S. Khim. 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology* 240: 53–75.

Culver, C. S., and A. M. Kuris. 2000. The apparent eradication of a locally established introduced marine pest. *Biological Invasions* 2: 245–253.

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications* 8: 309–322.

Federal Register. 2004. Mandatory ballast water management program for U.S. waters. *Federal Register* 69: 44952–44961.

Floyd, T., and J. Williams. 2004. Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the southern Gulf of St. Lawrence. *Journal of Shellfish Research* 23: 457–462.

Ford, M. A., and J. B. Grace. 1998. Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. *Journal of Ecology* 86: 974–982.

Fox, W. M., M. S. Johnson, S. R. Jones, R. T. Leah, and D. Copplestone. 1999. The use of sediment cores from stable and developing salt marshes to reconstruct historical contamination profiles in the Mersey Estuary, UK. *Marine Environmental Research* 47: 311–329.

Geller, J. B., E. D. Walton, E. D. Grosholz, and G. M. Ruiz. 1997. Cryptic invasions of the crab *Carcinus* detected by molecular phylogeography. *Molecular Ecology* 6: 901–906.

Griffiths, C. L. 2000. Overview on current problems and future risks. Pages 235–241 *in* G. Preston, G. Brown, and E. van Wyk (eds.), *Best Management Practices for Preventing and Controlling Invasive Alien Species*. Capetown: Working for Water Programme.

Grosholz, E. D. 2002. Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution* 17: 22–27.

———. 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences of the USA* 102: 1088–1091.

Grosholz, E. D., G. M. Ruiz, C. A. Dean, K. A. Shirley, J. L. Maron, and P. G. Connors. 2000. The impacts of a nonindigenous marine predator in a California bay. *Ecology* 81: 1206–1224.

Haderlie, E. C., and D. P. Abbott. 1980. Bivalvia: the clams and allies. Pages 355–411 *in* R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford, CA: Stanford University Press.

Hewitt, C. L., M. L. Campbell, R. E. Thresher, and R. B. Martin. 1999. *Marine biological invasion of Port Phillip Bay, Victoria*. Hobart, Australia: Centre for Research on Introduced Marine Pests.

Hidalgo, F. J., P. J. Baron, and J. M. Orensanz. 2005. A prediction come true: the green crab invades the Patagonian coast. *Biological Invasions* 7: 547–552.

Holland, A. F., D. M. Sanger, C. P. Gawle, S. B. Lerberg, M. S. Santiago, G. H. M. Riekerk, L. E. Zimmerman, and G. I. Scott. 2004. Linkages between tidal creek ecosystems and the landscape and demographic attributes of their watersheds. *Journal of Experimental Marine Biology and Ecology* 298: 151–178.

Hutchings, P. A., R. W. Hilliard, and S. L. Coles. 2002. Species introductions and potential for marine pest invasions into tropical marine communities, with special reference to the Indo-Pacific. *Pacific Science* 56: 223–233.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–386.

Kennish, M. J. 1992. *Ecology of estuaries: Anthropogenic effects*. Boca Raton, FL: CRC.

———. 2001. Coastal salt marsh systems in the US: A review of anthropogenic impacts. *Journal of Coastal Research* 17: 731–748.

Kuris, A. M. 2003. Eradication of introduced marine pests. Pages 549–556 *in* D. J. Rapport, W. L. Lasley, D. E. Rolston, N. O. Nielsen, C. O. Qualset, and A. B. Damania (eds.), *Managing for Healthy Ecosystems*. Boca Raton, FL: CRC.

Lafferty, K. D. 1992. Foraging on prey that are modified by parasites. *American Naturalist* 140: 854–867.

Lafferty, K. D., and A. K. Morris. 1996. Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* 77: 1390–1397.

Lee, H., W. Nelson, J. Lamberson, and D. A. Reusser. 2004. *Regional Assessment of the Invasive Macrobenthos in the Small West Coast Estuaries*. Washington, DC: Environmental Protection Agency; Environmental Monitoring and Assessment Program.

Lee, H., B. Thompson, and S. Lowe. 2003. Estuarine and scalar patterns of invasion in the soft-bottom benthic communities of the San Francisco Estuary. *Biological Invasions* 5: 85–102.

Levinton, J. 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. *American Naturalist* 106: 472–486.

Martin, W. E. 1972. An annotated key to the Cercariae that develop in the snail *Cerithidea californica*. *Bulletin of the Southern California Academy of Sciences* 71: 39–43.

Maryland Department of Natural Resources. 2004. *Invasive and Exotic Species: Nutria*. Baltimore: Wildlife and Heritage Service.

Meadows, P. S., and A. Meadows, eds. 1991. *The Environmental Impact of Burrowing Animals and Animal Burrows*. Oxford: Clarendon.

Nehring, S. 2002. Biological invasions into German waters: An evaluation of the importance of different human-mediated vectors for nonindigenous macrozoobenthic species. Pages 373–383 *in* E. Leppakoski, S. Gollasch, and S. Olenin (eds.), *Invasive Aquatic Species of Europe. Distribution, Impacts, and Management*. Dordrecht: Kluwer Academic.

Nicholls, R. J. 2004. Coastal flooding and wetland loss in the 21st century: Changes under the SRES climate and socio-economic scenarios. *Global Environmental Change—Human and Policy Dimensions* 14: 69–86.

Noonburg, E. G., and J. E. Byers. 2005. More harm than good: When invader vulnerability to predators enhances impact on native species. *Ecology* 86: 2555–2560.

Pederson, J., R. Bullock, J. T. Carlton, J. Dijkstra, N. Dobroski, P. Dyrynda, R. Fisher, L. Harris, N. Hobbs, G. Lambert, E. Lazo-Wasem, A. Mathieson, M. Miglietta, J. Smith, J. Smith III, and M. Tyrrell. 2005. *Marine Invaders in the Northeast: Rapid Assessment of Nonnative Marine Species of Floating Dock Communities*. Report of the August 3–9, 2003 survey. Cambridge, MA: MIT Sea Grant College Program.

Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. Pages 233–263 *in* R. J. Livingston (ed.), *Ecological Processes in Coastal and Marine Systems*. New York: Plenum.

Quayle, D. B. 1941. The Japanese "little neck" clam accidentally introduced into British Columbia waters. *Progress Report Fisheries Research Board of Canada Pacific Coast Station* 48: 17–18.

Rand, T. A., and S. M. Louda. 2004. Exotic weed invasion increases the susceptibility of native plants attack by a biocontrol herbivore. *Ecology* 85: 1548–1554.

Ray, G. L. 2005a. Invasive marine and estuarine animals of the North Atlantic. 19. ERDC/TN ANSRP-05-1. http://el.erdc.usace.army.mil/ansrp/pdfs/ansrp05-6.pdf.

———. 2005b. Invasive marine and estuarine animals of the Pacific Northwest and Alaska. 18. ERDC/TN ANSRP-05-6. http://el.erdc.usace.army.mil/ansrp/pdfs/ansrp05-6.pdf.

Reise, K., S. Gollasch, and W. J. Wolff. 2002. Introduced marine species of the North Sea coasts. Pages 260–266 *in* E. Leppakoski, S. Gollasch, and S. Olenin (eds.), *Invasive Aquatic Species of Europe: Distribution, Impacts, and Management*. Dordrecht: Kluwer Academic.

Robinson, T. B., C. L. Griffiths, C. McQuaid, and M. Rius. 2005. Marine alien species of South Africa: Status and impacts. *African Journal of Marine Science* 27: 297–306.

Rudnick, D. A., K. Hieb, K. F. Grimmer, and V. H. Resh. 2003. Patterns and processes of biological invasion: The Chinese mitten crab in San Francisco Bay. *Basic and Applied Ecology* 4: 249–262.

Ruesink, J. L., H. S. Lenihan, A. C. Trimble, K. W. Heiman, F. Micheli, J. E. Byers, and M. C. Kay. 2005. Introduction of nonnative oysters: Ecosystem effects and restoration implications. *Annual Review of Ecology Evolution and Systematics* 36: 643–689.

Ruiz, G. M., J. T. Carlton, E. D. Grosholz, and A. H. Hines. 1997. Global invasions of marine and estuarine habitats by non indigenous species: Mechanisms, extent, and consequences. *American Zoologist* 37: 621–632.

Ruiz, G. M., P. W. Fofonoff, J. T. Carlton, M. J. Wonham, and A. H. Hines. 2000. Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* 31: 481–531.

Ruiz, G. M., P. W. Fofonoff, A. H. Hines, and E. D. Grosholz. 1999. Nonindigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions. *Limnology and Oceanography* 44: 950–972.

Sanger, D. M., A. F. Holland, and G. I. Scott. 1999. Tidal creek and salt marsh sediments in South Carolina coastal estuaries: II. Distribution of organic contaminants. *Archives of Environmental Contamination and Toxicology* 37: 458–471.

Schwindt, E., and O. O. Iribarne. 2000. Settlement sites, survival and effects on benthos of an introduced reef-building polychaete in a SW Atlantic coastal lagoon. *Bulletin of Marine Science* 67: 73–82.

Schwindt, E., O. O. Iribarne, and F. I. Isla. 2004. Physical effects of an invading reef-building polychaete on an Argentinean estuarine environment. *Estuarine Coastal and Shelf Science* 59: 109–120.

Talley, T. S., J. A. Crooks, and L. A. Levin. 2001. Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes. *Marine Biology* 138: 561–573.

Torchin, M. E., J. E. Byers, and T. C. Huspeni. 2005. Differential parasitism of native and introduced snails: Replacement of a parasite fauna. *Biological Invasions* 7: 885–894.

Torchin, M. E., R. F. Hechinger, T. C. Huspeni, K. L. Whitney, and K. D. Lafferty. 2005. The introduced ribbed mussel (*Geukensia demissa*) in Estero de Punta Banda, Mexico: Interactions with the native cord grass, *Spartina foliosa*. *Biological Invasions* 7: 607–614.

Tyrrell, M. C., and J. E. Byers. 2007. Do artificial substrates favor nonindigenous fouling species over natives? *Journal of Experimental Marine Biology and Ecology* 342: 54–60.

Valiela, I., D. Rutecki, and S. Fox. 2004. Salt marshes: Biological controls of food webs in a diminishing environment. *Journal of Experimental Marine Biology and Ecology* 300: 131–159.

Verling, E., G. M. Ruiz, L. D. Smith, B. Galil, A. W. Miller, and K. R. Murphy. 2005. Supply-side invasion ecology: Characterizing propagule pressure in coastal ecosystems. *Proceedings of the Royal Society of London B, Biological Sciences* 272: 1249–1256.

Washington Department of Fish and Wildlife. 2000. Untitled document available at http://www.wa.gov/wdfw/fish/shelfish/beachreg/1clam.htm#manila.

Wasson, K., K. Fenn, and J. S. Pearse. 2005. Habitat differences in marine invasions of central California. *Biological Invasions* 7: 935–948.

Wasson, K., D. Lohrer, M. Crawford, and S. Rumrill. 2002. Nonnative species in our nation's estuaries: a framework for an invasion monitoring program. *National Estuarine Research Reserve Technical Report Series* 2002: 1.

Whitlow, W. L., N. A. Rice, and C. Sweeney. 2003. Native species vulnerability to introduced predators: Testing an inducible defense and a refuge from predation. *Biological Invasions* 5: 23–31.

Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *BioScience* 56: 203–209.

Zaklan, S. D., and R. Ydenberg. 1997. The body size-burial depth relationship in the infaunal clam *Mya arenaria*. *Journal of Experimental Marine Biology and Ecology* 215: 1–17.