

## 7.03 Functional Consequences of Invasive Species in Coastal and Estuarine Systems

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### Abstract

Rapid change is a major feature of modern estuaries and coasts. In numerous systems, invasive species are a primary force altering the structure and function of communities. Nonindigenous species take on nearly all possible ecological roles, serving as agents of disease, parasites, primary and secondary producers, predators, competitors, facilitators, and disturbers. Here, major functional impacts are assessed by considering invasive species as nutrient and biogeochemical modifiers, trophic transformers, and structural engineers. Both plant and animal invasions have the ability to dramatically alter habitat properties and energy flows, shifting ecosystems from one type or state to another, with different functional attributes. Invaders can also impact longer-term, evolutionary dynamics through alteration of selection regimes and hybridization. The ecosystem-level consequences involve changes to emergent structural and functional properties and to ecosystem services. Biodiversity, spatial heterogeneity, connectivity, succession, stability, and resilience all may be modified by invasion. Ecological impacts are often heavily intertwined with ecosystem services, in terms of both positive and negative consequences for humans. Invaders play key roles in fisheries, aquaculture, shoreline stabilization, remediation and restoration, and carbon sequestration. Several decades of invasion research allow us to identify the settings most likely to experience highly modified functions when invaded, and to synthesize the nature and magnitude of invasion effects on ecosystem function.

### 7.03.1 Introduction

Estuarine and coastal ecosystems are the marine environments most subject to alteration by humans. They have been converted to marinas, filled to create waterfront developments, and polluted by urban runoff, industrial discharge, and maritime activities. They also represent hubs of international travel, commerce, and aquaculture. Not surprisingly, then, these areas are also the sites of most marine species invasions (Rilov and Crooks, 2009). Ruiz et al. (2000) tallied 298 exotic invertebrate and algal species in coastal and estuarine waters of North America. Sliwa et al. (2009) recognized over 130 for Australia, while the Mediterranean has received 900 exotic species, including Lessepsian migrants (Zenetos et al., 2005, 2008). Scores more are reported from other areas that have received attention (Rilov and Crooks, 2009). Although these numbers sound impressive, they are almost certainly gross underestimates (Carlton, 2009). It has been estimated that there are thousands of introduced species in marine waters around the world, but most likely remain unrecognized because of lack of historical information, inadequate surveillance and monitoring, and waning taxonomic expertise (Carlton and Ruiz, 2005; Carlton, 2009). The pace of invasion also appears to be quickening with increasing globalization and efficiency of movement. Studies of ship ballast tanks suggest that thousands of species are on the move on the world's oceans at any one time, many destined to be delivered to regions where they would never reach naturally (Carlton, 1999). We can ask, then: Do all these invasive species matter? Are they simply replacing or duplicating the functions of native species within their invaded ecosystems?

Despite the ubiquity of invaders in many coastal waters and the sizable increase in our knowledge of invasion processes in the sea, we still know relatively little about the specific roles of each of the thousands of invasive species across the globe. The emerging picture, however, is impressive. Invading species in the ocean come in all flavors and sizes, from the smallest virus to large reef-forming bivalves, forest-forming plants, and expansive macroalgal carpets. They represent all major taxa, exhibit a tremendous diversity of lifestyles, and fill multidimensional niches – some new to a region and some attained by displacing other species. Within invaded ecosystems, invasive species may be primary producers, grazers, predators, competitors, facilitators, and agents of disturbance or disease. As such, an ecological evaluation of invasion consequences in coastal and estuarine systems is likely to reflect the key biological processes within these realms.

In this chapter, we discuss invasives as ecosystem components and synthesize what is known about the mechanisms by which they alter or assimilate into coastal and estuarine ecosystems. It is impossible to provide an exhaustive catalog of all species and associated literature here due to space constraint. There are recent books and reviews that have begun to approach this (Davis, 2009; Rilov and Crooks, 2009). Rather, we focus on characterizing the major structural and functional roles that invasive species play in these systems, and provide examples that illustrate the processes by which invasive species can alter ecological functions and ecosystem services. We document invasion modifications of flows of material and energy through the ecosystem, as well as alterations to the abiotic nature of ecosystems themselves, biogeochemical processes,

and food-web structure. We focus on cases where invasive species alter the outcomes of biotic interactions. All possible classes of ecological interactions may be modified, including competition, predation, ammensalism, facilitation, and even mutualism. We also discuss how invaders can alter emergent properties of ecosystems such as productivity, biodiversity, heterogeneity, connectivity, stability, and overall ecosystem functions. Such knowledge is fundamental to stewardship of the ocean – a functional understanding must underlie management practices and conservation decisions. Determinations about pre-invasion monitoring, species to target for eradication, effective restoration methods, maintenance of essential fish and invertebrate habitat, or preservation of threatened and endangered species all rely on understanding realized or potential impacts of invaders on ecosystem functions.

### 7.03.2 Functional Roles of Invaders in Ecosystems

The general answer to the question of what invaders do in (or to) ecosystems is simple. They can potentially fill any ecological role. A biological invasion is, at its essence, a natural event, and there is no reason to suspect that a broad typology of effects of anthropogenic invaders would be different from that for any species. Interactions between invasive and resident biota play out on local scales, however, and thus sometimes invaders have roles or exert effects beyond those of natives. The influence of invaders on localized processes can result in functional modifications to invaded ecosystems, through either alterations of established processes, or the addition or subtraction of new processes and functions.

In some instances, an invader will perform roles similar to those of native species. They may serve as a forage item or a competitor for space. The invader may do it more or less effectively than a native species, however, and thus affect the characteristics of largely established processes. These can alter the functional attributes of the ecosystem such as number of trophic pathways, interaction strengths, amplitudes, resilience, and temporal patterns. The vastly more rapid rates of anthropogenic invasion compared with natural invasions also assure that these changes are taking place much more quickly than at any time previously in history.

In other instances, local invader impacts go beyond modification of established functions, and, instead, alter the very nature of ecological processes that are occurring. Entire new trophic levels can be added, new habitats can be created or destroyed, or novel types of species interactions may emerge. For example, in areas of the species-poor Baltic Sea, invasive species have added a suite of novel functions, including surface-deposit feeding in soft muds (by the snail *Potamopyrgus antipodarum*), deep bioturbation (by the worm *Marenzelleria viridis*), and filter feeding in oligohaline and freshwater reaches (by zebra mussels, *Dreissena polymorpha*) (Olenin and Leppäkoski, 1999; Leppäkoski et al., 2002). Such invasions fundamentally 'change the rules of existence' for resident species (Vitousek, 1990). For these 'discrete trait invaders', we would expect major system-level effects (Chapin et al., 1996).

Of the myriad potential effects of any invader, what sorts of interactions would rise to the level of functional effects? Reduced to its core, an invasive species will interact with both

biotic and abiotic elements of invaded ecosystems (Figure 1). For the relatively short history of invasion biology, much of the focus on invader impacts has been cast in terms of interactions among biotic components. Invaders can utilize other species as food sources, or be eaten themselves; invaders can be parasites or be parasitized, or can compete for trophic resources. Many of these strictly biotic interactions, and especially pairwise interactions between natives and exotics, typically would not be considered to generate functional effects (Crooks, 2002). However, these interactions can trigger additional effects with extended ramifications. Initiation of trophic cascades is one example (Grosholz and Ruiz, 2009); invasion meltdowns provide another (Simberloff and Von Holle, 1999; Grosholz 2005). In some cases, invasions can do more than change strengths of interactions between trophic levels – they can substitute ‘new food webs for old’ (Elton, 1958) and fundamentally change the flow of energy in ecosystems.

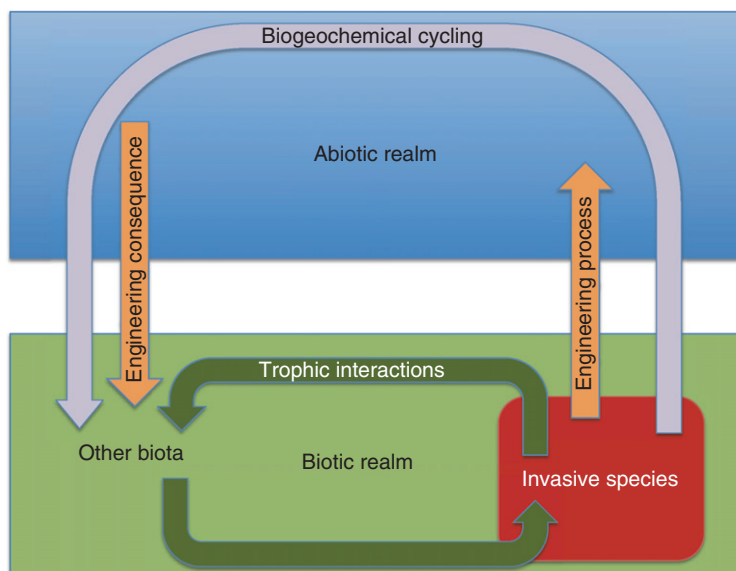
In addition to altering the flow of energy through food webs, invasive organisms will also interact with and modify the abiotic environment (Figure 1). This class of effects has received increasing attention in recent years (Crooks, 2002; Wallentinus and Nyberg, 2007; Bouma et al., 2009). Invaders have, for example, proved to be capable of modifying light, water motion, oxygenation, sediment dynamics, and geochemical environments. These sorts of interactions rise to the level of functional or ecosystem effects for two primary reasons. First, by definition, ecosystems contain both abiotic and biotic elements, and interactions between them can be considered to occur at the ecosystem level (when ecosystem is scale independent, *sensu* Pickett and Cadenasso (2002)). Second, by their very nature, the pathways of effects of one organism on another are often indirect and mediated by processes occurring in the abiotic realm. As such, it is likely that effects will simultaneously impact a wide variety of species. For example, if an invader is increasing or reducing erosion rates, it will affect whole suites of species depending on stable (or unstable) sediment.

It is useful to consider the two fundamental ways in which abiotic modifications can be mediated (Figure 1). In one case, invaders can alter nutrient and biogeochemical cycling. This can often be considered as flows of materials through processes occurring in both the biotic and abiotic realms (e.g., the carbon or nitrogen cycle), and is thus somewhat analogous to the flow of energy through biotic food webs. In the other case, invaders can alter the physical structure of the ecosystem and thereby alter habitats and their distribution – this has been referred to as ecosystem engineering (Jones et al., 1994; Crooks, 2002). Typically, flux models and mass-balanced approaches will not appropriately describe the engineering interactions. Instead, a whole new set of models and conceptual underpinnings is required to describe and predict the effect of species that shape habitats (Hastings et al., 2007).

Below, we consider the roles of invaders in altering nutrient and biogeochemical cycling, flow of energy through food webs, and the physical characteristics of ecosystems through ecosystem engineering. The effects of some invaders (e.g., some top predators) will largely be confined to one class of effect. However, for many species, their impacts will span more than one category. Net effects of these invaders on resident biota will often be the result of a complex and interacting suite of mechanisms (e.g., an exotic species can simultaneously alter a habitat and serve as a food resource), and it is typically difficult to determine the relative contribution of each. However, we will highlight the potential roles of the species in relation to the three broad classes of impacts, as described in the invasion literature.

### 7.03.3 Invader Impacts on Nutrient and Biogeochemical Cycling

Flows and fluxes of water, nitrogen, carbon, and trace elements are fundamental aspects of ecosystem function, as are fluxes of organic matter, particulates, and mineral sediments.



**Figure 1** Key processes by which invasive species shape ecosystem functions: trophic interactions, biogeochemical cycling, and abiotic engineering.

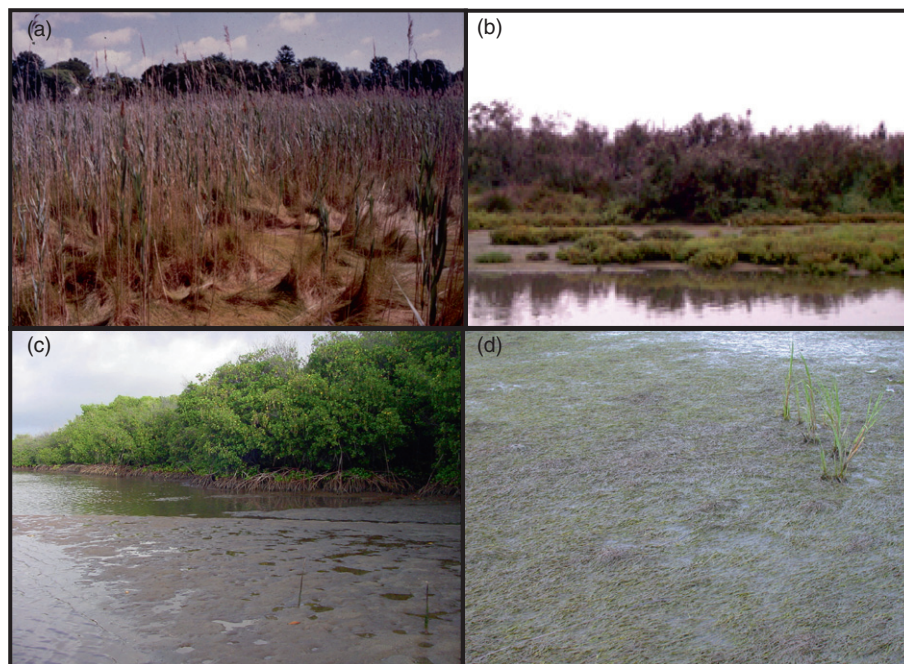
The exchange of materials and nutrients between habitats and assemblages on the seafloor and in the water column is referred to as 'benthic–pelagic coupling'. Benthic organisms often mediate this exchange directly, by filtering and depositing particulates, by taking up or releasing nutrients, by respiring and creating micro-niches within sediments that promote remineralization or denitrification, or by fixing nitrogen or hosting nitrogen fixers. Often microbial communities and their metabolic pathways act as intermediaries. Invasive species can create, disrupt, or redirect these processes with significant functional consequences for biogeochemical cycling (Davis, 2009).

### 7.03.3.1 Biodeposition, Nutrient Transfer, and Benthic–Pelagic Coupling

Perhaps no taxon has had larger effects on whole ecosystems than benthic molluscs that dwell at high densities in estuaries. Although the freshwater zebra mussel *D. polymorpha* and *Corbicula* clams are among the best-studied bivalve invaders, marine genera such as the clam *Corbula* (= *Potamocorbula*), the mussel *Musculista*, and the oyster *Crassostrea* all have tremendous filtration capacities that can remove phytoplankton efficiently and redirect particulate organic matter to the seabed in the form of feces and pseudofeces. These activities eventually release large amounts of regenerated nutrients that become available first to benthic algae on the seafloor and then to phytoplankton in the water column (Newell, 2004; Sousa et al., 2009). In the Bay of Brest (France), the introduced slipper limpet *Crepidula fornicata* provides an important source of organic matter and silica for phytoplankton through feces deposition. Silica

deposition by this species may represent up to 84% of river input, with up to 23% retention in mats of *C. fornicata*. With lowered Si:N ratios as a result of chronic eutrophication in this bay (Chauvaud et al., 2000), the trapped silica is critical in promoting diatom growth and is likely to keep harmful algal blooms (HABs) at bay (Ragueneau et al., 2002, 2005). In the oligotrophic Adriatic, the presence of the introduced Manila clam *Venerupis* (= *Ruditapes*) *philippinarum* increases outflux of ammonium, phosphorus, silicate, and carbon dioxide from sediments by 18, 15, 9, and 9 times, respectively (Bartoli et al., 2001).

Vascular plants also have major effects on nutrient transfer between the water column and benthos and on belowground nutrient cycling. In estuaries of the NE Pacific, the nonindigenous seagrass *Zostera japonica* and an invasive hybrid cordgrass (*Spartina foliosa* × *Spartina alterniflora*) both form dense beds in the intertidal zone, with *Zostera* at lower elevations (Figure 2). These macrophyte beds are net sinks for NO<sub>3</sub>, NO<sub>2</sub>, and dissolved phosphorus, and can convert unvegetated intertidal sediments from sources to sinks for these nutrients, with probable negative effects on phytoplankton productivity (Larned, 2003; Grosholz et al., 2009). Uptake may be highest in summer, when river inputs of nutrients to the estuarine water column are lowest. Notably, nutrient uptake by the native seagrass, *Z. marina*, is higher than for *Z. japonica*, due to greater biomass; hence, invader effects are likely to be significant only in otherwise unvegetated sediments (Larned, 2003). In the Yancheng Nature Reserve in China, invasive *S. alterniflora* marsh exhibited higher sediment and tissue sulfur levels and greater sulfur storage than native *Suaeda salsa* and *Phragmites australis* marsh or than unvegetated tidal flat. These higher sulfur concentrations are proposed to increase the competitive



**Figure 2** Invasive plants alter ecosystem architecture and introduce copious amounts of litter and detritus that are incorporated into the food web. (a) *Phragmites australis* in Connecticut, USA. Photograph by C. Whitcraft. (b) *Tamarix* spp. in Tijuana River estuary, California, USA. Photograph by T. Talley. (c) *Rhizophora mangle* on Molokai, Hawaii, USA. Photograph by A. Demopoulos. (d) Bed of invasive eelgrass, *Zostera japonica*, with invasive hybrid *Spartina* in Willapa Bay, Washington, USA. Photograph by C. Neira.

advantage of *S. alterniflora* and contribute to its successful expansion in China.

The introduction of vascular plants to unvegetated sediments (Figure 2) will usually increase belowground biomass through litter accumulation, and accelerate respiration rates, converting systems from net autotrophic to heterotrophic conditions (Hahn, 2003; Grosholz et al., 2009), and sometimes generating sulfide buildup (Neira et al., 2005, 2007). However, not all vascular plants shift nutrient cycling in the same direction relative to native vegetation. *Z. japonica* detritus decomposes more rapidly than the native seagrass (Hahn, 2003), but *Spartina* hybrid belowground sediments had lower respiration rates than those of native marsh vegetation, with slowed carbon and nitrogen turnover and accumulation of refractory organic matter (C. Tyler, personal communication; Grosholz et al., 2009). Invasive *P. australis* in the northeastern USA modifies N pools but the direction and magnitude of the effects vary with the system and its native species (Windham and Meyerson, 2003). *P. australis* can increase the standing stock of nitrogen in invaded systems due to its high biomass and refractory stems (Windham and Meyerson, 2003). Pore waters in at least some native salt-marsh stands have higher N concentrations than in *P. australis* stands. Uptake of dissolved organic nitrogen by invasive *P. australis* may explain this observation and contribute to its competitive dominance (Meyerson et al., 2009). Mangrove invaders (*Rhizophora mangle*) in Hawaii increase sediment oxygen demand and labile carbon is redirected toward microbial consumers relative to uninvaded sediments, where oxygen demand is lower and macrofauna play a larger role in C processing. Oxygen demand remained elevated even 2–6 years after removal of aboveground *R. mangle* biomass, indicating the persistent functional impacts of large plant invaders (Sweetman et al., 2010).

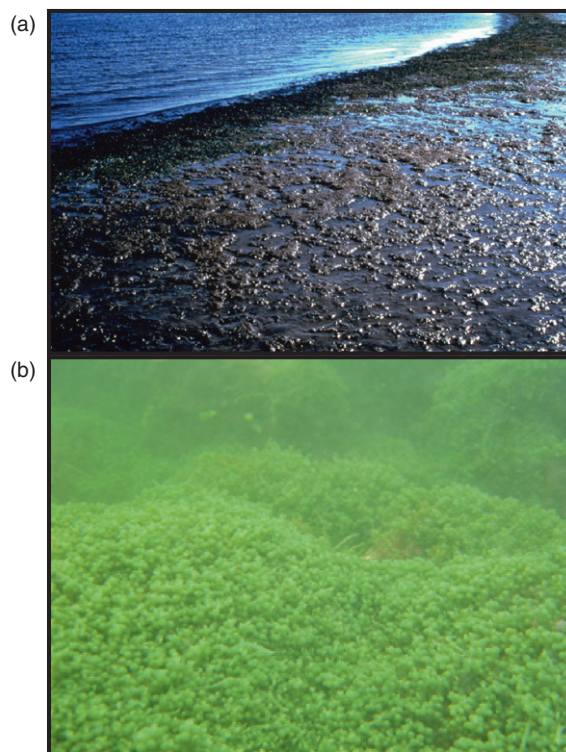
### 7.03.3.2 Nitrogen Fixation

With nitrogen being a key, often-limiting nutrient in most coastal marine settings, the introduction of new nitrogen via nitrogen fixation can regulate primary production. The invasive alga *Caulerpa taxifolia* appears to enhance N fixation by releasing photosynthate into the algal rhizosphere, as is done by seagrasses. This activates microbial fermentation, which stimulates sulfate-reducing microbes, many of which also fix nitrogen (Chisholm and Moulin, 2003). The additional N may promote success of *C. taxifolia* in highly oligotrophic Mediterranean waters. In a study of nitrogen fixer activity and diversity in southern California wetlands, Moseman et al. (2007) found elevated N fixation rates in sediments with invasive mussels (*Musculista senhousia*), lowered fixation rates in stands of the invasive mangrove (*Avicennia marina*), and no effect in tamarisk (*Tamarix*)-invaded sediments relative to adjacent mudflat or native marsh sediments. Both direct and indirect deposition of organic matter and fining of sediments by *M. senhousia* may enhance nitrogen fixer activity. Reduced diversity of N-fixing microbes, assessed using *nif-H* probes and Terminal Restriction Fragment Length Polymorphism (TRFLP), was observed in *Musculista*- and tamarisk-invaded sediments (Moseman et al., 2007). Altered diversity was not necessarily translated into altered function, although highest fixation rates were usually observed at low or intermediate diversity levels. These results

demonstrate that even similar types of invaders (i.e., the mangrove and tamarisk tree morphs) can have differing biogeochemical impacts.

### 7.03.3.3 Bioturbation

Bioturbation, the mixing of sediment, and bioirrigation, the pumping of solutes by animal activities, both exert major controls on redox conditions and biogeochemical processes within sediments. They also affect sediment stability and erosion, which will be covered more fully in Section 7.03.5. A wide variety of invasive species, including polychaetes, bivalves, and crustaceans, are bioturbators that affect invaded ecosystems. Invaders may increase or reduce rates of bioturbation relative to native faunal activities. Enhanced bioturbation has been reported in the Baltic Sea following invasion of the polychaete *Marenzelleria*, which burrows more deeply than the native *Nereis diversicolor* (Olenin and Leppäkoski, 1999). Burrowing activities increase microhabitat heterogeneity and control the distribution and fluxes of oxidants (oxygen, nitrate, and iron), thereby enhancing aerobic remineralization, sulfate reduction, ammonium oxidation, and denitrification (Kristensen and Kostka, 2005; Marinelli and Waldbusser, 2005; Bertics and Ziebis, 2009). Mat-forming organisms such as mussels (*M. senhousia*) or algae (*Caulerpa* spp.) that blanket the sediment surface (Figure 3) may have a reverse effect, homogenizing sediments by trapping fine particles and promoting dysaerobic or anaerobic conditions, or by limiting access to particles for subsurface feeders below.



**Figure 3** Mat-forming animals and plants modify or smother seafloor communities: (a) *Musculista senhousia*; (b) *Caulerpa racemosa* var. *cylindracea*.

### 7.03.4 Invader Alteration of Trophic Interactions and Energy Flow through Ecosystems

The direct effects of introduced marine species as either food sources for, or consumers of, resident species have long been of interest, yet there have been relatively few studies of the system-level trophic implications of these invasions. Those examples that do exist demonstrate a variety of interactions, including the existence of indirect effects and trophic cascades. Not surprisingly, given their basal position in the food chain, invasive autotrophs have received the most attention. Although there are fewer successful invasions of species at higher trophic levels, their functional impacts can be dramatic.

#### 7.03.4.1 Food-Web Effects of Invasive Vascular Plants

The introduction of vascular plants has functional effects on trophic pathways brought about in part by the addition of above- and belowground biomass (Posey, 1988; Grosholz et al., 2009). Many invasive vascular plants in marine systems produce copious amounts of litter and enter the food chain as detritus. The extent to which invasive primary producers are consumed as living material, however, depends in part upon the palatability of the tissues, and thus this becomes integral for understanding and predicting invader impacts.

Common approaches for assessing invader suitability as food sources include examining characteristics of the plants themselves (e.g., C:N ratios), or utilizing either naturally occurring or experimentally-altered stable isotope ratios to track invader-derived C and N through the food web. Invasive tamarisk (*Tamarix* spp.) in a southern California salt marsh (Figure 2(b)) had lower C:N ratios and higher degradation rates than most of the native high marsh plants, suggesting high palatability (Whitcraft et al., 2008). In the US Pacific Northwest, *S. alterniflora*, with a C:N ratio of 46–48, is notably less palatable for tidal invertebrates than a co-occurring invader, *Z. japonica* (C:N ratio of 17). This may explain the more rapid incorporation of *Z. japonica* than *S. alterniflora* into benthic invertebrates as determined from  $^{15}\text{N}$  enrichment experiments (Grosholz et al., 2009). In addition, *Z. japonica* is preferred by migrating waterfowl over the native eelgrasses (Lovvorn and Baldwin, 1996). In San Francisco Bay, however, Western Canada geese avoid the invasive *Spartina* hybrid almost entirely, due to its increased toughness, but readily consume up to 90% of the native Pacific Cordgrass (*S. foliosa*) at some sites (Grosholz et al., 2009). Thus, replacement of one primary producer by a congeneric species does not necessarily mean replacement of trophic function.

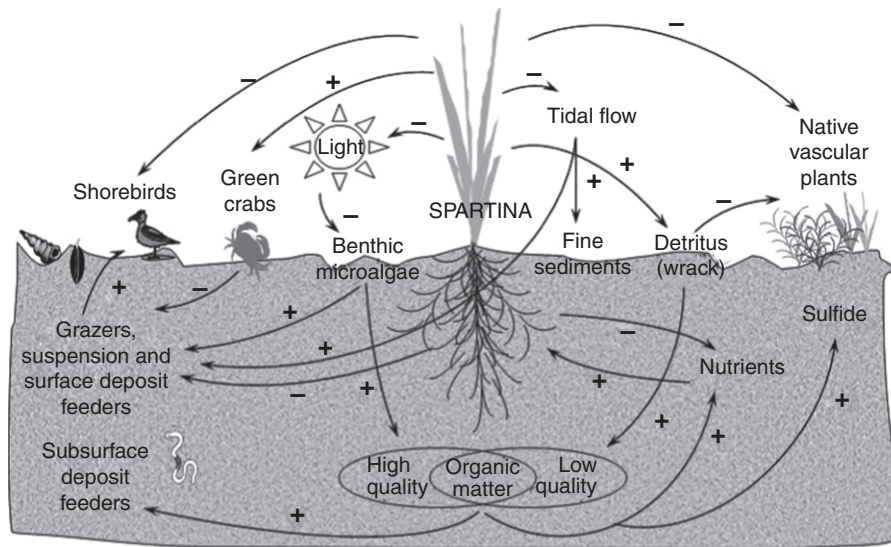
On the US East Coast, natural abundance stable isotope analyses revealed incorporation of invasive *P. australis* into the food-web supporting killifish in *Spartina* marshes (Wainright et al., 2000; Currin et al., 2003). Invasion of *S. alterniflora* marshes by *P. australis* in New Jersey led to a shift in arthropod food webs from live-plant to detritus-based, due to the loss of external herbivores such as plant hoppers that were consumed by many of the predatory arthropods such as dolichopodids and spiders. As the external plant feeders were replaced by less accessible, concealed stem feeders, the predatory arthropod assemblage became dominated by detritivores and algal feeders such as *Collembola* and chironomids (Gratton and Denno, 2005, 2006). These trophic shifts were reversed fairly rapidly

when *P. australis* was removed and *S. alterniflora* was restored. Because *P. australis* has a  $\delta^{13}\text{C}$  signature that is distinctive from that of the native *S. alterniflora* in this system, isotopic evidence readily documented the shift in the plants at the base of the arthropod food web (Gratton and Denno, 2006).

Research in NE Pacific wetlands has revealed the degree to which a number of invasive plants enter and alter food chains. The use of  $^{15}\text{N}$ -labeled plant detritus has revealed that detritus of invasive *Spartina* and *Tamarix* species is readily consumed by infaunal invertebrates typically considered to be detritivores or deposit feeders (e.g., oligochaetes and capitellid polychaetes) (Levin et al., 2006; Whitcraft et al., 2008; Grosholz et al., 2009). An increase in detritivores such as capitellid polychaetes and tubificid oligochaetes is typically observed following wetland plant invasion of tidal flats (Jackson, 1985; Neira et al., 2005; Wu et al., 2009). Dual isotopic labeling of invasive *Spartina* detritus (with  $^{15}\text{N}$ ) and microalgae (with  $^{13}\text{C}$ ) in San Francisco Bay demonstrated that species that consume microalgae (bivalves and amphipods) were more likely to experience density declines following *Spartina* invasion (Levin et al., 2006). Bottom-up effects in the form of reduced microalgal production and increased litter input (Grosholz et al., 2009) as well as simultaneous top-down effects in the form of enhanced disturbance and predation from the invasive green crab *Carcinus maenas* (Neira et al., 2006) probably both contributed to the dramatic declines in macrofaunal abundance following *Spartina* invasion, and to a shift from faunal reliance on fresh algal primary production to a detritus-based system (Figure 4).

Notably, Brusati and Grosholz (2007, 2008) found limited use of invasive hybrid *Spartina* by epifaunal consumers in San Francisco Bay based on natural abundance isotopic ratios. Similarly, for invasive mangroves in Hawaii, Demopoulos et al. (2007) found little evidence for incorporation of mangrove-derived carbon in detritivores. This was surprising given extensive consumption of mangrove detritus in native mangrove forests by tubificid oligochaetes, nematodes, and nereid polychaetes (Demopoulos et al., 2007). Clearly, the entry of invasive plants into wetland food webs can be limited and may ultimately reshape the trophic structure of the ecosystem.

Wetland plant invasion of tidal flats often increases primary productivity. The introduction of Atlantic cordgrass (*S. alterniflora*) and Japanese seagrass (*Z. japonica*) into Willapa Bay (Washington) tidal flats elevated primary production by 50% (Ruesink et al., 2006). However, impacts on production may vary temporally. For cordgrass in San Francisco Bay, the *Spartina* hybrid induces higher primary productivity and biomass than the native *S. foliosa* or *Salicornia* spp. However, the *Spartina* hybrid belowground biomass enhancement changes with invasion stage, nearly doubling from the growing edge to mature (30-year-old) meadows (Neira et al., 2007). *S. alterniflora* in Willapa Bay appears to have maximal biomass at 5–10 years and then declines (Grosholz et al., 2009). In its native habitat, *Spartina* exhibits a hump-shaped production function along an intertidal elevation gradient (Mendelssohn and Morris, 2000; Morris et al., 2002). Thus, significant changes in function can derive from production by a few invasive, high-impact species (Ruesink et al., 2006), but the effects may be both time dependent and location dependent.



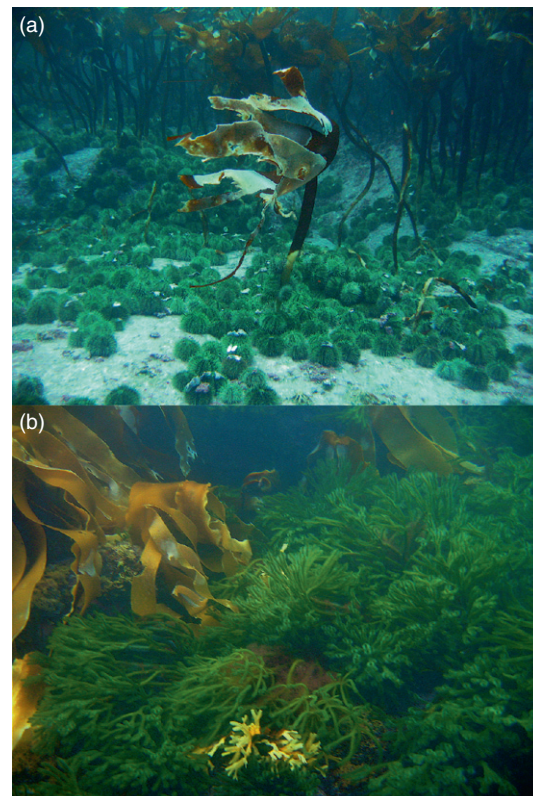
**Figure 4** Conceptual model of changes following cordgrass invasion of unvegetated tidal flats. Positive (+) and negative (-) effects on a range of physical, chemical, and biological processes are shown. From Grosholz, E.D., Levin, L.A., Tyler, C., Neira, C., 2009. Changes in community structure and ecosystem function following *Spartina alterniflora* invasion of Pacific estuaries. In: Silliman, B., Bertness, M., Grosholz, E. (Eds.), *Human Impacts on Salt Marshes: A Global Perspective*. University of California Press, Berkeley, CA, pp. 23–40.

#### 7.03.4.2 Food-Web Effects of Invasive Macroalgae

Like plant invasions, macroalgal invasions can increase primary productivity. *Sargassum muticum* invasion in Spain more than doubled primary production and increased the diversity of algal species, reducing dominance of the native *Gelidium spinosum* (Sanchez et al., 2005). Many epiphytic species were supported by the invader. Competition for light and increased space for epiphytes are explanations for the observed shifts in algal community structure (Sanchez et al., 2005). In the Mediterranean, there are approximately 85 introduced macrophyte species, of which 1 out of 10 have achieved status as invasives with marked ecological impacts. Most of these are large, perennial species, lack a resting stage, have vegetative reproduction, and have toxic metabolites, causing avoidance by grazers. Thus, although primary productivity is likely to be enhanced by these prolific invaders, the transfer of this production to higher trophic levels may be sharply inhibited by allelopathy (Boudouresque et al., 1996).

A majority of introduced seaweeds are unpalatable, and even those that are readily eaten are rarely controlled by herbivores (Williams and Smith, 2007). *C. taxifolia*, for example, forms continuous meadows in the NW Mediterranean and produces toxic secondary metabolites. These inhibit growth of native algae and inhibit grazing by fish and sea urchins (Galil, 2000). *C. taxifolia* also reduces the accessibility of benthic prey and inhibits the foraging activity of fishes such as red mullet (*Mullus surmuletus*) (Levi and Francour, 2004). Thus, most of its effects appear related to habitat modification (see below) rather than to direct trophic interactions.

The invasive green alga *Codium fragile* ssp. *tomentosoides*, which covers much of the Nova Scotia shallow sub-tidal (Figure 5(b)), is also relatively less palatable to the dominant herbivore (*Strongylocentrotus droebachiensis*) than the native kelp, *Laminaria longicuris* (Sumi and Scheibling, 2005). *Codium*'s replacement of kelp in Nova Scotia is aided by the



**Figure 5** Invasion of *Membranipora membranacea* and *Codium fragile* in Nova Scotia. (a) *Membranipora* damage to native kelp beds, with additional urchin grazing. (b) Stands of *Codium* invading native kelp beds. Photographs by Robert Scheibling.

destructive effects on kelp of a fouling invader, *Membranipora membranacea* (Scheibling and Gagnon, 2006) (Figure 5). Many other species reliant on kelp forests, such as sea urchins, are

likely to be harmed by *C. fragile* inhibition of kelps, combined with shading effects of the invasive brown alga *S. muticum* (Williams and Smith, 2007).

#### 7.03.4.3 Impacts of Invasive Benthic Grazers and Filter Feeders

Invasive grazers often have the potential to structure communities by consuming habitat-forming (engineering) or otherwise fundamental plants. Gastropods such as limpets, chitons, and snails are noteworthy for their voracious grazing on algae, with bare rock or denuded meadow a common outcome (see Section 7.03.5). Some herbivores, however, may facilitate spread of invasive seaweeds through fragmentation (Harris and Mathieson, 2000; Zuljevic et al., 2001).

Competition can also arise from the effects of exotic grazers, such as with the gastropod, *Batillaria attramentaria*, which competes with the native marsh snail *Cerithidea californica* for benthic diatoms in NE Pacific wetlands. Largely due to superior resource use efficiency (converting diatoms to tissue), *Batillaria* has displaced *Cerithidea* (Byers, 2000). A less-recognized part of this food chain is also likely to suffer, as the snails serve as a first intermediate host for trematode parasites. Eighteen native trematodes occur in *Cerithidea*, but only one non-native species (*Cercaria batillariae*) is found in *Batillaria* (Torchin et al., 2005). Modeling of snail competition suggests that *Cerithidea* will experience local extinction in 55–70 years when competing with *Batillaria*; their native trematodes may experience the same fate (Byers, 2009).

Parasites are rarely considered as keystone species themselves. However, Wood et al. (2007) have shown that by reducing the efficiency of invasive littorine grazing, trematode infestation can act to enhance algal cover in the New England rocky intertidal zone. Uninfected *Littorina littorea* consumed 40% more macroalgal biomass than snails infested by the diagenic trematode *Cryptocotyle lingua* (Wood et al., 2007).

Invasive muskrat in Europe and nutria (*Myocastor coypus*) in the SE USA both are voracious grazers, burrowers, and rooters that consume or destroy marsh vegetation over large areas. Introduced from South America for their fur, nutria have damaged between 321 and 415 km<sup>2</sup> of Louisiana marsh on the Mississippi Deltaic Plain (Keddy et al., 2009). Nutria grazing increases the sensitivity of vegetation to stress from flooding and salinity associated with subsidence (Grace and Ford, 1996). Experimental studies with nutria show that they eliminate effects of intentional fertilization enacted to increase production, but tend to amplify effects of other disturbances such as fire and herbicide, possibly through a dietary preference for newly growing vegetation (McFalls, 2004; Keddy et al., 2009). Control of nutria in SE Louisiana has been by harvest, but predator control, enabled by reducing harvest of alligators, and increasing their density and size, have been proposed (Keddy et al., 2009).

Suspension feeders can have differing effects on both primary and secondary productivity. In some cases, filter feeders can increase benthic algal production by enhancing water clarity, as has been demonstrated for the zebra mussel *D. polymorpha* (Cecala et al., 2008). Invasive suspension-feeding mollusks can also reduce system primary productivity (*Potamocorbula*; Alpine and Cloern, 1992) or shift the composition of phytoplankton (Thieltges et al., 2006), with

consequences for pelagic and benthic components of the ecosystem. Where suspension feeders invade in high numbers, they can increase overall production. Secondary production in Willapa Bay was boosted over 250% by two invasive bivalve species, the Pacific oyster (*Crassostrea gigas*) and the Manila clam (*V. philippinarum*), which are both now routinely harvested (Ruesink et al., 2006). Abundant and palatable invaders also may at least temporarily boost population sizes of native predators (Grosholz, 2005).

#### 7.03.4.4 Impacts of Invasive Higher Consumers

Invasive species in estuarine and coastal systems are more likely to reside near the bottom than near the top of food chains. As such, there are rather few studies of invasive predator effects; many of these are from enclosed seas or estuaries (see table 15.1 in Rilov, 2009). Cladocerans in the Baltic Sea, comb jellies in the Black Sea, copepods in Pacific estuaries, green crabs (*C. maenas*) and shore crabs (*Hemigrapsus sanguineus*) globally, whelks in Chesapeake Bay, and asteroids in Tasmania are among the better-studied exotic predators (Rilov, 2009).

Some of the most transformative predators have been planktonic. The comb jelly *Mnemiopsis leidyi* invading the Black and Caspian Seas, and the Sea of Azov, in the 1980s, consumed meso-zooplankton (fish eggs, fish, and invertebrate larvae), leading to mortality and starvation by fishes and benthic population losses as well (Leppäkoski et al., 2009; Rilov, 2009). Eventually, an introduced ctenophore *Beroe ovata* exhibited some control of *M. leidyi*, generating recovery of many components of the pelagic ecosystem (Dumont et al., 2004). In the Baltic Sea, the invasive cladoceran *Cercopagis pengoi* can alter zooplankton community structure and food webs (Telesh and Ojaveer, 2002). In estuaries of the NE Pacific, invasive predatory copepods from Asia have transformed the zooplankton assemblage structure. *Tortanus dextrilobatus* in San Francisco Bay preferentially consumes native copepods and may be facilitating other invasive copepods (Rilov, 2009).

The rapa whelk, *Rapana venosa*, a voracious gastropod predator, has invaded the Chesapeake Bay and the Black Sea. This has resulted in a major loss of oyster beds in the Black Sea where there are no predators on this invader (Harding, 2003). In Chesapeake Bay, control by larger native whelks, blue crabs, mud crabs, and spider crabs seems likely (Harding and Mann, 1999, 2003).

Crabs, with planktonic larvae, high adult mobility, and often commercial value, seem to be among the most successful invasive predators. The green crab *C. maenas*, a generalist predator, exerts strong 'top-down' influence on benthic assemblages on the US Pacific and Atlantic coasts (Grosholz et al., 2000; Whitlow et al., 2003; Floyd and Williams, 2004), including prey preferences that may benefit lower trophic levels through competitive release (Figure 4). In central California, the *C. maenas* invasion reduced densities of 20 invertebrate species monitored over a 9-year period, with the clams *Nutricola tantilla* and *Nutricola confusa*, and native shore crab, *Hemigrapsus oregonensis* exhibiting rapid, strong declines. Possible indirect effects were density increases in the polychaetes *Lumbrineris* sp. and *Exogone* sp., and tube-building tanaid crustaceans, *Leptochelia dubia*, but shorebird densities did not respond positively or negatively (Grosholz et al., 2000). In addition, through preferential consumption of the



larger invasive bivalve *V. philippinarum*, the green crab has allowed another invasive, suspension-feeding competitor, *Gemma gemma*, to flourish in San Francisco Bay tidal flats after decades of limited activity (Grosholz, 2005). *Venerupis* also protects the native clam *Protothaca* by taking the brunt of *Carcinus* predation (Byers, 2009). Another consequence of massive predation on *V. philippinarum* by *Cancer* crabs has been to increase the predator biomass and production in the system, ultimately intensifying mortality of some native prey species (Byers, 2005). In some situations, competition between native and invasive species may be a much lesser effect than the concomitant escalation of predator-induced mortality as a result of prey subsidies by the invasive competitor (Noonberg and Byers, 2005). In San Francisco Bay, green crab densities are enhanced by invasive *Spartina*. Experimental enclosure of green crabs demonstrated that crab disturbance and predation target many of the bivalve and amphipod species whose densities decline in *Spartina*-invaded sediments (Neira et al., 2006).

To date, there are no instances of invasive aquatic predators driving species to total extinction. Although such a consequence might be expected from invasion by specialist predators, most invasive predators are generalists. Additionally, many invasions may be too recent to have caused extinctions.

### 7.03.5 Ecosystem Engineering by Invaders

#### 7.03.5.1 Abiotic Ecosystem Characteristics

Alteration of the physical or chemical characteristics of ecosystems is one of the greatest influences of invaders (Crooks, 2002, 2009; Wallentinus and Nyberg, 2007; Sousa et al., 2009). Such alterations change living conditions for entire suites of resident biota – essentially altering the very nature of the habitats in which local species reside (Vitousek, 1990). On land, familiar examples of introduced habitat modifiers include grazing hoof stock that denude islands and increase erosion rates, and highly flammable grasses (e.g., cheat grass) that alter fire regimes. In the sea, biogenic ecosystem alterations are especially prevalent in benthic systems. Here, habitat characteristics, such as grain size, sediment stability, water clarity, and structural complexity, are shaped by a wide range of biological activities, including bioturbation, growth of carbonate tubes or shells, and feeding.

Invader modifications of abiotic conditions have long been recognized (e.g., cordgrass invasion in Elton (1958)), but these were often loosely treated as a variety of different types of effects. These included alterations to disturbance regimes, changes in primary productivity and the growth of vegetative structure, or miscellaneous examples of ecosystem modification (Vitousek, 1990; Williamson, 1996; Crooks, 2009). Only relatively recently has an overarching concept emerged to capture the broad characteristics of species that affect other biota by changing habitats. This concept, termed 'ecosystem engineering', provides a useful tool for considering the role of such species (Jones et al., 1994, 1997; Crooks, 2002). Under this framework, the effects of species that destroy structure, whether they are goats or grazing snails, are considered together with species that create structure, for example, pine trees or mussels. Also, the engineering concept, which involves modifications to the physical environment that then translate into

subsequent biotic effects, encompasses abiotic modifications arising from all manner of proximate mechanisms, such as herbivory, tissue growth, or burrowing.

Consideration of engineers in the marine environment, where the role of species in structuring habitats has long been studied (e.g., facilitation and trophic group ammensalism), has helped to shape thinking about ecosystem-level impacts of invasive species and to disentangle trophic status from other ecosystem-level processes (Crooks, 2002). On land, only plants serve directly as habitat (trees creating a forest) and animals largely serve to modify existing habitat structure. In the sea, however, this distinction does not hold. The bodies of sessile forms (mussels, corals, and tubeworms) all directly provide habitat to other species, in ways that are functionally similar to that of algae and wetland plants.

#### 7.03.5.2 Engineering Processes

A useful framework for considering invasive engineering and its effect on other biota is to separate the engineering process, which is the effect of the engineer on the abiotic environment, from the engineering consequence, which is the resultant effect of changes to the abiotic environment on the biotic constituents, including both other species and feedbacks to the engineer itself (Jones and Gutierrez, 2007; Crooks, 2009). In the marine environment, there are relatively few engineering processes that appear to account for many invader effects. We will first highlight how these engineering processes affect pelagic and benthic habitats, and next discuss case histories of engineering-impacts of invaders on other biota.

Although the water column, because of its expansive space, apparent lack of physical structure, and fluidity, seems less amenable to engineering than benthic habitats, it can be strongly affected by the activities of invasive organisms. Biofiltration by invasive bivalves, as noted earlier, can increase water clarity, penetration of light, and autotroph growth. Such effects have been extensively documented not only for invasive zebra mussels in freshwater systems (Phelps, 1994; Strayer et al., 1999), but also for the filter-feeding clam *Corbula amurensis* (Alpine and Cloern, 1992) and tubeworm *Ficopomatus enigmaticus* (Davies et al., 1989). Water clarity can also be affected by bioturbation activities of benthic organisms, especially in areas of limited water circulation (e.g., benthic-feeding fish in freshwater lakes; Richardson et al., 1995). The bodies of organisms themselves can also affect light penetration to the benthos; shading by the attached, invasive macroalgae *S. muticum* is one example (Staeher et al., 2000; Wallentinus, 2002; Britton-Simmons, 2004).

Invasive biota can also alter chemical properties in the sea. Although these changes influence biogeochemical cycling, some aspects represent modifications of the environment and habitats. For example, HAB (Harmful Algal Bloom) species, including species likely transported in ballast water, degrade water-column conditions by disruption of cells and release of toxins into the environment, as well as by generating (microbially-driven) hypoxic conditions (Van Dolah, 2000). Exotic phyto- or zooplanktonic species have also been reported to produce copious mucus, which can coat the seafloor (Hopkins, 2002; Laing and Gollasch, 2002). Within the seabed, burrowing activities of invasive organisms can increase oxygen penetration, expanding habitability of subsurface sediments for smaller invertebrates.

Oxygenating bioturbators include the invasive bivalve *Ensis americanus* in intertidal and sub-tidal sediments of the North Sea (Armonies, 2001) and the spionid polychaete *Marenzelleria* in the Baltic Sea (Olenin and Leppäkoski, 1999).

Organisms can modify the movement of water, and this is a particularly common effect of sessile benthic invaders (discussed subsequently in more detail). Local flows are modified through the insertion or removal of structure from the benthos into the water column. Such modifications to flow regime have effects on food availability, flux of larvae to the benthos, sediment stability, and deposition. In addition, invaders can directly contribute to sediments through creation or degradation of calcareous shells and tubes. For example, carbonate sediments are created by the invasive polychaete *F. enigmaticus* in South America (Figure 6; Schwindt and Iribarne, 2000; Schwindt et al., 2004b). Species able to live

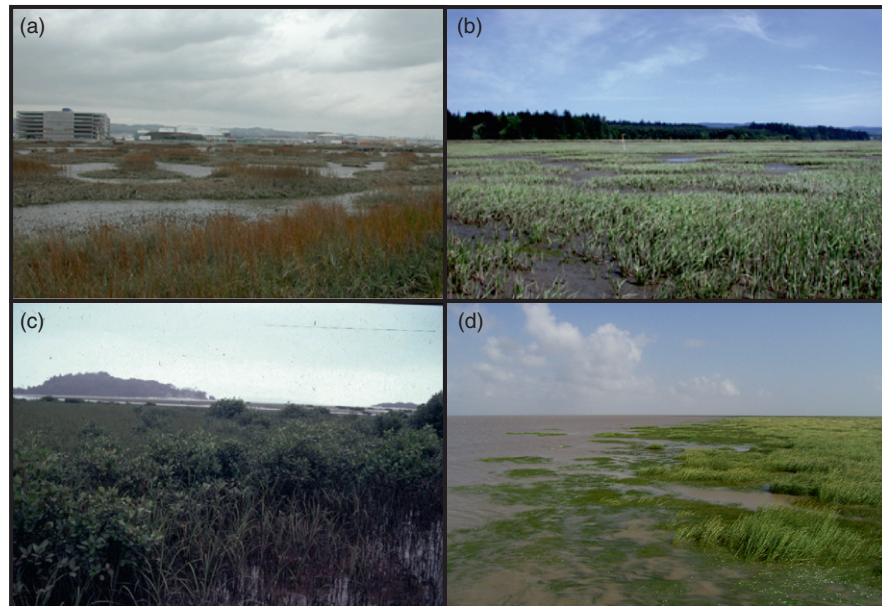
on the surfaces of other organisms can also alter the effective flow environment for the host species by creating drag. The exotic slipper limpet, *C. fornicata*, and 'oyster thief' algae, *C. fragile*, are both epibionts that increase drag and can cause dislodgement and loss of the mollusk species to which they attach (Steneck and Carlton, 2001; Thielges, 2005).

Indirect trophic modifications can result when plants invade an otherwise unvegetated foraging habitat. Both migratory and resident shorebirds, which forage on tidal flats at low tide, and estuarine fish, which forage on tidal flats at high tide, have experienced loss of foraging habitat in settings such as San Francisco and Willapa Bays, where open mud has been transformed into heavily vegetated marsh by invasive *Spartina* (Strong and Ayers, 2009) (Figure 7).

Modification of the physical architecture of the benthos through changed structural characteristics has effects that



**Figure 6** *Ficopomatus enigmaticus* transforms sediment to reef in Elkhorn Slough, California, USA. Photographs by B. Becker.



**Figure 7** *Spartina* invasions. (a) *Spartina* (*alterniflora* × *foliosa*) hybrid San Francisco Bay, USA; (b) *S. alterniflora* in Willapa Bay, Washington, USA; (c) *S. alterniflora* invading a New Zealand *Avicennia* forest. Photograph by T. Talley. (d) *S. alterniflora* invading Yangtze R. tidal flats. Photograph by A. Shang.

extend beyond hydrodynamics of the overlying water column. These are often considered together as the modification of habitat *per se*. Invaders that create structure, via their own bodies (e.g., plants, corals, and mussels) or dwelling structures (e.g., agglutinated worm tubes), can ameliorate environmental conditions such as temperature and water content, offer refugia from predation, provide visual cues for behavioral activities of motile fauna, slow water flow and increase particle deposition, and provide surfaces for settlement. All of these can occur (often concurrently) when structure is produced and habitat is created. Invaders that remove such structures, such as grazers that mow down emergent plants, will often have the opposite effect. This overlap in effects is possibly why there is such a robust response of ecosystems to structure creation or destruction by invasive species.

### 7.03.5.3 Ecosystem Engineering by Invasive Plants and Algae

Key abiotic mechanisms by which marine plants and algae act to engineer ecosystems include shading, flow reduction, altered sediment dynamics and content (enhanced deposition, reduced erosion, smaller grain size, and increased organic matter content), and substrate provision. They enhance living biomass above- and belowground, and often increase litter production with accompanying modification of geochemical conditions, humic and tannin substances, as well as organic matter quality. Those invaders with extensive root systems such as mangroves and cordgrasses often modify both above- and belowground conditions. These also stabilize sediments, reducing resuspension and erosion. The extensive aboveground root systems of mangroves (Figure 2(c)) and belowground rhizome systems of marsh grasses also act to stabilize sediments. They are so effective at erosion prevention that many early introductions occurred intentionally to stabilize shorelines and counter sediment loss (Wan et al., 2009).

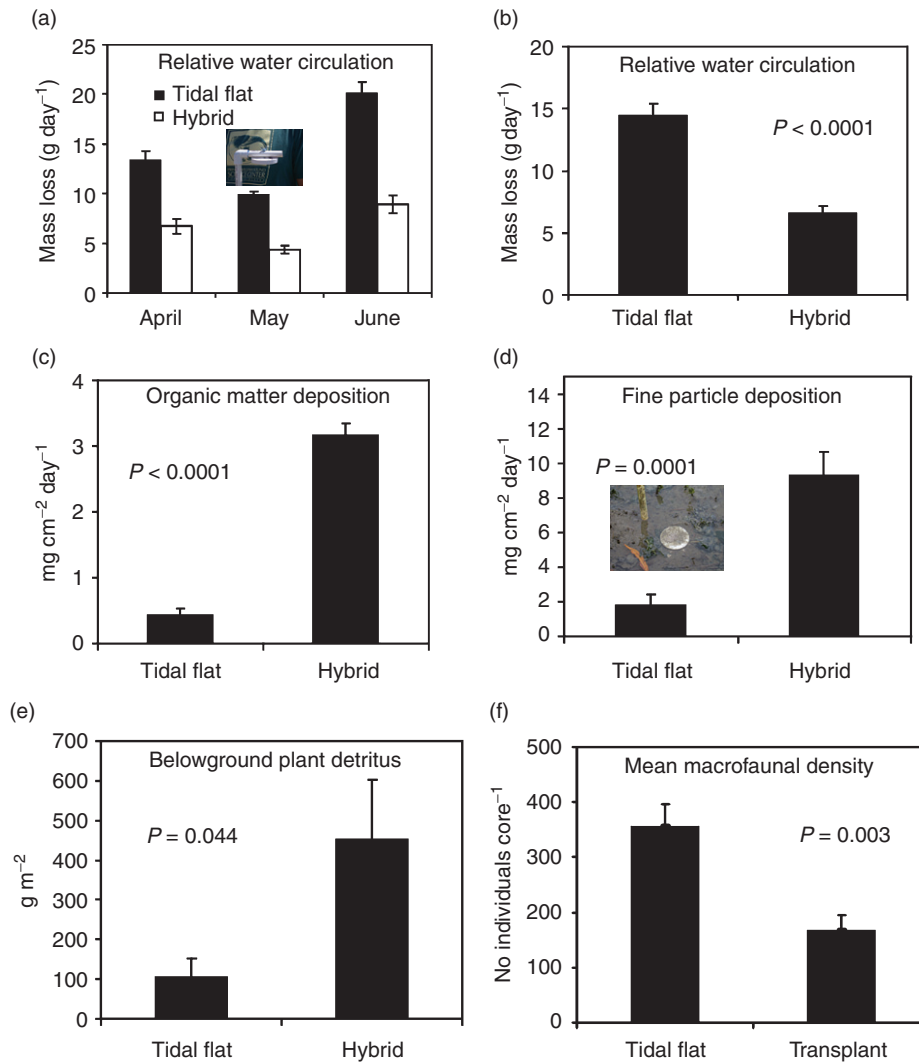
Ecosystem modification by invasive marine plants and algae is documented primarily for a few highly aggressive genera. For vascular plants, these are cordgrass (*Spartina*) (Figure 7), the common reed (*Phragmites*) (Figure 2(a)), Tamarisk (*Tamarix*) (Figure 2(b)), and eelgrass (*Zostera*) (Figure 2(d)); the most-studied algal invasions involve *Caulerpa* (Figure 3), *Codium* (Figure 5), and *Sargassum*. Many studies document consequences of plant and algae invasions for abundance or composition of primary producers, invertebrates, birds, and fish (summarized in Appendix 1), but few actually address the mechanisms involved. Some aspects of engineering are relatively well studied in vascular plant stands (Fonseca, 1996; Bos et al., 2007; Cuddington et al., 2007; Hastings et al., 2007; Bouma et al., 2009). However, experimental or manipulative studies aimed at identifying engineering effects of invasive marine plants and algae are limited. Removal, transplant, and mimic experiments can help identify specific invader effects and shed light on mechanisms. We will highlight these where such information is available.

Some of the effects of exotic cordgrass (*Spartina* spp.) are discussed in the context of trophic interactions (see previous section), but many of this invader's impacts stem from their ability to modify sedimentary and water-column conditions. Neira et al. (2006), using gypsum dissolution and flow

measurements, documented 2–4 times lower flow at the growing edge of an invasive *Spartina* hybrid meadow relative to the adjacent mudflat in San Francisco Bay (Figure 8). The hydrodynamic alterations triggered a cascade of sediment modifications including large increases in deposition of fine (silt/clay) particles high in organic C content, lower redox potential, and ensuing sulfide buildup and anoxia (Figure 8). As a result of the flow reduction, barnacle recruitment to artificial substrates was reduced and entrainment of suspended infauna in tube traps was elevated in the hybrid *Spartina* meadow relative to that on adjacent open mudflat. Sediments transplanted from the mudflat into *Spartina* habitat for 40 days exhibited changes comparable to those described above (Figure 9). Infauna present in the transplanted sediment blocks suffered loss of bivalves and amphipods, a 50% reduction in density and 30% reduction in species richness (Figure 9). Resulting faunal composition mirrored that in the unmanipulated *Spartina* habitat (Neira et al., 2006). These experiments suggested that lowered survivorship and changing composition of mudflat taxa in *Spartina*-invaded sediments result from engineering of abiotic conditions. However, increased crab predation (Neira et al., 2006; Figure 9) and altered food supply (Levin et al., 2006) also contribute to major changes in faunal density and composition, following *Spartina* invasion in this system.

As with *Spartina* invasions, *Phragmites* is often taller, denser, and has higher biomass than the native plants (Figure 2(a)). *Phragmites* blocks more light than native *Typha* or *Spartina* in the northeastern USA, with strong effects on the temperature of air and soil and the timing of the spring melt (Meadows, 2006; Meyerson et al., 2009). *Phragmites* increases marsh elevation to a greater extent than other species through higher accumulation of litter and organic matter (Windham and Lathrop, 1999; Meyerson, 2000; Rooth et al., 2003) rather than mineral accumulation (Leonard et al., 2002). Elevation changes reduce hydrologic flow and topographic variability, with detrimental effects on fishes (Able and Hagan, 2000; Able et al., 2003). X-radiographs reveal different subsurface sediment structure in invaded and adjacent uninvaded marshes of New England. Distinct laminae and very sparse rhizomes in *Phragmites* habitats contrast with bioturbated sediments having a dense root mat of thinner rhizomes in native *Spartina* marsh (Talley and Levin, 2001). Invasion of *P. australis* into *S. alterniflora* marshes caused only minor alteration of macrofaunal communities in meso- and oligohaline sections of Chesapeake Bay, USA, with avoidance by *Hydrobia minuta* and *Gammarus mucronatus* (Posey et al., 2003). However, Talley and Levin (2001) observed salinity dependence to *Phragmites* effects in Connecticut, USA. In the least saline regions, stands of *Phragmites* had greater species richness with more podurid insects, sabellid polychaetes, and peracarid crustaceans, and fewer arachnids, midges, and oligochaetes than the native *Spartina* stands. *Phragmites* invasion has been reported to increase mussel and shrimp densities but to decrease crab densities (Appendix 1) (Fell et al., 2003).

Lower in the intertidal zone, invasive seagrass can also transform either mudflat or native seagrass habitats (Williams, 2007). Experimental transplantation of the invasive seagrass *Z. japonica* on Oregon mudflats yielded reduced particle sizes and increased sediment organic content similar to the *Spartina* effects described above (Posey, 1988). Faunal effects differed,

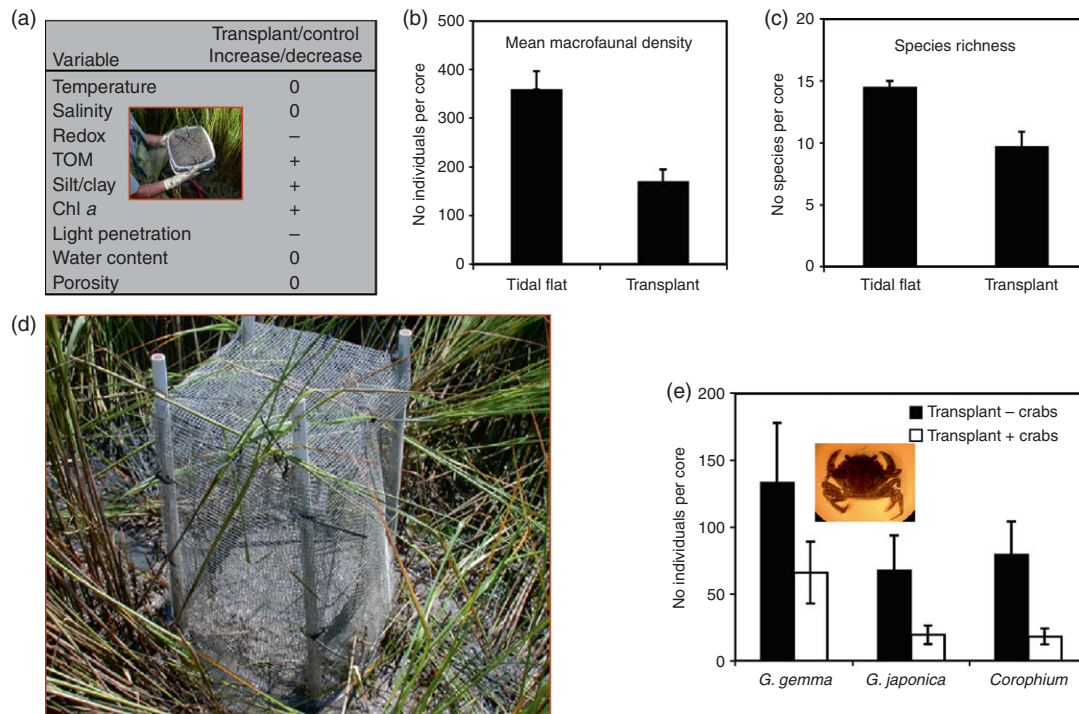


**Figure 8** Modification of the tidal flat ecosystem by invasive *Spartina* hybrid in San Francisco Bay. (a, b) Reduction in water flow as determined by gypsum loss. Increased deposition of (c) organic matter, (d) fine particles, and (e) belowground detritus within hybrid stands. Loss of macrofaunal density (f) within hybrid stands. Error bars represent 1 SE. Data from Neira, C., Grosholz, E.D., Levin, L.A., Blake, R., 2006. Mechanisms generating modification of benthos following tidal flat invasion by *Spartina* (*alterniflora* × *foliosa*) hybrid. *Ecological Applications* 16, 1391–1404.

however, in that invasive *Zostera* enhanced faunal densities and species richness relative to the uninvaded mudflat. Invasive *Heterozostera tasmanica* in Chile (Phillips et al., 1983; Ortiz and Wolff, 2002) and *Z. japonica* in the US Pacific NW (Posey, 1988) have had generally positive effects on system diversity.

Whereas the addition of non-native seagrasses can transform benthic ecosystems (Williams, 2007), the removal of native seagrasses can similarly impact ecosystem structure and function. In the 1930s a ‘wasting disease’ severely damaged or destroyed eelgrass meadows in the North Atlantic. This disease was brought about by the ‘cryptogenic’ (of unknown origin) species, *Labyrinthula zosterae*, a slime mold-like protist (Muehlstein et al., 1989; Ralph and Short, 2002; Minchin, 2007). In some benthic ecosystems of the North Sea, eelgrass meadows never recovered after the onset of this disease, and former meadows are now occupied by dense assemblages of the invasive razor clam *E. americanus* (Reise et al., 2002).

Perhaps the most destructive invasive autotrophs are *Caulerpa* species (*C. taxifolia* and *C. racemosa*), which have invaded the Mediterranean Sea and other areas and have become increasingly problematic over the past 25 years. Considered key ecosystem engineers, both *Caulerpa* species modify massive areas on landscape scales. They form continuous meadows that enhance siltation, block light, generally reduce diversity of underlying algae and invertebrates, and act to homogenize the seafloor ecosystems (Piazzi and Balata, 2008). *Caulerpa* stolons readily overgrow soft sediments, low-lying eelgrass, sponges, corals, and anemones. However, the *Caulerpa* invasion success and impact are partially dependent on substrate; it does best on algal turf and cannot penetrate extremely dense seagrass beds. *C. racemosa* can outcompete *C. taxifolia*, and also reduces the biomass of other invasive algae including *Acrothamnion preissii*, *Asparagopsis armata*, and *Womersleyella setacea* (Piazzi and Cinelli, 2003; Klein and Verlaque, 2007). Ecological impacts of *C. racemosa* are variable,



**Figure 9** Manipulative experiments documenting changes to (a) abiotic properties, (b) macrofaunal density, and (c) macrofaunal species richness in sediments transplanted from tidal flat to *Spartina* hybrid stands in San Francisco Bay. (d, e) Experiments including and excluding green crabs (*Carcinus maenas*), a species with enhanced densities in *Spartina* stands, document a role for predation in loss of invertebrates (the clam *Gemma gemma* and the amphipod *Grandidierella japonica*) following *Spartina* invasion. Error bars represent 1 SE.

and range from no effect (Casu et al., 2005), to reduced or enhanced densities of macrobenthos, including elevated density, diversity, and evenness of meiofauna (reviewed in Klein and Verlaque, 2007).

*Caulerpa* invasion into seagrass beds, when successful, is likely to alter system functions because it is typically less palatable to herbivores than seagrasses, and generally supports fewer epiphytes, which are an important element of overall productivity (Williams, 2007). In Australia, *C. taxifolia* supports larger numbers of epiphytes than the native seagrass *Zostera capricorni*, but fewer infauna reside beneath it (Gribben and Wright, 2006a; Prado and Thibaut, 2008; McKinnon et al., 2009). Fish densities do not differ in *C. taxifolia* beds and native Australian seagrass (*Zostera* and *Posidonia*) meadows, but species with seagrass affinities and recruits of several economically valuable species are less abundant in the invaded habitat (York et al., 2006). Foraging by some fish species such as mullet is retarded in *C. taxifolia* meadows (Levi and Francour, 2004). Ark shells (*Anadara trapezia*) exhibit enhanced recruitment but reproductive inhibition and decreased densities as adults under *Caulerpa* invasion (Gribben and Wright, 2006b; Wright et al., 2007). *Caulerpa* spp. can, under certain conditions, form dense mats that smother underlying substrates (Figure 4). Mats up to 15-cm-thick trap sediment and can clog animal feeding apparatuses, causing siltation of the assemblages (Piazzi et al., 2007). Underneath, an anoxic layer has been observed (Piazzi et al., 1997).

Large native macroalgae, such as kelps, are usually considered to have positive effects on faunal biomass and diversity (Dayton, 1985). Surprisingly, *S. muticum* invasions in the NE Atlantic appear to have had limited effect on algal (Olabarria

et al., 2009) and invertebrate assemblages (Strong et al., 2006), but as with vascular plants, the results are context dependent. *S. muticum* enhances diversity in soft-sediment ecosystems but has a negligible effect on rocky shore assemblages in the North Sea (Buschbaum et al., 2006). Off the coast of Scotland, *S. muticum* outcompetes the dominant native brown alga *Dictyota*, but supports more associated invertebrates (Harries et al., 2007). *S. muticum* invasions on the US Pacific coast act to inhibit native brown and red algae, including species preferred by grazing urchins (Britton-Simons, 2004). Experimental removal of invasive *S. muticum* in European subtidal rocky reefs has revealed strong effects of this species on light levels, but had no influence on flow (determined from alabaster dissolution), sedimentation, or nutrient regimes (Britton-Simons, 2004). The authors speculated that the strong inhibition of native algae was largely due to light limitation

While the Eastern Atlantic is invaded by *Caulerpa* and *Sargassum*, the NW Atlantic, SE Pacific, and SW Pacific are contending with invasion by *C. fragile* ssp. *tomentosoides* (Figure 5). This species, rated by Nyberg and Wallentinus (2005) as the most invasive alga, exploits disturbed settings, forming dense stands that inhibit recruitment of native kelps and other algae (Scheibling and Gagnon, 2006). In general, *Codium* fronds support a more diverse invertebrate epifauna than the native kelp *Laminaria* on the Canadian coast (Schmidt and Scheibling, 2006, 2007). The primordia enhance mussel recruitment but not growth (Bulleri et al., 2006). Widespread invasion of the same species primarily between 26° S and 30° S off Northern Chile is endangering farms that culture the alga *Gracilaria* (Neill et al., 2006).

Another brown algal invader, *Undaria pinnatifida*, has recently appeared in both the Atlantic and Pacific Oceans (Russell et al., 2008). Experimental removal demonstrates that this species reduces algal diversity (Casas et al., 2005). Competitive advantage has been attributed to lack of native herbivory, light, and nutrient and substrate use, but these mechanisms have not been verified (Casas et al., 2005). Similar reductions in biodiversity are observed for *Undaria* invasion in New Zealand (Battershill et al., 1998).

Exotic algae are also altering coral reefs. Since the 1950s, five algal species have become ecologically dominant in Hawaiian reefs. Among these, the red algae *Gracilaria salicornia*, *Kappaphycus alvarezii*, and *Euclima denticulatum*, introduced to Oahu, Hawaii for experimental aquaculture in the 1970s, are reducing coral diversity and causing coral mortality Smith et al., 2002). Like *Caulerpa* they exhibit mat-like morphologies and smother underlying taxa. In Florida reefs, the Pacific *Caulerpa brachypus* has become abundant (Jacoby et al., 2004).

Although the mechanisms and types of abiotic modifications induced by invasive plant and algal engineers are often similar across ecosystems and taxonomic realms, the community-level consequences will differ depending on invasion stage and context. Whether invasions enhance or reduce plant and animal densities, biomass, production, diversity, or heterogeneity may vary not only with the engineering effects of the invader, but also with whether the invaded setting is vegetated or unvegetated; cobble, sand, or mud; sub-tidal or intertidal; subject to strong top-down control agents; or exposed to other forms of disturbance or habitat degradation. All of these effects can be time dependent (Zipperer, 1996) or context dependent, with salinity (Talley and Levin, 2001), substrate (Hacker and Dethier, 2006), or location (Posey, 1988) modifying the outcome. Similarly, successional age of the plant stand may control the nature and magnitude of effects on resident invertebrate (Posey, 1988; Talley and Levin, 2001; Neira et al., 2007) and fish communities (Hunter et al., 2006) (see Appendix 1).

One determinant of the magnitude and/or direction of invasive engineer impact appears to be the presence of other resident engineers in the system. When plants invade previously unvegetated tidal flat sediments, macroinfaunal densities may decline (Figure 9; Neira et al., 2005; Brusati and Grosholz, 2006; Wu et al., 2009) or rise (Posey, 1988). Crab densities and biomass have been observed to increase in invasive plant patches (Neira et al., 2006; Wang et al., 2008), whereas mollusk densities and growth rates may decrease (Chen et al., 2005; Neira et al., 2005; Brusati and Grosholz, 2007) relative to unvegetated sediments. Shorebirds that use tidal flats generally avoid invasive marsh grass and mangrove stands (Rauzon and Drigot, 2002; Chen et al., 2004a) and will be displaced as plant meadow cover expands. Invasion by marine vascular plants of already-vegetated marsh or seagrass habitat can displace native plants (Ayers et al., 2004; Chen et al., 2004b; Li et al., 2009b), or other invaders (Zhi et al., 2007). However, their engineering effects tend to be less dramatic than when unvegetated sediments are invaded, because native plants have already modified flow, sediment, and nutrient regimes. For example, when *Spartina* invades marsh or seagrass habitat, animal densities may be unaffected (Chen et al., 2005; Neira et al., 2005; Brusati and Grosholz, 2007; Cottet et al., 2007; Bouma et al., 2009). However, *Spartina* invasion into Yangtze estuary marshes dominated by *Typha* and *Scirpus* caused loss of herbivores and detritivores (Chen et al., 2005), likely reflecting

trophic impacts of this invasion and highlighting the difficulty in determining mechanisms driving observed net effects.

#### 7.03.5.4 Ecosystem Engineering by Introduced Animals

The potential role of invasive animals in marine ecosystems is much broader than that on land. As highlighted earlier, animals, plants, and algae can play similar roles in marine ecosystems, and much of the research on the functional consequences of invasive marine animals has focused on their ability to create structure and thereby modify habitats (Crooks, 2002, 2009; Wallentinus and Nyberg, 2007). In addition, exotic marine animals also fill more traditional roles, as agents of disturbance, affecting either the abiotic environment (e.g., sediments) or other biogenic habitat providers (e.g., engineering plants).

##### 7.03.5.4.1 Animals as structure creators

Among the most evident effects of invasive marine animals is the creation of structure, primarily through the production of carbonate shells or tubes. Such structures provide surfaces for epibiont growth, as seen with the small clam *G. gemma* in California (Grosholz, 2005), the ark clam *Anadara demiri* in the Mediterranean (Morello et al., 2004), and oysters in the Wadden Sea (Markert et al., 2009). The creation of shell beds also enhances habitat complexity and offers refugia for a variety of infaunal and epifaunal organisms (Crooks, 2002; Gutierrez et al., 2003; Wallentinus and Nyberg, 2007; Crooks, 2009). Bivalves, particularly oysters and mytilid mussels, are the most-studied taxa (Ruesink et al., 2005; Crooks, 2009; Sousa et al., 2009), reflecting in part the ubiquity of these invaders as well as their demonstrated effects.

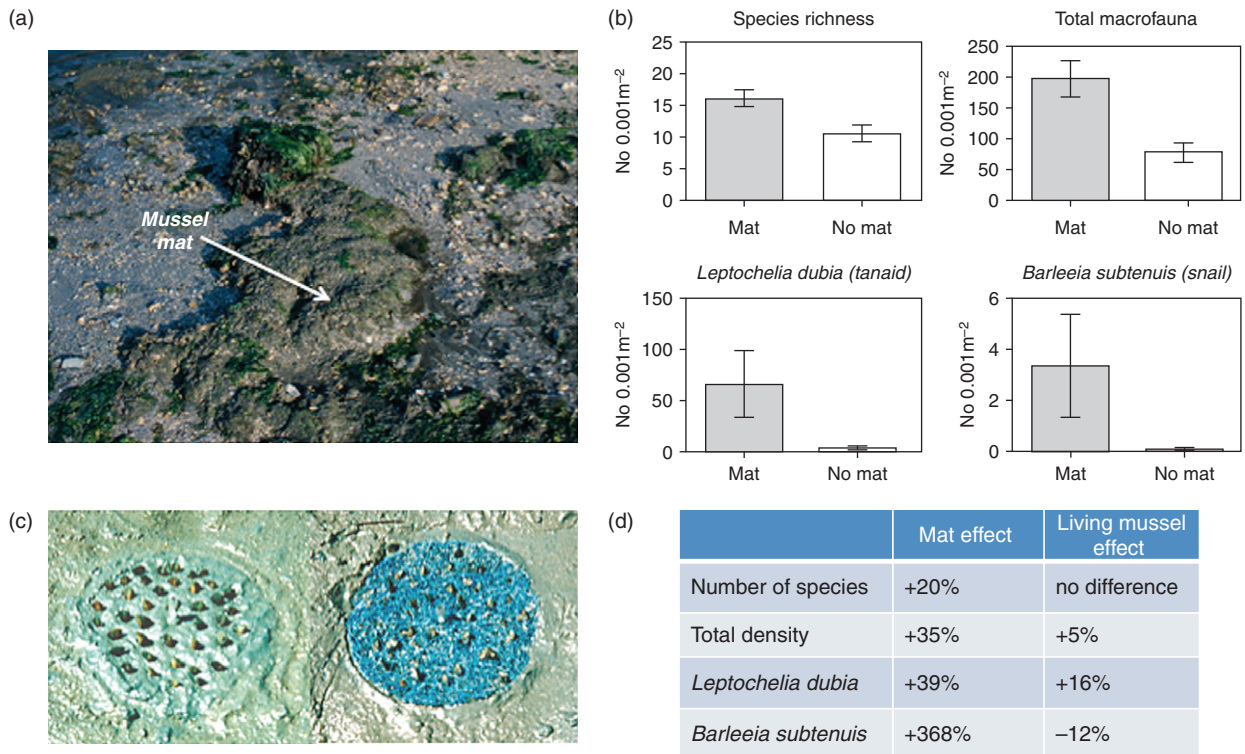
Oysters represent one of the most translocated of marine species, with invasive populations occurring throughout the world. As these species often create large reefs, marked ecosystem transformation is possible. This is true especially when the species invades soft-sediment systems that lack structural equivalents of oyster reefs, and thus novel hard-surface substrate is created (Ruesink et al., 2005). In Willapa Bay, Washington (USA), *C. gigas* (Pacific oyster) beds harbor increased diversities and densities of epifauna, including mussels and tube-building amphipods (Dumbauld et al., 2001; Hosack, 2003). In Argentina, the Pacific oysters form reefs on limestone outcrops, and both descriptive and experimental work demonstrate facilitation of most epifaunal (e.g., varunid and grapsid crabs, and peracarid crustaceans) and some infaunal forms, including polychaetes possibly responding to increased sedimentation within the oyster shell matrix (Escapa et al., 2004). Facilitative effects of oyster reefs are evident when oysters replace other bed-forming species. In Germany, comparisons of native mussel beds with structurally more complex oyster reefs revealed increased densities of sessile epifauna, motile species (e.g., *C. maenas* and *L. littorea*), and deposit-feeding oligochaetes associated with oysters (Markert et al., 2009; Troost, 2010). As expected, however, some species are displaced in areas invaded by oysters, including a snail and hermit crab in Argentina (Escapa et al., 2004). Similarly, in the Mediterranean, beds of Pacific oysters had increased densities of small meiofauna but decreased densities of larger macrofauna (Castel et al., 1989). Effects are linked to increased benthic–pelagic coupling, biodeposition of organic matter, and hypoxia (Castel et al., 1989).

Mytilid mussels are perhaps best known as being conspicuous elements of rocky shore and sub-tidal ecosystems, and their construction of dense and complex habitats shapes resident biotic assemblages (Crooks, 2009 and references therein). The effects of mytilids invading rocky shores often parallel, and can be predicted by, interactions observed with native mytilids, highlighting the robustness of engineer-induced consequences (Crooks, 2009). In South Africa, the invasion of rocky shores by *Mytilus galloprovincialis* has resulted in benthic communities that are fairly similar to those found in beds of the native mussel *Choromytilus meridionalis* (Branch and Steffani, 2004; Hammond and Griffiths, 2004). The primary effect of the invasion appears related to increased environmental tolerances of the invasive mussel, leading to an increased tidal range occupied by mussel beds and a concomitant expansion of the mussel bed community (Griffiths and Robinson, 2009).

The Asian mussel *M. senhousia* is a soft-sediment invader that can transform benthic habitats, creating a completely new type of habitat (Figures 3 and 10). This relatively small species, native to Asia, has invaded North America, Europe, and Australasia, where it can achieve remarkably high densities of over 100 000 individuals per square meter (Crooks, personal observation). *Musculista* uses its byssus to create cocoons or bags composed of sediment and detritus. At high densities, these cocoons become woven together to create surficial mats. In many invaded systems, this dense mat represents a novel habitat type on intertidal and shallow sub-tidal flats within which densities and diversities of small macrofauna can be substantially increased. Studies in southern California have

demonstrated densities up to 4 times greater in mussels mats than outside mats, and diversities over 50% higher (Figure 10) (Crooks, 1998). Most major macrofaunal taxa experienced some facilitation, with a tanaid crustacean (*L. dubia*) and small gastropod (*Barleeia subtenuis*) occurring in far greater numbers within mats (Figure 10). Surface-feeding guilds were generally more facilitated than were subsurface feeders. Experimental studies demonstrate that the effects can be primarily attributed to the presence of the mat and mussel shell structure, rather than to the activities of the living mussel (Figure 10) (Crooks, 1998; Crooks and Khim, 1999). Matrices of the shells and mats (as represented by structurally complex mimics) increased sediment organic content and fine sediments (Crooks, 1998; Crooks and Khim, 1999). In New Zealand, mussel beds were suggested locally to buffer increasingly brackish-water habitats from pH changes associated with increasing anthropogenic freshwater input, thus facilitating calcareous foraminifera (Hayward et al., 2008).

Although the pattern of facilitation within well-developed mats of large *Musculista* appears relatively robust, there are illustrative exceptions. In Australia, sediments with relatively low densities of small mussels exhibited macrofaunal community patterns comparable to those outside of mussel-inhabited areas (Buschbaum et al., 2009). In addition, for organisms too large to live within the mat matrix, dense aggregations of the mussel can have detrimental effects. Studies in California (Crooks, 2001) and New Zealand (Creese et al., 1997) have documented declines in surface-dwelling species that would tend to compete with *Musculista*. However, deeper-dwelling



**Figure 10** Observational and experimental assessment of the effects of the invasive mussel, *Musculista senhousia*, on benthic infauna in San Diego, California, USA. (a) dense mussel mat on an intertidal flat; (b) occurrence of infauna in areas with and without mats (error bars represent 1 SE); (c) experimental set-up distinguishing mat effects (artificial mats compared to no mats) and living mussel effects (living mussels compared to dead shells); (d) observed changes in infaunal properties attributed to the effects of mats and living mussels. See text for more details.

clams, including both suspension and deposit feeders, appear less affected by mussels and their mats (Crooks, 2001; Mistri, 2004). The inhibition of surficial forms, coupled with the relative lack of inhibition of deeper-dwelling suspension feeders, suggests that alteration of habitats and competition for space outweigh competition for food in producing observed effects. Dense *Musculista* mats can also inhibit beds of eelgrass (Reusch and Williams, 1998), presumably through modification of habitat conditions and preemption of space.

A variety of other structure-producing invaders also shape resident assemblages through engineering-related consequences. The tube-building polychaete worm, *F. enigmaticus*, has invaded estuarine systems in North America, South America, and Europe (Bruschetti et al., 2008). This worm creates dense and structurally complex tube networks (Figure 6). Initial discovery of the worm in San Francisco Bay even prompted reports of new "coral reefs" in the bay (Carlton, 1979). These calcareous reefs provide novel refugia for resident species, thus altering trophic relationships. The native crab, *Cyrtograpsus angulatus*, had much higher densities under worm reefs, and this in turn led to local increases in crab predation on benthic infauna as well as sediment reworking by crab burrows (Schwindt et al., 2002). In Elkhorn Slough, California, *Ficopomatus* reefs were found to facilitate a variety of other invasive species (Heiman et al., 2008). This was suggested to be a case of invasional meltdown (Simberloff and Von Holle, 1999; Simberloff, 2006), where one invasive species increases the establishment, survival, or impact of other invaders. Worm reefs also increase flux of materials to the seafloor through breakdown of the calcareous tubes, baffling of currents, and biodeposition of materials (Schwindt et al., 2002, 2004a, 2004b; Heiman et al., 2008). Filter-feeding activities of this worm are capable of decreasing chlorophyll *a* concentrations in the water, thus leading to decreased light attenuation (Bruschetti et al., 2008).

Another case of meltdown has been reported as a response to the invasion of the encrusting bryozoan *Watersipora subtorquata*. This bryozoan forms complex, calcareous structures in fouling communities, and these provide habitat for other species (Floerl et al., 2005). Because *Watersipora* is copper tolerant, its ability to cover surfaces painted with copper-based antifouling agents provides a refuge for species more sensitive to the effects of copper. This diminishes the effectiveness of this antifouling strategy and likely leads to increased survivorship and spread of other invasive species (Floerl et al., 2005).

Large-bodied, solitary tunicates are also responsible for biotic shifts in ecosystems where they have invaded. In the

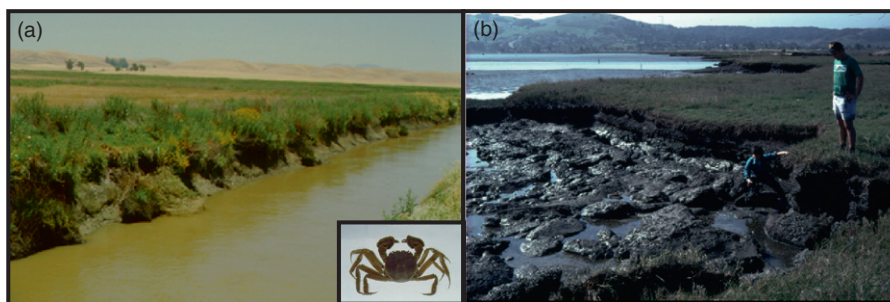
Mediterranean, the invasion of *Microcosmus sabatieri* creates complex surfaces which house a rich assemblage of peracarid crustaceans (Voultsiadou et al., 2007). On Chilean rocky shores, *Pyura praeputialis* has created complex, three-dimensional habitats (Castilla et al., 2004a). Castilla et al. (2004b) reported almost twice as many species in the biogenic habitat created by the tunicate than in adjacent habitats without the invader, including species that typically would be excluded from intertidal habitats.

Although sessile animal invaders are most typically associated with increasing structure within invaded ecosystems, mobile forms can provide resources for resident species directly. The shells of the Asian horn snail, *B. atramentaria*, provide substantial amounts of hard surfaces, facilitating populations of two other invaders, the Atlantic slipper shell (*Crepidula convexa*) and the Asian anemone (*Diadumene lineata*) (Wonham et al., 2005). *Batillaria* shells are also used by two native hermit crab species. The effects of introduced structure can be context dependent, however. Accumulated snail shells of the gastropod, *Maoricolpus roseus*, in a relatively high-energy and variable environment in Australia did not have demonstrable effects on resident biota, due to sediment movement and burial of shells (Nicastro et al., 2009).

Many of the above examples represent cases where the engineers create structure out of their own bodies (autogenic engineering). Animals also can create structure by their activities (e.g., allogenic engineering) as discussed above for *M. senhousia*. The invasive brackish-water amphipod, *Chelicorophium curvispinum*, can achieve densities in the hundreds of thousands per square meter and is able to modify benthic habitats by creating dense networks of mud tubes (van den Brink et al., 1993; Noordhuis et al., 2009).

#### 7.03.5.4.2 Animals as agents of disturbance

The converse of creating structure is removing it – acting as an agent of disturbance. This is the classic role of animals on land, and is also widespread among marine invaders. Disturbance can involve removal or modification of both biogenic material, typically through the proximate mechanism of grazing and herbivory, as well as abiotic materials (mud or rock). There are several examples of invasive crustaceans that burrow extensively into coastal sediments, plant tissues, and wood. These species illustrate how engineering disturbance can arise from nontrophic activities (Figure 11) (Talley and Crooks, 2007). The catadromous Chinese mitten crab (*Eriocheir sinensis*) (Rudnick et al.,



**Figure 11** Habitat disturbance and wetland loss caused by (a) *Eriocheir sinensis* (Chinese mitten crab) which weakens channel banks of the San Francisco Delta, USA and (b) *Sphaeroma quoianum* (isopod) which causes collapse of marsh edge and channel banks, Corte Madera marsh, San Francisco Bay, USA.



2003), for example, creates burrows in banks and levees (Figure 11(a)). Invasive, bioeroding isopods in the genus *Sphaeroma* have been implicated in the destruction of wetland ecosystems on both coasts of the United States. *Sphaeroma quoianum* is a species native to Australasia that was transported to the US west coast on boat hulls. It burrows into mud, soft rock, wood, and Styrofoam, largely to create living space and not for direct access to food resources (Talley et al., 2001; Talley and Crooks 2007; Davidson, 2008; Davidson et al., 2008). As an invader this isopod is commonly found at densities of over 10 000 m<sup>-2</sup> in burrows on vertical mud banks of tidal creeks and exposed bay fronts of salt marshes. Here, dense burrow networks decrease sediment stability and lead to collapse of mud banks, converting overlying marsh to tidal channels or mudflats (Figure 11(b)). At smaller scales, there is evidence that infauna inhabit burrows created by *S. quoianum* (Talley and Crooks, 2007; Davidson et al., 2009).

In Florida, a congener, *Sphaeroma terebrans*, has been implicated in massive changes to the distribution of mangroves (Carlton and Ruiz, 2005; Talley and Crooks, 2007). This species burrows into the prop roots of mangrove (*R. mangle*). Although it burrows into plant tissue, it too appears to primarily gain living space and not access to food. The invasive status and impacts of *S. terebrans* has been the subject of some debate, but there has been increasing evidence of damage inflicted by isopod burrowing, and suggestions that lower distribution limits of mangroves in the intertidal are now set by this invasive species (Rehm and Humm, 1973; Simberloff et al., 1978; Ribi, 1981; Brooks and Bell, 2002). Like *S. quoianum*, *S. terebrans* burrows also are reported to host a variety of other fauna (Thiel, 2000; Brooks and Bell, 2005).

Whereas the engineering effects of these species arise from nonfeeding activities, consumptive activities can produce strong structural effects as well. Massive removal of marsh vegetation by grazers reverses the strong engineering actions of plants. It is sometimes difficult to distinguish the degree to which impacts to other species are mediated by flow of energy through food webs (initiation of trophic cascades by removal of plant biomass), or by interactions that occur within the abiotic realm (increased light and water flow due to removal of structure).

One of the classic examples of habitat transformation by an invasive species involves the European periwinkle, *L. littorea*. It is currently the most abundant herbivorous snail of New England shorelines, and has had a strong influence on the distribution of macroalgae on both exposed and protected shorelines (Bertness, 1984). Experiments suggest that *Littorina* consumption of both Atlantic cordgrass (*S. alterniflora*) and macroalgae, both of which trap sediments, has altered the intertidal landscape in much of New England. This snail represents an example of an engineer whose primary role is to undo the ecological effects of other engineering species by grazing. Other such species include muskrats and nutria, which destroy vegetative structure by eating it (Grace and Ford, 1996; McFalls, 2004; Keddy et al., 2009). Spinoffs of extensive grazing include lower rates of organic accretion for the marsh and increased soil erosion. In the case of nutria in the Mississippi River Delta, grazing acts to exacerbate wetland loss where subsidence and sea-level rise are already converting marsh habitat to open water.

### 7.03.6 Evolutionary Impacts of Marine Invaders

Many of the functions altered by invaders will play out on timescales of years to decades. As highlighted in several cases (e.g., successional dynamics), invaders also will have dynamics that unfold over much-longer, evolutionary timescales (Crooks, 2005, 2011; Strayer et al., 2006). Evolutionary responses to invasion, in both the invader and recipient community, represent potential long-term, functional alterations (Mooney and Cleland, 2001; Cox, 2004; Sax et al., 2005; Suarez and Tsutsui, 2008).

The insertion of novel species is likely to exert selective pressure on resident biota. Although there is relatively little work on this in the context of anthropogenic invasions (Suarez and Tsutsui, 2008), studies on the native mussel (*Mytilus edulis*) on the east coast of North America indicate that they display an inducible defense, shell thickening, in response to the presence of the long-established, invasive predator, the crab *C. maenas* (Leonard et al., 1999). Interestingly, only mussels that currently co-occur with a more recently introduced and geographically restricted crab, *H. sanguineus*, display this inducible response (Freeman and Byers, 2006). Native mussels, taken from areas not within the current range of the exotic *Hemigrapsus*, do not display this response. This indicates an evolved ability to detect and respond to this invasive crab. More generally, phenotypic plasticity and the ability to elicit such responses represent an important adaptive mechanism related to invasions (Smith, 2009).

The genetic makeup of invading species is often of interest because it determines their physiological tolerances and habitat preferences, structural attributes, and ultimately their functional roles in an ecosystem. Where the invader occupies a habitat different from most native populations of the species, often it is an exotic strain that is unusually tolerant to particular conditions. This is the case for a *P. australis* lineage introduced to North America (Meyerson et al., 2009), or *Tamarix* spp. (Whitcraft et al., 2007), a riparian taxon that has invaded salt-marsh habitats. For example, the invasive *Phragmites* from Europe is more aggressive and more tolerant of saltwater and flooding (Vasquez et al., 2005), with different structural properties (e.g., higher culm density and aboveground biomass) than the native North American strains (Meyerson et al., 2009).

In some instances, hybridization between native and invasive plants or animals yields a more vigorous form that can occupy alternative physiological realms and ecological zones, and exhibits different phenology than the native. Cordgrasses in particular have a tendency to hybridize, and this process has played a large role in shaping their biogeography and functional impacts (Strong and Ayers, 2009) (Figure 12). Some of the hybrids are sterile, such as *S. townsendii*. Chromosome doubling in this species gave rise to fertile *S. anglica*, which has spread widely and altered ecosystems in locations or habitats not occupied by the original parental species (*S. alterniflora* and *S. maritima*). Hybridization of *S. alterniflora* and *S. foliosa* in San Francisco Bay has led to a form that is taller, denser, and has deeper roots, more inflorescences, more pollen and seed, and has a greater tidal range. Greater height of hybrids has attracted Clapper rails (*Rallus longirostris*). Hybrid *Spartina* has been demonstrated to exhibit greater toughness and less palatability than the parental forms in San Francisco Bay, leading to landscape dominance in the face of intense Canada goose grazing on



**Figure 12** Hybrid *Spartina* (a) *S. anglica*, Creekside Park, Marin County CA, USA. (b) *S. densiflora* at Humboldt Bay, CA, USA. (c) *S. densiflora* × *maritima* hybrids at the Piedras River, Huelva, Andalusia, Spain. (d) Encircled is a *S. densiflora* × *foliosa* hybrid plant at Creekside Park, CA, USA (*S. foliosa* is in foreground). (e) *S. alterniflora* × *foliosa* hybrids, San Bruno, CA, USA. (a) Photograph by D. Ayers. (b, c) Photographs by: J. Castillo. (d, e) Photograph by D. Ayers.

the native *Spartina* (Grosholz et al., 2009). *S. alterniflora* (from the North Atlantic) and *S. densiflora* (from South America) have also hybridized in the San Francisco Bay to form diploid and triploid hybrids (Ayers et al., 2008). Both hybrid forms are currently being eradicated, but it will be interesting to see, given the five forms of *Spartina* that have been present in San Francisco Bay (Strong and Ayers, 2009), how the genetic interactions develop, and with what ecological consequences.

Tamarisk invading the Tijuana River estuary in southern California (Figure 2(b)) exhibits multiple genetic sources and extreme hybridization. Genetic analysis of 37 samples yielded four *Tamarix* species and three hybrid forms among the haplotypes (Whitcraft et al., 2007). Although the different genetic types and species have slightly different growth forms, the ecological impacts of the different strains have not yet been determined (C. Whitcraft, personal communication). Invasive *Phragmites* also appears to be hybridizing with native strains (Meyerson et al., 2009).

Animal hybridization is less common, but seems to occur readily among *Mytilus* species, which have maternal genetic transmission. The highly invasive mussel *M. galloprovincialis* forms hybrids with *M. trossulus* in Japan (Skurikhina et al., 2004) and along the Pacific coast of the USA (Suchanek et al., 1997), and with *M. edulis* in Europe (Coustau et al., 2005). Ecological consequences of mytilid hybridization have not been reported.

### 7.03.7 Emergent Properties of Invaded Ecosystems

When invasive species affect other species and their linkages within ecosystems, the result may be patterns and properties that are novel or that cannot entirely be explained by the individual components. These patterns are considered emergent properties (Mayr, 1982; Corning, 2002) and may reflect the coherent response of complex systems to multiple interactions among component species and their environment. Hierarchical and self-organizing in nature, examples of emergent properties likely to be altered by invasion include productivity, habitat or community heterogeneity in space and time, trophic complexity, connectivity, succession, stability, resilience, and biodiversity. Evaluating emergent properties requires a holistic study of ecosystem-level processes, and there are few invaded systems for which this level of analysis has been conducted. However, it is possible to identify situations in which emergent properties might be affected by invaders (especially negatively), with the recognition that the full complement of potential invader effects (both positive and negative) would be virtually limitless.

#### 7.03.7.1 Productivity

Whole-system primary productivity is more often increased than reduced by successful higher plant or algal invaders, although invader dieback commonly occurs later in the

invasion process (Neira et al., 2007; Zhou et al., 2009). Systems made more diverse by invasive primary producers may be more productive as a result (Boyer et al., 2009; Power and Cardinale, 2009). In many cases, invasive plant and algal taxa are less palatable than natives (a factor that may contribute to invasion success), and so it is unclear how much of the added primary productivity is transferred to higher trophic levels. In addition, successful plant or macroalgal invaders commonly outcompete or inhibit growth of micro- or macroalgal taxa preferred by grazers.

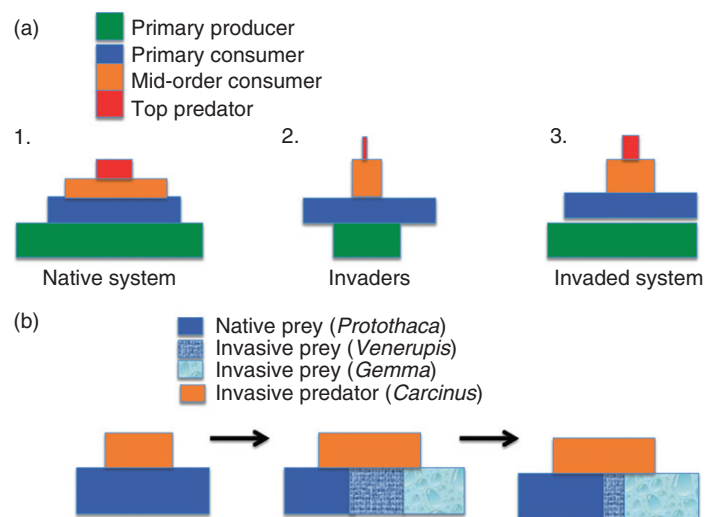
When viewed in aggregate, invasive species appear to be changing the shape of the trophic pyramid in many regions of the globe (Byrnes et al., 2007). A majority of invaders occupy lower trophic levels, as primary producers, suspension feeders, and detritivores, while simultaneously many systems are experiencing loss of top predators through overfishing or habitat degradation. The combined effect yields a skewed, bottom-heavy trophic pyramid in diverse regions such as the Wadden Sea, San Francisco Bay, the Gulf of the Farallones, and Australia (Figure 13) (Byrnes et al., 2007). In many instances, the most functionally significant trophic effects of invasive species involve second-order or indirect interactions. These interactions may be either facilitative or inhibitory, and can influence trophic levels above or below that of the invader species.

### 7.03.7.2 Habitat Structure

Biogenic modification of habitats, resulting in changes to emergent properties such as habitat complexity and heterogeneity, is achieved by the actions of ecosystem engineers (Section 7.03.5). Habitat complexity, considered as both the architecture of a given structural type (e.g., algal fronds) as well as heterogeneity of structures (e.g., various plant and algal morphs), is usually linked to biodiversity, with habitat complexity typically enhancing diversity (Crooks, 2002). Many invaders

can create more varied habitat, as well as remove it. Small-scale heterogeneity introduced to intertidal and sub-tidal habitats by a diverse, native assemblage of plant bed, animal burrowing, and reef-forming invertebrates can be lost when these taxa are displaced by meadow- or mat-forming invaders (e.g., *Spartina* and *Caulerpa*) that smother or overgrow natives. Invasive species may contribute to habitat complexity, either through creation of biogenic structure (*M. senhousia* and *F. enigmaticus*), or by altering existing structure and creating patchy landscapes (e.g., nutria). Replacement of one plant by another, or one reef by another, may not be a one-for-one exchange in terms of habitat complexity and outcome. For example, more complex habitats and community states have resulted from replacement of laminarian kelps by *Codium* in the Gulf of Maine (Harris and Jones, 2005) or replacement of *Gelidium* by *Sargassum* in Spain (Sanchez et al., 2005).

Although it is tempting to consider species that increase complexity as 'habitat creators', and species that remove structure as 'habitat destroyers', it is important to consider that habitat is 'in the eye of the beholder'. When invaders create one type of habitat, another is destroyed (Jones et al., 1997). An example of this comes from bioeroding isopods in marshes and mangroves. In each case, the burrowing isopod causes loss of vegetated wetlands. However, creek bottom or unvegetated soft bottom, as well as topographically complex creek bands, are created in its stead, and the species that use these habitats will benefit (Talley and Crooks, 2007). Another important caveat is that consequences of alterations to complexity will depend on scale. Where small organisms may view a biogenic structure as habitat, larger organisms (which are about the same size or which have comparable space requirements as the invader) might view these as competitors for space. Thus, one must use caution in attributing habitat creation or destruction to species without also using appropriate qualifiers – in the larger ecosystem context, both almost always occur simultaneously.



**Figure 13** (a) Conceptual illustration of changes in a coastal ecosystem trophic pyramid following invasion. (1) Uninvaded trophic structure; (2) trophic distribution of invaders; (3) altered trophic structure following 25% turnover of species, including local extinctions of top predators. (b) Within-trophic level shifts in native and invader bivalve prey composition induced by invasive green crab predation in San Francisco Bay. (a) Adapted from Byrnes, J.E., Reynolds, P.L., Stachowicz, J.J., 2007. Invasions and extinctions reshape coastal marine food webs. *PLoS ONE* 2, e295. (b) Based on Grosholz, E.D., 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences of the United States of America* 102, 1088–1091; and Byers, J.E., 2009. Invasive animals in marshes: biological agents of change. In: Silliman, B., Grosholz, E., Bertness, M. (Eds.), *Human Impacts on Salt Marshes: A Global Perspective*. University of California Press, Berkeley, CA, pp. 41–56.

### 7.03.7.3 Connectivity

Invasive species have the potential to impact the connectivity of ecosystems. In the broadest sense, anthropogenic introductions now routinely connect systems that would rarely or never be connected naturally, leading to 'hyperconnectivity' (Crooks and Suarez, 2006). Outside of the trajectories of invaders themselves, there has been little focus on metacommunity connectivity as an emergent effect of invasion, probably because quantification of realized connectivity is difficult even for native species (Cowan and Sponaugle, 2009). Many marine systems, including rock outcrops, kelp forests, seagrass beds, coral reefs, tidal flats, sand beaches, salt marshes, and mangrove swamps, function as meta-assemblages that are patchy in space and time. Connectivity of their constituent metapopulations is a key feature that drives ecosystem dynamics. Not only do early life-history stages provide key links between patches within an ecosystem, but they also often connect different systems, for example, linking coral reefs and mangroves, or marshes and seagrasses. Invasive species may disrupt native assemblage connectivity patterns by erecting structural barriers to dispersal, by consuming, trapping, or entraining larvae (the dispersal stage), by changing the reproductive output of competitors or prey, or by changing the phenology (gamete buildup and larval release times) of interacting natives. Concomitant local extinctions of native subpopulations through competition or habitat modification induced by invaders would also be expected to alter connectivities. When the local extinctions involve parasite hosts, the parasites themselves may suffer from impaired transmission of life stages (Torchin et al., 2005). Alternatively, invaders may enhance connectivity of native species by adding suitable habitat patches (e.g., hard substrate and plant meadows) that serve as stepping stones within the seascape, by increasing reproductive output through direct provision of food, or, indirectly, by consuming resource competitors.

### 7.03.7.4 Succession

Succession, a sometime consequence of connectivity, is another emergent feature that results from the interactions of different ecosystem components and processes in time. Invasion characteristics and impacts will be highly dependent on this temporal context (Strayer et al., 2006). Wetland plant invaders such as cordgrasses are known to exhibit successional stages including colonization, rapid growth, maturity, and dieback. Wetland sediments in each stage of *Spartina* invasion host distinct macroinfaunal assemblages adapted to differing geochemical, detritus, algal, and shade conditions (Neira et al., 2007). Other vascular plant (*P. australis*, Armstrong et al., 1996; *S. anglica*, Zhou et al., 1999) or algal (*Caulerpa* spp.) invaders that undergo similar growth and dieback scenarios might be expected to regulate succession of animal communities. Any engineering invader that transforms habitat types, from soft to hard substrate (Schwindt et al., 2002, 2004a, 2004b), from sand to mud (Thieltges et al., 2006), from mud to meadow (Grosholz et al., 2009), from channel bank to creek (Talley et al., 2001), from eutrophic to oligotrophic (Alpine and Cloern, 1992), or from meadow to forest (Whitcraft et al., 2007), will also produce emergent successional shifts in community dynamics.

### 7.03.7.5 Stability and Resilience

Invaders can destabilize ecosystems and sometimes cause state changes. Examples include the collapse of plankton systems from filtration or predation (Leppäkoski et al., 2009; Sousa et al., 2009), the shifts from autotrophic, algal-based to heterotrophic, detritus-based ecosystems following cordgrass invasion of tidal flats in San Francisco Bay (Levin et al., 2006; Grosholz et al., 2009), and the transition from sediments to cobble with the advent of a keystone grazer on the US Atlantic coast (Bertness, 1984). In Chesapeake Bay, the loss of oysters due to habitat destruction, overharvesting, and exotic disease has resulted in shifts from benthic to pelagic primary production, as well as from macrophytes and nekton to bacteria and jellyfish (Ruesink et al., 2005).

There is experimental evidence that higher native plant and animal diversity promote stability (Boyer et al., 2009) and resistance to invasion (Stachowicz et al., 1999, 2002, 2007). Diversity of macroalgae can promote faster recovery from heat stress in rocky shores (Allison, 2004) and microalgae are also more stable at higher levels of species richness (Watermann et al., 1999). Diversity of suspension-feeder assemblages, including exotic species, promotes increased long-term stability of organic matter input (Byrnes and Stachowicz, 2009). Does diversity generated from buildup of invasive species also have stabilizing effects? It seems not, if we can draw lessons from San Francisco Bay, where invasive species have failed to resist subsequent invaders and where invasion meltdown has occurred (Grosholz, 2005). Additional diversity of predators may not have any significant emergent influence on the structure or stability of the already-diverse prey communities (O'Connor and Bruno, 2009). Some evidence suggests that invader-caused changes in diversity may have greater effects when they are bottom-up than when they act from the top down.

### 7.03.7.6 Biodiversity

Invader impacts on ecosystem biodiversity are the net results of many interacting properties and processes, and are often scale-dependent. At local scales, invasive taxa can have varied effects on species diversity and richness, with responses depending on factors such as environmental setting, characteristics of responding taxa, and time since invasion. Some invaders, such as *Spartina* and *Caulerpa*, tend to reduce diversity of infaunal taxa through changes in abiotic conditions, food supply, and predation pressure. Other invaders, such as oysters, mussels, mangroves, and some macroalgae (*Sargassum* and *Codium*), tend to enhance local diversity, especially for species that utilize the three-dimensional biotic structures (Crooks, 2002, 2009).

Invasive species can also affect patchiness and landscape-level diversity. If ecosystem-modifying invaders increase patchiness (e.g., Figure 3(a)), creating a mosaic of areas with differing environmental conditions, it is likely that landscape-level diversity (encompassing both areas with and without invaders) will be increased due to turnover of species associated with the different patches (Wright et al., 2002). From a different perspective, however, it is possible that invaders are so pervasive that they effectively homogenize existing landscapes, smoothing over existing patchiness and diminishing landscape-level diversity (e.g., Figure 3(b)). Homogenization has occurred as

invasive cordgrasses spread over thousands of acres of shore in Europe, the US Pacific Northwest, China, and New Zealand (Li et al., 2009a; Strong and Ayers, 2009), and when the snail *L. littorea* converted vast stretches of New England coasts to rocky shores through its grazing activities (Bertness, 1984).

At regional scales, invasive species themselves add to the species pool. The species lists for many coastal systems are now considerably longer than they were historically, largely because invasion has outpaced extinction events, at least in the short term (Carlton, 1999). This raises questions about species saturation in ecological systems (Stachowicz and Tilman, 2005). Invaders may also create mutualistic or cascading interactions that increase system susceptibility to invasion, thereby contributing to 'invasion meltdown' (Simberloff and Von Holle, 1999). This has occurred following invasions by green crabs (*C. maenas*; Grosholz, 2005), cordgrass (*Spartina*; Grosholz et al., 2009), mangroves (*Rhizophora*; Demopoulos and Smith, 2010), and tubeworms (*Ficopomatus*; Heiman et al., 2008).

At global scales, rampant anthropogenic transport of a familiar suite of invasive species (e.g., *C. maenas* and *C. gigas*) has resulted in the converging of coastal faunas and floras. Species are shared across shores, oceans, and hemispheres, with distributions encompassing areas they would never reach naturally. This homogenization is leading to loss of gamma diversity (Bouma et al., 2009) and shows little sign of abatement.

### 7.03.8 Invaders and Ecosystem Services

Invasive marine species have the potential to dramatically affect goods and services provided by ecosystems. In many cases, invaders will have undesirable and costly impacts, and often there are strong correlations between ecological and economic impacts (Vila et al., 2010). One estimate for all invasive species (both terrestrial and aquatic) puts the annual environmental and economic costs at \$137 billion per year (Pimentel et al., 2000). Much of this represents impacts on land, but estimates associated with just two marine invaders, the green crab and shipworms, total almost \$250 million per year. We acknowledge, however, that invaders also may directly or indirectly provide benefits to humans. Although it is difficult to provide precise economic values associated with these costs and benefits, below we categorize impacts and provide examples.

#### 7.03.8.1 Aquaculture and Fisheries

Some of the direct economic impacts of invasive species derive from their utilization as fisheries and mariculture resources. The motivation to have new, productive, and reliable marine resources has spurred the transfer of marine organisms for centuries, and many of these organisms represent valuable economic commodities in places where they have been introduced. In addition, a number of accidentally introduced species have also developed into important resources for commercial and recreational harvest, as well as mariculture.

Mariculture and farming of intentionally introduced marine species represent a direct and tangible economic benefit, but one that is sometimes at odds with ecological impacts of these species. Examples of exotic species harvested within their introduced range include shrimp (*Litopenaeus vannamei*) and the

alga *K. alvarezii* (as a food additive) in Brazil (Ferreira et al., 2009), abalone (*Haliotis rufescens* and *H. discus hannai*) and the alga *Gracilaria* (for agar) in Chile (Castilla and Neill, 2009), and the kelp *U. pinnatifida* (for edible seaweed, wakame) in Spain (Wallentinus, 2002). In addition, as highlighted earlier, oysters have been moved all over the world, and culture of established populations or grow-out of adults represents a major resource in many coastal areas (Ruesink et al., 2005). As an extension of the engineering effects of oysters, shells of non-native oysters have been used as shelters to protect juvenile Dungeness crabs (*Cancer magister*), which is itself an economically valuable species (Fernandez et al., 1993).

One of the greatest growth markets in the seafood industry has been the development of farmed salmonids, representing an increase from 2% of the world supply of salmon in 1980 to 65% in 2004 (Knapp et al., 2007). The salmon species most widely farmed is the Atlantic salmon (*Salmo salar*); almost 2 million metric tons are now being produced in aquaculture facilities in Asia, the Pacific coast of North America, South America, and Europe (Knapp et al., 2007). Despite the food resources provided by these types of farming operations, there is concern about overfishing to provide fish meal for these predatory fish, deterioration of environmental conditions underneath pens, spread of disease or parasites, escape from containment, and hybridization with or displacement of closely related native species (Knapp et al., 2007).

Wild populations of invaders, including many species not intentionally introduced, have also developed into important local economic resources. On the Pacific Coast of North America, the manila clam (*V. philippinarum*), an early oyster hitchhiker, is now harvested from shorelines (Bourne, 1982). This clam has also been intentionally introduced for fisheries in the other parts of the world, including the United Kingdom and Italy (Granzotto et al., 2004; Jensen et al., 2004). In southern California, the exotic bay mussel *M. galloprovincialis* is cultured (Becker et al., 2007). In South America, the mussel *Perna perna* is harvested from Brazilian shorelines (Ferreira et al., 2009), the algae *Mastocarpus papillatus*, *Porphyra linearis* and *P. pseudolinearis*, and the tunicate *P. praeputialis* are now part of Chilean diets (Castilla and Neill, 2009). In the eastern Mediterranean, wild populations of species that have successfully traversed the Suez Canal, including penaeid prawns, the swimming crab *Portunus pelagicus*, and many fish, are also frequently harvested (Rilov and Galil, 2009).

Invasive species can also wreak havoc on already-established fisheries – this is one of the major economic sectors impacted by marine invasions in Europe (Vila et al., 2010). An extreme example comes from the collapse of fisheries in the Black Sea and Sea of Azov due to the invasion of the ctenophore *M. leidyi* in concert with overfishing and pollution (Leppäkoski et al., 2009; Rilov, 2009). Twelve years after its first record in the Black Sea, the biomass of *Mnemiopsis* was estimated at 100 million tons. Biomass in offshore areas was reported to be as high as 5 kg m<sup>-2</sup>. The extraordinary population explosion of this species caused a collapse of fish stocks through both predation and competition for food. It was estimated that the ctenophore could graze up to 70% of the ichthyoplankton stock. Annual losses were estimated at over \$200 million during the height of the invasion (IUCN, 2009). Since the late 1990s, *Mnemiopsis* populations have decreased, due at least, in part, to the accidental, ballast-borne invasion of

a *Mnemiopsis* predator, *B. ovata* (Leppäkoski et al., 2009; Rilov, 2009). This represents a case of biocontrol of an invader, albeit an unintentional one.

A variety of other impacts to fisheries have also been reported. The spread of disease agents represents a major threat to fisheries and aquaculture operations – the emergence of the white spot syndrome virus in shrimp facilities is one example (Seo and Lee, 2009). As highlighted previously, the slipper limpet *C. fornicata* and the alga *C. fragile* are both considered oyster pests due to their ability to foul and dislodge oysters (Gollasch et al., 2009). A predatory snail in the Black Sea, *R. venosa*, is impacting the oyster fishery (Harding, 2003), although this species is harvested itself and the shells are sold to tourists (Leppäkoski et al., 2009). The invasion of a shell-infesting sabellid worm damaged abalone fisheries in California (Kuris and Culver, 1999; Moore et al., 2007), and, in Hawaii, the invasion of the snowflake coral has impeded harvesting of black coral (IUCN, 2009). The *Caulerpa* invasion in the Mediterranean, which has had myriad ecological impacts (Meinesz, 1999), has negatively impacted the local bream (*Sarpa salpa*) fishery, as the fish is able to eat the alga but bioaccumulates its chemical defense toxins, making it inedible (IUCN, 2009). King crab, intentionally introduced into the Barents Sea, is now beginning to spread south. Although it is starting to be harvested, it also kills locally important fish and shellfish, and damages fishing gear (Jorgensen and Primicerio, 2007; IUCN, 2009).

### 7.03.8.2 Maritime Devices, Facilities, and Structures

As highlighted with the king crab, invasive species can also directly impact devices or structures placed in the marine environment. In the Mediterranean, thick swarms of the invasive jellyfish *Rhopilema nomadica* can clog water intake on power plants, with the cost of treatment at just two plants being \$50 000 annually (Rilov and Galil, 2009). Mitten crabs have had similar effects on water intake structures in Europe and California (Rudnick et al., 2003; Gollasch et al., 2009).

The growth of sessile biofouling organisms presents a major management issue, affecting ship maintenance, water transfer structures, and scientific instrumentation. Many of these biofoulers are exotic species (having been transported on ship bottoms), and in some places, such as parts of San Francisco Bay, invasive biofoulers far outnumber native species (Cohen and Carlton, 1995). One example of problematic, invasive biofoulers in San Francisco Bay are the large, solitary tunicates of the genus *Ciona*. This species can undergo rapid population growth; large masses of tunicates foul boat bottoms and floating docks, weakening the integrity of these structures (Blum et al., 2007; Crooks, personal observation). This tunicate has compromised local fisheries in Chile by fouling scallop culture lines (Castilla and Neill, 2009). Another particularly problematic fouling organism is the mussel genus *Mytilopsis*; their high densities and subsequent effects are reminiscent of those of the notorious zebra mussel, *D. polymorpha*. Concern about the incipient invasion of this species in a North Australian port led to an eradication program that poisoned and largely defaunated an entire harbor (Hewitt et al., 2009; IUCN, 2009).

Particularly problematic classes of invaders are bioeroding ecosystem engineers. The most notorious of these are the molluscan shipworms (*Teredo* spp.), which have plagued sailors and their ships for hundreds of years. These species are capable

of burrowing into wood, and have been known to destroy ships, seawall supports, pilings, and wharves (Carlton, 1979; Gollasch et al., 2009). For example, the naval shipworm (*Teredo navalis*) has destroyed wooden dyke gates in Holland, causing extensive flooding, and is the likely culprit that seriously damaged ships in the Spanish Armada prior to their attack on England in the sixteenth century (Hoppe, 2002; Reise et al., 2002; Gollasch et al., 2009).

Crustaceans are also important agents of destruction in marine systems. Mitten crabs create burrows, and their activities on levees can compromise the integrity of these structures (Rudnick et al., 2003; Gollasch et al., 2009). Limnoriid isopods (gribbles) have effects similar to those of shipworms. A program to clean heavily polluted and largely azoic portions of the Los Angeles/Long Beach Harbor, for example, led to the unintentional ecological release of gribbles found elsewhere in the system, and the subsequent destruction of some wharves (Reish et al., 1980). The burrowing activities of the isopod bioeroder *S. quoianum* (described earlier) can lead to the destruction of restored marshes (Talley et al., 2001; Talley and Crooks, 2007). There is also concern about its destruction of Styrofoam floats, which leads to the release of millions of particles of this substance into the water column (Carlton and Ruiz, 2005). In Europe, introduced muskrats have long been considered a pest because of their burrow-induced damage to levees (Storer, 1937).

### 7.03.8.3 Ecosystem Management

Exotic species interface with several forms of ecosystem management. First, exotic organisms are the subject of invasion prevention and control efforts. Although the eradication of established marine invaders is possible, it has proved to be notoriously difficult (Crooks and Rilov, 2009; Hewitt et al., 2009). It is widely held that prevention is far preferable to eradication, and the fields of marine vector control and risk assessment are gaining increased attention and sophistication (Gollasch, 2002; Hayes, 2003; Ruiz and Carlton, 2003; Campbell, 2009). Termed 'biosecurity', these efforts benefit greatly from detailed information on invasive species characteristics and impacts, which can be used to help prioritize control activities (Olenin et al., 2007; Hayes and Barry, 2008).

Beyond being direct targets of management, nonindigenous species are sometimes intentionally engaged to perform ecosystem functions deemed necessary or lacking (Ewel and Putz, 2004). There are several examples of uses (either proposed or realized) of already-established invaders for managing ecosystems. The dramatic biofiltration ability of dense populations of invasive (freshwater) bivalves has been employed to clean water (Reeders et al., 1989; Phelps, 2005), while the invasive *M. galloprovincialis* in southern California serves as an indicator of pollution in the Mussel Watch program (Crooks, personal observation; Goldberg, 1986). Although the use of already-established exotics for economic benefit is often not controversial, this is not the case when species are intentionally introduced for management purposes, given the rich history of unintended consequences of such introductions.

Vascular marsh plants have long been translocated to achieve shoreline stabilization and bioremediation. In Europe, *Phragmites* was used as a bioengineer to protect shorelines (Bakker, 1960), oxidize sediments (Armstrong and

Armstrong, 1988), and remove heavy metals such as Cu, Cd, Pb, Fe, and Ni from systems (Pevery et al., 1995). *S. alterniflora* also excretes heavy metals (Kraus et al., 1986). Several cordgrass (*Spartina*) species have been planted for shoreline stabilization and remediation in Europe, San Francisco Bay, and China (Campbell et al., 2009). The history of *Spartina* introductions provides an excellent model for examining the potential pros and cons of intentional species introductions. Although there have been benefits to protecting shorelines (Campbell et al., 2009; Wan et al., 2009), in many cases, the problems have been deemed to outweigh the benefits and substantial resources have been expended to remove these invaders (e.g., Hacker et al., 2001). There is no doubt, however, that in the face of climate-change factors such as sea-level rise and increased storminess, as well as natural disasters such as tsunamis, there will be increased interest and pressure to use the land-building and protective services provided by exotic plant species (Meyerson et al., 2009), perhaps trumping their status as native or exotic (Weis and Weis, 2003; Ewel and Putz, 2004). Thoughtful consideration of past lessons and current considerations should increase the predictive ability needed to steer these efforts, with the recognition that invaders are notoriously bad at following rules and thus likely to act in unexpected ways (Crooks, 2005, 2011).

#### 7.03.8.4 Aesthetic, Cultural, and Health Impacts

A final, broad class of invader effects relates to aesthetic and cultural values. Invasive species, by their very nature, contradict the often-stated goals of protecting and enhancing diversity of species native to a region. As discussed previously, the invasion of the same species all over the globe is leading to homogenization of biota and the loss of the uniqueness of individual areas (Lockwood and McKinney, 2001). Although such factors resist economic quantification, they often oppose the core beliefs of naturalists and conservationists.

Invaders sometimes have a more direct effect on humans. In the Mediterranean Sea, the 100-km jellyfish belt of invasive *Rhopilema* can inhibit beach use by swimmers and bathers (IUCN, 2009; Rilov and Galil, 2009). In Hawaii, invasive algae can smother corals and foul beaches (Figure 14), both effects are detrimental to the tourist industry (IUCN, 2009). Human health can also be affected by invaders. In California, cases of swimmer's itch have been attributed to an invasive

species of trematode flatworm (Grodhaus and Keh, 1958). In addition, there is global concern about the transport of pathogens, such as those that cause cholera, in ship ballast water (Ruiz et al., 2000). Similarly, many microalgal species capable of forming HABs have been transported around the world, increasing both ecosystem and human health risks (Hallegraeff, 1998; Wallentinus, 2002).

#### 7.03.9 Predicting Functional Consequences of Invasion

Although the study of marine invasions is still relatively young, the above-mentioned examples provide ample evidence that many invasive species have functional impacts at a variety of spatial and temporal scales. The greatest impacts of marine invasive plants, algae, and animals are found when the invasion transforms the ecosystem from one distinct habitat type (e.g., unvegetated sediments) to another (e.g., meadow, forest, or reef), or dramatically restructures existing food webs. To date, the largest plant effects on ecosystem structure and function are accorded to cordgrass, mangroves, and *Caulerpa*, with somewhat lesser influences of seagrass and other sub-tidal algal invaders. These functional effects appear tied to their potential to form large meadows that smother underlying organisms and alter light and sediment deposition regimes, their ability to support epiphyte primary and secondary production, and their palatability or competitive influence on other more palatable species. The largest animal impacts can resemble impacts of plants and algae, through the creation of novel habitats associated with biogenic structure (e.g., bivalve beds and worm reefs). Dramatic animal effects can also be induced by activities such as bivalve filtering, snail grazing, crustacean burrowing, and planktonic predation.

From this chapter we can identify those systems most likely to experience strong functional changes following invasion. The most transformative invader impacts have been identified in estuaries and salt marshes (e.g., Byers, 2009) and largely enclosed water bodies (e.g., Leppäkoski et al., 2009). This occurs, in part, because these systems are highly vulnerable to invasion. There is both a proliferation of invasion vectors that operate between these systems (i.e., they receive the most invasive propagules) and an intrinsic vulnerability, stemming from relatively low natural diversity and degraded environmental



**Figure 14** The invasive red alga *Eucheuma denticulatum* growing over reef-building corals in Kane'ohē Bay, Oahu, Hawaii. This alga was introduced to Hawaii in the 1970s for experimental aquaculture. Photographs by J. Smith.

conditions which can alter systems in ways that favor exotics over natives (Byers, 2002; Olyarnik et al., 2009; Preisler et al., 2009; Crooks et al., 2010). Beyond a preponderance of invaders, however, these systems also appear particularly amenable to change by ecosystem-modifying species. Compared to more open systems, they have a much greater proportion of benthic habitat, which is susceptible to restructuring by invasive plants and animals. Also, the relatively low turnover times in the pelagic components of estuarine and enclosed water bodies, compared to the open ocean, make them more vulnerable to the effects of predators (e.g., *Mnemiopsis*) and filterers (e.g., *Corbula*).

Within these vulnerable areas, key ecological realms where ecosystem-level alterations by invasion are most probable include:

- unvegetated habitats invaded by plants or algae;
- habitats structured by native ecosystem engineers (kelps, corals, and marsh plants) invaded by species with different functional attributes;
- habitats structured by strong abiotic controls (e.g., sediment characteristics, flow, oxygen, and productivity) that can be modified by invasive engineers; and
- low-diversity/low-redundancy systems, with foundation species whose roles may be lost.

Given the large and growing literature on the subject of species invasions, it is remarkable how many questions remain concerning the functional impacts of invaders, the mechanisms by which they act to alter ecosystem functions (especially in concert with the actions of other species), and their overall significance. Integration of physical and geochemical measurements, community ecological tools, field removal or transplant experiments, diet preference, and competition studies are required to document fully plant and animal invader impacts and mode of action. Such information is critical for effective detection, control, eradication, and restoration (e.g., Bulleri et al., 2008). Basic ecosystem-level questions that have emerged from our review include the following:

- How does the source, palatability, and degradability of primary production by invaders influence ecosystem structure and process?
- What are the consequences of substrate alteration by invaders (e.g., from sand to mud, from soft to hard, and from abiotic to biotic), and what mechanisms produce these changes?
- For invaders that create biogenic structure, what is the nature of the tradeoff between increased living space for some species versus usurpation of space for others, and how does this interact with local environmental conditions (substrate type, flow, and sedimentation)?
- Does the predator mode of action (direct or indirect) affect emergent properties of ecosystems?
- To what extent does disruption of facilitation among native species, or enhanced facilitation by invaders, alter emergent patterns and processes?
- Are bottom-up and top-down processes fixed in relative importance, or can a shift in weighting from one to another via invasion completely restructure ecosystems?

- What roles do parasites, disease, and symbionts play in invasion dynamics, and what are the functional consequences when these taxa are introduced or displaced?
- How does the lack of coevolutionary history affect invader impacts, and does this lack of history affect various functional processes (e.g., engineering vs. trophic) differently?

To answer these questions, invasion biologists will need to develop coordinated research programs that embrace ecological theory, adopt manipulative approaches, and focus on mechanisms underlying observed invader impacts. This type of research will ultimately inform conservation efforts and enhance maintenance of ecosystem services.

Fundamentally, we can also ask what general lessons about ecosystem structure and function can be learned from invasions. Have they revealed new types of biotic interactions and processes, producing 'no-analog systems' (Ricciardi, 2007; Williams and Jackson, 2007), or do they represent dramatically reshuffled biotas, but ones that will largely play by established rules (Lugo, 1994; Davis, 2009)? Although these questions are still the subject of debate, it is clear that invasions can cause substantial ecological surprises (Doak et al., 2008).

A large part of the interest in biological invasions stems from their conservation implications. Invaders capable of modifying ecosystem function clearly represent the sorts of strongly interacting species that merit particular concern (Soule et al., 2005). Considered more broadly, the addition of species through invasions represents a subset of the broader class of biotic modifications arising when species are either added to or removed from systems. As such, the study of invasions should inform efforts such as restoration, where the goal is to facilitate species' arrival into novel ecosystems. Assemblage change through species removals, as occurs by overharvesting, can similarly be informed by the general work associated with anthropogenic modification of species representation in ecosystems.

Biological invasions also represent an important element of global change. Anthropogenic invasions, in and of themselves, represent a major force of change operating in virtually all ecosystems across the globe. It is clear that introduced species, as well as natives, will respond to climatic forcing factors by appearing in and disappearing from systems. This will undoubtedly (but unfortunately) provide further opportunity to explore functional consequences of shifting biotic assemblages.

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**Appendix 1** Ecological consequences of invasion by marine plants and algae

<i>Invader</i>	<i>Location</i>	<i>Invaded ecosystem</i>	<i>Responder</i>	<i>Nature of response</i>	<i>References</i>
<b>Vascular plants</b>					
<i>Spartina alterniflora</i>	Yangtze R. estuary, China	<i>Phragmites australis</i> marsh	Arthropods	Reduced abundance, altered community composition, diet avoidance, increased dominance of <i>Spartina</i> feeders	Wu et al. (2009)
<i>S. alterniflora</i>	Yangtze R. estuary, China	<i>Spartina mariqueter</i> , <i>Scirpus</i> and <i>Phragmites</i> marsh	Nematodes, macrobenthos	No effect on nematode or macrobenthos density, altered trophic structure	Li et al. (2009a), Chen et al. (2007)
<i>S. alterniflora</i>	Yangtze R. estuary, China	<i>Spartina mariqueter</i> , <i>Scirpus</i> and <i>Phragmites</i> marsh	Birds (plovers and snipes)	Most species avoid <i>S. alterniflora</i> and use mudflat or <i>Scirpus</i> habitat. Only 1 of 15 species occurs in <i>S. alterniflora</i> habitat. Hooded crane also avoids this habitat.	Ma et al. (2003), Chen et al. (2004a)
<i>S. alterniflora</i>	Yangtze R. estuary, China	<i>Spartina mariqueter</i> , <i>Scirpus</i> and <i>Phragmites</i> marsh	Macrobenthos	No overall density difference in invasive and native marsh; enhanced density of <i>Assimina violacea</i> ; reduced density of four gastropods and bivalves; loss of herbivores and detritivores; increase in suspension feeders	Chen et al. (2005, 2007)
<i>S. alterniflora</i>	Yangtze R. estuary, China	<i>Phragmites</i> marsh, mudflat	<i>Sesarma dehaani</i>	Crab abundance and biomass higher in <i>Spartina</i> than tidal flat	Wang et al. (2008)
<i>S. alterniflora</i>	Yangtze R. estuary, China	<i>Spartina mariqueter</i> , <i>Scirpus</i> , <i>Phragmites</i>	Plants	<i>S. alterniflora</i> out competes native <i>S. mariqueter</i> ; <i>S. alterniflora</i> out competes <i>Phragmites</i> at high but not low salinity	Chen et al. (2004b), Wang et al. (2006), Li et al. (2009)
<i>S. alterniflora</i>	Coastal China	<i>Spartina anglica</i>	Plants	<i>S. alterniflora</i> out competes <i>S. anglica</i> in greenhouse experiments	Zhi et al. (2007)
<i>S. alterniflora</i>	Willapa Bay, Washington, USA	Mudflat	Clams	Lower densities of <i>Macoma</i> spp. and higher densities of <i>Venerupis philippinarum</i> in <i>Spartina</i> than mudflat; <i>Mya arenaria</i> variable	Ratchford (1995), Dumbauld et al. (1997)
<i>S. alterniflora</i> , <i>Zostera japonica</i>	Willapa Bay, Washington, USA	Intertidal mudflat	Macrobenthos	<i>S. alterniflora</i> habitat had a 50% reduction in species richness and 30% reduction in diversity (H') relative to mudflat and <i>Zostera</i> . No significant density effects were observed	Grosholz et al. (2009)
<i>S. alterniflora</i>	Willapa Bay, Washington, USA	Mudflat	Macrobenthos	Higher densities of macrofauna in spring in <i>Spartina</i> patches, but lower densities in August; enhancement of subsurface-deposit feeders in <i>Spartina</i> patches	Zipperer (1996)
<i>Spartina hybrid</i>	San Francisco Bay, USA	Unvegetated mudflat	<i>Balanus glandula</i> ; <i>Carcinus maenas</i>	<i>B. glandula</i> (barnacle) recruitment reduced by a factor of 9; crab densities higher in <i>Spartina</i> , <i>Spartina</i> preferred for consumption over <i>Phragmites</i>	Neira et al. (2006)
<i>S. hybrid</i>	San Francisco Bay, USA	Unvegetated mudflat	Other invasives	Invasive <i>Macoma petalum</i> , <i>Mya arenaria</i> , <i>Geukensia demissa</i> had 2–10 times higher densities at growing edge of the <i>Spartina</i> . High densities of <i>Urosalpinx cinerea</i> and <i>Ilyanassa obsoluta</i> also occurred.	Grosholz et al. (2009)
<i>S. hybrid</i>	San Francisco Bay, USA	Unvegetated mudflat, <i>S. foliosa</i>	<i>Macoma petalum</i>	Reduced clam densities and growth by a factor of 2 in vegetated sediments relative to open mudflat. Native and invader <i>Spartina</i> did not differ in effects.	Brusati and Grosholz (2007)

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Appendix 1 (Continued)

Invader	Location	Invaded ecosystem	Responder	Nature of response	References
<i>Spartina hybrid</i>	San Francisco Bay, USA	<i>S. foliosa</i> marsh, mudflats	Macrobenthos	<i>Spartina</i> hybrid reduces infaunal densities relative to mudflat; native <i>S. foliosa</i> enhances densities, different root systems may be responsible	Brusati and Grosholz (2006)
<i>S. hybrid</i>	San Francisco Bay, USA	Unvegetated mudflat, <i>Salicornia virginica</i> marsh	Macrobenthos	Invasion causes major reduction in macrobenthos density and biomass on mudflat, with loss of bivalves and amphipods; Lesser effects (minor composition changes) in <i>Salicornia</i> marsh	Neira et al. (2005), Levin et al. (2006)
<i>S. hybrid</i>	San Francisco Bay, USA	Unvegetated mudflat, <i>Salicornia</i> marsh	Macrobenthos	Macrobenthos exhibit four distinct communities linked to different stages of <i>Spartina</i> hybrid invasion; increasing successional stage involves reduced richness, increased dominance and shifts to detritivory by macrobenthos	Neira et al. (2007)
<i>Spartina anglica</i>	Germany	<i>Zostera noltii</i> , unvegetated	Macrobenthos	Diversity lower in vegetated than unvegetated habitats; shift from endo- to epi-benthic species in vegetated habitat; <i>Spartina</i> and <i>Zostera</i> communities similar, with no trophic shifts	Bouma et al. (2009)
<i>S. anglica</i>	Archachon Bay, France	<i>Z. noltii</i> , bare sediment	Macroinfauna, epifauna	No effect on infauna of <i>Spartina</i> relative to native <i>Zostera</i> ; added complexity enhances epifauna relative to bare substrate	Cottet et al. (2007)
<i>S. anglica</i>	Seafield Bay, Suffolk, England	Mudflat	Macrofauna	Reduced densities of bivalves and amphipods, elevated densities of tubificid oligochaetes in vegetated areas relative to mudflat	Jackson (1985)
<i>S. anglica</i>	Tasmania	Mudflat	Macrobenthos	Enhanced density and species richness	Hedge and Kriwoken (2000)
<i>S. anglica</i>	Washington State, USA	Cobble, mudflat, other	Macrobenthos	Effects are context dependent. Benthic diversity increased when <i>S. anglica</i> invaded	Hacker and Dethier (2006)
<i>S. anglica</i>	Krabbekreek, The Netherlands	Mudflat	<i>Arenicola marina</i>	<i>S. anglica</i> inhibits <i>Arenicola</i> establishment through root presence, high silt content and sediment compaction. Mutual exclusion occurs.	van Wesenbeeck et al. (2007)
<i>Phragmites australis</i>	New Jersey, USA	<i>S. alterniflora</i> marsh	<i>Geukensia</i> (mussel)	Densities of <i>Geukensia</i> were enhanced around <i>Phragmites</i> relative to <i>S. alterniflora</i>	McClary (2004)
<i>P. australis</i>	New Jersey, USA	<i>S. alterniflora</i> marsh	Arthropods	Invasive <i>Phragmites</i> causes a shift from free-living to concealed feeders; loss of spiders; free-living species are dominated by detritivorous collembola and chironomids, rapid recovery following invader removal	Gratton and Denno (2005)
<i>P. australis</i>		<i>S. alterniflora</i> marsh	Stem epifauna	<i>Phragmites</i> supports reduced density and diversity of stem epifauna relative to <i>S. alterniflora</i> ; but no differences occur in meiofauna	Robertson and Weiss (2005), Yuhas (2001)
<i>P. australis</i>	Connecticut River, USA	<i>S. alterniflora</i> marsh	Fish; mobile invertebrates	<i>Fundulus</i> densities were unaffected. Shrimp <i>Paelmonetes pugia</i> was more abundant and <i>Uca minax</i> was less abundant in <i>Phragmites</i> stands	Fell et al. (2003)
<i>P. australis</i>	New Jersey, Delaware, Maryland, USA	<i>S. alterniflora</i> marsh	Fish, crustaceans	Invasion stage determines <i>Phragmites</i> effects on <i>Fundulus</i> ; densities decline with increasing period of invasion; habitat quality declines as the invasion progresses. No effects on density are observed in some marshes.	Able et al. (2003), Fell et al. (2003), Osgood et al. (2003), Hunter et al. (2006)

<i>P. australis</i>	Connecticut, USA	<i>Spartina patens</i> , <i>Juncus</i> ; <i>Typha</i> tidal marshes, salinity gradient	Macrobenthos	Effects increase with age and decrease with increasing salinity; invaded sediments have reduced densities of epifaunal gastropods, <i>Succinea wilsoni</i> and <i>Stagnicola catascopium</i> , more podurid insects, sabellid polychaetes, and peracarid crustaceans, smaller area.	Talley and Levin (2001)
<i>Rhizophora mangle</i>	Hawaii, USA	Sand flat	Macrobenthos, epifauna	Emergent roots colonized by introduced barnacles and sponges; mangrove infauna supported more introduced species than the sand flat, mangrove infauna exhibited higher species richness (mainly annelids and amphipods) due to enhanced number of niches; dominance	Demopoulos and Smith (2010)
<i>R. mangle</i>	Hawaii, USA	Sand flat	Birds	Mangroves house water bird predators, sand flat species avoid mangrove for nesting, foraging	Allen (1998), Rauzon and Drigot (2002)
<i>R. mangle</i>	Hawaii, USA	Sand flat	Crabs	Facilitation by providing nursery grounds, predation refuge	
<i>Z. japonica</i> <i>Z. japonica</i>	British Columbia Oregon, USA	Tidal flat Tidal flat	Water birds Macrobenthos	Heavy consumption by brant, wigeon, mallard, and pintail Effects varied with age and location; general richness was enhanced	Baldwin and Lovvorn (1994) Posey (1988)
<b>Marine algae</b>					
<i>Sargassum muticum</i>	NW Spain	Temperate Intertidal	Algal assemblages	Limited impact, altered no. native taxa and two under story functional groups	Olabarria et al. (2009)
<i>S. muticum</i>	Northern Ireland	Soft substrate	Infauna	Increased abundance of small, opportunistic taxa at one site but not another; no effects on sediment characteristics	Strong et al. (2006)
<i>S. muticum</i>	Isle of Cumbrae, Scotland	Sub-tidal reef	Algae	Reduced densities of native brown algae ( <i>Dictyota</i> ) and enhanced densities of associated sessile epifauna, increased homogeneity	Harries et al. (2007)
<i>S. muticum</i>	North Sea	Rocky shore and soft sediments	Epibiota	<i>S. muticum</i> enhances diversity in soft sediment ecosystems but has negligible effects on rocky shores	Buschbaum, et al. (2006)
<i>S. muticum</i>	Washington State, USA	Sub-tidal reefs	Algae, urchins	Shading reduces abundance and growth of native brown and red algae, with indirect consequences for grazing urchins	Britton-Simons (2004)
<i>Caulerpa taxifolia</i>	Southeastern Australia	Temperate sub-tidal seagrasses ( <i>Halophila ovalis</i> , <i>Zostera capricorni</i> ), soft sediments	Epifauna, infauna	More epifauna and fewer infauna with invasion of unvegetated sediments; more epifauna than on <i>H. ovalis</i> ; fewer epifauna than on <i>Z. capricorni</i> ; reduced infauna in both seagrasses	McKinnon et al. (2009)
<i>C. taxifolia</i>	New South Wales, Australia	<i>Z. capricorni</i>	Epiphytes	More epiphytes on <i>Caulerpa</i> than <i>Zostera</i> ; filter feeders on bryozoans and ascidians in particular	Prado and Thibaut (2008)
<i>C. taxifolia</i>	New South Wales, Australia	Unvegetated estuary	<i>Anadara trapezia</i>	Reduced densities relative to unvegetated sediments, inhibition of reproduction; females more affected than males, enhanced recruitment	Gribben and Wright (2006a,b), Wright et al. (2007)
<i>Caulerpa racemosa</i> var. <i>cylindracea</i>	Mediterranean coast	Sub-tidal		Reduced alpha diversity in invaded assemblages, increased homogenization, reduced depth differences in communities following invasion; more turf-forming algae	Piazzi and Balata (2008)

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Appendix 1 (Continued)

Invader	Location	Invaded ecosystem	Responder	Nature of response	References
<i>Codium fragile</i> ssp. <i>tomentosoides</i>	Canada	Sub-tidal, <i>Laminaria longicuris</i> , <i>Laminaria digitata</i>	Benthic macrofauna	Selected species (4/11) prefer <i>C. fragile</i> canopy over removal or <i>Laminaria</i> habitat	Schmidt and Scheibling (2007)
<i>C. fragile</i> ssp. <i>tomentosoides</i>	Northern Adriatic Sea	Breakwaters along sandy shore	<i>Mytilus galloprovincialis</i>	<i>Codium</i> primordia enhance mussel recruitment, but not growth	Bulleri et al. (2006)
<i>C. fragile</i> spp. <i>tomentosoides</i>	Canada	Sub-tidal, <i>L. longicuris</i> , <i>L. digitata</i>	Epiphytes	<i>Codium</i> fronds support greater diversity including more amphipods, harpacticoid copepods, <i>Placa dendritica</i> (specialist herbivore) than <i>Laminaria</i> fronds	Schmidt and Scheibling (2006)
<i>C. fragile</i> ssp. <i>tomentosoides</i>	Canada	Sub-tidal, <i>L. longicuris</i> , <i>L. digitata</i> , <i>Desmarestia</i> spp.	Kelps	<i>Codium</i> exploits disturbance, forming dense stands that inhibit recruitment of kelps and other seaweeds	Scheibling and Gagnon (2006)
<i>Lophocladia lallemandii</i>	Mediterranean, Balearic Islands	<i>Posidonia oceanica</i> meadows	<i>Posidonia</i>	Reductions in seagrass shoot size, leaf biomass, and fraction of living shoots, lower sucrose content, probably indicating reduced photosynthesis	Ballesteros et al. (2007)
<i>Womersleyella setacea</i>	N. Aegean Sea, Greece	Sub-tidal	Animals: 278 spp.	Epifauna different on invader than native, enhanced species richness and abundance	Antoniadou and Chintiroglou (2007)
<i>Undaria pinnatifida</i>	Argentina (Patagonia)	Sub-tidal	Algae	Reduces diversity of native seaweed	Casas et al. (2005)

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