

Molluscan Invasions in Marine and Estuarine Communities

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ABSTRACT

The distributions of many species of marine and estuarine mollusks have been altered dramatically by human movements over the past 2,000 and more years. Vectors have included vessels, mariculture, the aquarium trade, intentional or accidental releases into the wild, and canals. Most marine mollusk distributions are held to be "natural" prior to the 19th century, whereas mollusk distributions during or since the 19th century are held to be potentially subject to human modification. However, that pre-19th century invasions occurred is clear, suggesting that the antiquity of human-mediated mollusk introductions has been extensively underestimated. The Asian oyster *Crassostrea gigas* was introduced to Europe by the 1500s, the Northern Hemisphere mussel *Mytilus* may have arrived in the Southern Hemisphere by the early 1500s, and shipworms have similarly been widespread by shipping. A subset of 38 Northern Hemisphere introduced mollusks reveals distinct geographic patterns: 63% originate in the North Atlantic Ocean/Mediterranean area, while 37% originate in the North Pacific Ocean. Within the Atlantic Ocean, the western Atlantic is a significantly stronger donor area, accounting for 75% of those North Atlantic taxa that have dispersed globally. Similarly, the western Pacific Ocean is also a strong donor region, exporting 93% of all those originating in the Pacific. Ecologically, in San Francisco Bay, California, the introduced in faunal or near-surface bivalves *Mya*, *Gemma*, *Venerupis*, *Musculista* and *Potamocorbula* may be sufficiently abundant as to control water column productivity. The European snail *Littorina littorea* (Linnaeus, 1758) has had vast and complex impacts on intertidal hard and soft bottom communities from Canada to the mid-Atlantic America. In general, far more attention must be paid to experimentally demonstrating the impacts of invasive species.

Key words: invasion, bioinvasion, exotic, alien, nonindigenous, introduced

INTRODUCTION

The natural structure of most shallow-water marine and estuarine communities has been altered dramatically by human activities over the past 2,000 and more years (Carlton, 1996c; Ruiz et al., 1997) Protist, invertebrate, vertebrate, algal, and seagrass populations have been either completely extirpated (removing entire populations) or decimated (severely reducing population size, often to a point of functional extinction). In contrast, numerous species have been accidentally or intentionally introduced by human activities to communities. The result is that both the diversity and relative abundance of species within many marine communities have been fundamentally changed.

Marine, including estuarine, mollusks provide an excellent platform to examine the scale of change in shallow-water ecosystems. No group of marine invertebrates is better known, thanks to a combination of a fossil, archeological, and long historical record. Best understood are changes in population size (examples are the global demise of most shallow-water edible shellfish populations) and the introduction of nonindigenous species.

Poorly understood is the scale of global extinction of marine mollusks in historical time (Carlton, 1993), in part because the subject has received little attention.

Biological invasions consist of species moved through human activities (introductions) and by natural means (range expansions) (Carlton, 1989). In understanding the importance of the human-mediated movement of mollusks, it is critical to note that such dispersal is not simply a matter of accelerating "normal" processes that "have always been happening" or that "would happen anyway." Natural movements of species are almost always along predictable corridors, whether these corridors are continental margins, transoceanic currents, or routes that open or are created over geological time. In contrast, human-mediated movements of species often involve the unpredictable and instantaneous global translocation of species independent of space or time barriers. Thus, there is no natural biotic flow between, for example, the temperate estuaries of southern Australia and the temperate estuaries of Western Europe. However, either by intent (such as a commercial species moved in the hold of an airplane) or by accident (such as a species living on the hull or in the seachest or in the ballast of a ship) a marine mollusk can be transported between Australia and Europe in a matter of hours to days.

I review here aspects of the global introductions of marine mollusks. A particular focus is placed on the potential scale of underestimation of the number of introductions that may have occurred.

HUMAN-MEDIATED DISPERSAL: MECHANISMS AND BIODIVERSITY OF TRANSPORTED ORGANISMS

The mechanisms by which marine organisms have moved or are now moved around the world by other-than-natural means is well documented, although the quantitative and qualitative aspects of these movements, relative to the diversity and abundance of species, are often poorly known. Potential vectors include vessels (ships and in the 20th century semisubmersible exploratory drilling platforms), aquaculture (mariculture), including the movement of commercial oysters, the aquarium and ornamental organism trade, intentional or accidental releases into the wild, plant (seagrass and marsh plant) transplantations, and canals (Carlton, 1985, 1987, 1992a, 1994; Carlton & Geller, 1993; Carlton et al., 1995; Cohen & Carlton, 1998; Minchin, 1996). Vessels in particular are now recognized as one of the major long-term homogenizers of coastal biotas (Carlton, 1985, 1996a; Carlton & Hodder, 1995; Zibrowius, 1992).

Historically, wooden vessels were floating biological islands, with extensive fouling communities on their hulls (that is, intertidal and sublittoral epibenthic assemblages), boring communities in their hulls, and additional suites of organisms in the sand ballast and rock ballast typically carried by pre-20th century ships. Intertidal organisms can occur at the ships' water line, and may include algae, limpets, and barnacles. Sublittoral fouling congregations may include a rich assemblage of algae, sponges, hydroids, sea anemones, sedentary polychaete annelids, sessile mollusks, barnacles, bryozoans, and ascidians. Vessels with interstices, holes, abandoned shipworm and gribble burrows, empty barnacles, empty but articulated bivalves (such as deeply cupped oysters), and other hollows and cavities, could further support such mobile organisms as flatworms, free-living polychaetes, crabs and other crustaceans, and fish. Boring communities included shipworms (teredinid bivalves) and gribbles (limnoriid isopod crustaceans) and associated commensal or symbiotic species.

While it is possible to derive an overall hypothetical picture of the general composition of fouling and boring mollusk assemblages (discussed below), we know little about the mollusks that may have been carried in sand ballast or rock ballast inside a vessel. Survival in this solid ballast in a ship's hold may have been dependant on how wet the ballast remained over a given length of time and, in the case of sand in particular, how anoxic the sediment became. Given relatively humid if not aqueous conditions, interstitial and small

sand-dwelling mollusks and rock-dwelling mollusks (especially in deeper rock crevices) may have been transported frequently.

Over the centuries, hundreds or thousands of species of mollusks must have been transported in hundreds of thousands of ship voyages. Carlton (1999) has suggested that on and in pre-18th century vessels the molluscan assemblages may have included smaller gastropods such as periwinkles (Littorinidae) carried in rock ballast, sea slugs (nudibranch opisthobranchs) associated with hydroid and bryozoan fouling, and such bivalves as chamsids (Chamidae), mussels (Mytilidae) and oysters (Ostreidae), and other gastropods such as limpets (Lottiidae), associated with hull fouling. Shipworms (Teredinidae) were presumably often common to abundant in wooden vessels; how many different species of shipworms a single vessel could support appears not to have been reported in the literature. In turn, shipworm burrows may have supported a secondary assemblage of nestling and other boring bivalves, such as hiatellids (Hiatellidae), venerids (Veneridae), petricolids (Petricolidae), and piddocks, including *Martesia* (Pholadidae).

In addition to these taxa, hull fouling in temperate waters likely also supported populations of the jingle shells *Anomia* and *Pododesmus* (Anomiidae), *Hiatella* (Hiatellidae), commensal and crevicolous clams in the family Lasaeidae (*Kellia* and *Lasaea*), and *Entodesma* (Lyonsiidae), and in tropical waters the wing oysters *Pinctada* and *Pteria* (Pteriidae), *Isognomon* (Isognomonidae), and the pen shells *Atrina*, *Streptopinna* and *Pinna* (Pinnidae). Benthic infaunal, soft-bottom epifaunal, and even salt marsh species may also occur in the interstices of ships' fouling, and this phenomenon may have been far more common in earlier times. For example, small (<1 cm) infaunal clams, such as *Mya arenaria* Linnaeus, 1758, and mussels, such as *Geukensia demissa* (Dillwyn, 1817), can occur embedded in hull-fouling communities.

Carlton (1999) further noted that chitons (Polyplacophora) may have occurred on ship anchors. I observed the attachment of a 1 cm-long individual of the chiton *Chaetopleura apiculata* (Say, 1834) on the anchor of a 40-meter vessel after the anchor had been in 10 meters of water near Woods Hole, Massachusetts, USA, overnight for about 14 hours. In earlier maritime history, with longer coastal residencies, anchors would have been available for colonization on and in bottom sediments, including mixed rubble and rock bottoms, for long periods of time. In turn, anchors may remain wet over considerable distances due to wave splash.

Marine organisms continue to move on and in ships in modern times. Wood hull boring communities are vastly reduced in number (except in local wooden vessels, especially in tropical waters), and few if any such ships regularly move around the world anymore. However, fouling communities, while not as vast as they once were, are still transported. Antifouling paints, increased ship speeds, and reduced port residencies have presumably changed the quality and quantity of such assemblages. In modern ships, water ballast has replaced dry and hard ballast and has received a good deal of attention as a dispersal mechanism (Carlton, 1985; Williams et al., 1988; Baldwin, 1992; Kelly, 1993; Carlton & Geller, 1993). It is probable that hundreds of species of mollusks are in motion in ship ballast water on an hourly basis around the world at the beginning of the 21st century. Ironically, these may include the larvae of some ship-worms, and thus shipworms may still be in motion around the world, despite the demise of ocean-going wooden ships.

Mollusks may also move in modern ships in seachests, a mechanism that requires far more study than it has received. Seachests (also known as sea inlet boxes or suction bays) are spaces in a ship's hull into which water is drawn in order to then be pumped into a ship's ballast system. The sea chest can provide a settlement area for both attached and mobile species. Richards (1990) found a population of the tropical muricid snail *Thais blandfordi* Melville, 1893, living on the walls of the seachest of a cargo vessel having served in the New Guinea archipelagoes. The cruise track of the vessel had included Saudi Arabia, Kenya, Malaysia, Singapore, and Papua New Guinea, and then via Hong Kong to Hull, England. The population structure of the snails suggested that they had reproduced in the sea chests. The snails had also survived British winter water temperatures before

returning to the tropics and being found in the harbor of Kimbe, Papua New Guinea, where Richards sampled the vessel. The snails had become sufficiently abundant to the point that they had blocked the pipes and filters of the water cooling system. Muricid snails have crawl-away young that emerge from deposited egg capsule. Young snails may thus have been drawn into the seachests on floating seaweed or debris, had survived feeding on barnacles, and had grown to adults in the sea chest.

TABLE 1. Conjectural examples (not necessarily actual records) of marine molluscan taxa whose global distribution has been susceptible to alteration by ship transport, arranged by ship "habitat."

	Hull fouling	In shipworm burrows	Fouling in seachests	Rock ballast	Water ballast ³
Polyplacophora	x	x	x ¹		x
Gastropoda					
Lottiidae	x	x	x	x	x
Fissurellidae	x	x	x		x
Assimineidae	x ²	x		x	x
Pomatiopsidae				x	x
Littorinidae		x	x	x	x
Calyptraeidae	x	x	x		x
Vermetidae	x	x	x		x
Muricidae		x	x		x
Ellobiidae	x ²	x		x	x
Siphonariidae	x	x	x	x	x
Opisthobranchia	x	x	x		x
Bivalvia					
Mytilidae	x	x	x		x
Arcidae	x	x	x		x
Pteriidae	x	x	x		x
Isognomonidae	x	x	x		x
Malleidae	x	x	x		x
Pinnidae	x	x	x		x
Pectinidae	x	x	x		x
Spondylidae	x	x	x		x
Anomiidae	x	x	x		x
Ostreidae	x	x	x		x
Chamidae	x	x	x		x
Lasaeidae	x	x	x		x
Veneridae	x	x	x		x
Petricolidae	x	x	x		x
Myidae	x	x	x		x
Hiatellidae	x	x	x		x
Pholadidae		x			x
Teredinidae	x	x			x
Lyonsiidae	x	x	x		x

¹Also potentially on anchors.

²Referred to by Carlton (1999) as "hull nestlers", that is, species living in cracks in the wood hull at or above the waterline.

³Those taxa with non-planktonic larvae could be taken into the ship with ballast water on floating seaweeds, sea-grasses, or debris.

Three interesting conclusions may be drawn from Richards' observation. First, seachests may be the modern day manifestation of the deep, sheltered galleries of empty shipworm burrows in pre-20th century (wooden) vessels, in terms of offering a protected microhabitat in the hull of the vessel for organisms not normally associated with external hull fouling. Second, the interpretation of the natural distribution of species with crawl-away young is thus further complicated by the advent of the seachest in the evolution of the ship. Three, taxa not normally associated with shipping may clearly be entrained and

moved by ships. *Thais blanfordi* is a species that lives in exposed reef habitats. Richards speculated that the vessel may have entrained these snails in the Indian Ocean near the barrier reef off Mombasa, Kenya. As this snail was carried into the vessel by some unknown means, so it presumably could be carried out (unless the snails had grown too large to escape through the grate holes), and thus *Thais* could potentially be introduced to a new region.

In summary, a wide diversity of gastropods and bivalves were or are thus susceptible to transport on ships. The taxa noted above, and additional taxa, are assembled in Table 1 by ship "habitat"-hull fouling, in shipworm burrows, as fouling in seachests, in rock ballast, and in water ballast. With few exceptions, external transport (on hull fouling) and internal transport (in seachests, in shipworm burrows, and in ballast water) serve as potentially viable mechanisms for most taxa. Rock ballast is necessarily-and *a priori-more* selective, and is here scored conservatively as involving primarily supralittoral or high intertidal species of gastropods. While the associated fauna of rock ballast was not recorded at the time of its use, as noted above, experimental studies recreating historical conditions would be of great value in evaluating this mechanism and in refining the nature of the transportable taxa.

THE POTENTIAL ANTIQUITY OF MARINE MOLLUSCAN INTRODUCTIONS

How long have human activities moved marine mollusks around the world? The evidence from maritime history indicates that mollusks have been moved for millennia *within* ocean basins and for at least centuries *between* ocean basins (Carlton, 1999). And yet, despite the potentially diverse array of species that may have been associated with shipping over these long lengths of time, few introductions are recognized that are linked to global shipping prior to the 19th century. This relatively late recognition is not surprisingly related to when the first reliable distributional records of mollusks become available. It is thus not surprising to note that most marine mollusk distributions have long been held to be "natural" prior to the 19th century, whereas mollusk distributions during or since the 19th century are held to be potentially subject to human modification.

That this dichotomy is an artificial one is illustrated by the following three examples:

(1) The Japanese oyster *Crassostrea gigas* (Thunberg, 1793) was transported to southern Europe by Portuguese explorers by the 1500s (Edwards, 1976). It was described from Europe as a different and presumptive native Atlantic species, *Crassostrea angulata* (Lamarck, 1819). Despite suggestions since the 1940s that the two species were the same, based upon morphological, behavioral, physiological and reproductive evidence, and despite the absence of a fossil or early archeological record in Europe (Ranson, 1967; Edwards, 1976), oyster biologists continued to use the junior synonym *C. angulata*, with the stated or implied view that it is native (Arakawa, 1990; Heral, 1990; Michinina & Rebor-dinos, 1997). In part this usage was no doubt reinforced by the intentional introduction of *C. gigas* into Europe commencing in the 1960s (Ribera & Boudouresque 1995; Zibrowius, 1992), and the concomitant desire to be able to refer to the pre-existing stocks by a separate name. Ó Foighil et al. (1998) have again clearly demonstrated that *C. angulata* and *C. gigas* are the same species based upon molecular genetic studies (mitochondrial cytochrome oxidase I gene sequences).

(2) It was recognized as early as the 1940s that the northwestern Atlantic Ocean clam *Mya arenaria* did not occur in modern Europe until the 1500s. Petersen et al. (1992) have pushed the date of arrival back another 200 years or more, discovering Danish midden shells dated to the 1200s-1300s. *Mya* may thus have been brought to Europe from America by Vikings (perhaps intentionally as a new food), and may have been reintroduced by later explorers and colonists returning from North America as well. Alternatively, as *Mya* occurs in ship fouling (as noted above) it may also have been transported in the once-richer vessel fouling communities of earlier centuries.

(3) The northern hemisphere mussels in the genus *Mytilus* may have arrived in the Southern Hemisphere, on the east coast of South America and in the South Pacific Ocean, by the early 1500s, when these regions were first explored by European vessels (Haws, 1975). The sibling species of mussels *Mytilus trossulus* Gould, 1850 (of the North Pacific Ocean), *Mytilus edulis* Linnaeus, 1758 (of the North Atlantic Ocean), and *Mytilus galloprovincialis* Lamarck, 1819 (of the Mediterranean Sea), are all common ship fouling organisms and have been transported globally for centuries. As is true with many introductions (Carlton, 1979b), introduced populations of Northern Hemisphere *Mytilus* carried to the Southern Hemisphere were given a host of new names (Table 2). Thus, *Mytilus galloprovincialis* arrived sometime before 1819 in Australia (where it was renamed as *Mytilus planulatus* Lamarck, 1819), and *Mytilus edulis* arrived by the 1840s in eastern South America (where it was renamed as *Mytilus platensis* Orbigny, 1846). Other invasions by this species continued throughout the 19th and 20th centuries, and both *M. edulis* and *M. galloprovincialis* continued to be redescribed around the world until the 1970s (Table 2).

TABLE 2. The introduction and redescription of *Mytilus* species around the world.

Introduced to	Redescribed as/by (*)	= <i>Mytilus</i>	Reference
Southern Hemisphere			
Pacific Ocean			
New Zealand	<i>aoteanus</i>	Powell, 1958	<i>galloprovincialis</i> Koehn, 1991
Australia	<i>planulatus</i>	Lamarck, 1819	<i>galloprovincialis</i> Koehn, 1991
Argentina	<i>platensis</i>	Orbigny, 1846	<i>edulis</i> Seed, 1992
Chile	<i>chilensis</i>	Hupé, 1854	<i>edulis</i> Seed, 1992
Indian Ocean			
Kerguelen Islands	<i>desolationis</i>	Lamy, 1936	<i>edulis</i> Koehn, 1991
	<i>kerguelensis</i>	Fletcher, 1938	<i>edulis</i> Koehn, 1991
Atlantic Ocean			
South Africa	—	—	<i>galloprovincialis</i> Grant & Cherry, 1985; Griffiths et al., 1992
Northern Hemisphere			
Pacific Ocean			
California	<i>diegensis</i>	Coe, 1945	<i>galloprovincialis</i> McDonald & Koehn, 1988
Russia (Pacific)	<i>zhirmunksii</i>	Scarlato & Starobogatov, 1979	<i>galloprovincialis</i> Seed, 1992
Japan, China	—	—	<i>galloprovincialis</i> Wilkins et al., 1983

*Literature references to original descriptions are given in Soot-Ryen (1955) and Seed (1992).

Curiously, the primarily northeastern Pacific Ocean *Mytilus trossulus* appears to have failed as a colonizer in the Southern Hemisphere (although it may owe its presence in the North Atlantic Ocean to ship dispersal), either because of competition with already-present introduced populations of *M. edulis* and *M. galloprovincialis*, or with native southern mytilids, or because of other factors. This lack of invasion success is, however, in concert with other elements of the temperate northeastern Pacific Ocean biota which, with few exceptions, have failed to depart the eastern Pacific and colonize other parts of the world, as discussed further below.

SHIPWORMS AS A MODEL GUILD FOR EARLY HISTORIC INTRODUCTIONS

Shipworms provide a particularly compelling guild of mollusks through which to analyze the long-term role of global shipping in altering aboriginal marine invertebrate distributions. While the very name "shipworm" suggests an intimate association with vessels, the possibility that many shipworm species—particularly those in marine bays and estuaries that were converted to ports and harbors—could in fact owe a good deal of their modern distribution to shipping appears, curiously, to have never been extensively explored on a global basis. While shipworm workers have consistently referred to the possible role of ships (Edmondson, 1942, 1962; Turner, 1966), drifting wood has almost always been offered as an equally viable alternative to explain now-cosmopolitan distributions. Indeed, a leading paradigm of shipworm biogeography may be taken to be as follows, here rendered as a modified syllogism:

Shipworms live in wood.
Wood floats.
Wood floats in ocean currents.
Thus, shipworm distributions are natural.

A potential flaw in this deductive argument is the assumption that shallow-water dwelling species of shipworms can survive while floating in wood across the high seas during the weeks or months involved in a transoceanic or interoceanic voyage, and then arrive alive to make a "landfall" on a distant shore in a condition sufficient to reproduce. Neither detailed quantitative observations nor experimental evidence appear to be available to support this assumption. In contrast, Edmondson (1962) noted that when open-ocean wood is examined, such wood is almost always occupied by shipworm species that are not found in harbors—that is (and somewhat predictably!) oceanic wood is colonized by a pelagic shipworm guild. In the Central and North Pacific Ocean these include *Teredo princepsae* Sivickis, 1928 (= *Teredo gregoryi* Dall, Bartsch & Rehder, 1938) and *T. triangularis* Edmondson, 1942. Edmondson (1962) further considered *Uperotus clavus* (Gmelin, 1791) and *Teredo palauensis* Edmondson, 1959, to be species that have adopted a "typically oceanic existence." Of course, it is not impossible that these species, too, may have been subjected to ship-mediated dispersal. *Teredo palauensis*, which Turner (1966) considered as possibly conspecific with *Teredothyra excavata* (Jeffreys, 1860), was first described from the hull of a wrecked ship in the Caroline Islands that may have picked it up while at sea.

Vessels with shipworms would have made direct harbor-to-harbor transits in a matter of days and weeks. Carlton (1999) has further suggested a "port renewal" hypothesis, wherein ocean-going ships periodically return to coastal waters, permitting the fouling community to be revitalized under the trophic, salinity, temperature, and other conditions in which they evolved. Such port-returns may have further led to intensive periods of larval release, triggered by more eutrophic and warmer coastal waters (while inhibited by cold, high salinity, oligotrophic ocean waters).

None of this argument contradicts the potential for shipworms to be naturally transported for short or even longer distances within the tropical and subtropical Atlantic, Pacific, and Indian Oceans in drifting wood, coconut husks, and mangrove roots. In these regions, sorting out aboriginal distributions from ship-created ones may now be impossible.

Turner (1966) recorded the remarkable case of the dispersal of the warm-water shipworm *Teredo furcifera* von Martens, 1894, by a vessel travelling largely in the Northern Hemisphere. The *Bounty II* left Tahiti for the Hawaiian Islands in September 1961. It was drydocked (length of time unknown) in Honolulu "where some but not complete work was done to repair damage by shipworms," and then proceeded to the Los Angeles area (San Pedro and Long Beach), where it remained in the water until spring 1962, at which time it was drydocked again (and again, length of time unknown). The vessel then proceeded

north for stops in British Columbia, Washington, and California (all in marine or brackish waters), before proceeding through the freshwater Panama Canal. It then visited marine or brackish ports in Louisiana and Florida, proceeded north to the cold water marine port of Boston, crossed the ocean to France and England, then south to the Canary Islands, and crossed the ocean westbound again to New York State. It proceeded to a shipyard in November 1962, where it remained in the water until October 1963. The winter of 1962-1963 was characterized by "severe freezing" conditions at the site where the vessel was docked. When plankton was removed from the *Bounty II* in October 1963, *T. furcifera* was found to be alive and to have produced larvae, presumably in the summer of 1963 in New York.

TABLE 3. Examples of introduced and cryptogenic shipworms (Teredinidae) around the world

Species	Type Locality ¹	Reproductive Mode
<i>Teredo bartschi</i> Clapp, 1923	Florida	LLT
<i>Teredo clappi</i> Clapp, 1923	Florida ²	LLT
<i>Teredo furcifera</i> von Martens, 1894	Molucca Islands	LLT
<i>Teredo navalis</i> Linnaeus, 1758	Netherlands	LST
<i>Bankia bipalmulata</i> (Lamarck, 1801)	India	O
<i>Bankia carinata</i> (Gray, 1827)	Sumatra ³	O
<i>Bankia fimbriatula</i> Moll & Roch, 1931	Scotland ⁴	O
<i>Lyrodus affinis</i> (Deshayes, 1863)	Reunion	LLT
<i>Lyrodus bipartitus</i> (Jeffreys, 1860)	England ⁵	LLT
<i>Lyrodus massa</i> (Lamy, 1923)	Yemen and Arabia	LLT
<i>Lyrodus medilobatus</i> (Edmondson, 1942)	Hawaiian Islands	LLT
<i>Lyrodus pedicellatus</i> (Quatrefages, 1849)	Spain	LLT

O = oviparous (free-swimming larvae, in water column for days to weeks); LST = larviparous, held short-term (free-swimming larvae, in water column for days); LLT = larviparous, held long-term (larvae in water column for hours)

¹The type locality may not be where the species is native; this caveat especially pertains to the seven taxa first described from the Northern Hemisphere.

²Described from specimens collected from the keel of ship.

³The material reported by Turner (1966) as *Bankia carinata* at a great depth (7,488 meters) in the Banda Sea (eastern Indonesia) may bear reexamination.

⁴Described from "teak wood" (drifting from tropical waters in the Gulf Stream to Scotland, or discarded imported tropical wood).

⁵Described from shells in wood that came ashore in England from the Gulf Stream.

It thus perhaps not surprising that the same suite of species of *Teredo*, *Bankia* and *Lyrodus* are today found in temperate or tropical ports and harbors around the world (Table 3). I suggest that all of these common harbor ship-worm species have had their natural distributions broadly and deeply altered by shipping. For any given location, consideration must be given to whether the species and populations in question should be regarded as native, introduced, or cryptogenic. In some regions of the world, the historical record is clear and the arrival of certain species can be more easily detected. For many regions this is not the case. Noting that certain shipworms can survive for long periods with their pallets closed (Turner, 1966), a compelling test of the hypothesis that neritic shipworms do not survive long transoceanic or interoceanic voyages would be to experimentally subject neritic species to oceanic conditions for the length of time that it would take to transit selected high seas routes. It would be of further interest to examine in greater detail the biogeography of species with an oviparous life cycle, such as in the genus *Bankia*, compared to those with both long- and short-term incubated larvae, such as in the genera *Teredo* and *Lyrodus* (Table 3). Species in the genus *Bankia*, with long-term planktotrophic larvae, may represent more panmictic stocks, whereas those with shorter-term larvae-and thus possibly more subject to the establishment of isolated populations via dispersal as adults-may represent more genetically unique populations, either through founder effects or later genetic changes.

INTRODUCTIONS OF MARINE MOLLUSKS: SYSTEMATIC, BIOGEOGRAPHIC, AND ECOLOGICAL OVERVIEWS

No global review of the total number of marine mollusks transported by human activity is available. I estimate the total number of introduced marine bivalves, gastropods, and chitons to be about 100 species, but many cryptogenic taxa could increase that number significantly. This number includes invasions through the Suez Canal (Por, 1978; Spanier & Galil, 1991).

To illustrate the systematic, geographic, and ecological breadth of these invasions, I examine here a subset of 38 introduced species the evolutionary origins of which are known to be in the Northern Hemisphere (Table 4, arranged by source region). Omitted from this table are opisthobranch (nudibranchs and sacoglossans) and pyramidellid gastropods, invasions through the Suez Canal, species of uncertain establishment, certain intracontinental introductions, primarily such freshwater taxa as the bivalves *Corbicula* and *Dreissena* and the snail *Potamopyrgus*, and terebratulids, discussed above, the geographic origins of introduced or cryptogenic species being as yet uncertain.

A wide phylogenetic and ecological breadth of taxa are subject to human-mediated geographic alteration. These include salt-marsh and high intertidal taxa (the ellobiid *Myosotella*, the pomatiopsid *Cecina*, the periwinkle *Littorina saxatilis* (Olivi, 1792), the mussel *Geukensia*), intertidal and sublittoral soft bottom species (Batillariidae, Nassariidae, Melongenidae, Corbulidae, Myidae, Pharidae, Petricolidae, Veneridae, Pectinidae, Semelidae) and intertidal and sublittoral hard bottom (including fouling) species (Littorinidae, Calyptraeidae, Vermetidae, Muricidae, Mytilidae, Ostreidae, Dreissenidae, Trapezidae, Lanternulidae). Similarly, transport is not selective for any feeding mode, and includes omnivores, herbivores, carnivores, grazers, and suspension feeders.

Geographic patterns are distinct (Table 5). In terms of donor regions, 24 taxa (63%) originate in the North Atlantic Ocean/Mediterranean area, while 14 (37%) originate in the North Pacific Ocean. Within the Atlantic Ocean, the western Atlantic is a significantly stronger donor area, with 18 taxa or 75% (versus 6 from the North Atlantic (*Mytilus edulis*) and Eastern Atlantic/Mediterranean) having dispersed globally from Atlantic North America. Similarly, the western Pacific Ocean is a strong donor region, with 13 taxa (versus one from the Eastern Pacific), or 93% of those originating in the Pacific, having been exported (Table 5).

In terms of receiver regions, Eastern North Pacific shores are comparatively strongly invaded, with 28 species (Table 5) more than twice the total of 13 species that have invaded the entire North Atlantic/Mediterranean/Black Sea region (Table 4).

Carlton (1992b, 1996a) and Cohen & Carlton (1995) have briefly reviewed some of the ecological impacts of molluscan invasions. In many regions, introduced mollusks are now the most abundant infaunal or epifaunal species present. In the northeastern Pacific Ocean, in San Francisco Bay, the infaunal or near-surface bivalves *Mya*, *Gemma*, *Venerupis*, *Musculista* and *Potamocorbula* may be sufficiently abundant as to control water column productivity (Cloern, 1982; Officer et al., 1982; Alpine & Cloern, 1992; Cohen & Carlton, 1995). The introduced mussels *Mytilus galloprovincialis* and *Geukensia demissa* likely add significantly to this role in San Francisco Bay but remain unstudied in this regard. In Pacific Northwest embayments, *Mya arenaria* may be the only common large clam at the upland end of many estuaries (Carlton, 1979a). Griffiths et al. (1992) conclude that the introduced *Mytilus galloprovincialis* is the dominant mussel throughout the Western Cape region of South Africa, largely displacing the native mussel *Aulacomya ater* (Molina, 1782). In New Zealand, the introduced *Mytilus galloprovincialis* forms aggregations up to several hundred square meters in area intertidally and subtidally in New Zealand, where it overgrows serpulid polychaetes, bryozoans, hydroids, and coralline algae, and is often locally the most abundant and competitively dominant epifaunal invertebrate (Witman & Grange, 1998). In Europe, Pacific North America, and elsewhere, large intertidal and shallow sublittoral reefs of the Pacific oyster *Crassostrea gigas* (Heral, 1990; Barber, 1997),

may play similar ecological roles in terms of altering water column phytoplankton densities and in terms of benthic community structure.

TABLE 4. Examples of introductions of marine mollusks originating in the Northern Hemisphere (*) = see footnote

Geographic Origin/Species	Invading	References
Eastern Atlantic—Mediterranean Species		
Gastropoda		
Littorinidae		
<i>Littorina littorea</i> (Linnaeus, 1758) (periwinkle) (*)	Atlantic North America	Carlton, 1992b; Vadas & Eimer, 1992; Zibrowius, 1992
Ellobiidae		
<i>Myosotella myosotis</i> (Draparnaud, 1801) (marsh snail)	Atlantic and Pacific North America	Carlton, 1992b
Bivalvia		
Mytilidae		
<i>Mytilus galloprovincialis</i> Lamarck, 1819 (mussel)	Pacific Ocean (New Zealand, Australia; Japan; Russia; California); South Africa	Carlton, 1992b; Geller et al., 1994; MacKenzie et al., 1997
Ostreidae		
<i>Ostrea edulis</i> Linnaeus, 1758 (oyster) (*)	Atlantic North America	Barber, 1997; MacKenzie et al., 1997
Corbulidae		
<i>Corbula gibba</i> (Olivi, 1792) (corbula) (*)	Australia	Healy & Lamprell, 1996
Western Atlantic Species		
Gastropoda		
Littorinidae		
<i>Littorina saxatilis</i> (Olivi, 1792) (periwinkle) (*)	Pacific North America	Carlton & Cohen, 1998
Vermetidae		
<i>Vermetus alii</i> Hadfield & Kay, 1972, in Hadfield et al. 1972 (wormsnail) (*)	Hawaiian Islands	Hadfield et al., 1972; Kay, 1979
Calyptraeidae		
<i>Crepidula fornicata</i> (Linnaeus, 1758) (slipper snail)	Europe; Pacific North America; Mediterranean	Carlton, 1992b; Zibrowius, 1992; Blanchard, 1995; Minchin et al., 1995; Eno et al., 1997
<i>Crepidula convexa</i> Say, 1822 (slipper snail)	Pacific North America	Carlton, 1992b
<i>Crepidula plana</i> Say, 1822 (slipper snail)	Pacific North America	Carlton, 1992b
Melongenidae		
<i>Busycotypus canaliculatus</i> (Linnaeus, 1758) (whelk) (*)	Pacific North America	Carlton, 1992b
Nassariidae		
<i>Ilyanassa obsoleta</i> (Say, 1822) (mudsnail) (*)	Pacific North America	Carlton, 1992b
Muricidae		
<i>Urosalpinx cinerea</i> (Say, 1822) (oyster drill)	Europe; Pacific North America	Carlton, 1992b; Eno et al., 1997
Bivalvia		
Mytilidae		
<i>Geukensia demissa</i> (Dillwyn, 1817) (mussel)	Pacific North America	Carlton, 1992b
Dreissenidae		
<i>Mytilopsis leucophaeata</i> (Conrad, 1831) (false mussel)	Europe	Oliver et al., 1998
Ostreidae		
<i>Crassostrea virginica</i> (Gmelin, 1791) (oyster)	British Columbia (Boundary Bay); Hawaiian Islands (Oahu: Pearl Harbor)	Carlton, 1992b; Carlton & Mann, 1996; Barber, 1997; MacKenzie et al., 1997
Pectinidae		
<i>Argopecten irradians</i> (Lamarck, 1819) (scallop)	Western Pacific Ocean (China)	Chew, 1990; Wang, 1995; MacKenzie et al., 1997
Myidae		
<i>Mya arenaria</i> Linnaeus, 1758 (softshell clam)	Europe; Black Sea; Pacific North America	Carlton, 1992b; Zolotarev, 1996; Eno et al., 1997; MacKenzie et al., 1997
Pharidae		
<i>Ensis directus</i> Conrad, 1843 (razor clam)	Europe	Rasmussen, 1996; Eno et al., 1997

(continued)

TABLE 4. (Continued)

Geographic Origin/Species	Invading	References
Western Atlantic Species		
Bivalvia (continued)		
Tellinidae		
<i>Macoma "balthica"</i> (Linnaeus, 1758) (*)	Pacific North America	Meehan et al., 1989
Petricolidae		
<i>Petricolaria pholadiformis</i> (Lamarck, 1818) (angel wing)	Europe; Mediterranean and Black Sea; Pacific North America	Zibrowius, 1992; Carlton, 1992b; Eno et al., 1997
Veneridae		
<i>Mercenaria mercenaria</i> (Linnaeus, 1758) (quahog) (*)	Europe; Mediterranean; Pacific North America	Zibrowius, 1992; Eno et al., 1997; MacKenzie et al., 1997
<i>Gemma gemma</i> (Totten, 1834) (gem clam)	Pacific North America	Carlton, 1992b
North Atlantic Species		
Bivalvia		
<i>Mytilus edulis</i> Linnaeus, 1758 (mussel) (*)	Indian Ocean (Kerguelen Islands); Southwest Atlantic Ocean (Argentina); Southeast Pacific Ocean (Chile)	Koehn, 1991; Seed, 1992
Eastern Pacific Species		
Gastropoda		
Calyptraeidae		
<i>Crucibulum spinosum</i> (G. B. Sowerby I, 1824) (cup-and-saucer shell)	Hawaiian Islands	Kay, 1979
Western Pacific Species		
Gastropoda		
Pomatiopsidae		
<i>Cecina manchurica</i> A. Adams, 1861 (supralittoral snail)	Pacific North America	Carlton, 1992b
Muricidae		
<i>Rapana venosa</i> Valenciennes, 1846 (whelk) (*)	Black Sea, Mediterranean	Zibrowius, 1992; Zolotarev, 1996
<i>Ocenebrellus inornatus</i> (Récluz, 1851) (oyster drill) (*)	Pacific North America	Carlton, 1992b
Batillariidae		
<i>Batillaria attramentaria</i> (G. B. Sowerby II, 1855) (cerith)	Pacific North America	Carlton, 1992b
Nassariidae		
<i>Nassarius fraterculus</i> (Dunker, 1860) (basket snail; nassa)	Pacific North America	Carlton, 1992b
Bivalvia		
Mytilidae		
<i>Musculista senhousia</i> (Benson, 1842) (mussel)	Pacific North America; New Zealand; Australia; Mediterranean	Carlton, 1992b; Zibrowius, 1992; Reusch & Williams, 1998
Ostreidae		
<i>Crassostrea gigas</i> (Thunberg, 1793) (oyster)	Europe; Mediterranean; Pacific Ocean (widespread)	Grizel & Heral, 1991; Carlton, 1992b; Zibrowius, 1992; Gouilletquer & Heral, 1997; Eno et al., 1997; MacKenzie et al., 1997; Kunz-Jacques, 1997; Barber, 1997
Corbulidae		
<i>Potamocorbula amurensis</i> (Schrenck, 1861) (corbula) (*)	Pacific North America	Carlton et al., 1990; Alpine & Cloern, 1992; Duda, 1994; Kimmerer et al., 1994
Psammobiidae		
<i>Nuttallia obscurata</i> (Reeve, 1857) (*)	Pacific North America	Forsyth, 1993; Gillespie, 1995; Merilees & Gillespie, 1995
Semelidae		
<i>Theora lubrica</i> Gould, 1861 (semele)	Pacific North America; New Zealand	Climo, 1976; Carlton, 1992b
Veneridae		
<i>Venerupis philippinarum</i> (A. Adams & Reeve, 1850) (little-neck clam) (*)	Pacific North America; Europe, Mediterranean Hawaiian Islands	Carlton, 1992b; Zibrowius, 1992; Laruelle et al., 1994; Gouilletquer & Heral, 1997; MacKenzie et al., 1997; Gouilletquer, 1997
Western Pacific Species		
Bivalvia (continued)		
Trapezidae		
<i>Neotrapezium liratum</i> (Reeve, 1843) (trapezium) (*)	Pacific North America	Carlton, 1992b
Laternulidae		
<i>Laternula marilina</i> (Reeve, 1860) (lantern shell) (*)	Pacific North America	Miller et al., 1999

Notes: Bivalvia

Ostrea edulis is widely held in aquaculture (mariculture) systems around the world, and while adventitious specimens can be found occasionally in the wild near those systems, permanently reproducing wild populations appear to be established outside its native Europe only in eastern North America from Maine to Rhode Island.

Potamocorbula amurensis occurs in Pacific North America in San Francisco Bay, California, only. Bernard et al. (1993) placed *P. amurensis* in synonymy with the earlier *P. ustulata* (Reeve, 1844). I examined (1997) the syntypes of *P. ustulata* (ex Cuming coll., type locality Singapore) in The Natural History Museum, London, and compared them to a population of *Potamocorbula* collected in San Francisco Bay in November 1996. The latter closely match the *P. amurensis* of Asian literature (Carlton et al., 1990). The syntypes of *P. ustulata* of the same size as *P. amurensis* from San Francisco Bay are heavy, thick, well-calcified shells, the umbones of which are thus not subject to being easily broken; they further have a deeply incised pedal retractor scar above the anterior adductor muscle scar, and the pallial sinus is a distinct albeit shallow indentation. *Potamocorbula amurensis* is a comparatively thin, fragile shell, whereby the inner curve of the umbo is subject to breakage when the internal resilium plug in the right valve under the umbo breaks away; the pedal retractor scar is not incised, and the pallial sinus is only a very minor undulation of the pallial line. I tentatively regard the two as separate species, pending further consideration on to what extent some of these characteristics may be phenotypic. *Corbula gibba* has been found in Australia in Port Phillip Bay, Victoria, but is likely to spread along the mainland and into Tasmania.

Nuttallia obscurata occurs from British Columbia to Oregon (C. Mills & J. Chapman, pers. comm., 1998). *Macoma "balthica"*: The population of this Atlantic *Macoma* in San Francisco Bay is genetically similar to Western Atlantic Ocean stocks. If the *Macoma* of Atlantic North America is distinct from European *M. balthica*, then the name *Macoma petalum* (Valenciennes, 1821) may apply to the Atlantic American and San Francisco Bay populations (Meehan et al., 1989; Cohen & Carlton, 1995).

Mercenaria mercenaria occurs in Pacific North America in Alamos Bay, in southern California, only. *Venerupis philippinarum* goes by perhaps a greater variety of names than any other species on this list. The name *Venerupis philippinarum* is used following Carlton (1992b) and Coan & Scott (1997) and the arguments set forth therein. Other specific names in use are *japonica* Deshayes, 1853, and *semidecussata* Reeve, 1864, with these and *philippinarum* variously placed in the genera *Tapes*, *Venerupis*, and *Ruditapes*.

Neotrapezium liratum is known from Ladysmith Harbor, British Columbia (Carlton, 1992b), but may be more widespread but overlooked in the Pacific Northwest.

Laternula marilina is known only from Humboldt Bay, California (Miller et al., 1999) and may be more widespread but overlooked in the Pacific Northwest. Gastropoda

Littorina saxatilis is cryptogenic in both the Mediterranean Sea (Zibrowius, 1992) and in at least two locations in South Africa (Reid, 1996). Curiously, it was first described from Venice in 1792, making it perhaps one of the earlier introductions of a marine mollusk. It occurs in Pacific North America in San Francisco Bay, California.

Ocenebrellus inornatus is known in most literature as *Tritonalia japonica* (Dunker, 1860), *Ocenebra japonica* or *Ceratostoma inornatum*; see Amano & Vermeij, 1998. *Rapana venosa* is a senior synonym of *Rapana thomasi* Crosse, 1861. *Busycotypus canaliculatus* occurs in Pacific North America in San Francisco Bay, California, only. *Ilyanassa obsoleta* occurs in Pacific North America only in three locations: San Francisco Bay, California, Willapa Bay, Washington, and Boundary Bay, British Columbia.

Vermetus alii is here tentatively regarded as originating from the subtropical western Atlantic Ocean, although alternatively it may originate from the subtropical eastern Pacific (R. Bieler, pers. comm., 1996); it is here regarded as introduced to the Hawaiian Islands.

In other regions, introduced gastropods have become both aspect dominants and community structural engineers. The European snail *Littorina littorea* (Linnaeus, 1758) has had vast and complex impacts on intertidal hard- and soft-bottom communities from Canada to the mid-Atlantic American coast (Carlton, 1992b; Vadas & Elner, 1992; Bertness, 1999), altering the abundance and distribution of numerous other plants and animals. The Atlantic mudsnail *Ilyanassa obsoleta* (Say 1822) may have had a similar range of impacts on soft-bottom communities in San Francisco Bay, but, while its negative impact on a native mudsnail has been demonstrated (Race, 1982), much of its ecosystem-level interactions in California remain to be studied. The Atlantic slipper limpet *Crepidula fornicata* (Linnaeus, 1758), is locally very abundant in western Europe, although little appears to be available on its ecological impact, although it is regarded as a nuisance and competitor in the oyster industries (Eno et al., 1997). A range of carnivorous molluscivores, including the Atlantic drill *Urosalpinx* and whelk *Busycotypus* and the Asian drill *Ocenebrellus* and whelk *Rapana*, have been transported by a variety of means around the

world, and may have local significant impacts, although quantitative, experimental data are lacking for all introduced populations.

TABLE 5. Donor and receiver regions of introduced mollusks originating in the Northern Hemisphere

	DONOR REGION							TOTAL ALL
	North Atlantic-Mediterranean				North Pacific			
	NA	EA/M	WA	TOTAL	EP	WP	TOTAL	
Gastropoda	0	2	8	10	1	5	6	16
Bivalvia	1	3	10	14	0	8	8	22
TOTAL	1	5	18	24	1	13	14	38
RECEIVER REGION: NORTHERN HEMISPHERE								
	North Atlantic-M-BS			North Pacific				
	M/BS	EA	WA	EP	WP	HAWAII		
Gastropoda	2	2	2	12	0	2		
Bivalvia	6	6	1	16	3	3		
RECEIVER REGION: SOUTHERN HEMISPHERE								
	WSP	ESP	WSA	SA	IO			
Gastropoda	0	0	0	0	0			
Bivalvia	5	1	1	1	1			

Abbreviations: BS, Black Sea; EA, Eastern Atlantic Ocean; EP, Eastern Pacific Ocean; ESP, Eastern South Pacific Ocean (Chile); IO, Indian Ocean; M, Mediterranean Sea; NA, North Atlantic Ocean; SA, South Africa; WA, Western Atlantic Ocean; WP, Western Pacific Ocean; WSA, Western South Atlantic Ocean (Argentina); WSP, Western South Pacific Ocean (Australia, New Zealand).

CONCLUDING REMARKS

Three general conclusions or observations arise from the current data and knowledge about marine bioinvasions, with particular reference to the patterns of molluscan introductions under discussion here.

First, human-mediated dispersal-potentially ancient-offers a set of alternative hypotheses to the presumptions of "naturalness" embedded in many if not most classical interpretations of the historical biogeography of a vast number of species. The fact that a given species *could* disperse naturally does not prove that it did so, nor does the fact that a given species occurred or occurs in or on the bottom of a ship (or with commercial oysters, or with other vectors) prove that it was dispersed by that means either. Rather, a great many species populations must be regarded today as cryptogenic—neither clearly native or introduced-until further data are gathered (Carlton, 1996b). There can be little doubt, however, that a staggering number of species were *subjected* to broad and repeated dispersal by human activities centuries before the first biological surveys commenced. Carlton (1999) estimated that between 900 and 1,500 coastal species of marine organisms now regarded as naturally distributed may in fact have been dispersed by ships between the years 1500 and 1800 alone. It is predictable that work would reveal the pre-18th or pre-19th century absence of certain now-common species in selected areas of the world where careful comparative analyses of the fossil, archeological, and modern faunas had not yet been undertaken.

Second, biogeographic patterns that emerge from the molluscan invasion data in hand now bear further consideration at broader systematic and geographic levels. These include the apparent predominance of the western sides of oceans (the eastern sides of continents) as donor areas, and possible explanations for this predominance, in terms of the complex interplay of the evolutionary histories of these biotas, the scale of regional productivity, and the probabilities over time and space of interfacing with constantly changing patterns of human-dispersal vectors. These patterns further include more detailed consi-

deration of the northeastern Pacific Ocean as a region particularly remarkable for its role as a receiver (versus donor) area. Only one molluscan species, the slipper limpet *Crucibulum spinosum* (G. B. Sowerby 1,1824), appears to have departed the Pacific coast of North America, a pattern in concert with the low export diversity among other taxa (Carlton, 1979a, who noted that only a few Pacific American crustaceans have colonized other regions of the world). The depth and breadth of this phenomenon remain to be adequately explored.

Third and last, we may appeal to the need for far greater quantitative and experimental data on the ecological impacts of marine invasions, including those by mollusks. While invasive species often become the aspect dominant members of many communities -thus leading to the expectation or prediction that a given invasive species is having a significant ecological impact-more attention must be paid to experimentally demonstrating the actual mechanisms of such impacts. Without such data, both the predictive level of invasion ecology, and a full understanding of the importance of invasions in altering community and ecosystem structure, will remain limited.

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