Marine Bioinvasions: The Alteration of Marine Ecosystems by Nonindigenous Species

By James T. Carlton

Empty of cargo, the ship ballasted up—pumping or gravitating the brackish river water under the ship into its ballast tanks and into a large central cargo hold.

SOMETIME IN 1979 or perhaps 1980 a bulk cargo ship pushed off from a port in the Americas, with a load of wheat or iron ore, bound for a Russian port on the Black Sea. Perhaps it was winter, and the vessel needed more weight to keep it down in stormy seas. Or perhaps the vessel was "high on the nose," and needed extra weight to keep its bow down just a little more. The ship "ballasted up," pumping water into its bottom ballast tanks, and adding another 1,000 metric tons to a forepeak tank. The voyage went well; cargo and water were released on the north shore of the Black Sea, 22 days later.

In the fall of 1982, while towing a meter net for routine plankton sampling, a Russian oceanographic research vessel captured a 5-cm-long comb jellyfish previously unknown in the Black Sea. It was identified in Moscow as the American ctenophore *Mnemiopsis leidyi*, a common species from Cape Cod to Brazil (Vinogradov *et al.*, 1989). By 1988 the standing stock of *Mnemiopsis* was calculated in terms of hundreds of thousands of metric tons. The comb jelly is well-known as an insatiable consumer of zooplankton. By 1989, anchovy (*Engraulis encrasicolus*) landings had fallen from hundreds of thousands of tons to tens of thousands of tons (Harbison and Volovik, 1994).

Sometime in 1984, perhaps, a bulk cargo vessel departed the dock in a Chinese river port, headed for California to load wood products. Empty of cargo, the ship ballasted up—pumping or gravitating the brackish river water under the ship into its ballast tanks and into a large central cargo hold. With 25,000 metric tons of water aboard, the vessel could safely head for the open sea and a 14-day crossing to a brackish water port in the northern part of San Francisco Bay. Once in the Bay, most of the Asian ballast water was to be pumped out, making "room"—in terms of both weight and space—for 30,000 metric tons of cargo.

In October 1986, a marine biology class, taking benthic grab samples in shallow water in the northern part of San Francisco Bay, found a small clam new to the Bay—a 2.5 cm long, wrinkly skinned bivalve later to be identified as the brackish water corbula *Potamocorbula amurensis*. By 1988 the standing stock of *Potamocorbula* reached 10,000 individuals per square meter (Carlton *et al.*, 1990). By 1990 the spring phytoplankton bloom in the north Bay had essentially disappeared (Alpine and Cloern, 1992).

In 1985—or a year or two earlier—another bulk cargo vessel cast off lines in a Black Sea port for a month's voyage to the Great Lakes, to load wheat. In full freshwater ballast, the vessel was ready for a long voyage across the Mediterranean and up through the North Atlantic Ocean. Perhaps it was summer or fall (the lakes are closed for the entry of seagoing vessels in the middle of winter), and the waters of the Great Lakes were relatively warm—warm enough so that the plankton in the Black Sea ballast water would not die immediately from the stress of freezing water. Arriving in western Lake Erie—or while passing through Lake St. Clair, a small body of water between Lakes Erie and Huron—the ship discharged its ballast water.

On June 1, 1988, biologists pulling up benthic grabs from the floor of Lake St. Clair brought up a clump of bivalve mollusks new to the Great Lakes. By 1990 the zebra mussel *Dreissena polymorpha*—whose arrival in North America had been predicted since the 1920s—occurred by the tens, and even the hundreds of thousands, per square meter on virtually every submerged hard substrate in the shallow waters of Lakes Huron

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and Erie (Mills *et al.*, 1993). Water pipes 1.0 meter in diameter were narrowed to a 30-cm core, the remainder of the pipe being a thick layer of zebra mussels.

On a spring day in May 1996 a bulk cargo vessel, or a container ship, or some other type of vessel, takes on water in San Francisco Bay that will be discharged two days later in Puget Sound. The Bay, that day, is rich with invertebrate larvae—the larvae of the clam *Potamocorbula*, or the larvae of the recently introduced Atlantic green crab *Carcinus maenas*, or the larvae of the latest invader, the Chinese mitten crab *Eriocheir sinensis*. None of these species now occur in Puget Sound.

Despite the above stories of the invasions of San Francisco Bay, the Black Sea, or the Great Lakes, is the captain of this ship ballasting up on this May day aware—in even the broadest sense—of the potential contents of his ballast "cargo"? And even if he were (and chances are he's not), what could he do about it?

Biological invasions in the sea consist of natural range expansions (that is, the often predictable ebb and flow of organisms due to changing climates or currents) and human-mediated introductions. The latter are usually unpredictable, and, because of the transport vectors discussed below, independent of the natural barriers of space and time (Carlton, 1987, 1989). Thus it is that a Japanese shore crab can appear in New Jersey, or an Australian barnacle in England, or a Chesapeake Bay comb jellyfish in the Black Sea.

Introductions of nonindigenous marine organisms by human activities are not new. We have been changing the face of coastal zone biotas for centuries, if not millennia, through the insertion of nonnative animals and plants. Peterson *et al.* (1992) have discussed the possibility that Viking explorers brought the North American clam *Mya arenaria* back to Europe as early as the 13th century. It appears too, that Portuguese traders may have intentionally brought the Japanese oyster *Crassostrea gigas* back to southern Europe in the 15th century—where it was subsequently described as a new species, *Crassostrea angulata*, under which name it remains today (Edwards, 1976). By the 13th and 14th centuries, wooden vessels had set into motion the transglobal dispersal of wood-boring shipworms (teredinid bivalves) and gribbles (isopod crustaceans), in patterns that render discerning their aboriginal distributions extraordinarily difficult.

That organisms naturally drifted in wood along continental margins for eons is unquestionable; that they drifted in wood from southern Australia to the North Atlantic Ocean, and survived that voyage (if indeed it could even take place) over a period of several years, is not as clear. That thousands of wooden ships, their hulls riddled with boring organisms and covered with thick mats of fouling organisms, moved between these two regions in a matter of weeks or months, is well-known.

The deep burrows created by wood-boring organisms in sailing vessels served as ocean-going refuges for many other mobile organisms, organisms that would be swept off the outer hull of the ship in the normal course of operations—animals such as crabs, shrimp, and small fish. The level of shipworm activity in tropical waters was sufficiently well-known to the British Admiralty by the 16th century that English ships were advised—indeed forbidden—to go into certain South American waters. The hulls themselves supported massive fouling communities (including hydroids, mussels, sea squirts, sea weeds, and scores of other organisms) that in turn provided intricate habitats for many nestling organisms typically not associated with such communities, such as clams or worms more normally found living in soft harbor muds, or mussels more typically associated with salt marshes, all of whose larvae could and do settle into thick fouling beds. Although we can "picture" such communities, based on studying modern fouling assemblages, there are no data that indicate just how diverse fouling communities were on ancient sailing vessels. Some insights have been gained, however, by studying fouling communities on modern-day replicas of historical vessels, whose sailing patterns mimic in part those of ancient voyages (Carlton and Hodder, 1995).

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The transport of living organisms went on, too, deep inside the ship. Almost always before the 1880s, but running well into the 1920s, vessels carried rock and sand for ballast (and an amazing diversity of other heavy materials as well, ranging from old roof tiles to scrap metal), and this ballast was discharged on shores around the world (Carlton, 1992c). Carried in this maritime ballast were numerous shore-dwelling organisms, including beach plants, shore-hopping talitrid amphipods, and insects. Lindroth (1957), for example, in a scholarly and elegant treatise, traced the role of ships' ballast and the subsequent introduction of European beetles to North America. The Chilean–New Zealand sandhopper *Transorchestia chiliensis* was brought by beach ballast to the Oakland Estuary in San Francisco Bay presumably sometime in the late 19th or early 20th centuries, and today survives (as the only known population of the subspecies *T. c. enigmatica*) on a 100-m stretch of shoreline on an urbanized lake in the middle of the City of Oakland.

Rock ballast may have been the means, too, by which the common European shore periwinkle *Littorina littorea* found its way in modern times to North America, although this snail is also a prime candidate for intentional release by European colonists as a new coastal food resource, because it was for centuries (and regionally remains) a popular food item in western Europe.

The arrival of *Littorina littorea* in America in the 1840s further illustrates that introductions are not limited to bays, ports, and harbors—the urbanized aquatic "weedy lots." *Littorina* colonized rocky shores, marshes, and mudflats from Newfoundland to New Jersey in 40 years, and subsequently became the characteristic tidepool snail of New England (Brenchley and Carlton, 1983). In turn, *Littorina* changed the face of the rocky shores, profoundly altering the expression of both plant and animal communities (Lubchenco, 1978; Brenchley and Carlton, 1983; Carlton, 1992b). In the mid–19th century, the Indian Ocean wood boring isopod *Sphaeroma terebrans* began invading the mangrove communities of South, Central, and southern North America (Carlton and Ruckelshaus, 1996). In the 1950s, the Indo-Pacific mantis shrimp (stomatopod) *Gonodactylus aloha* was introduced to Hawaii, displacing the native species *Pseudosquilla ciliata* (Kinzie, 1984) on shallow coral reefs. In the 1980s, the Mediterranean mussel *Mytilus galloprovincialis* colonized the open wave-swept rocky shores of South Africa (Branch *et al.*, 1991). Forty years earlier it had begun to occupy similar habitats in southern California.

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After 500 years of seagoing vessels moving in every conceivable pattern and touching upon virtually every kilometer of coastline of the inhabited world, discerning the natural patterns of distributions of the thousands of species that could have been carried is thus difficult. This work requires retrospective time-based (paleontological, archeological, and historical) studies, spatial (biogeographic) studies, and a combination of both (evolutionary studies, looking at probable species relationships, and using molecular genetic techniques to "track" dispersal routes and the links between peripheral, disjunct populations and possible parental stocks).

Such work is tedious and time-consuming, and requires a species-by-species approach, but such work is slowly revealing which species in some communities are introduced and which are native (Carlton and Iverson, 1981; Meehan *et al.*, 1989; Chapman and Carlton, 1991; Geller *et al.*, 1993), thereby permitting us to begin to reconstruct the aboriginal nature of certain marine communities. That much of the reorganization of these communities occurred before the first biological surveys took place, and before Linnaeus and others even began bestowing Latin names onto animals and plants, guaranteed that the scale of this phenomenon would be—and largely still remains—buried in antiquity. In the meantime, the history of thousands of species that could have been transported by ships remains unknown. While by default such taxa are classically treated as "native," a more rigorous characterization is to think of such organisms as "cryptogenic," that is, neither clearly native or exotic (Carlton, 1996a)—as pieces of a yet unconstructed puzzle, as we try to assemble a picture of how modern coastal marine and estuarine communities came to be formed, and the extent to which they owe their modern diversity to human-mediated supplementation and transformation.

Although many details of the introduction of marine organisms remain to be resolved, it is clear that by the end of the 19th century an extensive reorganization of some fraction of the world's coastal marine biota had quietly and often cryptically taken place. The 20th century opened with an equally quiet yet profound change in global maritime commerce, a change that was to eventually set the stage for a vast new network of invasions.

In the 1880s ship building technology changed, and the first serious commitment to iron ships was well underway. The existence of bulk-headed, metal-walled spaces, combined with motor-driven pumps, permitted ships to begin to switch from carrying rocks for ballast to carrying water for ballast (Carlton, 1985). Within 20 years, water ballast was in use by thousands of ships. Water was drawn into the vessel either by pumping, or by simply letting the water flow in by gravity until pumping was required.

And with that water plankton, fish, pieces of seaweed with attached organisms, and waterlogged pieces of wood rubbed off the piers, flowed into the vessel. For the first time in the history of human endeavor and the history of the ocean, large parcels of plankton-rich water were being transported virtually instantaneously across and between oceans. No longer were the vast expanses of the open ocean a barrier to the planktonic larvae or adults of most coastal-dwelling species, nor were continents a barrier to species living in the Atlantic or Pacific Oceans.

The first clear ballast water "signal" came from the North Sea, when in 1903 the Chinese diatom *Biddulphia sinensis* was discovered in Europe. The ballast game was afoot. By the 1910s the Chinese mitten crab *Eriocheir* appeared in German rivers; it too was thought to have been transported by ballast water. For the next 60 years transported species would dribble from the ballast faucet all over the world, but in apparently relatively small numbers (Carlton, 1985; Williams *et al.*, 1988).

In the 1970s and 1980s, for reasons that remain at the doorstep of competing hypotheses (Carlton, 1996b), the number of invasions believed to be linked to the transport and discharge of ballast water began to blossom. Perhaps coastal waters were changing for the better due to several decades of intensive campaigns to improve water quality—thus making donor regions more diverse and recipient regions more susceptible to invasions. Perhaps the increased speed of vessels since World War II led to higher plankton survival, or perhaps the increased number of vessels carrying non–petroleum contaminated ballast water led to more successful inoculations. For whatever reasons, the world began to itch with new invasions of marine animals and plants. That it wasn't simply the appearance that there were more invasions, due to more scientists being aware of the phenomenon, or because of more thorough exploration, appears to be the case: in fact, since the 1970s, the number of scientists exploring the coastal zone and capable of identifying even common marine organisms has been in a steady, and sometimes steep, decline (Carlton, 1993; National Research Council, 1995).

Carlton (1985) reviewed what was known of ballast invasions and many of the available records up until the early 1980s (reporting of new invasions often lags behind actual introductions by several years). Soon thereafter, the ballast flood gates were about to open (Table 1)—the Chinese clam *Potamocorbula* was to be collected only 1 y later in San Francisco Bay, the Eurasian zebra mussel *Dreissena* 2 y after that in the Great Lakes, and most of the western world was to first hear of the invasion of the Black and Azov Seas by the American comb jelly *Mnemiopsis* in 1989 (Vinogradov *et al.*, 1989). In 1986 the first specimens of red-tide causing Japanese dinoflagellates were discovered in southern Australia, waters that receive vast amounts of ballast water from Japanese ports. Also in the 1980s the Japanese seaweed *Undaria pinnatifida* was discovered in the same waters (Sanderson, 1990), and in 1986 the Japanese starfish *Asterias amurensis* was found in Tasmania (Buttermore *et al.*, 1994). All were linked to ballast water, with the dinoflagellates in particular being linked to the transport of their cyst stages in the large amounts of sediment that accumulate in ballast tanks and ballasted cargo holds (Hallegraeff, 1993).

In 1986 the Indo-Pacific swimming crab *Charybdis helleri* appeared in the Caribbean, apparently via ballast water by way of eastern Mediterranean populations (themselves established by coming through the Suez Canal); in 1995, it was discovered in Florida (Lemaitre, 1995). In 1988 the Japanese shore crab *Hemigrapsus sanguineus* appeared in New Jersey—an unexpected arrival given the much greater preponderance of ballast water released on the mid-Atlantic coast not from Asia but from Europe and the Mediterranean.

And in 1989 one of the more remarkable invasions seen in many decades appeared in France and Monaco in the northern Mediterranean: a form of the ubiquitous subtropical green algae *Caulerpa taxifolia* (Boudouresque *et al.*, 1994). This alga now occupies many thousands of square meters of sea floor in the shallow sublittoral zone, in regions formerly supporting diverse arrays of other erect macroscopic organisms, such as sponges, gorgonians, and other seaweeds (A. Meinesz, personal communication). For many hundreds of meters in waters only 1–2 m deep along the shoreline of northern Italy, *Caulerpa* now forms "astroturf"-like green sheets (JTC and A. Meinesz, personal observations, Imperia, Italy, June 1995). *Caulerpa* appears to owe its origins and its freedom in the Mediterranean not, however, to ballast water, but to releases from the aquarium industry.

Scores of other invasions have been recorded in the 1980s and 1990s from those countries with the remaining resources and taxonomic expertise to detect new invasions (Carlton and Geller, 1993). From scores of other coastal countries of the world, with few or no active marine ecological or taxonomic programs, the literature is silent on new species invasions.

It's May, 1996 and the ship noted earlier has finished ballasting in San Francisco Bay, about to take a load of plankton up to Puget Sound. Or perhaps the ship is in the Great Lakes, ballasting up zebra mussel larvae, now that America is a major donor region of zebra mussels. Or perhaps it is in a Tasmanian port, ballasting up the larvae of the seastar *Asterias* to be donated to another port elsewhere in the world. If told of what he is about to do, relative to the transport of exotic species, the ship captain may well wonder what the concern is: he's been moving ballast water for decades, and surely "everything that could have been introduced would have been introduced by now." But here our ability to predict fails the Captain.

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That zebra mussels were released in the Great Lakes for decades before they were discovered by scientists in 1988 seems almost certain. That the Great Lakes—or American waters in general—were "immune" to the invasion of the zebra mussel seemed like a tempting conclusion as of May, 1988. But as long as the corridor remains open—or "fluid" in this case—we know that the potential for invasion also remains. A vessel may move a species between two ports for 100 years, and then the species "takes" in the 101st year. One of the commonest fouling organisms of western Europe is the seasquirt *Ascidiella aspersa*. It seems probable that it has been on the bottoms of many vessels visiting American ports for almost 400 years. Why, then, did it appear in New England fouling communities in the mid-1980s?

With our ability thus being low to predict the relationship between the existence of a transport mechanism and the probability of introduction of any given species, a logical route is to reduce the scale of the mechanism. In 1990, Australia, Canada, and the United States brought before the United Nations International Maritime Organization (IMO) the issue of ballast water and the introduction of nonindigenous, particularly so-called "nuisance," species. As of 1996, IMO is considering amendments to the international regulations

Table 1
Examples of recent invasions in marine and freshwater ecosystems

Species (Native Region)	Introduced To (Mechanism of Introduction; 1st Date of Collection)	Reference
Chlorophyta		
Caulerpa taxifolia (subtropical regions) (green alga)	Mediterranean; France and Italy (AQ; 1989)	Boudouresque *et al.*, 1994
Rhodophyta		
Antithamnion nipponicum (Japan) (red alga)	Long Island Sound: Connecticut (BW/SF; 1986)	Foertch *et al.*, 1995
Phaeophyta		
Undaria pinnatifida (Japan) (kelp)	Australia (BW/SF; 1980s)	Sanderson, 1990
Dinoflagellata		
Alexandrium catenella (Japan) (dinoflagellate)	Australia (BW; 1986)	Hallegraeff, 1993
Ctenophora		
Mnemiopsis leidyi (Americas) (combjelly)	Black and Azov Seas (BW; 1982)	Vinogradov *et al.*, 1989 Harbison and Volovik, 1994
Annelida: Polychaeta		
Marenzelleria viridis (North America) (spionid worm)	Western Europe (BW; 1983)	Essink and Kleef, 1993
Mollusca: Bivalvia		
Perna perna (South America) (brown mussel)	Gulf of Mexico: Texas (BW/SF; 1990)	Hicks and Tunnell, 1993
Pinctada margaritifera (Tropical Pacific Ocean) (pearl oyster)*	Florida (BW/SF; 1990)	Chesler, 1994; Carlton and Ruckelshaus, 1996
Potamocorbula amurensis (Asia; brackish water corbula)	San Francisco Bay (BW; 1986)	Carlton *et al.*, 1990
Dreissena polymorpha (Eurasia; zebra mussel)	Great Lakes (BW; 1988)	Mills *et al.*, 1993
Dreissena bugensis (Eurasia; quagga mussel)	Great Lakes (BW; 1990)	Mills *et al.*, 1993
Crustacea: Copepoda		
Pseudodiaptomus marinus (China, Japan) (copepod)	San Francisco Bay (BW; 1986)	Orsi and Walter, 1991
Pseudodiaptomus forbesi (China) (copepod)	San Francisco Bay (BW; 1987)	Orsi and Walter, 1991
Crustacea: Isopoda		
Sphaeroma quoyanum (New Zealand) (boring pillbug)	Oregon (SF; 1995)†	Herein
Crustacea: Cladocera		
Bythotrephes cederstroemi (Eurasia) (water flea)	Great Lakes (BW; 1984)	Mills *et al.*, 1993
Crustacea: Decapoda		
Carcinus maenas (North Atlantic) (shore crab)	California (?; 1989–1990)	Cohen *et al.*, 1995; Grosholz and Ruiz, 1995
Callinectes sapidus (Northwest Atlantic) (blue crab)*	Hawaii (PR?; 1985)	Eldredge, 1995
Charybdis helleri (IndoPacific) (swimming crab)‡	Florida (BW/SF; 1995)	Lemaitre, 1995
Hemigrapsus sanguineus (Japan; shore crab)	New Jersey (BW; 1988)	McDermott, 1991
Bryozoa		
Membranipora membranacea (Europe; moss animal)	Maine to New York (BW; 1987)	Berman *et al.*, 1992
Echinodermata		
Asterias amurensis (Japan) (North Pacific seastar)	Australia; Tasmania (BW/SF; 1986)	Buttermore *et al.*, 1995
Chordata: Tunicata		
Styela clava (Japan) (Stalked sea squirt)§	Oregon (SF; 1995)	Herein
Ascidiella aspersa (Europe) (sea squirt)	Massachusetts to Connecticut (BW/SF; ca. 1985)	Carlton, 1993
Chordata: Pisces		
Gymnocephalus cernuus (Europe) (ruffe)	Great Lakes (BW; 1987)	Mills *et al.*, 1993
Proterorhinus marmoratus (Eurasia; goby)	Great Lakes (BW; 1990)	Mills *et al.*, 1993
Neogobious melanostomus (Eurasia; goby)	Great Lakes (BW; 1990)	Mills *et al.*, 1993

BW, in ships' ballast water; SF, in ships' fouling or boring; AQ, public aquarium release; PR, private release by individual.
* Not known if established.
† Previously known from Humboldt Bay, California to Baja California; discovered in 1995 in Coos Bay, Oregon.
‡ Previously known in 1987–1988 from Cuba, Colombia, and Venezuela.
§ Previously known from San Francisco Bay to San Diego Bay; discovered in 1993–1994 in Coos Bay by R. Emlet and A. Moran (personal communication, 1995).

(known as MARPOL) that govern marine pollution from ship-generated sources, amendments that would require vessels around the world to undertake ballast management practices.

These practices include releasing original ballast water in midocean, when and where it is safe to do so, and thus arriving in the destination port with planktonic organisms that could not survive in coastal waters. As exchange of ballast water would put ship and crew at risk under heavy weather conditions, alternative ballast management strategies are now being extensively studied by IMO and by the above countries. These focus on both "micromanagement" scenarios (asking ships not to ballast up "red water" or other discolored water next to them, as such water might represent a toxic dinoflagellate bloom) and to direct treatment of the water by mechanical, thermal, chemical or other means. Ballast management at all of these levels—from open-ocean exchange, to local control, to new ship technology—will provide the basis for extensively reducing ballast water introductions (Carlton *et al.*, 1995).

How can invasions impact marine ecosystem function? Invasions can alter the energy flow, the species interactions, and virtually all other aspects of community structure. As noted earlier, the brackish water corbula *Potamocorbula*, along with a less abundant but earlier introduction, the Atlantic softshell clam *Mya arenaria*, are apparently responsible for extremely low chlorophyll levels in the water column in the northeastern portions of San Francisco Bay (Alpine and Cloern, 1992). The removal of one of the bases of the food chain—the phytoplankton—from large regions of San Francisco Bay obviously could have extensive impacts on the seasonal abundance of their predators, the herbivorous zooplankton (such as copepods and mysids) and, in turn, upon zooplanktivorous fish. Also noted earlier was the remarkable success of the Atlantic Ocean combjelly fish *Mnemiopsis* in the Black and Azov Seas. A carnivore, it consumes zooplankton (including larval fish) voraciously, and when it occurs in high densities, it is capable of removing most copepods from a given mass of estuarine water. In each case, the insertion of a single species into a relatively large ecosystem has fundamentally altered energy flow and subsequent species interactions, perhaps irreversibly. Invasions representing the same trophic guild can, in turn, produce similar profound effects. Cloern (1982) and Officer *et al.* (1982) thus provided compelling evidence that in south San Francisco Bay three species of introduced clams (from New England and from Japan) are also the primary controllers of phytoplankton biomass.

In other regions, species known to play an important ecosystem role in one region have become abundant in a new area, but their impact in the latter site may remain unknown or poorly understood. An example is the American Atlantic marsh mussel *Arcuatula demissa* (*Geukensia demissa*), a species known to be important in the biogeochemical cycling of phosphorus between the water column and sediments in Georgia marshes (Kuenzler, 1961). *Arcuatula* has been common to abundant in San Francisco Bay since the 1890s, and yet its role in processing phosphorus in that estuary remains unknown.

Not all invasions are inherently "bad," of course. Intentional releases such as the Atlantic striped bass *Morone saxatilis* in California in the 1870s led to more than 100 years of popular sport fishing. Accidental releases such as the Japanese clam *Venerupis philippinarum* in British Columbia and the State of Washington in the 1930s (transported unintentionally with Japanese oysters) led to multi-million dollar shellfisheries resources now largely based in clam farms. These species have of course altered the ecosystems they are in, and neither species would likely be intentionally introduced today in the United States because of the concerns over the potential levels of such alterations.

Although intentional releases of nonnative species to enhance local fisheries or start new mariculture operations continues actively around the world (Carlton, 1992a), such releases are often of species whose biology and ecology are known to some extent, and thus we can enter into discussions over the wisdom of such releases, based on the available data and based on the predicted outcomes—both in terms of ecological impact and of resource development. Equally challenging are new research directions that will provide genetically altered species for fisheries enhancement, with the intent that such species be released in the wild.

But accidental releases—by such means as ballast water—play invasions roulette with potentially much higher stakes, because the species involved are not often not recognized as being present until after they have become well-established. That major finfish fisheries can be readily impacted is illustrated by the invasion of the comb jelly *Mnemiopsis* in the Black Sea and the demise of the anchovy fishery. Central American shrimp viruses transported in 1994–1995 to Texas coast shrimp facilities offer another example of such fisheries impacts. That marine and coastal protected areas are not immune to invasions is well illustrated by the diversity and predominance of introduced marine invertebrates and plants in some National Estuarine Research Reserves (Carlton, 1989).

That marine and coastal protected areas are not immune to invasions is well illustrated by the diversity and predominance of introduced marine invertebrates and plants in some National Estuarine Research Reserves.

Given the vast kaleidoscope of invasions around the world, what are the critical research needs at the close of the 20th century as we anticipate the potential of a new century of invasions? Key questions focus on the ecology, biogeography, prevention, and control of exotic species. In terms of ecology and biogeography, there are now many hundreds if not thousands of individual case histories of aquatic invasions, ranging from simple records to anecdotal descriptive accounts to, in rare cases, experimental studies. Coupled with these are growing data sets on specific transport vectors. A critical need exists to begin to elucidate patterns, if such exist, on how many, where, when, and why invasions have been relatively successful and unsuccessful, through comparisons of different marine provinces. An important focus will be to look at the resistance or susceptibility to invasions in distinct communities within and between provinces.

Equally important is research to significantly slow the rate of invasions, by identifying those vectors that function to transport the preponderance of species and then by designing management interfaces to interrupt the vector with sophisticated quarantine barriers. These embody challenging problems: vector interruption does not necessarily mean disruption or cessation of the vector itself. Thus a major focus of prospective ballast water management technologies is to minimize the impact on ship speed, ship cargo handling, and ship port residency while maximizing the reduction of viable organisms transported. Finally, research on control mechanisms that seek to limit the spread and abundance of introduced species that are already well-established is virtually nonexistent for all but a few of the higher-profile (in terms of economic or other social impacts) species.

A result of decades of invasions is that, in regions such as San Francisco Bay or Long Island Sound or Puget Sound, the biota is now technically richer (often by scores or hundreds of species) in terms of the number of species that have been added since the mid-19th century. This phenomenon presents a perhaps confusing picture to the public and to governmental agencies relative to our normal celebrations that regions with "higher diversity" are in some manner "better." In turn, we know of no species that have been completely lost from these regions because of these invasions, although the abundance of the native species and how they interacted may be highly altered.

It is, in fact, the latter that we have lost. San Francisco Bay and hundreds of sites all over the world are apparently richer places in terms of the absolute number of species now present. But gone, and in many regions, only gone since the late 19th century, are the original communities that inhabited these regions, and thus we are in fact far poorer in terms of natural biodiversity at the community and ecosystem level.

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There is still much to preserve and to cherish in the world's oceans. Reducing the number of invasions will do much to keep it that way.

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