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INTRODUCED MARINE AND ESTUARINE MOLLUSKS OF NORTH AMERICA: AN END-OF-THE-20TH-CENTURY PERSPECTIVE

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ABSTRACT A review of the introduced marine and estuarine (brackish water) bivalves and prosobranch and pulmonate gastropods of the Atlantic, Gulf and Pacific coasts of North America reveals an established fauna of 36 non-indigenous species. Sixteen species are native to temperate or tropical coasts of North America, and have been transported to regions of the continent where they did not occur in historical time; the remaining 20 species are from Europe, the Mediterranean, South America, the Indo-Pacific, and the northwestern Pacific. The movement of Pacific (Japanese) and Atlantic commercial oysters to the Pacific coast, and ship fouling, boring. and ballast water releases. have been the primary human-mediated dispersal mechanisms. Regional patterns are striking: 30 species are established on the Pacific coast, 8 on the Atlantic coast, and 1 on the Gulf coast (three species occur on both coasts); 19 (63%) of the Pacific species occur in San Francisco Bay alone. These patterns may be linked to a combination of human-mediated dispersal mechanisms and regional geological-biological Pleistocene history: at least 27 species of Japanese and Atlantic coast mollusks were introduced to the American Pacific coast by the oyster industry, in large part into geologically young regions with low native molluscan diversity. With the exception of a few species, there is little experimental elucidation of the ecological impact of the introduced marine mollusks in North America. Negative effects by introduced gastropods on native gastropods have been demonstrated on both the Atlantic and Pacific coasts; for one species, the Atlantic pulmonate marsh snail *Ovatella* on the Pacific coast, experimental evidence suggests that its establishment did not arise at the expense of native species. No introduced marine mollusk in North America has had a greater ecological impact than the periwinkle *Littorina littorea,* which colonized the Atlantic coast from Nova Scotia to New Jersey in the 30 year period between 1860 and 1890. and subsequently altered the diversity. abundance. and distribution, of many animal and plant species on rocky as well as soft bottom shores. Future marine invasions. through ballast water release and perhaps through aquaculture activities. can be expected with confidence.

KEY WORDS: mollusks, introductions, invasions, nonindigenous, exotics

INTRODUCTION

> "A good deal of chess play has also been done with clams...."
> -Charles S. Elton (1958)

At the close of the 20th century we are witnessing rapidly growing interest in the phenomenon of biological invasions of coastal waters. As a result of an increasing number of unintentional invasions of marine organisms due to the release of ballast water through international shipping activities, and of increasing pursuit of the intentional use and release of marine organisms for mariculture purposes and for open sea fisheries enhancement, concern is growing relative to the potential ecological, genetic, economic, and social risks that may be associated with future invasions

I review here the diversity, distribution, regional invasion patterns, and ecological impacts of the introduced marine and estuarine (brackish water) bivalves and prosobranch and pulmonate gastropods of the Atlantic, Gulf, and Pacific coasts of North America. Introduced species (exotic, non-indigenous, alien, or invader species) are those taxa transported by human activity to regions where they did not exist in historical time (Carlton 1987). While there has been no previous continent-wide review of the introduced mollusks, Quayle (1964), Hanna (1966) and Carlton (1975, 1979a, 1979b) have provided regional lists and treatments for the Pacific coast. Abbott (1974), Bernard (1983) and Turgeon (1988) list many of the species discussed here. I include all species which have been recorded as free-living outside of mariculture operations. One species, the Japanese sea scallop *Patinopecten yessoensis,* is included because of its current mariculture use and potential to become naturally established. I have excluded opisthobranch mollusks (sacoglossans, nudibranchs and pyramidellids), pending a global and/or continental review of the candidate species. There are no introduced polyplacophorans (chitons) or scaphopods (tusk shells) in North America. I also exclude most records of single specimens of living mollusks whose anomalous presence outside their recorded ranges appears to be due to discarding through hobby (aquarium) or fishing activities.

Mechanisms of introduction of non-indigenous marine organisms to North American waters have been reviewed by Carlton (1985, 1987, 1989, 1992a). The most important human activities have been or are the following: (1) the transportation of organisms on the outside (fouling species) or on the inside (boring species) of ships, (2) the transportation of organisms inside vessels in solid ballast, such as rocks, sand, and detritus, (3) the movement of oysters, and the concomitant movement of organisms on the oyster shells or in associated sediments and detritus, (4) the intentional release of species for fisheries purposes, and (5) the release of larvae, juveniles, or adults of marine organisms in the ballast water of coastal, transoceanic, and interoceanic vessels. I review below the relative importance of each of these mechanisms to the established introduced mollusks in North America.

METHODS

Field, museum, and literature work from 1962 to 1979 are summarized by Carlton (1979a). Field work during that period was conducted from Vancouver Island to southern California; 18 museums or private collections on the west and east coasts of the United States and Canada were studied. From 1979 to 1992 field work was conducted from Newfoundland to Virginia. as well as on the Pacific coast. and museum collections were revisited to examine additional species. Throughout both periods I corresponded with malacologists and other biologists and undertook continual literature reviews. The records and dates recorded here are thus based upon field work. museum collections. personal communications, and the literature. and form the basis of a monograph now in preparation. I present here an abstract of this work.

RESULTS

Regional Patterns of Invasion

Table 1 is a comprehensive synthesis of the introduced marine and estuarine mollusks reported since the early 19th century in North America. The introduced mollusks can be placed into 4 categories (Table 2): established (naturally reproducing populations are known), establishment not certain (no recent records, but the species may still be present), not established (not found in recent surveys or, if present, naturally reproducing populations are not known), and cryptogenic (Carlton 1987; status as introduced or native is not known).

Thirty-six species of non-indigenous marine and estuarine mollusks are established on the Pacific, Atlantic. and Gulf coasts of North America (Table 3). Sixteen species are native to temperate or tropical coasts of North America, and have been transported to regions of the continent where they did not occur in historical time. Thus, 14 species (Table 2) native to the Atlantic coast have been transported to the Pacific coast (Table 3 indicates 15 species on this route; this includes the European Ovatella, established on the American Atlantic coast). At least 3 species *(Rangia cuneata, Mytilopsis leucophaeata* and *Teredo burtschi)* have been transported from their apparently native southern ranges to more northem localities (shown in Table 3 as 1 species from the Gulf of Mexico and 2 species from the northwest Atlantic, respectively). The remaining 20 species include 4 from Europe, 1 questionably from Europe (the shipworm ***Teredo*** navalis), 1 from the Mediterranean (the mussel ***Mytilus galloprovincialis),*** 1 from South America (the mussel ***Perna perna).*** 1 questionably originating in the Indo-Pacific (the shipworm *Lyrodus pedicellatus),* and 12 from the northwestern Pacific.

Four species (Table 2) are questionably established; field work has not been focused on locating these species in recent years, and they may still be present. Seven species have not become regionally established: the Atlantic periwinkles *Littorina littorea* and *Tectarias muricatus,* once found living in California and the Gulf of California respectively; the European snail *Truncatella subcylindrica,* found in 1880 to be common at Newport, Rhode Island; the Asian clam *Laternula limicola,* found over a period of several years in Coos Bay, Oregon in the 1960s; the European oyster *Ostrea edulis,* widely released on the American Pacific coast, and the South American mytilid *Mytella charruana* which appeared in numbers in Jacksonville, Florida in 1986. Of these, *Littorina littorea* and *Ostrea edulis* have become established on the Atlantic coast, The Japanese sea scallop *Patinopecten yessoensis* while present in mariculture operations in British Columbia has not been reported in natural sets.

Cryptogenic species include (Table 1) the pulmonate limpet *Siphonaria pectinata* and the shipwonn *Teredo navalis.* Nineteenth century or earlier shipping has been implicated in creating the modem distributions of both species, but details of their historical biogeography in the north Atlantic Ocean remain uninvestigated.

Regional patterns (Table 3) are striking: 30 species are established on the Pacific coast, 8 on the Atlantic coast, and 1 on the Gulf coast (3 species, the snail *Ovatella,* the clam *Corbicula,* and the shipworm *Teredo bartschi* occur on both the Atlantic and Pacific coasts). Most (27 species) of the introduced mollusks on the Pacific coast originate either from Asia or the Atlantic coast of North America. Of the Pacific species, 5 are recorded from only 1 locality: the Atlantic whelk *Busycotypus* and the Asian clam *Potamocorbula* occur only in San Francisco Bay, the Atlantic clam *Mercenaria* occurs only in Colorado Lagoon, Alamitos Bay, the Atlantic oyster *Crassostrea virginica* now survives only in the Serpentine and Nicomekl Rivers of the Boundary Bay region, British Columbia, and the shipworm *Lyrodus takanoshimensis* has been reported only from Ladysmith Harbor, British Columbia. I do not include here the clam *Macoma "balthica"* whose San Francisco Bay population appears to arise from an Atlantic coast stock, as this genotype may in fact be widespread in central California embayments.

Four species are restricted to the Pacific Northwest (Washington and British Columbia): the Japanese snails *Cecina manchurica* and *Nassarius fraterculus,* the Japanese clam *Trapezium liratum* and the Pacific oyster *(Crassostrea gigas* (which rarely reproduces south of Willapa Bay, WA). Two additional species reported only from British Columbia are the questionably established *Clanculus ater* and *Subia conica.* Four Atlantic species are well established in a few restricted localities: the slipper limpet *Crepidula convexa* occurs only in San Francisco and Boundary Bays (newly recognized in British Columbia by Robert Forsyth); the mudsnail *Ilyanassa obsoleta* occurs only in San Francisco, Willapa. and Boundary Bays; the angelwing clam *Petricola pholadiformis* occurs only in San Francisco. Newport, and Boundary Bays, and the gem clam *Gemma gemma* is restricted to 5 bays in central California (Bodega Harbor (not Bodega Bay), Tomales Bay. Bolinas Lagoon, San Francisco Bay, and Elkhom Slough). Seven oyster-associated introductions occur in British Columbia/Washington and in California, but for reasons that remain unclear do not occur "naturally" in Oregon bays and estuaries: these are the Japanese snail *Batillaria attramentaria* and the Atlantic gastropods *Ilyanassa obsoleta, Crepidula convexa. C. fornicata, C. plana,* and *Urosalpinx cinerea;* the fifth species, the Japanese clam *Venerupis philippinarum,* occurs in Netarts Bay, Oregon only by virtue of an intensive planting program (the only bay in Oregon where the Japanese oyster drill *Ceratostoma inornatum* is also established).

The Asian clam *Theora lubrica* and the Atlantic mussel *Geukensia demissa* occur disjunctly in San Francisco Bay and again in southern California bays. The abundant and widespread freshwater clam *Corbicula fluminea* appears occasionally in estuarine situations in Oregon and California. The tropical Atlantic shipworm *Teredo bartschi* has been introduced to at least 2 sites in western Mexico, and is probably more widespread than these records indicate.

Of the 30 introduced species on the Pacific coast, then. only 12 are relatively widespread. These are the gastropods *Crepidula fornicuata, Crepidula plana, Batillaria attramentaria, Urosalpinx cinereu. Ceratostoma inornatum,* and *Ovatella myosotis,* and the bivalves *Mytilus galloprovincialis, Musculista senhousia, Venerupis philippinarum, Myra urenaria, Teredo navalis,* and *Lyrodus pedicellutus.*

TABLE 1.

Introduced marine and estuarine mollusks of North America (exclusive of opisthobranch gastropods). *Common names* after Turgeon 1988; (*) species listed without common name in Turgeon 1988; (+) species not listed in Turgeon 1988.

Species	NATIVE **TO/Introduced To (date of collection) /MECHANISM (M) (see keys, below)**	**References and Remarks**
GASTROPODA: Prosobranchia		
Trochidae		
Clanculus ater Pilsbry. 1911 (+ topsnail)	NW PACIFIC/NE Pacific: BC: Queen Charlotte Sound (1964). M: BW?	Clarke. 1972. Not reported since 1964; status not known.
Pomatiopsidae		
Cecina manchurica A. Adams, 1861 (+ Manchurian cecina)	NW PACIFIC/NE Pacific: BC (date?); WA: Whatcom Co. (1961); Willapa Bay (1963) M: COI	Morrison, 1963a, Duggan, 1963, Carlton, 1979a. Kozloff and Price, 1987:210. High intertidal, common, co-occurring with Ovatella *myosotis.* found by digging down inside piles of old oyster shells in damp. rich organic debris (Willapa Bay, 1977. JTC), a microhabitat similar to the one in its native Japan (Davis, 1979: 117). Also at base of salt marsh plant *Salicornia.*
Littorinidae		
Lirrorina littorea (Linnaeus, 1758) (common periwinkle)	NE ATLANTIC/NW Atlantic: (< 1840) Canada to VA/NW ATLANTIC/NE Pacific: see remarks. M: Atlantic: SB or IR; Pacific: DA	Carlton, 1982, Carlton et al. 1982, Vermeij. 1982a.b. Lubchenco, 1978, 1983, 1986. Brenchley, 1982, Brenchley and Carlton, 1983, Kemp and Bertness, 1984. Bertness. 1984, Blackstone, 1986, Yamada and Mansour. 1987, Petraitis, 1989: Became extinct in North America in precontact times: reestablished through either intentional release (for food) or accidentally with ballast rocks. Collected in San Francisco Bay in 1968-1970 and again in 1977 (Carlton, 1969. 1979a). but not found since despite sporadic searches throughout the bay (JTC, personal observations). Now one of the most predominant mollusks of the Atlantic rocky shore, and in some regions the marshes and mudflats, from Newfoundland to New Jersey.
Tectarius muricatus (Linnaeus, 1758) (beaded periwinkle)	NW ATLANTIC/Mexico: Gulf of California (1986, 1988). M: ?	Bishop. 1992, Chaney, 1992. No records since 1988.
Truncatellidae		
Truncatella subcylindrica (Linnaeus, 1767) (+)	NE ATLANTIC/NW Atlantic: RI: Newport (1880). M: SB?	Burch (1962) is the most recent to repeat this early record of Verrill (1880). who found this species to be common; it has not been collected since.
Potamididae		
Barillaria attramentaria (Sowerby, 1855) *(= Batillaria zonalis* auctt.) (Japanese false cerith)	NW PACIFIC/NE Pacific: BC (1959) to WA (1920s), but not Grays Harbor or Willapa Bay: CA: Tomales Bay (1941); Monterey Bay Elkhom Slough (1951). M: CO1	Hanna, 1966, MacDonald, 1969a, 1969b. Whitlatch, 1974, Carlton, 1979a. Whitlatch and Obrebski, 1980, Yamada, 1982. Abundant locally on mudflats.
Hipponicidae		
Sabia conica (Schumacher, 1817) (*hoofsnail)	NW PACIFIC/NE Pacific: BC: Queen Charlotte Sound: Table Island (1940); Vancouver Island (1963). M: BW?	Cowan, 1974, Carlton, 1979a, Kay, 1979. Current status not known.
Calyptraeidae		
Crepidula convexa Say, 1822 (convex slippersnail)	NW ATLANTIC/NE Pacific: BC: Boundary Bay (R. Forsyth, personal communication, 1991); CA: San Francisco Bay (1898); M: COI	Hanna, 1966, Carlton and Roth, 1975. Carlton, 1979a. Very common on snail shells on mudflats along shores of San Francisco Bay.

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TABLE 1.

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Species	**NATIVE TO/Introduced To (date of collection) /MECHANISM (M) (see keys, below)**	**References and Remarks**
Crepidula fornicata (Linnaeus, 1758) (common Atlantic slippersnail)	NW ATLANTIC/NE Pacific: WA: Puget Sound (1905?); Grays Harbor (1970s); Willapa Bay (1937): CA: Humboldt Bay (S. Lamed, collector, 1989); Tomales Bay?; San Francisco Bay (1898). M: COI	Hanna, 1966, Carlton, 1979a
Crepidula plana Say. 1822 (eastern white slippersnail)	NW ATLANTIC/NE Pacific: WA?: Puget Sound?; Willapa Bay (1937); CA: San Francisco Bay (1901). M: COI	Carlton, 1979a, Wicksten, 1978 (as *Crepidula perforans)*
Muricidae		
Ceratostoma inornatum (Recluz. 1851) (= *Ocenebra japonica* (Dunker. 1860)) (+ Japanese oyster drill)	NW PACIFIC/NE PACIFIC: BC (1931); WA: south to Puget Sound (1924); Willapa Bay (present populations since 1960s?); OR: Netarts Bay (1930-34); CA: Tomales Bay (1941); Morro Bay?; M: COI.	Chew, 1960, Hanna, 1966, Squire. 1973. Radwin and D'Attilio, 1976, Carlton, 1979a. Locally common on oyster beds in the Pacific Northwest.
Urosalpinx cinerea (Say. 1822) (Atlantic oysterdrill)	NW ATLANTIC/NE Pacific (1890 and later years): BC: Boundary Bay; WA: Puget Sound and Willapa Bay; CA: Humboldt, San Francisco, Tomales, and Newport Bays. M: COI	Carlton, 1979a; populations last reported in Humboldt Bay in 1950 are still present (S. Lamed. collector, 1989). Locally common on oysters and rocks.
Melongenidae		
Busycotypus canaliculatus (Linnaeus, 1758) (channeled whelk) Nassariidae	NW ATLANTIC/NE Pacific: CA: San Francisco Bay (1938). M: COI?	Stohler, 1962, Carlton, 1979a (who reviews evidence for retention of 1938 date).
Nassatiidae		
Ilyanassa obsoleta (Say. 1822) (= *Nassarius obsoletus)* (eastern mudsnail)	NW ATLANTIC/NE Pacific: BC: Boundary Bay (1952); WA: Willapa Bay (1945); CA: San Francisco Bay (1907). M: CO1	Hanna. 1966, Carlton, 1979a. Race, 1982 Astronomically abundant in San Francisco Bay.
Nassarius fraterculus (Dunker. 1860) (Japanese nassa)	NW PACIFIC/NE Pacific: BC: Boundary Bay (1959); WA: Puget Sound region (1960). M: COI	Hanna, 1966, Carlton, 1979a, Cernohorsky. 1984:184-185
Pulmonata		
Melampodidae		
Ovatella mysotis (Draparnaud. 1801) (= *Phytio setifer* (Cooper. 1872)) (*European ovatella)	NE ATLANTIC/NW Atlantic: Nova Scotia to West Indies: Bermuda; NW ATLANTIC/NE Pacific: BC: Boundary Bay (1965) to Mexico: Scammons Lagoon (1972). M: Atlantic: SB; Pacific: COI	Stimpson, 1851, Morrison. 1963a, Abbott. 1974, Carlton, 1979a, Berman and Carlton, 1991. Earliest Pacific coast record is 1871 (San Francisco Bay): earliest record on Atlantic coast is 1841 (Massachusetts). Very common in high salt marsh and drift habitats.
Siphonariidae		
Siphonaria pectinata (Linnnaeus, 1758) (striped falselimpet)	MEDITERRANEAN?/NW Atlantic (19th century or earlier): FL to Mexico, Caribbean Cuba, and northern South America. M: S	Morrison, 1963b, 1972. Morrison believed this species to be introduced from the Mediterranean on ships R. T. Abbott (personal communication, 1990) concurs. G. Vermeij (personal communication, 1990) questions this conclusion based on habitat and broad Western Atlantic distribution. Cryptogenic (see text).
BIVALVIA		
Mytilidae		
Mytilus galloprovincialis Lamarck. 1819 (= *M. edulis* auctt). (+ Mediterranean mussel)	MEDITERRANEAN/NE Pacific: Northern CA (date?) to southern CA (1880s?), Mexico M: S	McDonald and Koehn, 1988, Koehn. 1991. Seed. 1992. Late twentieth century distribution probably enhanced by ballast water transport as well as ship fouling. An abundant fouling mussel.

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TABLE 1.

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Species	**NATIVE TO/Introduced To (date of collection) /MECHANISM (M) (see keys, below)**	**References and Remarks**
Musculista senhousio (Benson, 1842)	NW PACIFIC/NE Pacific: BC: Boundary Bay (R. Forsyth. personal communication. 1991); Puget Sound (1959); northern CA: Bodega Harbor (1971) to Elkhorn Slough (1965), earliest record for Pacific coast is 1941 (San Francisco Bay); southern CA: Newport Bay (1977) to San Diego Bay (1976); Mexico: Papilote Bay. south of Ensenada (1970). M: Pacific NW, northern CA: COI; southern CA-Mexico: BW?	Hanna, 1966, Morton, 1974, Carlton, 1979a. Abundant locally in dense mats over soft bottoms.
Geukensia demissa (Dillwyn, 1817) (ribbed mussel)	NW ATLANTIC/NE Pacific: CA: San Francisco Bay (1894), southern CA: Alamitos (1957), Anaheim (1972) and Newport (1940) Bays, Bolsa Chica Lagoon, Orange Co. (M. Wicksten, personal communication, 1979). M: San Francisco Bay: COI: southern California: S?/COI?	Hanna, 1966, Carlton, 1979a, Sarver et al.. 1992. Juvenile *Geukensia* occur in fouling on ships, suggesting a mechanism for intracoastal transport from San Francisco Bay to southern California. Abundant in marshes, mudflats, and at bases of retaining walls in San Francisco Bay.
Perna perna (Linnaeus. 1758) (+edible brown mussel)	EASTERN SOUTH AMERICA/Gulf of Mexico: TX: Port Aransas (1990) to Port Mansfield (1991). M: BW/S	Hicks and Tunnell, 1993. Also recorded from Namibia to Mozambique (Kennelly, 1969).
Mytella charruana (d'Orbigny. 1846) (+, charru mussel)	EASTERN SOUTH AMERICA/NW Atlantic: FL: Jacksonville (1986). M: BW?/S?	Lee, 1986. Appeared briefly in large numbers in seawater intake of power plant in 1986. but disappeared by 1987 (H. Lee. personal communication, 1992). Perhaps released in ballast water of oil tankers from Venezuela.
Pectinidae		
Patinopecten yessoensis (Jay. 1856) (+Japanese sea scallop)	NW PACIFIC/NE Pacific: BC (1984-85). see remarks. M: IR	Raised in open sea aquaculture operations in BC (T. Carey, personal communication, 1990). but naturally reproducing populations not reported as of 1992.
Anomiidae		
Anomia chinensis Philippi. 1849 (= *Anomia lischkei* Dautzenberg and Fischer, 1907) (+ Chinese jingle)	NW PACIFIC/NE Pacific: WA: Samish Bay (1924). Willapa Bay (1952): OR: Tillamook Bay (<1970s). M: COI	Carlton, 1979a. Current status not known. May be established (Hanna, 1966, Abbott. 1974), although Bernard (1983) believed otherwise.
Ostreidae		
Crassostrea gigas (Thunberg. 1793) (Pacific oyster)	NW PACIFIC/NE Pacific: Cultured from AK to Mexico: well established in BC, WA, sporadically reproducing south to CA: Tomales Bay. NW Atlantic: Sporadic plantings along Atlantic and Gulf coasts since 1930s. No established populations reported as of 1992, despite reported unauthorized private plantings of 1000s of bushels in Chesapeake Bay about 1988-90. M: IR.	Pacific: Galstoff, 1932, Barrett, 1963, Hanna, 1966, Quayle, 1969, Carlton, 1979a, Bourne, 1979, Chew, 1979, Ketchen et al. 1983, Foster. 1991:41. Atlantic: Galtsoff, 1932, Nelson, 1946; Turner, 1949, 1950, Mann, 1979, Mann et al. 1991. Experimental introductions in 1875 in WA (Barrett, 1963:48-49) were followed by regular attempts throughout the Pacific Northwest starting in 1902; CA plantings began in 1928.
Crassostrea virginica (Gmelin, 1791) (eastern oyster)	NW ATLANTIC/NE Pacific: BC: Boundary Bay only (since 1917-1918). Population in Willapa Bay WA is now extinct (K. Sayce, personal communication, 1990)	Elsey, 1933, Barrett, 1963, Hanna. 1966, Carlton, 1979a, Bourne, 1979. Plantings began in 1869-1870 in San Francisco Bay with completion of Transcontinental Railroad. and continued along entire Pacific coast in subsequent years.

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TABLE 1.

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Species	**NATIVE TO/Introduced To (date of collection) /MECHANISM (M) (see keys, below)**	**References and Remarks**
Ostrea edulis Linnaeus, 1758 (edible oyster)	NE ATLANTIC/NW Atlantic: ME (1949) and RI (1991). NE Pacific: See remarks. M: Maine: IR; Rhode Island: ?	Loosanoff, 1962, Welch, 1966, Hidu and Lavoie, 1991. May be established in bays and harbors of Rhode Island (J. D. Karlsson, collector, 1991). Raised in aquaculture facilities on the Pacific coast. but not known to be naturally established (rare natural settlement has occurred in Tomales Bay CA (Davis and Calabrese, 1969)). Raised along NW Atlantic coast with small natural sets north to Halifax County. Nova Scotia (M. Helm, personal communication, 1990).
Mactriade		
Rangia cuneata (Sowerby, 1831) (Atlantic rangia)	GULF OF MEXICO/NW Atlantic: FL east coast to Chesapeake Bay (1955); NY: Hudson River (1988, C. Letts, collector). M: to Chesapeake Bay: COI?/BW?, to Hudson River: BW	Hopkins and Andrews. 1970. Newly established in lower Hudson River perhaps due to release as larvae in ballast water from Atlantic or Gulf coasts
Tellinidae		
Macoma "balthica" (Linnaeus, 1758) (Baltic macoma)	NW ATLANTIC/NE Pacific: San Francisco Bay. M: COI	Meehan et al. 1989. The genetic similarity of San Francisco Bay populations to NW Atlantic populations (as opposed to specimens from Europe or further north on the Pacific coast) suggest that the San Francisco *M. "balthica"* were probably introduced in the 19th century. Very common.
Semelidae		
Theora lubrica Gould. 1861 (Asian semele)	NW PACIFIC/NE Pacific: CA: Los Angeles Harbor. Anaheim Bay. Newport Bay (earliest southern CA record, 1968): San Francisco Bay (1982). M: BW	Seapy, 1974, Carlton et al. 1990. It is of interest to note the increase of this species in 1978-79 in polluted environments in the Inland Sea of Japan (Sanukida et al. 1981). the source of much ballast water carried to the NW Pacific, and its appearance in the early 1980s in San Francisco Bay. Intracoastal movement to San Francisco Bay from southern CA is also possible.
Dreissenidae		
Dreissena polymorpha (Pallas. 1771) (+ zebra mussel)	NE ATLANTIC/NW Atlantic: estuarine populations in NY: Hudson River (summer 1992, up to 5/00, W. Walton, personal communication, 1992). M: from Europe to the Great Lakes (1988), BW: within North America: see Carlton, l992b	Griffiths et al. 1991, Strayer, 1991, Hebert et al. 1991. Carlton. 1992b. Nalepa and Schloesser, 1992. Ballast water in coastal vessels and ballast, bilge, or incidental water in small sailing vessels could transport zebra mussels between estuaries along the Atlantic coast. Usually in low densities in brackish water (W. Walton. personal communication, 1992).
Mytilopsis leucophaeata (Conrad. 1831) (dark falsemussel)	NW ATLANTIC-GULF OF MEXICO/NW Atlantic: NY: Hudson River (1937); MA: no locality (Marelli and Gray, 1985: 118), perhaps Boston: Charles River? M: S/BW	Rehder, 1937, Jacobson. 1953. Specimens are believed to have been collected from the lower Charles River, near Boston (R. T. Abbott, personal communication, 1990; R. Turner, personal communication. 1992). Native (?) from Chesapeake Bay south.

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TABLE 1.

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Species	NATIVE TO/Introduced To (date of collection) /MECHANISM (M) (see keys, below)	References and Remarks
Trapeziidae		
Trapezium liratum (Reeve, 1843) (+ Japanese trapezium)	NW PACIFIC/NE Pacific: BC: Ladysmith Harbor (1949?); WA: Willapa Bay? (1947?). M: COI	Carlton, 1979a. Populations are present in BC (R. Forsyth, personal communication, 1991). Status in WA not known. Never established in CA; report in Abbott (1974) of appearance "prior to 1935" based upon interceptions in Pacific oyster shipments. Nestling in fouling communities.
Corbiculidae		
Corbicula fluminea (Muller, 1774) (= *C. manilensis* auctt.) (Asian clam)	NW PACIFIC/NE Pacific: estuarine populations in OR: Siuslaw River; CA: Smith River, San Francisco Bay; NORTH AMERICA/NW Atlantic: estuarine populations in Chesapeake Bay: James River. Freshwater populations throughout the United States, northern Mexico. M: from Asia to N. America (1920s-1930s), IR; within North America: see Counts, 1986	Counts, 1986, 1991; estuarine populations: Diaz, 1974, Carlton. 1979a, Nichols et al. 1990, Counts, 1991:105. Abundant locally, but in lower densities in brackish water.
Veneridae		
Venerupis philippinarum (A. Adams and Reeve, *1850) (= Tapes semidecussata* Reeve, 1864; = *T. japonica* Deshayes, 1853: also placed in subgenus *Ruditapes).* (Japanese littleneck)	NW PACIFIC/NE Pacific: BC (1936) to CA: Monterey Bay: Elkhorn Slough (1949). OR: Netarts Bay (see remarks). M: COI except for OR: IR	Fisher-Piette and Metivier, 1971 (specific taxonomy and synonymy), Bourne, 1982, Anderson et al. 1982, Bernard. 1983. Ketchen et al. 1983. Generic placement follows E. Coan and P. Scott (personal communication, 1992). Intentional plantings in OR: Netarts Bay sporadically from 1960s-1980s resulted in a naturally reproducing population (Gaumer and Farthing, 1990); also planted in other OR bays, where specimens should be expected. Common to abundant in coarser sediments.
Gemma gemma (Totten, 1834) (amethyst gemclam)	NW ATLANTIC/NE Pacific: CA: Bodega Harbor (1974) to Elkhorn Slough (1965); earliest record 1893, San Francisco Bay. M: COI	Carlton, 1979a. Records from north of Bodega or south of Monterey Bay are based upon misidentifications. Abundant in soft sediments.
Mercenaria mercenaria (Linnaeus, 1758) (northern quahog)	NW ATLANTIC/NE Pacific: CA: Alamitos Bay (1967). M: IR	Crane et al. 1975, Murphy, 1985a, 1985b. The only established population on the Pacific coast of this common Atlantic species is in this small CA bay. Hertz and Hertz (1992) report a single live specimen from Mission Bay, San Diego. probably from discarded bait or food.
Petricolidae		
Petricola pholadiformis (Lamarck, 1818 (false angelwing)	NW ATLANTIC/NE Pacific: WA: Willapa Bay (1943); CA: San Francisco Bay (1927), Newport Bay (1972). M: COI	Hanna, 1966, Carlton, 1979a. In higher shore hard shale, clay, mud substrates.
Myidae		
Mya arenaria Linnaeus, 1758 (softshell)	NW ATLANTIC/NE Pacific: AK (1946) to Monterey Bay: Elkhorn Slough (<1911). M: COI	Carlton, 1979a. Bernard, 1979. Became extinct on Pacific coast from southern AK south in late Tertiary; reestablished (earliest record 1874, San Francisco Bay) through accidental introduction with Atlantic oysters. Now one of the most common upper bay clams from WA to San Francisco Bay.

continued on next page

TABLE 1.

continued

Species	NATIVE TO/Introduced To (date of collection) /MECHANISM (M) (see keys, below)	References and Remarks
Corbulidae		
Pommocorbula amurensis (Schrenck, 1861) (+ Amur river corbula)	NW PACIFIC/NE Pacific: CA: San Francisco Bay (1986). M: BW	Carlton et al. 1990, Nichols et al. 1990. In densities of tens of thousands per square meter in estuarine reaches of San Francisco; to be expected in other CA bays through intracoastal transport of larvae in ballast water.
Teredinidae		
Lyrodus pedicellatus (de Quatrefages. 1849) (= *Teredo diegensis* Bartsch. 1927) (blacktip shipworm)	INDO-PACIFIC?/NE Pacific: CA: San Francisco Bay (1920); Monterey Bay (1935): Santa Barbara to San Diego Bay (earliest southern CA record 1871). M: S	Kofoid and Miller, 1927, Turner, 1966, Ecklebarger and Reish. 1972, Carlton. 1979a
Lyrodus takanoshimensis Roth. 1929 (+)	NW PACIFIC/NE Pacific: BC: Ladysmith Harbor (1981). M: COI (in wooden oyster boxes)	Popham 1983.
Teredo barrschi W. Clapp. 1923 (Bartsch shipworm)	NW ATLANTIC/NW Atlantic: NJ: Bamegat Bay (1974), CT: Long Island Sound: Waterford (1975): NE Pacific: Gulf of California: La Paz (<1971): Mexico: Sinalao (1978-79). M: S	NW Atlantic: Hoagland and Turner, 1980. Hoagland, 1981, 1986, Richards et al. 1984. Gulf of California: R. Turner in Keen, 1971:282, Hendrickx, 1980. Reported by Abbott (1974) as introduced to CA, a record based upon specimens from San Diego Bay in the 1920s (Kofoid-and Miller. 1927). May no longer be present in Bamegat Bay in thermal effluents, but still established in Long Island Sound heated power plant effluents at Millstone.
Teredo novalis Linnaeus. 1758 (naval shipworm)	NE ATLANTIC?/NE Pacific: BC: Pendrell Sound (1963): WA: Willapa Bay (1957); OR: Coos Bay (1988): CA: San Francisco Bay (1913): southern CA? NW ATLANTIC: see remarks. M: S	Turner, 1966. Carlton, 1979a. Coos Bay record: JTC. field records. Cryptogenic in NW Atlantic: early American records include reports both from visting vessels (Russell, 1839, MA) and from established populations (DeKay. 1843, NY). Grave (1928) enigmatically noted. "The date of its first appearance in [Woods Hole] is not known," noting records as early as 1871. If introduced, it may have arrived centuries ago with visits of earliest European vessels.
Teredo furcifera von Martens in Semon, 1894 (+)	NW ATLANTIC (Caribbean north to FL)/NW Atlantic: NJ Bamegat Bay (1974). M: S	Hoagland and Turner, 1980, Richards et al., 1984. Probably only temporarily established in Barnegat Bay in thermal effluents of power plant (K. E. Hoagland, personal communication, 1992) and may no longer be present there. Turner (1966) records an earlier nonestablished population in NC.
Laternulidae		
Laternula limicola (Reeve, 1863) (= *L. japonica* auctt.) (+)	NW PACIFIC/NE Pacific: OR: Coos Bay (1963). M: BW	Keen, 1969. Not recorded in Coos Bay since 1965, and not re-discovered there despite intensive searching from 1986-1989 (JTC and students, field records).

Mechanisms of introduction

S = Ships (fouling and boring)
SB = Ships (solid ballast: rocks. sand)
BW = Ships (ballast water)
COI = Fisheries: Accidental release with commercial oyster industry
IR = Fisheries: Intentional release
DA = Fisheries: Accidental release with discarded algae (seaweed) in shellfish packing

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TABLE 1.

continued

Species	NATIVE TO/Introduced To (date of collection) /MECHANISM (M) (see keys, below)	**References and Remarks**

Regions (as used here:)
Northwest (NW) Pacific = Asia: China. Japan, Korea
Northeast (NE) Pacific = Pacific coast of North America: Alaska to Mexico
Northwest (NW) Atlantic = Atlantic coast of North America: Canada to Florida
Northeast (NE) Atlantic = Europe: northern and western

AK	Alaska	NJ	New Jersey
BC	British Columbia	NW	Northwest
CA	California	NY	New York
CT	Connecticut	OR	Oregon
FL	Florida	RI	Rhode Island
MA	Massachusetts	TX	Texas
ME	Maine	VA	Virginia
NC	North Carolina	WA	Washington
NE	Northeast		

It is of interest to note that 19 (63%) of the 30 species occur in San Francisco Bay. Only the embayments of the Pacific Northwest approach this number of established species. with Willapa Bay having 12 species, Puget Sound 11 species, and Boundary Bay 13 species. These numbers will increase with further exploration (for example, *Trapezium liratum, Crepidula convexa* and *Crepidula plana* should be expected more widely than now reported in Washington and British Columbia) and with new introductions.

Four of the introduced mollusks on the Atlantic coast are from Europe and 3 (as noted above) are southern species now established in northern localities. Only 2 species are widespread, the European periwinkle *Littorina littorea,* and the Gulf of Mexico clam *Rangia cuneata.* The European oyster *Ostrea edulis,* long restricted to Maine. now occurs in Rhode Island as well, although the means of introduction of this population (whether by transport from Maine as a ship-fouling organisms, or by intentional release, or by escape from aquaculture facilities) is not yet known. The shipworm *Teredo bartschi* occurs within the thermal plume of a nuclear power plant in Long Island Sound; the status of the population of this species. and of another southern teredinid, in New Jersey is not clear. Estuarine populations of 2 typically freshwater bivalves, the Asian clam *Corbicula fluminea* and the European zebra mussel *Dreissena polymorpha,* are known from limited locations.

The sole clearly introduced marine mollusk in the Gulf of Mexico, *Perna perna,* is from South America. Were it not for this recent report, there would be no certain records of introduced mollusks in the Gulf fauna.

Regional Patterns of Mechanisms of Introduction

The human-mediated dispersal mechanisms that have led to the introduction of non-indigenous mollusks to North American coasts have played strikingly different regional roles (Table 4). Far exceeding all other mechanisms in terms of number of species successfully transported and introduced is the now largely historical movement of the Atlantic oyster *Crassostrea virginica* and the Pacific (Japanese) oyster *Crassostrea gigas* to the bays and estuaries of the Pacific coast of North America from the 1870s to the 1930s. and from the 1900s to the 1970s, respectively (Table 1). Atlantic oyster importation ceased due to lack of breeding success and because of competition with the increasing importation and culture of the Pacific oyster. Pacific oyster importations stopped after sufficient natural sets and regional aquaculture operations were able to supply adequate amounts of seed.

These industries led to the introduction of at least 22 mollusks to the Pacific coast (Table 4: the 20 species shown for COI plus the 2 species of oysters); 9 are from Japan and 13 are from the Atlantic. Intentional fishery releases added another 2 species (the Asian clam *Corbicula fluminea* and the Atlantic quahog *Mercenaria mercenaria,* which curiously did not become established through the oyster industry) to the Pacific coast fauna.

Prior to these industries and releases. only a few species of mollusks had been transported to or within North America. The earliest introduction may have been the cryptogenic shipworm *Teredo navalis* to the New England coast. The European snail *Littorina littorea,* prehistorically present in the northwestern Atlantic, was returned to North America before 1840 either intentionally (released by European settlers in eastern Canada to establish a periwinkle fishery) or accidentally (with ballast stones). A late 18th century-early 19th century introduction to the Atlantic coast with ballast stones may have been the European marsh snail *Ovatella myosotis* (subsequently then transported with oysters to the Pacific coast). On the Pacific coast, mid-19th to early 20th century ship-mediated introductions included the shipworms *Teredo navalis* and *Lyrodus pedicellatus,* as well as the Mediterranean mussel *Mytilus galloprovincialis,* whose introduced status was long overlooked in California due to its previous identification as the "native" *Mytilus edulis.*

Ballast water has played a small role in terms of the numbers of introduced species, although at least 2 of the species introduced by this means are ecologically and/or economically significant invasions. For a number of species, the role of ballast water as a mechanism is submerged among a number of other mechanisms that are not easily distinguished from each other. Thus, ballast water or ship fouling may have led to the 20th century movement of the North American native dreissenid *Mytilopsis leucophaeata* to the Hudson River. Either mechanism may also have played a role in the appearances of the South American bivalves *Mytella*

TABLE 2.

Introduced marine and estuarine mollusks of North America: Established and other species arranged by donor region. *Regions:* See Table 1, footnote.

	Donor Region	**Receiver Region**
ESTABLISHED		
Cecina manchurica	NW Pacific	NE Pacific
Batillaria attramentaria	NW Pacific	NE Pacific
Ceratostoma inornatum	NW Pacific	NE Pacific
Nassarius fraterculus	NW Pacific	NE Pacific
Muscullsta senhousia	NW Pacific	NE Pacific
Crassostrea gigas	NW Pacific	NE Pacific
Theora lubrica	NW Pacific	NE Pacific
Trapezium liratum	NW Pacific	NE Pacific
Corbicula fluminea	NW Pacific	NE Pacific
	N America	NW Atlantic
Venerupis philippinarum	NW Pacific	NE Pacific
Potamocorbula amurensis	NW Pacific	NE Pacific
Lyrodus takanoshimensis	NW Pacific	NE Pacific
Lyrodus pedicellatus	Indo-Pacific?	NE Pacific
Littorina litrorea	NE Atlantic	NW Atlantic
Ovatella myosotis	NE Atlantic	NW Atlantic
Ostrea edulis	NE Atlantic	NW Atlantic
Dreissena polymorpha	NE Atlantic	NW Atlantic
Mytilus galloprovincialis	Mediterranean	NE Pacific
Teredo navalis	NE Atlantic?	NE Pacific
Crepidula convexa	NW Atlantic	NE Pacific
Crepidula fornicata	NW Atlantic	NE Pacific
Crepidula plana	NW Atlantic	NE Pacific'
Urosalpinx cinerea	NW Atlantic	NE Pacific
Busycotypus canaliculatus	NW Atlantic	NE Pacific
Ilyanassa obsoleta	NW Atlantic	NE Pacific
Ovatella myosotis	NW Atlantic	NE Pacific
Geukensia demissa	NW Atlantic	NE Pacific
Crassostrea virginica	NW Atlantic	NE Pacific
Macoma "balthica"	NW Atlantic	NE Pacific
Gemma gemma	NW Atlantic	NE Pacific
Mercenaria mercenaria	NW Atlantic	NE Pacific
Petricola pholadiformis	NW Atlantic	NE Pacific
Mya arenaria	NW Atlantic	NE Pacific
Perna perna	South America	Gulf of Mexico
Rangia cuneata	Gulf of Mexico	NW Atlantic
Teredo bartschi	NW Atlantic	CT: Long Island Sound
	NW Atlantic	NE Pacific
Mytilopsis leucophaeata	NW Atlantic	NY: Hudson River
ESTABLISHMENT NOT CERTAIN		
Clanculus ater	NW Pacific	NE Pacific
Sabia conica	NW Pacific	NE Pacific
Anomia chinensis	NW Pacific	NE Pacific
Teredo furcifera	NW Atlantic	NJ: Barnegat Bay
NOT ESTABLISHED		
Littorina littorea	NW Atlantic	NE Pacific
Ostrea edulis	NE Atlantic	NE Pacific
Tectarius muricatus	NW Atlantic	NE Pacific
Truncatella subcylindrica	NE Atlantic	NW Atlantic
Mytella charruana	South America	NW Atlantic
Patinopecten yessoensis	NW Pacific	NE Pacific
Laternula limicola	NW Pacific	NE Pacific
CRYPTOGENIC		
Siphonaria pectinata	Mediterranean?	NW Atlantic?
Teredo navalis	NE Atlantic?	NW Atlantic?

charruana in Florida and *Perna perna* in Texas. Ballast water or the movement of commercial oysters may have transported the clam *Rangia cuneata* from the Gulf of Mexico to Chesapeake Bay, from where it may have spread down the coast to Florida, and from where it may have been carried in ballast water to the Hudson River.

On the California coast, a complex mixture of ballast water, ship fouling, or the movements of shellfish may have led to the

TABLE 3.

Summary of introduced marine and estuarine mollusks (excluding opisthobranchs) of North America.

	Established	Establishment Not Certain	Not Established	Cryptogenic
To Pacific coast (Northeast Pacific) from:				
Northwest Pacific	12	3	2	
Indo-Pacific?	1			
Northwest Atlantic	15		2	
Northeast Atlantic?	1			
Northeast Atlantic			1	
Mediterranean	1			
Subtotal	30	3	5	
To Atlantic coast (Northwest Atlantic) from:				
Northeast Atlantic	4		1	1?
Gulf of Mexico	1			
Northwest Atlantic	2	1		
South America			1	
North America	1			
Subtotal	8	1	2	1
To Gulf of Mexico from:				
Mediterranean				1?
South America	1			
Subtotal	1			1
Total	39(*)	4	7	2

(*) Total of 36 species; *Ovatella, Corbicula,* and *Teredo bartschi* are each scored twice (see Table 2). because they originate from different donor regions depending upon the recipient regions.

transportation of the Atlantic mussel *Geukensia demissa* from central California to southern California and of the Japanese mussel *Musculista* senhousia from the northern Pacific coast to southern California. Superimposed upon these potential intracoastal mechanisms and routes is the probability that Asian mollusks have been introduced more than once to the Pacific coast; early introductions of the mussel *Musculista* are linked to the commercial Pacific oyster industry, while its appearance in the 1970s in southern California may be due to ballast water release directly from Asian ports. Similarly, the Asian clam *Theora lubrica* may have been introduced in separate incidents from Asia to both central and southern California; nearly 15 years separate its initial discovery in southern California bays (to where it was probably introduced in the ballast water of ships returning from Indonesia and southeast Asia during the Vietnam War) from its later discovery in San Francisco Bay. The latter invasion may be linked (Table 1, remarks) to an increase in *Theora's* population in regions which now supply large amounts of ballast water to the Bay.

In contrast to these complex dispersal histories, 2 bivalves have appeared in North America whose introduction is clearly linked to ballast water release. These are the Asian corbulid clam *Potamocorbula amurensis* and the Eurasian zebra mussel *Dreissena polymorpha*. *Potamocorbula* established large populations in San Francisco Bay in the 1980s (Carlton et al. 1990, Nichols et al. 1990). at the same time *Dreissena* was establishing large populations in the Great Lakes (Griffiths et al. 1991). *Dreissena* is included here by virtue of its spread into brackish (oligohaline) waters (Table 1). A second species of *Dreissena* (May and Marsden 1992), whose specific name remains unclear, also introduced by ballast water into the Great Lakes, has not appeared (as of November 1992) in estuarine environments in North America.

DISCUSSION

Regional Patterns and Mechanisms of Introduction

The striking differences between the number of molluscan invasions on the Atlantic, Pacific, and Gulf coasts of North America (Table 3) may be due to a combination of human-mediated dispersal events and regional geological and biological Pleistocene history. The two are difficult to separate.

A global mechanism for the potential introduction of nonindigenous mollusks to all shores is shipping. With the ebb and flow of human colonization and commerce, shipping has had a differential impact upon different regions at different times. Societal changes (the colonization of new lands, the opening and closing of ports due to political changes, the birth of new or the demise of old commodities, regional and world wars) and shipping changes (the replacement of wood with iron ships, increased vessel speed. the development of more effective antifouling paints, the advent of ballast water in the 1880s) have led to new invasions in largely unpredictable manners. Colonization and commercial shipping have occurred on a regular basis between Europe and Atlantic America since the early 17th century (or for about four centuries). While contact between Europe and Pacific America is just as old, regular shipping did not commence until the early 19th century, or about two centuries later (Carlton 1987). Despite this two century dichotomy, shipping does not contribute significantly to the regional differences in invasions between the Atlantic and Pacific coasts (Table 4).

A major mechanistic distinction occurs, however. in the history of commercial oyster movements to the two coastlines. Massive inoculation of the Pacific coast of North America for 60 years between 1870 and the 1930s with millions of tons of living oysters

TABLE 4.

Introduced marine and estuarine mollusks: Mechanisms of introduction of established species (M) in parentheses indicates one of two possible transport mechanisms; see key, Table 1 footnote.

	To:		
	Atlantic Coast	Pacific Coast	Gulf Coast
MECHANISM			
Shipping: Fouling/Boring	*Mytilopsis* (BW) *Teredo*	*Mytilus* *Geukensia (COI)* *Lyrodus pedicellatus* *Teredo* (2 spp.)	*Perna* (BW)
Shipping: Solid Ballast	*Littorina* (IR) *Ovatella*		
Shipping: Water Ballast	*Rangia (**)* *Mytilopsis* (S) *Dreissena* (*)	*Theora* *Potamocorbula* *Musculista* (COI)	*Perna (S)*
Commercial Oyster Industry	*Rangia* (**)	*Cecina* *Batillaria* *Crepidula* (3 spp.) *Ceratostoma* *Urosalpinx* *Busycotypus* *Ilyanassa* *Nassarius* *Ovatella* *Geukensia* (S) *Musculista* (BW) *Macoma* *Trapezium* *Venerupis* *Gemma* *Petricola* *Mya* *Lyrodus takanoshimensis*	
Intentional Release	*Littorina* (SB) *Ostrea* *Corbicula* (**)	*Crassostrea* (2 spp.) *Venerupis* (Oregon) *Mercenaria* *Corbicula* (***)	

* *Dreissena* was transported to North America in ballast water from Europe (Carlton, 1992b). but its occurrence in the oligohaline zone of the lower Hudson River is probably due to natural transport as larvae or as juveniles on floating materials from the upper River basin.

** *Rangia* may owe its reappearance on the Atlantic coast in Holocene times either to the transportation of oysters from the Gulf of Mexico to Chesapeake Bay or to its transportation as larvae in ballast water from the Gulf. Ballast water is the probable mechanism of its recent introduction to the oligohaline portions of the Hudson River. Genetic analyses would be of interest to establish whether the Hudson River population originates from the Atlantic coast (such as Chesapeake Bay) or the Gulf coast, if indeed these potential parental populations are genetically distinct.

*** *Corbicula* was probably transported and released intentionally in Western North America no later than the 1920s-1930s (perhaps in more than one incident): subsequent dispersal from western to eastern America has been both through anthropogenic means (the use of the clam as bait, for example). and by natural dispersal along water corridors.

from Japan and from the Atlantic coast led to the simultaneous unintentional inoculation of scores if not hundreds of species of associated protists, invertebrates, algae, seaprasses, and perhaps fish. No such introductions of exotic oysters on this scale occurred on the Atlantic coast of North America.

As a result, 27 species of Asian and Atlantic mollusks have become established on Pacific shores. The bays and estuaries of the Pacific coast where these species are established are geolopically young (recently flooded, < 10,000 years old) and do not have a diverse native biota, suggesting that these systems were relatively susceptible to invasion (Carlton 1975, Carlton 1979b. Nichols and Thompson 1985). Only one introduced species, the Mediterranean mussel *Mytilus galloprovincialis*, occurs in open coast, high energy environments on the Pacific coast; all remaining species are restricted to bays and estuaries. While the extraordinarily diverse molluscan fauna of these open coast rocky shores may thus. in turn, resist invasion, few human-mediated mechanisms serve to transport rocky shores species, and it may be that few if any non-indigenous species from comparable habitats around the world been released into these communities. Thus, on the Pacific coast, there was an apparently coincidental combination of biotically depauperate regions subjected to invasions by a transport mechanism that served to bring species appropriate to those habitats from other regions of the world.

It is of interest to note that in a parallel sense the most significant molluscan invasion of the Atlantic shore also occurred in a geologically young (recently deglaciated, <10,000 years old), biotically depauperate environment. The European periwinkle *Littorina littorea* invaded hard and some soft bottom intertidal communities of the Atlantic coast in the presence of relatively few native herbivorous or omnivorous gastropods. Why, however, other western European rocky shore gastropods failed to colonize American Atlantic shores during centuries of intensive shipping is not clear. It may be that European populations of the common periwinkle *Littorina saxarilis* have been mixed in with aboriginal populations and thus gone undetected. However. it is clear that a variety of other small to medium size European snails (such as trochids and patellid limpets) either were not introduced or were not successful. Here again transport mechanisms may have been rare, with little solid (rock) ballast originating from these habitats (which may suggest that ballast rocks may not have been the means of introduction of *Littorina littorea* to America).

The near absence of recorded introduced mollusks in the Gulf of Mexico may be linked. as with the Atlantic coast, to the absence of large scale importations of commercial oysters or other shellfish from other regions. Pre-ballast water shipping contributed few or no clear introductions. although a detailed biogeographic analysis of the shipworms of the Gulf of Mexico would be of interest. The recent appearances of the South American fouling bivalves *Mytella* and *Perna* in Florida and Texas may suggest that the global increase in ballast water-mediated invasions (Carlton 1985, 1987) may be an active mechanism that will add to the non-indigenous mollusks of the Gulf. The movement of the zebra mussel *Dreissena polymorpha* down the Mississippi River and its arrival (perhaps by 1993) in the oligohaline waters of that delta will add a second species to the list of Gulf marine and estuarine invasions.

Ecological Impacts

With the exception of a few species. there is little experimental elucidation of the ecological impact of the introduced marine mollusks in North America. Carlton (1979b) reviews general ecological considerations. including a remarkable, albeit anecdotal, early account of the interactions between the introduced Atlantic marsh mussel *Geukensia demissa* and the California clapper rail. Nichols and Thompson (1985) document the persistence of an "introduced mudflat community" in San Francisco Bay. where all of the mollusks are introduced *(Macoma "balthica"* indicated as native in their paper. was later shown to be a probable introduction to the Bay (Meehan et al. 1989)).

Remaining largely uninvestigated is the alteration of benthic community dynamics by the abundant introduced bivalves on the Pacific coast. such as *Mytilus galloprovincialis, Geukensia demissa, Musculista senhousia, Mya arenaria, Crassostrea virginica, Venerupis philippinarum,* and *Gemma gemma.* All of these species can occur in great densities. Certain community-level interactions for some of these species (such as *Geukensia, Mya,* and *Gemma)* are known in their donor regions, but are applied with difficulty to the Pacific coast where different suites of potentially interacting species occur. Only the most recent bivalve introduction, the Asian clam *Potamocorbula amurensis,* has been the subject of intensive observational studies relative to its rapid predominance in certain parts of San Francisco Bay, reaching densities of >10,000 per square meter at sites where the former biota has become rare or absent (Nichols et al. 1990). *Potamocorbula* thus joins *Mya, Musculista,* and *Gemma* as species potentially critically important in regulating phytoplankton dynamics in the Bay (Carlton et al. 1990).

On the Pacific coast and Atlantic coasts, interactions between several pairs of native and introduced gastropods have been examined. Interactions between the introduced European periwinkle *Lirtorina littorea* and native gastropods on the Atlantic coast have been studied by a number of workers. In experimental studies. Petraitis (1989) found that *Littorina littorea* negatively affected the growth of the native limpet *Tectura testudinalis.* Yamada and Mansour (1987) also experimentally demonstrated that *Littorina littorea* can depress the growth rate of the native rocky shore snail *Littorina saxatilis.* Brenchley (1982) documented that *Littorina littorea* was the most abundant consumer of eggs of the native mudsnail *Ilyanassa obsoleta* in mid-intertidal habitats on the Atlantic coast. Brenchley and Carlton (1983) further demonstrated that there has been a historical change in the distribution of *Ilyanassa* due to competitive exclusion by *Littorina littorea,* with microhabitat displacement in the mid intertidal zone of 70% of *Ilyanassa,* calculated from littorinid removal experiments. *Littorina* also limits both the upper and lower distribution of *Ilyanassa.*

On the other hand, Race (1982) found that the Atlantic *Ilyanassa obsoleta,* introduced to San Francisco Bay, in turn limits the distribution of the native mudsnail *Cerithidea californica.* by means of competitive interactions and by predation on *Cerithidea's* egg capsules. Whitlatch and Obrebski (1980) found that while the introduced Japanese snail *Batillaria* and the native Pacific coast snail *Cerithidea* can be sympatric in Tomales Bay, CA, similar-sized individuals exclude each other when feeding on the same size diatoms.

Berman and Carlton (1991) examined the potential interactions between the introduced Atlantic marsh snail *Ovatella myosotis* and the native Pacific coast marsh snails *Assiminea californica* and *Littorina subrotundata.* No observational or experimental evidence of competitive superiority by *Ovatella* could be found, and they concluded that the establishment of the introduced species in high shore. semiterrestrial environments did not arise at the expense of the native species.

While the introduced freshwater bivalves *Corbicula fluminea* and *Dreissena polymorpha* have had and are having profound impacts on the communities in which they have invaded (references in Table 1), ecological interactions of these species in brackish water remain largely uninvestigated.

Perhaps no introduced marine mollusk in North America has had a greater impact than the periwinkle *Littorina littorea,* which colonized most of the Atlantic coast from Nova Scotia to New Jersey in only 30 years, between 1860 and 1890 (references in Table 1). Perhaps because little or no economic impact has been associated with this invasion, it has attracted relatively little notice globally as a classic example of an invasion, aquatic or terrestrial. *Littorina* has fundamentally altered the distribution and abundance of algae on rocky shores (references in Table 1), altered hard-bottom, soft-bottom, and salt marsh habitat dynamics (Bertness 1984) negatively interacted with native gastropods (reviewed above), dramatically altered the hermit crab shell resource (providing an abundant larger shell) and modified shell utilization and preference patterns of the native hermit crab *Pagurus longicarpus* (Blackstone 1986), and as grazing herbivores and vacuuming omnivores, may have important impacts on a wide variety of small invertebrates. such as barnacles, whose newly settled larvae are consumed in large numbers (see "Life Habit" review in Brenchley and Carlton 1983).

In summary, all but the snail *Ovatella* of the abundant species of introduced mollusks that have been studied have been shown to have dramatic impacts on the pre-existing structure of the communities in which they have invaded. These results would suggest that the extensive populations of those species not yet studied may also have had. or are having, substantial impacts on population dynamics and interactions among co-occurring species, both native and introduced. Numerous fruitful investigations remain to be undertaken.

Future Invasions

Predictions of what species will invade, and where and when invasions will occur, remain one of the more elusive aspects of biological invasion science (Mooney and Drake 1986; Drake et al. 1989). Thousands of species of marine and estuarine mollusks that occur in Europe. Africa. South America, Asia, and Australia overlap in basic environmental requirements with habitats that occur in North America. Selecting probable invasion candidates from this vast fauna. and predicting competitive, predatory, or other interactions with previously established molluscan species or ecological equivalents as potential mediators of successful establishment, is a frustrating task. It is doubtful. for example, if an examination of the Asian biota would have identified the clam *Potamocorbula amurensis,* among a background of scores of other estuarine taxa, as a high profile potential invader.

Nevertheless certain limited projections may be made. The New Zealand fresh and brackish water snail *Potamopygus antipodurum,* established in western Europe. and occurring in densities of up to 800,000 snails per square meter. is a probable future invader of eastern North American fresh and oligohaline habitats (JTC. C. L. Secor, and E. L. Mills, in preparation). Abundant fouling bivalves in India and Asia, such as the mussels *Modiolus striatulus* and *Limnoperna fortunei* (Morton 1977). may yet reach North America. If large scale inoculations of the Pacific oyster *Crassostrea gigas* on the Atlantic coast commence in the 1990s (as opposed to the many smaller previous releases). successful establishment may take place (presumably the species will be raised on the Atlantic coast from larvae or clean seed. and the introduction of associated organisms with large stocks of adult oysters will not take place).

Also predictable are the eventual detection of natural sets of the Japanese sea scallop *Patinopecten yessoensis* in British Columbia, the spreading of the European edible oyster *Ostrea edulis* from Rhode Island south and west into Long Island Sound, the establishment of the periwinkle *Littorina littorea* in San Francisco Bay if not elsewhere on the Pacific coast, the establishment of the New Zealand green lipped mussel *Perna canaliculus* (Carlton 1992a: 16) in California (to where it is now imported daily in large numbers for direct human consumption) and the spreading of the Asian clam *Potamocorbula amurensis* from San Francisco Bay to other bays on the Pacific coast.

Broadly, the recent appearances of *Rangia cuneata* in the Hudson River, of *Perna perna* in Texas, of two species of the zebra mussel *Dreissena* in the Great Lakes and thus much of the rest of North America, and of *Potamocorbula amurensis* in San Francisco Bay, argue strongly that future, ballast-water mediated invasions will continue to be a regular phenomenon in North America. On any day, perhaps any hour, it is likely that the larvae of dozens of species of mollusks are released into coastal waters of North America by ballast water. Similarly, steadily increasing local, national, and global pressures to expand mariculture industries through the importation of new candidate species will almost certainly mean the accidental (or intentional) release of novel species.

These predictions arise from the projection that the basic mechanisms of human-mediated transport of non-native species outlined at the beginning of this paper will remain in place for many years to come. This forecast is despite the existence of a number of international guidelines (including those of the International Council for the Exploration of the Sea, Carlton, 1989) that exist to prevent the release of detrimental species through fisheries and mariculture activities, and despite growing international awareness of the role of ballast water in transporting exotic species transoceanically and interoceanically. While our inability to always distinguish between certain mechanisms of introduction of exotic species may make full control difficult, identifying and quantifying the role of such mechanisms, followed by cooperative management efforts, are the necessary precursors to eventually modifying the rate of “chess play” of new invasions.

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