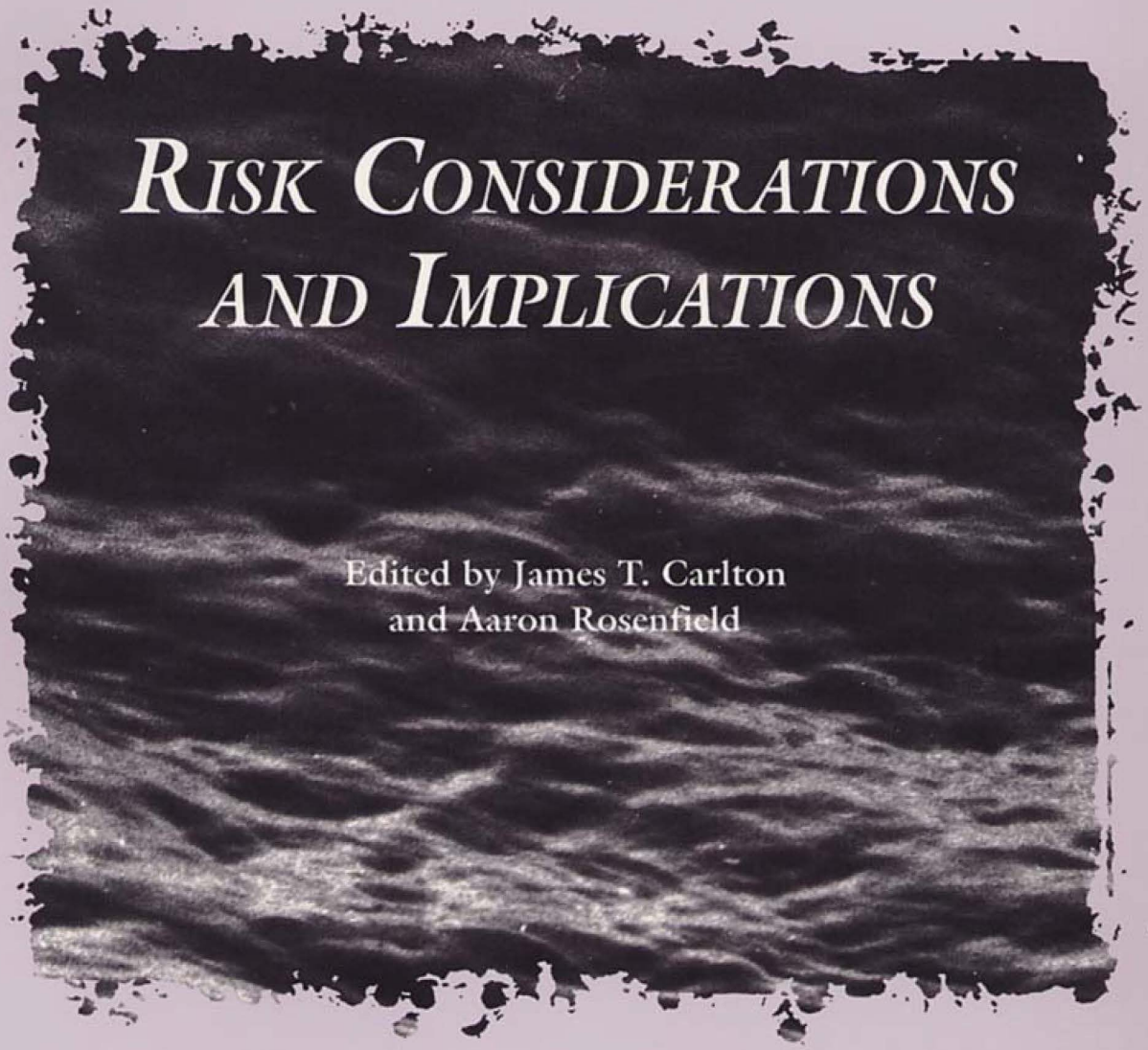
Molluscan Introductions and Transfers

Risk Considerations and Implications



Edited by James T. Carlton
and Aaron Rosenfield

A Maryland Sea Grant Publication
College Park, Maryland

Molluscan Introductions and Transfers

MOLLUSCAN INTRODUCTIONS AND TRANSFERS

RISK CONSIDERATIONS AND IMPLICATIONS

A Symposium Proceedings

Edited by James T. Carlton
and Aaron Rosenfield

A Maryland Sea Grant Publication
College Park, Maryland

Published by the Maryland Sea Grant College, University of Maryland, College Park.

Publication of this book is supported by grant #NA46RG0091 from the National Oceanic and Atmospheric Administration to the Maryland Sea Grant College and by Grant #NA90AA-D-SG184.

The papers in this book were presented at a special symposium, Molluscan Introductions and Transfers: Risk Considerations and Implications, presented at the 82nd Annual Meeting of the National Shellfisheries Association and the Shellfish Institute of North America, held April 4-5, 1990 in Williamsburg, Virginia. All the papers are reprinted with the permission of the Journal of Shellfish Research.

Copyright © 1994 Maryland Sea Grant College.

All rights reserved. No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording, or any information storage or retrival system, without permission in writing from Maryland Sea Grant.

Sea Grant is a federal-state-university partnership encouraging the wise stewardship of our marine resources through research, education and technology transfer.

University of Maryland Publication UM-SG-TS-94-02
ISBN: 0-943676-58-4

For information on Maryland Sea Grant publications, contact:

Maryland Sea Grant College
0112 Skinner Hall
University of Maryland System
College Park, Maryland 20742

Printed on recycled paper.

Contents

NOTE: When referencing these papers, please cite the original source: *Journal of Shellfish Research*. Volume, page numbers and year for each paper are as follows: Carlton and Rosenfield, 11(2):487, 1992; Carlton, 11(2):489-505, 1992; Carriker, 11(2):507-510, 1992; Mann, Burreson and Baker, 10(2):379-388, 1991; Lipton, Lavan and Strand, 11(2):511-519, 1992; Hackney, Kilgen and Kator, 11(2):521-533, 1992; Gaffney and Allen, 11(2):535-538, 1992; Ford, 11(2):539-546, 1992.

Contributors

Standish K. Allen, Jr.
Haskin Shellfish Research Laboratory
Rutgers University
Port Norris, New Jersey 08349

Patrick K. Baker
Virginia Institute of Marine Science
School of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062

Eugene M. Burreson
Virginia Institute of Marine Science
School of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062

Melbourne R. Carriker
College of Marine Studies
University of Delaware
Lewes, Delaware

James T. Carlton
Maritime Studies Program
Williams College—Mystic Seaport
50 Greenmanville Avenue
Mystic, Connecticut 06355

Susan E. Ford
Haskin Shellfish Research Laboratory
Rutgers University
Port Norris, New Jersey 08349

Patrick M. Gaffney
College of Marine Studies
University of Delaware
Lewes, Delaware 19958

Cameron Ray Hackney
Department of Food Science and Technology
Virginia Polytechnic Institute and Technology
and State University
Blacksburg, Virginia 24601

Howard Kator
School of Marine Science
Virginia Institute of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062

Marylin B. Kilgen
Department of Biology
Nicholls State University
Thibodaux, Louisiana 70310

Eileen F. Lavan
Marine Environmental and Estuarine Studies Program
University of Maryland
College Park, Maryland 20742

Douglas W. Lipton
Department of Agricultural and Resource Economics
University of Maryland
College Park, Maryland 20742

Roger Mann
Virginia Institute of Marine Science
School of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062

Aaron Rosenfield
Northeast Fisheries Science Center
National Marine Fisheries Service
Oxford, Maryland 21654

Ivar E. Strand
Department of Agricultural and Resource Economics
University of Maryland
College Park, Maryland 20742

Introduction to the Special Symposium on Mulluscan Introductions and Transfers: Risk Considerations and Implications

James T. Carlton and Aaron Rosenfield

The collection of papers that appears within these proceedings is the outcome of a Symposium entitled "Introductions and Transfers of Mollusks: Risk Considerations and Implications". The Symposium was held as part of the 82nd Annual Meeting of the National Shellfisheries Association in April 1990 in Williamsburg, Virginia. One paper from this Symposium was published earlier in this *Journal* (Mann et al. 1991). In addition to those papers that appear here, six other papers were presented orally during the Symposium. Unfortunately these latter papers were not completed in time to be included in this issue of the *Journal of Shellfish Research*. Although the editors would like to allow additional time, it was concluded that further delays would risk outdating the papers submitted by the rest of the Symposium participants.

The Mollusca occur world wide in extraordinary diversity, abundance, and distribution both in aquatic and terrestrial habitats. They are readily available and harvestable; with common sense and a little knowledge and care they are among the easiest of the invertebrates to collect, manipulate, transport, and maintain for extended periods using relatively uncomplicated conditions and inexpensive holding facilities. It is no wonder their exploitation for food, ornamentation, dye materials, tools, construction material, music, toys, utensils, money, and shell collections has been practiced for millennia. More recent imaginative and remarkable advances have been made in the use of mollusks for aquaculture, genetic engineering (including the development of transgenics), toxicology, and biomedicine. The use and application of mollusks in fields such as these necessarily involve the shipment and importation, that is, the translocation of mollusks from one location to another. As can be deduced from the title of this Symposium considerable apprehension and concern exists today over the risks or dangers associated with the potential movement of molluscan species from one ecosystem to another. These movements create a strong potential for the introduction of new species or the infusion of new genetic material into regions where they may have profound impacts on native species.

In very recent years the subject of the natural and human mediated invasions of nuisance species into ecosystems where they have not been resident before has and continues to be the subject of a great deal of attention. This attention is particularly strong among individuals and groups associated with intentional movements of molluscan species, not only for aquaculture purposes but also for scientific study, aquarium use, new product development and depuration. In addition others are interested in the unplanned, accidental translocation of exotic mollusc species and transfers or indigenous species, either of which when released into new environments may become nuisances themselves or act as carriers for other plants or animals that become pests, parasites, pathogens, or competitors with resident organisms. There are always risks associated with translocation of animals and plants resulting in impacts that could be either positive or negative from the viewpoints of environmental and resource sustainability. Careful consideration must be given to the ecological, genetic, sociological, economic, aesthetic and political impacts that may result from undesirable introductions regardless if they are deliberate or accidental. On the other hand, the use of mollusks for purposes of aquaculture, stock enhancement and improvement, sanitation, recreation, science and technology, education, and food production could bring enormous benefits. However, such programs must be well thought out and carefully designed, and must be considerate of maintaining environmental integrity and ecological balance.

This Symposium thus considers some of these risks and benefits involved with both known and anticipated introductions and transfers of mollusks, and discusses the potential implications, past, present, and future, of these movements.

We are most grateful to the National Marine Fisheries Service Office of Research and Environmental Information for providing funding for this Symposium, and particularly to Dr. Glenn A. Flittner and Dr. Carolyn Brown for their generous support and help in planning and conducting the Symposium.

LITERATURE CITED

Mann, R., E. M. Burreson & P. K. Baker. 1991. The decline of the Virginia oyster fishery in Chesapeake Bay: considerations for introduction of a non-endemic species, *Crassostrea gigas* (Thunberg, 1793). *J. Shellfish Res.* 10:373–388.

Introduced Marine and Estuarine Mollusks of North America: An End-of-the-20th-Century Perspective

James T. Carlton

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 bartschi*) have been transported from their apparently native southern ranges to more northern 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 *Tectarius 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 shipworm *Teredo navalis*. Nineteenth century or earlier shipping has been implicated in creating the modern 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 *Sabia 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 Elkhorn 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 fornicata, Crepidula plana, Batillaria attramentaria, Urosalpinx cinerea, Ceratostoma inornatum*, and *Ovatella myosotis*, and the bivalves *Mytilus galloprovincialis, Musculista senhousia, Venerupis philippinarum, Myra arenaria, Teredo navalis*, and *Lyrodus pedicellatus*.

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		
Littorina 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		
Batillaria 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: Elkhorn Slough (1951). M: COI	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.

continued on next page

TABLE 1.

continued

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. Larned, 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 oyster drill)	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. Larned, 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).
Nassariidae		
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: COI	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 myosotis (Draparnaud, 1801) (=*Phytia 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 (Linnaeus, 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.

continued on next page

TABLE 1.

continued

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

continued on next page

TABLE 1.

continued

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/oo, W. Walton, personal communication, 1992). M: from Europe to the Great Lakes (1988), BW; within North America: see Carlton, 1992b	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.

continued on next page

TABLE 1.

continued

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		
Potamocorbula 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 Roch, 1929 (+)	NW PACIFIC/NE Pacific: BC: Ladysmith Harbor (1981). M: COI (in wooden oyster boxes)	Popham 1983.
Teredo bartschi W. Clapp, 1923 (Bartsch shipworm)	NW ATLANTIC/NW Atlantic: NJ: Barnegat 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 Barnegat Bay in thermal effluents, but still established in Long Island Sound heated power plant effluents at Millstone.
Teredo navalis 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 Barnegat 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

continued on next page

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
Musculista 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 littorea	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, seagrasses, 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 geologically 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 saxatilis* 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 *Littorina 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 *Potamopyrgus antipodarum*, 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.

ACKNOWLEDGMENTS

For generously supplying records and advice, I thank R. Tucker Abbott, the late Frank Bernard, Timothy Carey, John Chapman, Kenneth Chew, Eugene Coan, Michael Helm, K. Elaine Hoagland, Robert Forsyth, John Karlsson, the late Myra Keen, Scott Larned, Harry Lee, Christopher Letts, Roger Mann, James McLean, Arleen Navarret, Kathleen Sayce, Paul Scott, Rudolf Stohler, Ruth Turner, Geerat Vermeij, William Walton, and Mary Wicksten. My graduate students at the University of Oregon Institute of Marine Biology (OIMB), including Patrick Baker, Jody Berman, Chad Hewitt, and John Megahan, my postdoctoral associates at OIMB, including Richard Everett, Jonathan Geller, and Gregory Ruiz, and my constant field companion, Debby Carlton, were my coworkers in the field in Coos Bay. This work began as a revision of G (no period follows his first name, G) Dallas Hanna's 1966 Pacific coast monograph, an undertaking I began in 1969 under the aegis of the late Allyn G. Smith, the late Leo G. Hertlein, the late Doc Hanna, Charles R. Stasek, and Victor Zullo, all then at the California Academy of Sciences in San Francisco. This work was supported in part by a National Science Foundation (NSF) National Needs Postdoctoral Fellowship at the Woods Hole Oceanographic Institution, by NSF Grant No. DAR-8008450 and by the NOAA/Oregon Sea Grant College Program, project R/EM-19. Stimulus to prepare this brief overview was provided by the organization of a special symposium, "Molluscan Introductions and Transfers: Risk Considerations and Implications," held at the 82nd Annual Meeting of the National Shellfisheries Association on April 4–5, 1990, in Williamsburg, Virginia.

LITERATURE CITED

Abbott, R. T. 1974. American Seashells. 2nd ed. Van Nostrand Reinhold, N.Y., 663 pp.

Anderson, G. J., M. B. Miller & K. K. Chew. 1982. A guide to Manila clam aquaculture in Puget Sound. University of Washington, Sea Grant Program, WSG-82-4, 45 pp.

Barrett, E. M. 1963. The California oyster industry. *Calif. Dept. Fish Game Fish Bull.* 123:1–103.

Berman, J. & J. T. Carlton. 1991. Marine invasion processes: interactions between native and introduced marsh snails. *J. Exp. Mar. Biol. Ecol.* 150:267–281.

Bernard, F. R. 1979. Identification of the living *Mya* (Bivalvia: Myoida). *Venus (Jap. J. Malacol.)* 38:185–204.

Bernard, F. R. 1983. Catalogue of the living Bivalvia of the Eastern Pacific Ocean: Bering Strait to Cape Horn. *Can. Spec. Publs. Fish. Aquatic Sci.* 61:1–102.

Bertness, M. D. 1984. Habitat and community modification by an introduced herbivorous snail. *Ecology* 65:370–381.

Bishop, J. A. 1992. *Tectarius muricatus* (Linnaeus, 1758) from the northern Gulf of California, Mexico. *Festivus* 24:81–82.

Blackstone, N. W. 1986. Variation of cheliped allometry in a hermit crab: the role of introduced periwinkle shells. *Biol. Bull.* 171:379–390.

Bourne, N. 1979. Pacific oysters, *Crassostrea gigas* (Thunberg). In: British Columbia and the South Pacific Islands. In Exotic Species in Mariculture, R. Mann, ed., MIT Press, Cambridge, MA, 1–53.

Bourne, N. 1982. Distribution, reproduction, and growth of Manila clam, *Tapes philippinarum* (Adams and Reeve) in British Columbia. *J. Shellfish. Res.* 2:47–54.

Brenchley, G. A. 1982. Predation on encapsulated larvae by adults: effects of introduced species on the gastropod *Ilyanassa obsoleta*. *Mar. Ecol. Prog. Ser.* 9:255–262.

Brenchley, G. A. & J. T. Carlton. 1983. Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. *Biol. Bull.* 165:543–558.

Burch, J. 1962. How to know the Eastern land snails. Wm. C. Brown Co. Publs., Dubuque, Iowa, 214 pp.

Carlton, J. T. 1969. *Littorina littorea* in California (San Francisco and Trinidad Bays). *Veliger* 11:283–284.

Carlton, J. T. 1975. Introduced intertidal invertebrates. In: Light's Manual: Intertidal Invertebrates of the Central California Coast, R. I. Smith & J. T. Carlton, eds. 3rd ed., University of California Press, Berkeley, pp. 17–25.

Carlton, J. T. 1979a. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. dissertation, University of California, Davis, 904 pp.

Carlton, J. T. 1979b. Introduced intertidal invertebrates of San Francisco Bay. In: San Francisco Bay: The Urbanized Estuary, T. J. Conomos, ed., American Association for the Advancement of Science, Pacific Division, San Francisco, pp. 427–444.

Carlton, J. T. 1982. The historical biogeography of *Littorina littorea* on the Atlantic coast of North America, and implications for the interpretation of the structure of New England intertidal communities. *Malacol. Rev.* 15:146.

Carlton, J. T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Ocean. Mar. Biol. Ann. Rev.* 23:313–371.

Carlton, J. T. 1987. Mechanisms and patterns of transoceanic marine biological invasions in the Pacific Ocean. *Bull. Mar. Sci.* 41:467–499.

Carlton, J. T. 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conserv. Biol.* 3:265–273.

Carlton, J. T. 1992a. The dispersal of living organisms into aquatic ecosystems: the mechanisms of dispersal as mediated by aquaculture and fisheries activities. In: Dispersal of Living Organisms into Aquatic Ecosystems, A. Rosenfield & R. Mann, eds. The University of Maryland, College Park, Maryland, pp. 13–45.

Carlton, J. T. 1992b. Dispersal mechanisms of the zebra mussel *Dreissena polymorpha*. In: Zebra Mussels: Biology, Impacts, and Control, T. F. Nalepa & D. W. Schloesser, eds., Lewis Publishers, Inc. (CRC Press), Boca Raton, FL, pp. 677–697.

Carlton, J. T., D. P. Cheney & G. J. Vermeij, eds. 1982. Ecological effects and biogeography of an introduced marine species: the periwinkle, *Littorina littorea*. Abstract from a Minisymposium and Workshop, Nahant, 1981. *Malacol. Rev.* 15:143–150.

Carlton, J. T. & B. Roth. 1975. Phylum Mollusca: shelled gastropods. In: Light's Manual: Intertidal Invertebrates of the Central California Coast, R. I. Smith & J. T. Carlton, eds., 3rd ed., University of California Press, Berkeley, pp. 467–514.

Carlton, J. T., J. K. Thompson, L. E. Schemel & F. H. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. *Mar. Ecol. Prog. Ser.* 66:81–94.

Cernohorsky, W. O. 1984. Systematics of the family Nassariidae (Mollusca: Gastropoda). *Bull. Auckland Inst. Mus.* 14, 356 pp.

Chaney, H. W. 1992. A note on exotic species. *Festivus* 24:83.

Chew, K. K. 1960. Study of food preference and rate of feeding of Japanese oyster drill, *Ocinebra japonica* (Dunker). U.S. Fish Wildlife Serv. Spec. Sci. Rept. Fish. No. 365, 27 pp.

Chew, K. K. 1979. The Pacific oyster (*Crassostrea gigas*) in the west coast in the United States. In Exotic Species in Mariculture, R. Mann, ed., MIT Press, Cambridge, MA, 54–82.

Chew, K. K. 1990. Global bivalve shellfish introductions. *World Aquaculture* 21:9–22.

Clarke, A. H., Jr. 1972. *Clanculus microdon ater* Pilsbry in British Columbia. *Can. Fld. Natl.* 86:165–166.

Counts, C. L., III. 1986. The zoogeography and history of the invasion of the United States by *Corbicula fluminea* (Bivalvia: Corbiculidae). *Amer. Malacological Bull. Spec. Bull.* 2:7–39.

Counts, C. L., III. 1991. *Corbicula* (Bivalvia: Corbiculidae). Part 1. Catalog of fossil and recent nominal species. Part 2. Compendium of zoogeographic records of North America and Hawaii, 1924–1984. *Tryonia* 21:1–134.

Cowan, I. McT. 1974. *Sabia conica* (Schumacher) on the Pacific coast of North America. *Veliger* 16:290.

Crane, J. M., L. G. Allen & C. Eisemann. 1975. Growth rate, distribution, and population density of the northern quahog *Mercenaria mercenaria* in Long Beach, California. *Calif. Fish Game* 61:68–94; errata, 61:261.

Davis, G. M. 1979. The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. *Acad. Natl. Sci. Phil. Mon.* 20, 120 pp.

Davis, H. C. & A. Calabrese. 1969. Survival and growth of larvae of the European oyster (*Ostrea edulis* L.) at different temperatures. *Biol. Bull.* 136:193–199.

DeKay, J. E. 1843. Zoology of New York. Part V. Mollusca. Carroll & Cook, Albany, 271 pp.

Diaz, R. J. 1974. Asiatic clam, *Corbicula manilensis* (Philippi), in the tidal James River, Virginia. *Ches. Sci.* 15:118–120.

Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek & M. Williamson, eds., 1989. Ecology of biological invasions: A global perspective. John Wiley & Sons, 528 pp.

Duggan, E. P. 1963. Report of non-indigenous marine shells collected in the state of Washington. *Veliger* 6:112.

Eckelbarger, K. J. & D. J. Reish. 1972. Effects of varying temperatures and salinities on settlement, growth, and reproduction of the wood-boring pelecypod, *Lyrodus pedicellatus*. *Bull. So. Calif. Acad. Sci.* 71:116–127.

Elsey, C. R. 1933. Oysters in British Columbia. *Bull. Biol. Bd. Can.* 34:1–34.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen and Co., Ltd., London, 181 pp.

Fisher-Piette, J. & B. Metivier. 1971. Revision des Tapetinae (mollusques bivalves). *Mem. Mus. Natn. Hist. Nat. Paris (Zool.)* 71:1–106.

Foster, N. R. 1991. Intertidal bivalves: a guide to the common marine bivalves of Alaska. University of Alaska Press, Fairbanks, AK, 152 pp.

Galtsoff, P. S. 1932. Introduction of Japanese oysters into the United States. *U.S. Bur. Fish. Fish. Circular* 12: 16 pp.

Gaumer, T. & P. Farthing. 1990. Welcome stranger. *Oregon Wildlife* 46:10–11.

Grave, B. H. 1928. Natural history of shipworm, *Teredo navalis*, at Woods Hole, Massachusetts. *Biol. Bull.* 55:260–282.

Griffiths, R. W., D. W. Schloesser, J. H. Leach & W. P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Can. J. Fish. Aquat. Sci.* 48:1381–1388.

Hanna, G D. 1966. Introduced mollusks of western North America. *Occ. Pap. Calif. Acad. Sci.* 48:1–108.

Hebert, P. D. N., C. C. Wilson, M. H. Murdoch & R. Lazar. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. *Can. J. Zool.* 69:405–409.

Hendrickx, M. E. 1980. Range extensions of three species of Teredinidae (Mollusca: Bivalvia) along the Pacific coast of America. *Veliger* 23: 93–94.

Hertz, J. & C. M. Hertz. 1992. Unusual finds at Mission Bay, San Diego. *Festivus* 24:61–62.

Hicks, D. W. & J. W. Tunnell. 1993. Invasion of the south Texas coast by the edible brown mussel, *Perna perna* (Linnaeus, 1758). *Veliger* 36(1) *in press*.

Hidu, H. & R. E. Lavoie. 1991. The European oyster, *Ostrea edulis* L. in Maine and eastern Canada. In: Estuarine and marine bivalve mollusk culture, W. Menzel, ed. CRC Press, Inc., Boca Raton, FL, pp. 35–46.

Hoagland, K. E. 1981. Life history characteristics and physiological tolerances of *Teredo bartschi*, a shipworm introduced into two temperate zone nuclear power plant effluents. *Proc. Third Intern. Conf. Waste Managmt. & Utilization Conference*, S. S. Lee & S. Sengupta, eds., 14 pp.

Hoagland, K. E. 1986. Effects of temperature, salinity, and substratum on larvae of the shipworms *Teredo bartschi* Clapp and *T. navalis* Linnaeus (Bivalvia: Teredinidae). *Amer. Malacol. Bull.* 4:898–899.

Hoagland, K. E. & R. D. Turner. 1980. Range extensions of teredinids (shipworms) and polychaetes in the vicinity of a temperate-zone nuclear generating station. *Mar. Biol.* 58:55–64.

Hopkins, S. H. & J. D. Andrews. 1970. *Rangia cuneata* on the east coast: thousand mile range extension, or resurgence? *Science* 167:868–869.

Jacobson, M. K. 1953. *Congeria leucophaeata*(Conrad) in the Hudson River. *Nautilus* 66:125–127.

Kay, E. A. 1979. Hawaiian Marine Shells. University of Hawaii Press, 653 pp.

Keen, A. M. 1969. *Laternula* living on the Pacific coast? *Veliger* 11:439.

Keen, A. M. 1971. Sea Shells of Tropical West America. 2nd ed. Stanford University Press, Stanford, CA, 1064 pp.

Kemp, P. & M. D. Bertness. 1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proc. Natl. Acad. Sci.* 81:811–813.

Kennelly, D. H. 1969. Marine shells of southern Africa. Books of Africa, Cape Town, SA, 123 pp.

Ketchen, K. S., N. Bourne & T. H. Butler. 1983. History and present status of fisheries for marine fishes and invertebrates in the Strait of Georgia, British Columbia. *Can. J. Fish. Aquat. Sci.* 40:1095–1119.

Koehn, R. K. 1991. The genetics and taxonomy of species in the genus *Mytilus*. *Aquaculture* 94:125–145.

Kofoid, C. A. & R. C. Miller. 1927. Biological section. In: Marine borers and their relation to marine construction on the Pacific coast, C. L. Hill & C. A. Kofoid, eds., San Francisco, CA, pp. 188–343.

Kozloff, E. N. & L. H. Price. 1987. Phylum Mollusca: Class Gastropoda. In: Marine invertebrates of the Pacific Northwest, E. N. Kozloff, eds., University of Washington Press, Seattle, WA, pp. 193–302.

Lee, H. G. 1987. Immigrant mussel settles in Northside generator. *The Shell-O-Gram* (Jacksonville Shell Club, Jacksonville, FL) 28:7–9.

Loosanoff, V. L. 1962. Gametogenesis and spawning of the European oyster, *O. edulis*, in waters of Maine. *Biol. Bull.* 122:86–94.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat.* 112:23–39.

Lubchenco, J. 1983. *Littorina* and *Fucus:* effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64: 1116–1123.

Lubchenco, J. 1986. Relative importance of competition and predation: early colonization by seaweeds in New England. In: Community ecology, J. Diamond & T. J. Case, eds., Harper and Row, NY, pp. 537–555.

MacDonald, K. B. 1969a. Quantitative studies of salt marsh mollusc faunas from the North American Pacific coast. *Ecol. Mono.* 39:33–60.

MacDonald, K. B. 1969b. Molluscan faunas of Pacific coast salt marshes and tidal creeks. *Veliger* 11:399–405.

Mann, R., ed. 1979. Exotic species in mariculture. MIT Press, Cambridge, MA, 363 pp.

Mann, R., E. M. Burreson & P. K. Baker. 1991. The decline of the Virginia oyster fishery in Chesapeake Bay: considerations for introduction of a non-endemic species, *Crassostrea gigas* (Thunberg, 1793). *J. Shellfish Res.* 10:379–388.

May, B. & J. E. Marsden. 1992. Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. *Can. J. Fish. Aquatic Sci.* 49:1501–1506.

Marelli, D. C. & S. Gray. 1985. Comments on the status of recent members of the genus *Mytilopsis* (Bivalvia: Dreissenidae). *Malacol. Rev.* 18:117–122.

McDonald, J. H. & R. K. Koehn. 1988. The mussels *Mytilus galloprovincialis* and *M. trossulus* on the Pacific coast of North America. *Mar. Biol.* 99:111–118.

Meehan, B. W., J. T. Carlton & R. Wenne. 1989. Genetic affinities of the bivalve *Macoma balthica* from the Pacific coast of North America: evidence for recent introduction and historical distribution. *Mar. Biol.* 102:235–241.

Mooney, H. A. & J. A. Drake, editors. 1986. Ecology of biological invasions of North America and Hawaii. Ecological Studies 58. Springer-Verlag, 321 pp.

Morrison, J. P. E. 1963a. *Cecina* from the state of Washington. *Nautilus* 76:150–151.

Morrison, J. P. E. 1963b. Notes on American *Siphonaria*. *Ann. Repts. Amer. Malacol. Union* 1963:7–9.

Morrison, J. P. E. 1972. Mediterranean *Siphonaria:* west and east—old and new. *Argamon (Israel J. Malacol.)* 3:51–62.

Morton, B. 1974. Some aspects of the biology, population dynamics, and functional morphology of *Musculista senhousia* Benson (Bivalvia, Mytilidae). *Pac. Sci.* 28:19–33.

Morton, B. 1977. An estuarine bivalve (*Modiolus striatulus*) fouling raw water supply systems in west Bengal, India. *J. Inst. Water Engin. Sci.* 31:441–453.

Murphy, R. C. 1985a. Factors affecting the distribution of the introduced bivalve, *Mercenaria mercenaria*, in a California lagoon—the importance of bioturbation. *J. Mar. Res.* 43:673–692.

Murphy, R. C. 1985b. Bivalve contribution to benthic metabolism in a California lagoon. *Estuaries* 8:330–341.

Nalepa, T. F. & D. W. Schloesser, eds., 1992. Zebra Mussels: Biology, Impacts, and Control. Lewis Publishers, Inc. (CRC Press), Boca Raton, Fl.

Nelson, T. C. 1946. On the need for developing new strains of oysters through selective breeding of domestic stock, cross breeding with other species and the introduction of species from other areas. *Proc. Natl. Shellfish. Assoc.* 1946:1–7.

Nichols, F. H. and J. K. Thompson. 1985. Persistence of an introduced mudflat community in South San Francisco Bay, California. *Mar. Ecol. Prog. Ser.* 24:83–97.

Nichols, F. H., J. K. Thompson & L. E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. *Mar. Ecol. Prog. Ser.* 66:95–101.

Petraitis, P. S. 1989. Effects of the periwinkle *Littorina littorea* (L.) and of intraspecific competition on growth and survivorship of the limpet *Notoacmea testudinlis* (Muller). *J. Exp. Mar. Biol. Ecol.* 125:99–115.

Popham, J. D. 1983. The occurrence of the shipworm, *Lyrodus* sp., in Ladysmith Harbour, British Columbia. *Can. J. Zool.* 61:2021–2022.

Quayle, D. B. 1964. Distribution of introduced marine Mollusca in British Columbia waters. *J. Fish. Res. Bd. Can.* 21:1155–1181.

Quayle, D. B. 1969. Pacific oyster culture in British Columbia. *Fish. Res. Bd. Can. Bull.* 169, 192 pp.

Race, M. S. 1982. Competitive displacement and predation between introduced and native mud snails. *Oecologia* 54:337–347.

Radwin, G. E. & A. D'Attilio. 1976. Murex shells of the world. An illustrated guide to the Muricidae. Stanford University Press, Stanford, CA, 284 pp.

Rehder, H. A. 1937. *Congeria leucophaeata* (Con.) in the Hudson River. *Nautilus* 50:142–143.

Richards, B. R., R. E. Hillman & N. J. Maciolek. 1984. Shipworms. In: M. J. Kennish & R. A. Lutz, eds., Ecology of Barnegat Bay, New Jersey. Springer-Verlag, New York, pp. 201–225.

Russell, J. L. 1839. Familiar notice of some of the shells found in the limits of the Essex County, Massachusetts: with reference to descriptions and figures. *J. Essex Co. Nat. Hist. Soc.* (Salem, MA), 1:47–76.

Sanukida, S., H. Okamoto & M. Hitomi. 1981. On the behavior of the indicator species of marine bottom pollution. *Bull. Jap. Soc. Sci. Fish.* 47:863–869.

Sarver, S. K., M. C. Landrum & D. W. Foltz. 1992. Genetics and taxonomy of ribbed mussels (*Geukensia* spp.). *Mar. Biol.* 113:385–390.

Seapy, R. R. 1974. The introduced semelid bivalve *Theora* (*Endopleura*) *lubrica* in bays of southern California. *Veliger* 16:385–387.

Seed, R. 1992. Systematics, evolution, and distribution of mussels belonging to the genus *Mytilus:* an overview. *Amer. Malacol. Bull.* 9: 123–137.

Squire, D. R. 1973. The Japanese oyster drill, *Ocenebra japonica* Dunker, in Netarts Bay, Oregon. *Proc. Natl. Shellfish. Assoc.* 63:10.

Stimpson, W. 1851. Shells of New England. A revision of the synonymy of the testaceous mollusks of New England. Phillips, Sampson, and Co., Boston, 56 pp.

Stohler, R. 1962. *Busycotypus canaliculatus* in San Francisco Bay. *Veliger* 4:211–212.

Strayer, D. L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. *Can. J. Fish. Aquatic Sci.* 48:1389–1395.

Turgeon, D. D., ed. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks. *Amer. Fish. Soc. Spec. Publ.* 16:1–277.

Turner, H. J. 1949. Growth of the North Pacific oyster in New England. In: Report on investigations of methods of improving the shellfish resources of Massachusetts. Commonwealth of Massachusetts, Woods Hole Oceanographic Institution, pp. 8–10.

Turner, H. J. 1950. Growth of the North Pacific oyster, *Ostrea gigas*, in Massachusetts. In: Report on investigations of methods of improving the shellfish resources of Massachusetts. Commonwealth of Massachusetts, Woods Hole Oceanographic Institution, p. 31.

Turner, R. D. 1966. A survey and illustrated catalogue of the Teredinidae (Mollusca: Bivalvia). *Mem. Comp. Zool. Harvard Univ.*, 265 pp.

Vermeij, G. J. 1982a. Phenotypic evolution in a poorly dispersing snail after arrival of a predator. *Nature* 299:349–350.

Vermeij, G. J. 1982b. Environmental change and the evolutionary history of the periwinkle (*Littorina littorea*) in North America. Evolution 36:561–580.

Verrill, A. E. 1880. Occurrence at Newport, R.I., of two littoral species of European shells not before recorded as American. *Amer. J. Sci.* 20:250–251.

Welch, W. R. 1966. The European oyster, *Ostrea edulis*, in Maine. *Proc. Natl. Shellfish. Assoc.* 54:7–23. (not 1963 as usually cited)

Whitlatch, R. B. 1974. Studies on the population ecology of the salt marsh gastropod *Batillaria zonalis*. *Veliger* 17:47–55.

Whitlatch, R. B. & S. Obrebski. 1980. Feeding selectivity and coexistence in two deposit-feeding gastropods. *Mar. Biol.* 58:219–225.

Wicksten, M. K. 1978. Checklist of marine mollusks at Coyote Point Park, San Francisco Bay, California. *Veliger* 21:127–130.

Yamada, S. B. 1982. Growth and longevity of the mud snail *Batillaria attramentaria*. *Mar. Biol.* 67:187–192.

Yamada, S. B. & R. A. Mansour. 1987. Growth inhibition of native *Littorina saxatilis* (Olivi) by introduced *L. littorea* (L). *J. Exp. Mar. Biol. Ecol.* 105:187–196.

Introductions and Transfers of Mollusks: Risk Considerations and Implications

Melbourne R. Carriker

Writings on ecological biogeography provide a global historical perspective for presentations to be given at this symposium (Ekman 1953, Briggs 1974, Vermeij 1978, Pielou 1979, Cox and Moore 1985, Mooney and Drake 1986). In the course of geologic epochs, floral and faunal populations of the world have become naturally distributed into generally defined geographic areas whose boundaries have expanded or retreated over the centuries. In quite recent geologic history, however, humans have been altering this pattern critically, wittingly and sometimes unwittingly, manipulating artificially the redistribution of many species populations. Molluscs have been no exception. These introductions and transfers have occurred, sometimes beneficially, more often in muddled uncontrolled ways, and occasionally with "disastrous backlash consequences" to the receiving communities (Odum 1971, Rosenfield and Kern 1979, Mooney and Drake 1986). Elton is quoted as writing ". . . about this spate of invasions . . . make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora" (Dobson and May 1986)!

In this overview I introduce the symposium, consider the significance of artificial dispersal of marine molluscs, and whether the reportedly worrisome problems of these invasions are exaggerated or real. Speakers in the symposium will no doubt set me straight, and bring us all up-to-date on the problems, advantages, and safety practices related to human-directed introductions and transfers of commercial and potentially commercial marine molluscs.

That dispersal has been occurring with increasing intensity, is confirmed by many biological surveys. Results of these show that marine molluscan biota, especially commercial estuarine and coastal populations, continue to be moved about widely (for example, Korringa 1942, Allen 1953, Carriker 1955, Hanna 1966, Ansell 1968, Mann 1979, Counts 1983). Large scale global intermingling, fueled by an increasing commercial market for edible molluscs, will undoubtedly accelerate its pace.

But why the flap over the fact that several molluscan species populations are becoming geographically homogeneous? Why not adopt the noninterference attitude of "let nature take its course"? Some would suggest that, anyway, little can be done about the problem, and besides some invasions can be beneficial. Take for example, the case of the early, little-controlled importation of *Crassostrea gigas* to the West Coast of the United States, which reaped a valuable commercial industry, a recreational fishery, and a seed-producing operation (Bourne 1979, Chew 1979).

But alas! because an introduction has been profitable in one venture does not guarantee that others will be also. Courtney and Robins (1989) put it this way: "What is happening is at best a lottery in which an occasional lucky or even well thought-out success is replayed, only to result in losses in the form of noncorrectable environmental mistakes of varying severity."

If invasions do constitute a gamble, we should next explore the consequences of uncontrolled introductions and transfers. Three major sequels come to mind: a) a wide spectrum of other organisms can piggyback on or in the invaders, b) potential genetic changes can occur in both invaders and residents, and c) physical alteration of the invaded habitat can result (Sindermann 1970, 1977, Vermeij 1978, Bourne 1979, Rosenfield and Kern 1979, Courtney and Taylor 1986, Ward 1986, Fisher 1988). Let's consider these consequences in more detail:

a) Organisms carried on, or within invaders, for example, could include:

- Disease microorganisms (viruses, bacteria, fungi, yeasts, sporozoans, ciliates, dinoflagellates),
- Multicellular parasites (copepods, trematodes, cestodes, odostomid snails, pinnotherid crabs),
- Predators, especially their larvae and young (muricid and naticid snails, conchs, octopuses, crabs),
- Competitors contending for food and space (barnacles, bryozoans, sea squirts, chitons, limpets, other commercial bivalves).

In this lengthy list, disease microorganisms and parasites with a single host and with direct waterborne transmission and short generation times, are potentially the most pernicious in cultivated molluscan populations (Sindermann 1970, 1977, Dobson and May 1986). The likelihood of introductions of disease microorganisms is very high (Fisher 1988); and because checks and balances in the new habitat are rarely the same as in the original environment, invading microorganisms are less apt to be restrained. Because of their long association with, and natural immunity to their hosts, pathogens carried by invaders can have deleterious effects on unprotected resident species. Unquestionably, diseases will continue a significant problem in mariculture; the limiting factor in their control is the meager knowledge available about them (Sindermann 1970). Nonetheless, Sindermann (1970) is optimistic about their eventual control. Little, also, is known about multicellular parasites: how they become established in new hosts remains essentially unexplored (Fisher 1988).

b) The genetic consequences of introductions and transfers of molluscan species can be examined instructively with reference to how readily they will hybridize. In this context, closely related invading and native species will produce hybrids differing in fitness from that of the natives. If survival and reproduction of these hybrids is greater than that of the natives, it is probable that invaders carry genes, which in combination with natives genes, are advantageous. The rapid introgression of favorable genes will likely decrease the distinctiveness of the native species—with unpredictable consequences. If fitness of hybrids is inferior to that of the natives, then introgression of alien genes will probably decrease the fitness of hybrids in the short term; whether reduced fitness persists, will be determined by whether or not it is eliminated by natural selection. As to whether distantly related species will hybridize, is probably not possible to predict. If they should,

little genetic interaction can be expected. It is thus quite clear that it is possible to assess only short term genetic interactions between invaders and natives; those occurring after acclimation of invaders to the invaded habitat are not foreseeable (S. Allen, personal communication). It is also evident that monitoring of these hybrid species, if they occur, is difficult—if not impossible (Andrews 1979, Newkirk 1979, Courtney and Taylor 1986, Regal 1986, Pimentel et al. 1989, Tiedje et al. 1989).

c) A third consequence of uncontrolled molluscan invasions could include alteration of the ecosystem by invaders as well as by their genetically modified descendents. Changes could take place in the physical structure of the habitat, redistribution of populations, or trophic interactions, resulting in a modified ecological balance not necessarily commercially beneficial. Unfortunately, it is not yet possible accurately to predict the ecological impact of molluscan invaders (Courtney and Taylor 1986, Pimentel et al. 1989).

Indisputably, then, intentional and accidental spreading of molluscan species about the rim of the world-ocean can be dangerously risky. But why some species are extremely successful invaders, while close relatives may not be (Ehrlich 1986), and some habitats are colonized while others are not, is still a puzzle (Cox and Moore 1985). Ekman (1953) observed almost four decades ago that organisms become distributed in conformity with their genetic nature, which is adapted to specific environmental conditions.

It follows, consequently, that successful geographic dispersal is the product of an interaction between physiological properties of the organism and the quality of the environment. A case in point is estuarine species, which though broadly tolerant to a widely fluctuating complex of ecological factors (Hedgpeth 1957, Carriker 1967), only rarely invade oceanic habitats; and conversely, oceanic species seldom successfully move into sharp estuarine gradients. On the other hand, successful invasion by estuarine species into other brackish waters, especially at similar latitudes does occur—not only undesignedly on bottoms of ships and in their holds, but also through intentional human ventures (Allen 1953). Natural barriers to dispersal are also imposed by latitudinal thermal zones along coasts, as well as by differences in aerial exposure on intertidal-subtidal reaches. Human enterprises, ironically enough, have aided the insidious, highly successful spread of some species by inadvertently making available ecologically "open" habitats (Mooney et al. 1986); deplorable examples are the catastrophic invasion of human-made waterways by Asian clams of the genus *Corbicula* (Counts 1983, Mooney et al. 1986), and the devastating infestation of the Great Lakes by the zebra mussel *Dreissena polymorpha* (Garton and Haag 1989) called "an ecological disaster of oil-spill proportions" (D. Israelson, Toronto Star, Canada, March 12, 1990). Most recently word has come (Williams 1990) that there are at least three projects in the greater Caribbean region raising Pacific giant clams (*Tridacna* sp.); whether these molluscs have been properly screened for potential pathogens has yet to be determined.

Can biological (morphological, physiological, reproductive, genetic, behavioral, etc.) characteristics of successful invaders be identified with any degree of reliability? Probably not. Nonetheless, Ehrlich (1986) has come up with the following possible attributes of potentially successful invaders: abundance in the native habitat, polyphagous, short reproductive cycles, high genetic variability, fertilized females able to colonize alone, larger in size than most relatives, associated with *Homo sapiens*, and able to function well in a wide range of physical-chemical environmental factors. At this stage in the advancement of biology, identification of even a few of these attributes would not be easy, if indeed possible. Hence, it is no surprise that prediction with certainty of successful invasions is not yet within our grasp (Mooney and Drake 1986).

In view of the serious risks of introductions and transfers, concerned biologists and managers in many countries have been developing strict policies and procedures to control them. The latest revision of guidelines for control encompasses a worldwide program. The guidelines are summarized in the ICES "Codes of practice and manual of procedures for consideration of introductions and transfers of marine and freshwater organisms" (Turner 1988). A section on molluscs is included. A rigorous procedure for limiting risks of introductions of shellfish diseases has also been prepared by Sindermann (1970, 1977), who cautions that even with safeguards a disease in the enzootic phase could escape detection.

As might be anticipated, not all aspects of the "Codes" are acceptable to everyone. Some sections are controversial, others are difficult to implement, and some aspects of control have not been addressed. With references to the latter, Mann (1979) noted that the document deals almost exclusively with the limiting of adverse biological effects of introductions, and does not speak to supportive socioeconomic and political pressures that may favor introductions. As he emphasizes, the guidelines should be implemented in a practical way and in a realistic time scale, or they will be ignored. Notwithstanding its deficiencies, the "Codes" is an important guide and must continue to evolve and fine-tune to international needs a) as new knowledge on invading species, their diseases, parasites, predators, and competitors becomes available, and b) as the "Codes" program is more widely adopted and tested across international boundaries.

The biological characteristics of many marine molluscs, especially bivalves and gastropods, simplify the arduous task of control of introductions and transfers. For one thing, although they create the same range of inherent ecologic, pathologic, and genetic problems as other organisms, most commercial adult bivalves and gastropods are capable of no, or only localized movement on their own; thus risks attending their handling can be controlled more effectively than those of more motile species (Turner 1988). For another, many species of molluscs can now be raised in hatcheries to the F2 and F3 generation, shelled species can be disinfected upon arrival at their destination, fertilized eggs can be disinfected before shipment, and hatchery-raised shelled pediveligers can be transported for setting in tanks near planting grounds. It goes without saying, that all steps in introductions and transfers should be computer-recorded so that original sources and history of movements can be traced readily.

As already stated, attention on introductions and transfers has been focused primarily on the biological aspects, and little on the socioeconomic and political considerations (Mann 1979). Several writers have touched on the latter; some of their thoughts follow: Managers, when considering the introduction of a foreign species, should seriously question why a local native species would not be commercially adequate (Courtney and Robins 1989). Foreign species should probably be considered only if there is a demonstrated scientific need or a high potential for commercial success (Mann 1979, Rosenfield and Kern 1979). Approval of introductions should be based only on biological decisions—not on management or political mandates alone. Federal and state agencies should support, more than now done, research on the biology of potential introductions, making available a biological base for management

and control (Courtney and Robins 1989). Coastal universities should be urged to expand basic interdisciplinary graduate training on commercial and potentially commercial species (including such subjects as culture, nutrition, behavior, physiological pollution, ecology, genetics, microbiology, parasitology, and predation) (Regal 1986, Fisher 1988, Courtney and Robins 1989, Tiedje et al. 1989). Integrated resource management, which incudes a multidisciplinary, integrated approach at all involved levels of government and industry (Tiedje et al. 1989), not only enhances multiple uses of resources, but also reduces sociopolitical conflicts (Cairns 1988). This approach, it should be noted, finds immediate application in the chaotic zebra-mussel dilemma in the Great Lakes.

Persons knowledgeable in the subject of introductions and transfers suggest that requests for them should be examined with extreme care by a single national body (perhaps an interjurisdictional and interagency council with peer reviews) to insure, insofar as possible, that exotic species will be beneficial (Bourne 1979, Courtney and Taylor 1986, Fisher 1988, Turner 1988, Courtney and Robins 1989).

In a provocative suggestion, Cairns (1988) points out that inasmuch as employment of rigorous procedures in control of introductions and transfers would avoid exceedingly expensive litigation problems that could result from movements of these organisms, funds thus freed could be redirected to constructive research, training, and control activities. The idea merits discussion, but its implementation might be difficult!

With reference to my opening question in this overview, I answer that the intrusive problems of invasions are unequivocally real and challenging. Nevertheless, I close optimistically, and affirm that through international goodwill and by creative cooperation (Wooster 1969) the frustrating, complex problem of human-coupled movements of molluscan populations can be controlled, and done so beneficially and minimally disruptively: biologically, socioeconomically, and politically . . . an appropriate goal for proponents of controlled malacological zoogeography!

LITERATURE CITED

Allen, F. E. 1953. Distribution of marine invertebrates by ships. *Australian J. Mar. Freshwat. Res.* 4:307–316.

Andrews, J. D. 1979. Scenario for introduction of *Crassotrea gigas* to the Atlantic Coast of North America. In: R. Mann, Ed., Exotic Species in Mariculture, pp. 225–231. MIT Press, Cambridge, Massachusetts.

Ansell, A. D. 1968. The rate of growth of the hard clam *Mercenaria mercenaria* (L.) throughout the geographical range. *J. Cons. Perm. Int. Explor. Mer.* 31((3):364–409.

Bourne, N. 1979. Pacific oysters, *Crassostrea gigas* Thunberg, in British Columbia and the South Pacific Islands. In: R. Mann, Ed., Exotic Species in Mariculture, pp. 1–53. MIT Press, Cambridge, Massachusetts.

Briggs, J. C. 1974. Marine Zoogeography. McGraw-Hill Book Co., New York, 475 pp.

Chew, K. K. 1979. The Pacific Oyster (*Crassostrea gigas*) in the West Coast of the United States. In: R. Mann, Ed., Exotic Species in Mariculture, pp. 54–82. MIT Press, Cambridge, Massachusetts.

Cairns, J. Jr. 1988. Integrated resource management: the challenge of the next ten years. In: W. J. Adams, G. A. Chapman, and W. G. Landis, Eds., Aquatic Toxicology and Hazard Assessment, pp. 559–566. Tenth Vol., ASTM STP 971, Amer. Soc. Testing Materials, Philadelphia.

Carriker, M. R. 1955. Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura*. Spec. Sci. Rept.: Fish. No. 148, U.S. Fish & Wildl. Serv., Washington, DC, 150 pp.

Carriker, M. R. 1967. Ecology of estuarine benthic invertebrates: a perspective. In: G. H. Lauff, Ed., Estuaries, pp. 442–487. Publ. No. 83, Amer. Assoc. Adv. Sci., Washington, DC.

Counts, C. L. III. 1983. Bivalves in the genus *Corbicula* Muhlfeld 1811 (Mollusca: Corbiculidae) in the United States: systematics and zoogeography. Ph.D. Dissertation, University of Delaware, Newark, xxii + 451 pp.

Courtney, W. R. Jr. & C. R. Robins. 1989. Fish introductions: good management, mismanagement, or no management? *Aquatic Sci.* 1(1): 159–172.

Courtney, W. R. Jr. & J. N. Taylor. 1986. Strategies for reducing risks from introductions of aquatic organisms: a philosophical perspective. *Fisheries* 11(2):30–33.

Cox, C. B. & P. D. Moore. 1985. Biogeography, An Ecological and Evolutionary Approach. 4th Ed. Blackwell Sci. Publ., Boston, 244 pp.

Dobson, A. P. & R. M. May. 1986. Pattern of invasions by pathogens and parasites. In: H. A. Mooney and J. A. Drake, Eds., Ecology of Biological Invasions of North American and Hawaii, pp. 58–76. Ecological Studies 58, Springer-Verlag, New York.

Ehrlich, P. R. 1986. Which animal will invade? In: H. A. Mooney and J. A. Drake, Eds., Ecology of Biological Invasions of North America and Hawaii, pp. 79–95. Ecological Studies 58, Springer-Verlag, New York.

Ekman, S. 1953. Zoogeography of the Sea. Sidgwick and Jackson Limited, London, 417 pp.

Fisher, W. S. Ed. 1988. Disease Processes in Marine Bivalve Molluscs. Amer. Fish. Soc. Spec. Publ. 18. Bethesda, Maryland, 315 pp.

Garton, D. W. & W. R. Haag. 1989. Relationship between shell length, metabolism and heterozygosity in the introduced zebra mussel *Dreissena polymorpha*. *Amer. Zool.* 29(4): Abstr. 31, p. 7A.

Hanna, G. D. 1986. Introduced mollusks of Western North America. Occ. Papers Calif. Acad. Sci. 48, 108 pp.

Hedgpeth, J. W. 1957. Estuaries and lagoons. II. Biological aspects. In: J. W. Hedgpeth, Ed., Treatise on Marine Ecology and Paleoecology, pp. 693–729. Geol. Soc. Amer., Memoir 67.

Korringa, P. 1942. *Crepidula fornicata*'s invasion in Europe. *Basteria* 7(1/2):12–23.

Mann, R. Ed. 1979. Exotic Species in Mariculture. MIT Press, Cambridge, Massachusetts, 363 pp.

Mooney, H. A. & J. A. Drake, Eds. 1986. Ecology of Biological Invasions of North America and Hawaii. Ecological Studies 58. Springer-Verlag, New York, 321 pp.

Mooney, H. A., S. P. Hamburg & J. A. Drake. 1986. The invasions of plants and animals into California. In: H. A. Mooney and J. A. Drake, Eds., Ecology of Biological Invasions of North America and Hawaii, pp. 250–272. Ecological Studies 58. Springer-Verlag, New York.

Newkirk, G. F. 1979. Genetic aspects of the introduction and culture of nonindigenous species for aquaculture. In: R. Mann, Ed., Exotic Species in Mariculture, pp. 192–211. MIT Press, Cambridge, Massachusetts.

Odum, E. P. 1971. Fundamentals of ecology. 3rd Ed. W.B. Saunders Co., Philadelphia, 574 pp.

Pielou, E. C. 1979. Biogeography. John Wiley & Sons, New York, 351 pp.

Pimentel, D., M. S. Hunter, J. A. LaGro, R. A. Efroymson, J. C. Landers, F. T. Mervis, C. A. McCarthy & A. E. Boyd. 1989. Benefits and risks of genetic engineering in agriculture. *BioScience* 39:606–614.

Regal, P. J. 1986. Models of genetically engineered organisms and their ecological impact. In: H. A. Mooney and J. A. Drake, Eds., Ecology of Biological Invasions of North America and Hawaii, pp. 111–129. Ecological Studies 58. Springer-Verlag, New York.

Rosenfield, A. & F. G. Kern. 1979. Molluscan imports and the potential for introduction of disease organisms. In: R. Mann, Ed., Exotic Species in Mariculture, pp. 165–189. MIT Press, Cambridge, Massachusetts.

Sindermann, C. J. 1970. Principal Diseases of Marine Fish and Shellfish. Academic Press, New York, 369 pp.

Sindermann, C. J. 1977. Disease diagnosis and control in North American marine aquaculture. Development in Aquaculture and Fisheries Science, 6. Elsevier Sci. Publ. Co., New York, 329 pp.

Tiedje, J. M., R. K. Colwell, Y. L. Grossman, R. E. Hodson, R. E. Lenski, R. N. Mack & P. J. Regal. 1989. The release of genetically engineered organisms: a perspective from the Ecological Society of America. Special Feature. The planned introduction of genetically engineered organisms: ecological considerations and recommendations. *Ecology* 70(2):296–315.

Turner, G. E., Ed. 1988. Codes of practice and manual of procedures for consideration of introductions and transfers of marine and freshwater organisms. Internat. Coun. Explor. Sea, Copenhagen, Denmark. Cooperative Res. Rept. No. 159, 44 pp.

Vermeij, G. J. 1978. Biogeography and Adaptation. Patterns of Marine Life. Harvard University Press, Cambridge, Massachusetts, 332 pp.

Ward, J. E. & C. J. Langdon. 1986. Effects of the ectoparasite *Boonea* (= *Odostomia*) *impressa* (Say) (Gastropoda: Pyramidellidae) on the growth rate, filtration rate, and valve movements of the host *Crassostrea virginica* (Gmelin). *J. Exp. Mar. Biol. Ecol.* 99:163–180.

Williams, E. H. 1990. Pacific giant clams. *Caribbean Mar. Sci. Newsletter* 1990(1):5.

Wooster, W. S. 1969. The ocean and man. In: The Ocean, Scientific American Book, pp. 123–130. W. H. Freeman and Co., San Francisco.

The Decline of the Virginia Oyster Fishery in Chesapeake Bay: Considerations for Introduction of a Non-Endemic Species, *Crassostrea gigas* (Thunberg, 1793)[1]

Roger Mann, Eugene M. Burreson and Patrick K. Baker

ABSTRACT The Chesapeake Bay oyster fishery for *Crassostrea virginica* (Gmelin) is in a state of continuing decline. Two diseases, *Haplosporidium nelsoni* and *Perkinsus marinus* have effectively eliminated oysters from many sections of the Bay. Despite over 30 years of disease activity the native oysters have developed neither tolerance nor absolute resistance to these diseases, and do not exhibit any recovery in disease endemic areas in Virginia. Repletion programs have completely failed to recover to permanent production areas lost to disease. Present fishery management activities are limited to a controlled retreat away from the disease in an arena where disease distribution is salinity and temperature (and hence climate) related and, therefore, beyond human influence. Disease resistance is the pivotal issue. This commentary builds on the reality that without resistance to both diseases no recovery to sustained, stable production on all formerly productive oyster bottom is possible. It is improbable that such resistance can be developed in *Crassostrea virginica*. A consideration is made of the case for introduction of a non-endemic species, *Crassostrea gigas* (Thunberg) to assist in attaining this goal.

KEY WORDS: *Crassostrea gigas*, oyster, introductions

INTRODUCTION

The premeditated movement of aquatic species for aquaculture and fishery enhancement purposes has been an active component of animal husbandry for over two thousand years. Present day activity is essentially international in scope. Stimuli for such movements are many and variable, from biological control to development of local and national economies to revitalization of depressed economies suffering from native species depletion caused by disease, overexploitation, pollution or some combination thereof. Elton (1958), in his classic text on introduced species, comments on the extensive movement of oysters around the globe as part of commercial fishery activity. In this commentary we examine arguments for introduction of the Pacific or Japanese oyster, *Crassostrea gigas* (Thunberg), to Chesapeake Bay to supplement production that is currently supported only by depleted stocks of native *Crassostrea virginica* (Gmelin).

Comprehensive guidelines for consideration of and effecting introductions have been developed independently by ICES (International Council for the Exploration of the Seas), EIFAC (European Inland Fisheries Advisory Commission) and AFS (the American Fisheries Society). These guidelines emphasize the following:

(a) a clear rationale for introduction,
(b) selection of candidate species, including a consideration of associated pests, parasites and diseases,
(c) testing, utilizing quarantine systems, before a decision to proceed with introduction,
(d) introduction using quarantine procedures and monitoring after release to provide data for subsequent considerations for introductions.

Our commentary will focus on items (a) through (c) of the above list, including a brief discussion of the legal climate in this particular case, and conclude with a description of future efforts in data collection to allow a balanced decision concerning large scale fishery rejuvenation efforts in Virginia.

Developing the Rationale: Historical Perspective and Current Situation

Why should an attempt be made to restore or rejuvenate the oyster resource of Chesapeake Bay? Although the initial, and perfectly defensible, response to this question would probably be because it supports a commercially valuable industry we believe that the direct commercial exploitation aspect is of quite secondary importance. Benthic communities of Chesapeake Bay in precolonial times were dominated by intertidal oyster reefs. Oyster reefs were important geological as well as biological structures. Reefs supported extensive communities that, in turn, provided the base levels of food webs that eventually support comercially important finfish and crab species, important trophic interactions that are often underestimated in current attempts to "manage" finfish and crab stocks on a species by species basis. Demise of this productive benthic community has perhaps resulted in comparable demise of the commercial finfish and crab stocks. Limiting fishing effort on other species will have only marginal positive impacts. Further, the role of the oyster in harvesting primary productivity in Chesapeake Bay cannot be understated. The calculations offered by Newell (1989) are illuminating—a two order of magnitude decrease in filtration capacity compared to pre-1870 oyster stocks! Whereas the resident oyster population once had the capacity to filter the waters of the bay in 3.3 days, the present stocks can only manage the same task in approximately 325 days—and the stocks are still declining. A healthy and substantial oyster stock in Chesapeake Bay would probably be the single most effective mechanism of simultaneously harvesting microplankton, reducing the impact of eutrophication, sustaining a directly harvestable resource, improving water quality and maintaining a diverse and stable food web. Unfortunately, four centuries of neglect, mismanagement and wholesale mining of the oyster resource (both living and shell, the latter for industrial purposes—see Haven, Hargis and Kendall 1978, Kennedy and Breisch 1981) has resulted

[1]Contribution number 1714 from the Virginia Institute of Marine Science, School of Marine Science, College of William and Mary.

in the present scenario where sparse, disease ravaged populations survive in disparate, low salinity sanctuaries as subtidal crusts of living material overlaying a base of reef material. The importance of the oyster as a cornerstone species in Chesapeake Bay surpasses that of the directed fishery in both ecological and economic terms, yet it is the latter that embodies a disproportionate political power and which, by default, will eventually drive decision processes concerning restoration and rejuvenation including possible introductions. With this political reality clearly stated we will proceed with a greater focus on the directed commercial fishery aspect of the discussion.

The oyster (*Crassostrea virginica*) resource of Chesapeake Bay has been in continuing decline since the turn of the century (Haven, Hargis and Kendall 1978, Kennedy and Breisch 1981, Hargis and Haven 1988). Prior to 1960, average annual oyster production was 3.5 million bushels in Virginia and 2.2 million bushels in Maryland. Virginia oyster production in the 1980s decreased from over 1.0 million bushels in 1981 to 209,000 bushels in 1989. Current estimates for public fishery market oyster production in Virginia in the 1990–91 season are at an all time low of 43,000 bushels. The continuing decline due to overfishing has been assisted by the action of two diseases, *Haplosporidium nelsoni* (commonly known as MSX) and *Perkinsus marinus* (commonly known as "Dermo"). *Haplosporidium nelsoni* and *P. marinus* were at record high levels of abundance during 1986 and 1987 as a result of continuing drought conditions over the Chesapeake Bay watershed (Burreson and Andrews 1988). During 1986 and 1987, estimated overall mortality on public beds in Virginia was between 70 and 90% each year, the highest values recorded in 28 years of continuous monitoring (E. M. Burreson, unpublished data). During 1988 *P. marinus* spread to all monitored oyster beds in the Virginia portion of Chesapeake Bay. Since that time some abatement has occurred in low salinity areas (Burreson, unpublished data, May 1991) but the disease remains endemic to the majority of formerly productive oyster bottom. The combined effect of both oyster diseases has been the recent elimination of commercial oyster production from essentially all waters in the Virginia portion of the bay with the exception of three oyster bars in the upper James River and very limited areas in the upper Rappahannock River. Many oyster bars in the Maryland portion of the bay have also been denuded by the diseases. The remaining locations in Virginia, about 5% of the total public oyster grounds, are the subject of continuing, intense fishing pressure. Between 1987 and 1989 approximately 90% of the entire Virginia harvest came from the upper James River, although this declined to approximately 68% in the 1990–91 public oyster season. The magnitude of destruction and the economic implications are obvious.

In order to allow recolonization of formerly productive oyster beds, the distribution of diseases must be forced in a downstream direction by a decline in ambient salinity due to increased streamflow in the tributaries of Chesapeake Bay. Conditions typical of the 1950–1980 period still result in large, salinity related disease endemic areas and associated unproductive oyster bottom. Given the drought conditions of the 1980s in the middle Atlantic region, which exacerbated disease related losses, a marked and sustained change to wetter climatic conditions in the watershed is needed. Current, admittedly limited, understanding of the impacts of predicted global warming suggest this is unlikely. Furthermore, even a temporary increase in rainfall would result in only a temporary reduction in disease pressure. The life cycle and growth of the native oyster are such that even colonization of a presently denuded, high salinity oyster bed would require a minimum of three years without serious disease losses before a single crop of marketable oysters would be attained. Clearly, management around typical, rather than atypical, rainfall and streamflow conditions is unpredictable and imprudent.

The subject of natural disease resistance and the development of disease resistance in cultured stocks of the native oyster, *Crassostrea virginica*, has received considerable attention. Distinction should be made between tolerance to a greater parasite burden, wherein mortalities will eventually occur but at a decreased rate, and resistance, where no parasite related losses are observed. The notion that disease resistance would allow recolonization of presently barren areas, with the ensuing rejuvenation of the industry, is untenable with respect to Chesapeake Bay for several reasons. Natural populations, with their enormous fecundities, have failed to produce extensive beds of tolerant, let alone resistant oysters through natural selection as demonstrated by the continued and almost total absence of oysters from high salinity areas of the bay. This is probably due, at least in part, to the large gene pool of unselected oysters, especially for *H. nelsoni*, in the upper reaches of the major tributaries in Virginia and in the upper portion of the bay in Maryland. Efforts at Rutgers University to select such strains by manipulative breeding have resulted in some improvement in survival in response to challenge by *H. nelsoni* after 25 years of research and over eight generations of selection (Ford and Haskin 1987). Improvement in survival in response to *H. nelsoni* challenge is not correlated with the activity of a particular cellular or humoral defense mechanism (Douglass 1977, Ford 1986), but appears to be the result of an overall physiological superiority in which tolerant oysters, by more efficiently utilizing available energy, are able to inhibit the development of the disease (Myhre 1973, Newell 1985, Barber, Ford and Haskin 1988a,b); however, these strains are potentially useless in Chesapeake Bay because of the presence of *P. marinus* as well as *H. nelsoni*. Resistance to both diseases, as opposed to tolerance of a higher parasite number, is essential to reestablishing stable oyster populations on all formerly productive oyster bottom in the Virginia portion of Chesapeake Bay. The unusual intensification of both diseases in recent years and the resulting high oyster mortality dictate that the time required to select native *C. virginica* for disease tolerance and, eventually, resistance using traditional methods may not be adequate to deal with current economic needs. Alternative approaches to restore a productive resource and thereby rejuvenate the industry must be considered. The introduction of a non-endemic oyster species to reestablish productive bottom in currently denuded, disease endemic areas, is such an alternative.

Legal and Permitting Requirements Related to Introductions of Non-endemic Species: Can Introductions Be Effected in Virginia?

Federal and state legislation applies in two related areas. These are respectively: experimentation with non-endemic species, compliance with ICES guidelines and U.S. Federal Law (the Lacey Act); and permitting requirements for study of non-endemic species in the Commonwealth of Virginia. U.S. Federal Law, in the form of the Lacey Act Amendments of 1981, Public Law 97-79, contains provisions for control of movement of non-endemic species into the U.S.A. and across state lines. In essence the Lacey Act is complied with if approval for possession is obtained at the state level. The appropriate section of the "Laws of Virginia relating to the Marine Resources of the Commonwealth: 1984 Edi-

tion" are found under section 28.1-183.2 entitled "Importing Fish or Shellfish for Introduction into Waters of the State." Such importations are unlawful unless written permission is obtained from the Commissioner of the Virginia Marine Resources Commission—the designated state regulatory agency. A written request containing all pertinent information (i.e., species, origin, quantities, time period, etc.) must be submitted at least 30 days prior to importation. The Director of the Virginia Institute of Marine Science must approve all requests prior to approval by the Commissioner. Provided appropriate permission is granted by the aforementioned Director and Commissioner then the legal prerequisites are fulfilled.

Neither the Lacey Act nor the Laws of Virginia address the legal and moral obligations of either informing or even seeking comment on proposed introductions from neighbouring legal jurisdictions if they are likely to be affected by such introductions. Indeed, there appears to be no specific instructions requiring such action. Formal interstate advisory and management bodies do exist but their legal authorities on the issue of introductions appear limited. Although the present discussion focusses on the Virginia portion of the Chesapeake Bay, any introduction of reproductively active, non-endemic species will potentially have impact in both Maryland and North Carolina waters if pelagic larval stages are widely dispersed and survive. Even wider geographical impact may occur over time in the event of establishment in the recipient environment. Clearly, the ability of neighbouring states to influence the permitting process through alternate legal challenges remains untested.

Selection of Species for Introduction: Why Crassostrea gigas?

When considering the selection of species for introduction it is important to effectively match the donor and recipient environments to insure greatest possibility of successful survival of the introduced species. The Chesapeake Bay environment can be characterized as having a continental climate with large air and water temperature ranges; large temporal and spatial salinity variation; a geologically young, sedimentary basin that has been extensively dredged to facilitate past and current commercial shipping; a region where salinity related endemic diseases currently limit native oyster distribution, and an irretrievably altered watershed that currently serves as home to over 14 million people. In summary, this is a high stress environment that is drastically altered from that prior to colonial settlement—the environment in which *Crassostrea virginica* flourished to form reefs that were major geological features as well as dominant components of the benthic community of Chesapeake Bay. The magnitude of change over the past four centuries should be underscored. Despite continuing efforts to improve water quality in the bay it must be realized that the cumulative abuses of urban and agricultural development to the bay watershed make the goal of restoration of the bay to its former pristine condition (as described in Captain John Smith's logs) untenable. Intertidal oyster reefs no longer exist in the bay, they have been tonged and dredged to subtidal depths generally exceeding one meter. The quantitative change in oyster reef structure associated with their degradation from intertidal to subtidal features is illustrated by the fact that present, immediate subsurface shell deposits have been radiocarbon dated at several hundred years before present (DeAlteris 1988).

It is appropriate to begin a search for an alternate species within the genus *Crassostrea*—reef forming species tolerant of mid to subtropical latitude, high stress environments. Tables 1–3 summarize species in the genus *Crassostrea*, and compare published data describing their temperature and salinity tolerances as both larval and adult forms. Caution must be applied in literature review in determining the geographic origin of *C. virginica* under examination (see comments in Hedgecock and Okazaki 1984, Reeb and Avise 1990, concerning lack of genetic uniformity throughout the zoogeographic range of this species), and, where possible, which geographic type of *C. gigas* (there are four, named by prefecture of origin, Hokkaido, Myagi, Hiroshima and Kumamoto, see comments in Torigoe 1981, Quayle 1989, Kusuki 1990) is being described. Geographic types of *C. gigas* are characterised by distinct growth rates and forms (so much so that they serve quite different commercial markets) that may have different temperature and salinity optima and tolerances. Such information on geographic type is rarely given, therefore data in tables 1–3 encompasses all types. For the present comparative purpose this is acceptable in that it may overestimate rather than underestimate possible ranges of *C. gigas* in the Chesapeake Bay. In general, the Myagi strain has been the focus of work in the hatchery based fishery of the Pacific coast of North America; however, there has been much intentional interbreeding of introduced stocks and precise pedigrees are lacking. The predominant oyster of that and the European fisheries can better be described as Myagi-like. Several other species lack adequate documentation for complete comparison; however, it is evident that strong similarities exist between *C. virginica* and *C. gigas*.

Crassostrea gigas is actively cultured elsewhere in the world, especially so as an introduced species. *Crassostrea gigas* has been extensively (both accidentally and intentionally) moved beyond its native oriental range for culture purposes to locations in the Pacific basin (Costa Rica through Alaska, Australia, New Zealand), and the Atlantic basic (North Sea through Mediterranean and Atlantic Coast of Morocco). Comprehensive summaries of these activities are given in Mann (1979, 1981) and Menzel (1990). *Crassostrea gigas* is the basis of the largest oyster fisheries in the world. During 1987 the leading oyster producing countries in the world were Korea and Japan with production of 303,233 and 258,776 metric tons respectively, this product being predominantly

TABLE 1.

Crassostrea species: Distribution and Synonyms. Source material: 1. Ahmed, 1971; 2. Boffi, 1979; 3. Carreon, 1969; 4. Chen, 1972; 5. Dang, 1972; 6. Durve, 1967; 7. Kamara et al., 1976; 8. Kong and Luh, 1977; 9. Mann, 1981; 10. Menzel, 1974; 11. Newball and Carriker, 1983; 12. Shafee and Sabatie, 1986; 13. Tebble, 1966; 14. Torigoe, 1981; 15. Zenkevitch, 1963.

Atlantic coast of North America: virginica (= rhizophorae), 11.
Brasil: brasiliensis (= rhizophorae = virginica?), 2, 7
Western Europe, English Channel to Morocco (now rare): angulata, 10, 13.
Europe, North Sea through Mediterannean to Morocco: gigas, 9, 12.
Pacific coast of North America: gigas, 9, 12.
Japan, Korean Peninsula through Vietnam: gigas, araikensis (= rivularis), nippona, 5, 14.
India: gryphoides, madrasensis, rivularis (= araikensis), 1, 6.
Thailand/Malaysia: belcheri (= nippona?), 4, 8.
Philippines: iredali (= madrasensis or even = rivularis?), 3.
West Africa: gasar (= tulipa), 7.
Black Sea: taurica, 15.

TABLE 2.

Temperature and salinity ranges of adults of Crassostrea species. Optimum ranges given in parentheses.

Species	Temperature (C)		Salinity (ppt)		Reference
	Growth	Spawning	Growth	Spawning	
virginica	5–34 (28–32)	18–25 (23)	>5 (12–27)	>8	7,8,20,21,22,31
angulata	20–30	20	21–43	<33	3,4,16
araikensis		7–40 (30–40)			5,11,16
gasar	25–30	5–34	14–20		1,28,29
gigas	3–35 (11–34)	16–30 (20–25)	10–42 (35)	10–30 (20–30)	2,4,15,18,19,24,25
gryphoides	19–33	27–31	4–40 (30–40)	13–29	11,13,23
iredali	30–33	<45	>15		4
madrasensis	26 (30)	1–41 (8–25)	17–35 (20–35)		16,17,26,27,30
nippona	no data				
rhizophorae			22–40 (26-37)		4,5,12
taurica	3–28	17–18			32

Reference: 1. Ajana, 1980; 2. Allen et al., 1988; 3. Amemiya, 1926; 4. Bardach et al., 1972; 5. Boveda and Rodriguez, 1967; 6. Breese and Malouf, 1977; 7. Butler, 1949; 8. Chanley, 1958; 9. Davis, 1958; 10. Davis and Calabrese, 1964; 11. Desai et al., 1982; 12. Dos Santos and Nascimento, 1985; 13. Durve, 1965; 14. His et al., 1989; 15. Hughes-Games, 1977; 16. Jhingran and Gopalakrishnan, 1974; 17. Joseph and Madhyastha, 1984; 18. King, 1977; 19. Le Gall and Raillard, 1988; 20. Loosanoff, 1958; 21. Loosanoff, 1969; 22. Loosanoff and Davis, 1952; 23. Mane, 1978; 24. Muranaka and Lannan, 1984; 25. Nell and Holliday, 1988; 26. Rao, 1951; 27. Rao and Nayor, 1956; 28. Sandison, 1966; 29. Sandison and Hill, 1966; 30. Stephen, 1980; 31. Wells, 1961; 32. Zenkevitch, 1963

C. gigas. By comparison the United States, ranking third, produced 217,632 metric tons (a mix of *C. gigas* and *C. virginica*) and France, producing predominantly *C. gigas* after initial introduction of the species some 15 years earlier, ranked fourth at 123,162 metric tons. *Crassostrea gigas* is elegantly suited for hatchery production as demonstrated by the enormous success of the hatchery-based industry in the U.S. Pacific Northwest. Commercial production based on hatchery produced seed oysters in the Northwest far exceeds present oyster production from the entire Chesapeake Bay. Domestic oyster production cannot satisfy the market need and the United States has, since 1985, held the dubious distinction of being the world's leading importer of oysters in fresh and frozen form.

The native northern European oysters *Ostrea edulis* and *Crassostrea angulata* were decimated by disease in the mid 1970s. Production of the former fell from 15,000 tons to the present day level of 2,500 tons per year. Production of the latter fell from 60,000 tons per year to zero. The industry was saved from economic extinction by the introduction of *C. gigas*. European *C. gigas* production (including French) now employs over 20,000 people and produces approximately 140,000 tons of oysters per year, this representing over 80% of the total production. Further,

TABLE 3.

Temperature and salinity ranges of Crassostrea larvae. Optimum ranges given in parentheses. Reference material as in Table 2

Species	Temperature (C)	Salinity (ppt)	Reference
virginica	20–33	8–39 (10–29)	3,9,10
angulata		21–43 (28–35)	3,4,16
araikensis	20–28 (26–28)	10–30 (20)	5
gigas	18–35 (30)	19–35	2,14,15
rhizophorae	<30 (25)	20–40 (28)	12

no data available for gasar, gryphoides, iredali, madrasensis, nippona and taurica.

C. gigas appears resistant to challenge by both *Bonamia ostreae* and *Marteilia refringens*, diseases that continue to decimate native European oysters. The analogies with Chesapeake Bay are painfully obvious.

Risk Analysis for Introduction of Diseases with Crassostrea gigas

The argument in support of possible use of *Crassostrea gigas* in restoration of the presently unproductive areas of the bay has, to this juncture, appeared positive. Questions of diseases associated with *C. gigas* in its native and introduced range remain—are there such diseases and could they be transferred to the bay with an introduction? *Crassostrea gigas* has, in its native range, no known diseases that have been associated with large-scale mortalities (Koganezawa 1975). In addition, it has been used successfully as an introduced species in areas where the native oysters have been decimated by diseases. *Crassostrea gigas* has been resistant to the local diseases and no new disease introductions have been positively documented even though, in certain areas, *C. gigas* has been introduced with few, if any, control measures. For example, *C. gigas* is not susceptible to *Bonamia ostreae* and *Marteilia refringens*, diseases that have caused massive mortalities in *Ostrea edulis*, the native species in western Europe, and it has not been susceptible to similar protozoan diseases where it has been introduced in Australia and New Zealand. In addition, *C. gigas* is resistant to the viral diseases that caused mass mortalities of the Portuguese oyster in France. The Japanese oyster is the basis for the hatchery-based industry in the Pacific Northwest and no new diseases (that cause measurable mortality) have been introduced into that region (Glude 1975) even though there have been periodic importations of *C. gigas* since 1902 and early introductions were effected without any control measures being enforced. Andrews (1980) reviewed oyster introductions around the world and discussed potential problems with such importations and precautions necessary to avoid disease introductions.

The extensive movement of *C. gigas* has provided, in addition to the native range, many potential sources for broodstock for a

proposed introduction. For the present discussion we will essentially limit our consideration of source broodstock to that from the state of Washington. Despite the fact that the pedigrees of these stocks are not definitively documented, the stocks are mostly of Myagi Prefecture origin but many years of hatchery breeding may have resulted in some limited crossing with stocks from other sources, they do have a known and documented history concerning associated pests, parasites, and diseases. The listing below includes only those organisms reported from *C. gigas* that are actual or potential disease agents in oysters or other bivalve molluscs. It does not include the numerous parasites, mostly metazoan, found in oysters world-wide that have never been implicated in host mortality.

1. Diseases of Unknown Etiology.

Hematopoietic Neoplasia. This disease results in a massive tissue invasion of abnormal blood cells and is analogous to leukemia in vertebrates. It has been implicated in large-scale mortalities of mussels in the state of Washington and of soft-shell clams in Chesapeake Bay. The syndrome has been reported in *C. gigas*, *C. virginica*, and *O. lurida*, but has not been associated with mortality in these species. A virus has been suggested as the cause for this disease, but the evidence is weak.

Potential implications: This syndrome is already present in Chesapeake Bay and has been observed occasionally in *C. virginica*.

2. Viral Diseases.

a. Oyster Velar Virus. This disease affects oyster larvae and has been reported from two hatcheries in the state of Washington (Elston and Wilkinson 1985). It has been observed occasionally in hatcheries from March to August in larvae greater than 150 μm in shell height. Infection results in loss of motility and death of larvae. Measured losses of hatchery production up to 50% have been recorded, but there is no established link between the disease and mortality since it has not been experimentally transmitted. There have been no reported outbreaks of the disease in recent years (R. A. Elston, Battelle Center for Marine Disease Control, Sequim, WA, personal communication).

Potential implications: This virus is primarily a hatchery problem where larvae are held at high density in tanks, but even in hatcheries the virus has never caused mortality over 50%. It is not expected to be a problem in nature where density of larvae is much lower than in hatcheries and transmission of viral particles between larvae is greatly reduced.

b. Hemocytic Infection Virus (HIV) and Gill Necrosis Virus (GNV). These iridoviruses have been reported from *C. gigas* in France. Both viruses were implicated in mass mortalities of the Portuguese oyster *C. angulata* in France during the 1970s (Comps and Bonami 1977), but neither virus causes mortality in *C. gigas* in the same area (Comps 1988). In fact, Comps (1988) states that the ability of *C. gigas* to resist mortality from these viruses resolved a very serious economic problem associated with the total elimination of the Portuguese oyster.

There has been some speculation that *C. gigas* is a carrier for these viruses and that one or both of them was introduced into France with importations of *C. gigas* from Japan. According to Henri Grizel, IFREMER, France, (personal communication, 12 March 1990) the lesions characteristic of the viral infections were observed in *C. angulata* prior to introduction of *C. gigas*, which suggests that the viruses were already present in France. Unfortunately, no attempt was made to isolate viruses at that time, so we will never know with certainty if the viruses were already present.

Potential implications: GNV and HIV have never been observed in *C. gigas* from the Pacific Northwest. In addition, the very characteristic gill lesion caused by GNV has never been observed (R. A. Elston, personal communication, 14 March 1990).

There are many reports in the literature of other viruses in oysters and other marine molluscs, including five different viruses from the eastern oyster, *C. virginica* (Johnson 1984). There is no firm evidence that any of these viruses (other than HIV and GNV) can be pathogenic to their hosts.

3. Bacterial Diseases.

a. Bacillary Necrosis. Many species of bacteria in the genus *Vibrio* are present naturally in seawater. They are not normally pathogenic, but can become so because of adverse environmental conditions, usually high temperature. These bacteria have been implicated in often complete mortality of larvae in hatcheries from various regions of the world. Juvenile oysters have also been reported to be affected in hatcheries in Maine. Affected oyster species include *C. gigas*, *C. virginica* and *Ostrea edulis* (Elston 1984, Sindermann and Lightner 1988).

Potential implications: Vibrios and other bacteria that may cause this problem are present naturally in seawater. Rigorous hatchery sanitation measures usually are sufficient to prevent mortalities. The Virginia Institute of Marine Science oyster hatchery has experienced no problem of this type.

b. Nocardiosis. This disease is caused by the actinomycete bacterium *Nocardia* and often results in raised green to yellow nodules on the mantle. It is apparently at least partially responsible for the historically reported phenomenon of summer mortality in adult *C. gigas* in the Pacific Northwest (see Friedman, Beattie, Elston and Hedrick 1991). Similar nodules have been observed in other oysters from other areas, including *C. virginica* (Elston, Beattie, Friedman, Hedrick and Kent 1987), but the cause of the nodules has not been determined in those cases.

Potential implications: This is a husbandry disease with local environmental sources of the bacterium in Washington and British Columbia which is restricted to certain embayments. It is not a disease of major concern in those areas.

c. Rickettsiae. Rickettsiae are obligate intracellular organisms and have been reported from digestive diverticula epithelial cells in *C. gigas*, *C. virginica*, and many other bivalve molluscs (Kinne 1983), but are not known to be responsible for mortality.

Potential implications: Rickettsiae have already been reported from *C. virginica* in Chesapeake Bay.

4. Protozoan Diseases.

a. *Marteilia refringens*. This parasite has been responsible for massive mortality of the native oyster *Ostrea edulis* in France. *Marteilia refringens* has also been reported in *C. gigas* in France (Cahour 1979), but prevalence and intensity were low and only early stages of development were observed. The infections were considered to be transient and no mortality has been observed in *C. gigas*.

Potential implications: This parasite is known only from Europe and does not develop normally in *C. gigas*. There is little chance of importing this parasite if the broodstock is limited to *C.*

gigas from the state of Washington, and ICES guidelines for quarantine of broodstock are followed.

b. *Haplosporidium* spp. A parasite that is morphologically similar to *Haplosporidium nelsoni* (MSX) has been observed in *C. gigas* in Korea (Kern 1976). Prevalence was very low, only 0.28% in 1,438 oysters examined, and no mortality has been reported. One of the four infected oysters contained spores and they were restricted to epithelium of the digestive diverticula, as they are in *H. nelsoni*. Another haplosporidan was reported in a single *C. gigas* from California (Katkansky and Warner 1970). Spores were observed throughout the connective tissue, similar to *Haplosporidium costale* (SSO) in *C. virginica*, but spore size was intermediate between *H. nelsoni* and *H. costale*. Plasmodial stages of a haplosporidan were observed in a single *C. gigas* from Washington (Pereya 1964).

Potential implications: There has been speculation that the two haplosporidans from Korea and California are *H. nelsoni* and *H. costale* respectively and that they were introduced to Chesapeake Bay region with unauthorized private plantings of *C. gigas* during the 1950s; however, there is no direct evidence and it remains only speculation. There is no danger of importing these, or any other, parasites with *C. gigas* if initial broodstock are kept in quarantine and only uninfected progeny from the hatchery are used in susceptibility studies or possible introductions.

c. *Marteilioides chungmuensis*. This parasite infects eggs of *C. gigas* in Japan and Korea (Comps, Park and Desportes 1986). It is related taxonomically to important oyster pathogens such as *Marteilia refringens* discussed above, but *M. chungmuensis* is not known to cause mortality. This parasite may be what Becker and Pauley (1968) observed in eggs of *C. gigas* in California. Less than 10% of the eggs were infected in any one female oyster and there was no evidence of oyster mortality.

Potential implications: Transmission studies have never been attempted with this parasite and the life cycle is unknown; however, this parasite infects eggs suggesting that quarantine of broodstock may not provide sufficient control. This parasite is apparently not pathogenic and it has never been reported from the Pacific Northwest.

d. *Mikrocytos mackini*. This parasite infects vesicular connective tissue cells and causes abscess-type focal inflammatory lesions in the mantle and gonad of *C. gigas*. It is known only from British Columbia, Canada although a similar parasite has been observed in *C. gigas* from Hawaii (Farley, Wolf and Elston 1988). Average mortality of 34% was observed during early occurrences of the disease before growers learned proper management techniques to avoid mortality (Bower 1988). Oysters less than two years of age are not affected and mortality of older oysters is reduced when held high in the intertidal zone.

Potential implications: This parasite is not known from the state of Washington. Quarantine of broodstock and use of progeny for field studies would prevent introduction of the parasite even if it were present.

5. Metazoan Parasites.

***Mytilicola orientalis*.** This highly modified copepod inhabits the digestive tract of *C. gigas* in Japan. It was introduced to the Pacific Northwest with early shipments of *C. gigas* seed from Japan and is now endemic along the west coast of the United States (Sindermann and Lightner 1988). This parasite has been implicated in sporadic mortalities of *C. gigas*, but the evidence has never been very strong. A recent, thorough, ten year study (Davey 1989) on a related species in mussels found no evidence of host mortality and the author argues forcefully that *Mytilicola* has been wrongly indicted in previous mortalities.

Potential implications: This parasite infects adult oysters and can be easily controlled by quarantine of broodstock in the hatchery.

In summary, quarantine of broodstock in a hatchery and the use of first generation offspring for any field studies, that is compliance with ICES guidelines for introduction of non-native organisms, will prevent introduction of all disease agents listed above except viruses, bacteria and the ovarian parasite *Marteilioides chungmuensis*, which is not known to cause mortality. If broodstock were limited to one source, the state of Washington, such problems could be minimized in that no pathogenic viruses are known in adult *C. gigas* from Washington and *M. chungmuensis* is absent from that area. There are no published reports of a serious disease outbreak in *C. gigas* from Washington and there are no documented disease introductions (that have resulted in measurable mortality) from the numerous introductions of *C. gigas* that have occurred around the world. Some incidental parasites have been introduced, but such introductions would not have occurred if ICES guidelines had been followed.

***Susceptibility of* Crassostrea gigas *to Diseases Endemic to Chesapeake Bay:* Perkinsus marinus *and* Haplosporidium nelsoni**

Of the two diseases endemic to the bay *Perkinsus marinus* is the only one amenable to laboratory experimentation. *Haplosporidium nelsoni* challenge can only be adequately effected by in situ exposure in *H. nelsoni* endemic areas. All stages of *P. marinus* are infective and the addition of finely minced, infected oyster tissue has been found to be very effective at initiating new infections in previously unexposed oysters in laboratory systems (Meyers, et al. 1991).

The susceptibility of both *C. virginica*, originating from Mobjack Bay broodstock, and *C. gigas*, F1 animals cultured at Gloucester Point, VA from a broodstock imported from Washington state in February 1989 and maintained in quarantine under ICES guidelines throughout study, to *P. marinus* was examined in two separate experiments by Meyers, et al. (1991). In the first experiment of 83 days duration 40% of the *C. gigas* became infected compared to 100% of the *C. virginica*. In the second experiments prevalence was high in both species after 60 days, but differed in intensity with moderate to high levels in *C. virginica* but low levels in *C. gigas*. Cumulative mortality over a 150 day period was 100% for *C. virginica* but only 25.1% for *C. gigas*. Other evidence suggests that *C. gigas* mortalities were not disease related. In summary, *C. gigas* consistently exhibited much higher tolerance of *P. marinus* than did *C. virginica*.

Where non-endemic material is introduced to a quarantined system for subsequent disease challenge the question arises as to the status of the stock before challenge begins. The ICES procedures are designed to preclude the possibility of vertical transmission of a disease from the introduced parent stock. Experience with application of ICES guidelines with oyster movements elsewhere, through the Conwy laboratory in the United Kingdom for example, indicates their effectiveness. Given the continuing quarantine maintenance regime for *C. gigas* in our laboratory, where sanitation procedures limit water and food availability and thereby provide continuing stress on maintained animals, it is probable that

disease, if present, would have already manifested itself; however, no evidence of disease organisms has been seen in histological sections of sampled animals.

The Dilemma: Where to Now?

To this point we have presented arguments to support the following:

(1) Native oyster populations continue to be decimated by endemic diseases, leaving large areas of formerly productive bottom unproductive in disease endemic areas.
(2) Current management practices have failed to reclaim to permanent production areas lost to disease.
(3) Selected strains of native oysters, developed at Rutgers University, have developed tolerance to *H. nelsoni;* however, the surviving population in the Chesapeake Bay has developed neither tolerance nor resistance to the two endemic diseases when they occur in combination as demonstrated by their absence from disease endemic areas.
(4) It is timely to consider another oyster species that may have improved tolerance or resistance to the endemic diseases to assist in reclamation of currently unproductive bottom.
(5) A survey of the available literature, although limited, suggests that *Crassostrea gigas* has salinity and temperature tolerances similar to the native oyster.
(6) Laboratory challenges of *Crassostrea gigas* with *Perkinsus marinus* strongly suggest that it is much more tolerant than the native species of oyster.

From this basis we will proceed to present arguments in favor of continuing examination of the proposed introduction and the benefits that will accrue. It is important to underscore that any further pursuit of this line of investigation in terms of disease challenge will necessitate de facto introduction of *Crassostrea gigas* into Chesapeake Bay waters. This is the only way to effect meaningful challenge with *H. nelsoni*. Despite the availability of ICES protocols to insure practically minimal introduction of associated pests, parasites and diseases, and triploid induction techniques to minimize spawning (review by Beaumont and Fairbrother 1991), there is no practical manner to absolutely insure that no spawning of stock introduced for experimental purposes will occur. A comprehensive examination of such issues as temperature and salinity tolerances of the various life history stages of *C. gigas*, and laboratory examination of susceptibility to local predators and physical environment can only provide greater ability to evaluate possible establishment and range extension in Chesapeake Bay. They cannot provide an avenue to eliminate the possibility of spawning. In situ *H. nelsoni* challenge of *C. gigas* has already been the subject of pointed debate among academics, regulatory bodies and industry at both an intra and interstate basis. Effecting such a study cannot be accomplished without limited risk of development of a self sustaining, resident population of *C. gigas* in Chesapeake Bay. Proceeding with such *H. nelsoni* challenges are an integral and necessary component of identification of disease tolerant or resistant stocks, be they of native or non-endemic origin. Eventually, a balanced decision must be made by regulatory agencies concerning the competing pressures to expedite rejuvenation of an ailing industry and consider the unpredictable biological consequences of introduction of a non-endemic species.

A major source of debate subsumed in the question of in situ testing is the possible impact of a resident *C. gigas* population in Chesapeake Bay and competitive interaction with the native species, *C. virginica*, both within the bay and potentially outside the bay if *C. gigas* were to spread to either the north or the south of the bay mouth. During the period 1940 through 1960 testing of *C. gigas* was conducted in the lagoon systems of the Delmarva peninsula and Delaware Bay. Resident populations have not resulted although these may have been precluded by the nature of the introductions. Adequate documentation is unavailable. The Delmarva coastal lagoons and intertidal flats still maintain considerable oyster resources. On the Atlantic seaboard north of the mouth of Delaware Bay, where *P. marinus* is absent, the native oyster continues to exist as disjunct populations of various sizes, but always at levels well below historical records. These regions have again suffered variously from disease, including *H. nelsoni*, sustained harvesting and degrees of environmental degradation. Recent efforts to revive the Connecticut oyster industry through extensive shell planting and resource management are meeting with some success. Limited, culture based production exists in New England, and both cultured and wild caught oysters are available from the Canadian Maritime provinces. Investigations at Rutgers University, described earlier, concerning increased tolerance to *H. nelsoni* offer some hope of expanded oyster production in this geographic region but large scale production and reintroduction of the native species remains an enormous task. With respect to possible establishment of *C. gigas* south of Chesapeake Bay, the data of tables 2 and 3 are of limited use in estimating range extension in that definitive temperature and salinity tolerance tests have not been published for *C. gigas*. Such data are clearly desirable. Some further information may be obtained from detailed examination of current oriental culture practices within the native range of *C. gigas* (see Kusuki 1990); however, caution must again be applied in determining which geographic type of *C. gigas* is being described.

Competitive interactions in a two species scenario in Chesapeake Bay with *C. gigas* in higher salinities and *C. virginica* in lower salinities are difficult to predict because only a few meaningful analogies exist. One such analogy is the Chinese culture of *C. gigas* relative to that of the Suminoe oyster, *Crassostrea rivularis*. The latter species is, like the Myagi type of *C. gigas*, fast growing and often quite large; however, it is generally acknowledged by Chinese workers (personal communication to Roger Mann) to tolerate lower salinities. What limits the distribution of each of the *Crassostrea* species in the Chinese fisheries? This is not adequately documented, thus limiting our predictive capability for Chesapeake Bay if a reproductively active population of *C. gigas* is introduced. The second analogy is the estuarine environment of the Gironde on the Charente River in western France (the major seed oyster producing area for *C. gigas*) and in south west France where harvest pressure is comparatively light, allowing greater densities of oysters to develop (Heral and Deslous-Paoli 1990). The former location can be used as an analogy to the James River seed oyster beds and the latter location as an analogy to a situation in Chesapeake Bay where *C. gigas* is introduced as a reproductively active population to currently unproductive bottom in disease endemic areas and allowed to proliferate without excessive harvest pressure. Such a situation would obviously necessitate several prerequisites including regulatory approval to effect in situ disease challenge, a demonstrated resistance to *H. nelsoni*, and a further regulatory decision to effect refurbishment by release of reproductively active *C. gigas* cultured through ICES protocols. The argument for a comprehensive examination of both the Chi-

nese and French sites is compelling. The third and final region of interest is Queensland, New South Wales and Victoria in Australia where the introduced *C. gigas* is competing with the native and highly prized Sydney rock oyster, *Saccostrea (Crassostrea) commercialis* (review by Pollard and Hutchings 1990). Unlike the French or Oriental situations, this Australian site allows a unique opportunity to study a confrontation of an introduced and native species in progress, where *C. gigas* is the introduced species of interest. In this situation we can pointedly examine the predictive value of temperature-salinity tolerances or similar physical data relative to other biological variables such as spawning and settlement periodicities. At present the further spread of *C. gigas* in New South Wales is controlled by the management activity of removing oyster settlement substrate shortly after settlement occurs (P. H. Wolf, Dept. State Fisheries, N.S.W., Australia; personal communication to Roger Mann). *Saccostrea commercialis* is more tolerant of exposure than *C. gigas* and selective mortality occurs before the substrate is returned to the water. Whether or not *C. gigas* and *S. commercialis* could eventually coexist if control activity ceased remains unanswered, although it is relevant to note that *C. gigas* is now cultured in preference to *S. commercialis* in New Zealand due to its higher growth rate and comparable market price, and a substantial fishery for *C. gigas* now exists in Tasmania (Pollard and Hutchings 1990).

There is little question that the future of the Virginia oyster industry in its present form is very bleak if a disease resistant oyster is not identified. In addition to the biological impacts, the sociological, political and economic impacts of a continuing decline in oyster production are widespread and demand responsible action in a viable time frame. Identification of a disease resistant oyster is only the beginning of the solution, irrespective of whether that be *C. gigas* or any other species of oyster. If disease resistance is demonstrable and a decision to proceed with introduction is forthcoming, then a hatchery based program functioning under ICES protocols must be implemented on a sufficient scale to provide seed in a timely manner to maintain and rebuild the depressed resource and the industry it supports. The present industry relies upon a naturally reproducing resource and a critical decision would relate to development and protection of actively spawning broodstock regions, similar to that operated in the Gironde, rather than the clearly untenable option of attempting to continually supply seed for extensive planting in the current "put and take" mode of operation. Alternatively, utilization of triploid oysters, both native and otherwise, in species specific, intensive culture operations may be economically attractive. Rejuvenation of the Virginia oyster industry is a task of immense proportions and will require revision and diversification of many current practices if formerly unproductive bottom is to be reclaimed to stable production, and production levels increased to allow continued competitiveness in an international marketplace for the end product. Based on the available information we believe that serious consideration should be given to the utilization of an introduced species, *C. gigas*, as part of that effort.

ACKNOWLEDGMENTS

Preparation of this manuscript was supported in part by funding from the National Oceanic and Atmospheric Administration, Office of Sea Grant, and the Council on the Environment, Commonwealth of Virginia. We are indebted to our colleagues, Dr. Bruce J. Barber, Mr. Michael Castagna, and Dr. Roger I. E. Newell for much discussion concerning introduced species. Thanks are also due to colleagues who disagree, often very strongly, with the viewpoints expressed in this manuscript for continually forcing us to provide rational arguments to support our conclusions.

LITERATURE CITED

Ahmed, M. 1971. Oyster species of West Pakistan. *Pakistan J. Zoology* 3(2):229–236.

Ajana, A. M. 1980. Fishery of the mangrove oyster, *Crassostrea gasar* Adanson (1757) in the Lagos area, Nigeria. *Aquaculture* 21(2):129–137.

Allen, M. J., R. J. Wolotira, Jr., T. M. Sample, S. F. Noel & C. R. Iten. 1988. Life history and harvest information for the Pacific oyster, *Crassostrea gigas* (Thunberg, 1793). NWAFC Tech. Mem. Ser.

Amemiya, I. 1926. Notes on experiments on the early developmental stages of the Portuguese, American, and English native oysters, with special reference to the effect of varying salinity. *J. Mar. Biol. Assoc. U.K.* 31(1):161–175.

Andrews, J. D. 1980. A review of introductions of exotic oysters and biological planning for new importations. *Mar. Fish. Rev.* 42(12):1–11.

Barber, B. J., S. E. Ford & H. H. Haskin. 1988a. Effects of the parasite MSX (*Haplosporidium nelsoni*) on oyster (*Crassostrea virginica*) energy metabolism. I. Condition index and relative fecundity. *J. Shellfish Res.* 7:25–31.

Barber, B. J., S. E. Ford & H. H. Haskin. 1988b. Effects of the parasite MSX (*Haplosporidium nelsoni*) on oyster (*Crassostrea virginica*) energy metabolism. II. Tissue biochemical composition. *Comp. Biochem. Physiol.* 91A:603–608.

Bardach, J. E., J. H. Ryther & W. O. McLarney. 1972. Aquaculture: The Farming and Husbandry of Freshwater and Marine Organisms. John Wiley & Sons, Inc., New York, NY: 868 pp.

Beaumont, A. R. & J. E. Fairbrother. 1991. Ploidy manipulation in molluscan shellfish: A review. *J. Shellfish Res.* 10(1):1–18.

Becker, C. D. & G. B. Pauley. 1968. An ovarian parasite (Protista incertae sedis) from the Pacific oyster, *Crassostrea gigas*. *J. Invertebr. Pathol.* 12:425–437.

Boffi, A. V. 1979. Molluscо Brasileiros de Interesse Medico e Economico. Simbolo S.A. Industrias Graficas, Sao Paulo, Brasil; 182 pp.

Boveda, J. V. P. & R. J. Rodriguez. 1987. Supervivencia de la ostra de mangle *Crassostrea rhizophorae* (Gilding, 1828) a las variaciones de temperatura, salinidad y pH. Sociedad de Ciencias Naturales la Salle Memoria 47(127–128):217–231.

Bower, S. M. 1988. Circumvention of mortalities caused by Denman Island oyster disease during mariculture of Pacific oysters. *Amer. Fish. Soc. Spec. Publ.* 18:246–248.

Breese, W. P. & R. E. Malouf. 1977. Hatchery rearing techniques for the oyster *Crassostrea rivularis* Gould. *Aquaculture* 12:123–126.

Burreson, E. M. & J. D. Andrews. 1988. Unusual intensification of Chesapeake Bay oyster diseases during recent drought conditions. *Proc. Oceans* 88:799–802.

Butler, P. A. 1949. Gametogenesis of the oyster under conditions of depressed salinity. *Biol. Bull.* 96(3):263–269.

Cahour, A. 1979. *Marteilia refringens* and *Crassostrea gigas*. *Mar. Fish. Rev.* 41(1–2):19–20.

Carreon, J. A. 1969. The malacology of Philippine oysters of the genus *Crassostrea* and a review of their shell characters. *Proc. Nat. Shellfish. Assoc.* 59:104–115.

Chanley, P. E. 1958. Survival of some juvenile bivalves in water of low salinity. *Proc. Nat. Shellfish Assoc.* 48:52–65.

Chen, T. P. 1972. Status and problems of coastal aquaculture in Thailand. 74–83. *In* Pillay, T. V. R. (ed.). Coastal Aquaculture in the Indo-Pacific Region. Whitefriars Press, Ltd., London, U.K.

Comps, M. 1988. Epizootic diseases of oysters associated with viral infections. *Amer. Fish. Soc. Spec. Publ.* 18:23–27.

Comps, M. & J. R. Bonami. 1977. Infection virale associe des mortalits ches l'huitre *Crassostrea gigas* th. *C.R. Acad. Sci. Paris, Ser. D* 285:1139–1140.

Comps, M., M. S. Park & I. Desportes. 1986. tude ultrastructurale de *Marteilioides chungmuensis* n. g., n. sp. parasite des ovocytes de l'huitre *Crassostrea gigas* Th. *Protistologica* 22(3):279–285.

Dang, L. V. 1972. Coastal aquaculture in Vietnam. 103–108. *In* Pillay, T. V. R. (ed.). Coastal Aquaculture in the Indo-Pacific Region. Whitefriars Press, Ltd., London, U.K.

Davey, J. T. 1989. *Mytilicola intestinalis* (Copepoda: Cyclopoida): a ten year survey of infested mussels in a Cornish estuary, 1978–1988. *J. Mar. Biol. Assoc. U.K.* 69:823–826.

Davis, H. C. 1958. Survival and growth of clam and oyster larvae at different salinities. *Biol. Bull.* 114(1):57–70.

Davis, H. C. & A. Calabrese. 1964. Combined effects of temperature and salinity on development of eggs and growth of larvae of *M. mercenaria* and *C. virginica*. *U.S. Fish Wildl. Ser. Fish. Bull.* 63(3):643–655.

DeAlteris, J. T. 1988. The sedimentary processes and geomorphic history of Wreck Shoal, an oyster reef in the James River, Virginia. Ph.D. dissertation, Virginia Institute of Marine Science, College of William and Mary.

Desai, K. M., B. Patel & H. Dave. 1982. Laboratory rearing of eggs and larvae of edible oysters of the Gulf of Kutch. Proceedings of the Symposium on Coastal Aquaculture, Cochin, India, 1980 6:704.

Dos Santos, A. E. & I. A. Nascimento. 1985. Influence of gamete density, salinity, and temperature on the normal development of the mangrove oyster, *Crassostrea rhizophorae* Guilding, 1828. *Aquaculture* 47(4);335–352.

Douglass, W. R. 1977. *Minchinia nelsoni* disease development, host defense reactions, and hemolymph enzyme alterations in stock of oysters (*Crassostrea virginica*) resistant and susceptible to *Minchinia nelsoni* caused mortality. Ph.D. Dissertation. Rutgers University, New Brunswick, NJ. 232 p.

Durve, V. S. 1965. On the seasonal gonadal change and spawning in the adult oyster *Crassostrea gryphoides* (Schlotheim). *J. Mar. Biol. Assoc. India.* 7(2):328–344.

Durve, V. S. 1967. On the nomenclature of two Indian backwater oysters. *J. Mar. Biol. Assoc. India.* 9(1):173–178.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen and Co. Ltd., London. 181 p.

Elston, R. A. 1984. Prevention and management of infectious diseases in intensive mollusc husbandry. *J. World Maricult. Soc.* 15:284–300.

Elston, R. A., J. H. Beattie, C. Friedman, R. Hedrick & M. L. Kent. 1987. Pathology and significance of fatal inflammatory bacteraemia in the Pacific oyster, *Crassostrea gigas* Thunberg. *J. Fish Dis.* 10:121–132.

Elston, R. A. & M. T. Wilkinson. 1985. Pathology, management and diagnosis of oyster velar virus disease (OVVD). *Aquaculture* 48:189–210.

Farley, C. A., P. H. Wolf & R. A. Elston. 1988. A long-term study of "microcell" disease in oysters with a description of a new genus, *Mikrocytos* (g. n.), and two new species, *Mikrocytos mackini* (sp. n.) and *Mikrocytos roughleyi* (sp. n.). *Fish. Bull.* 86(3):581–593.

Ford, S. E. 1986. Comparison of hemolymph proteins between resistant and susceptible oysters, *Crassostrea virginica*, exposed to the parasite *Haplosporidium nelsoni* (MSX). *J. Invert. Pathol.* 47:283–294.

Ford. S. E. & H. H. Haskin. 1987. Infection and mortality patterns in strains of oysters *Crassostrea virginica* selected for resistance to the parasite *Haplosporidium nelsoni* (MSX). *J. Parasitol.* 73:368–376.

Friedman, C. S., J. H. Beattie, R. A. Elston & R. P. Hedrick. 1991. Investigation of the relationship between the presence of a Gram-positive bacterial infection and summer mortality of the Pacific oyster, *Crassostrea gigas* Thunberg. *Aquaculture.* 94(1):1–16.

Glude, J. B. 1975. A summary report of Pacific coast oyster mortality investigations 1965–1972. Proc. 3rd U.S.-Japan Meeting on Aquaculture, 1974:1–28.

Hargis. W. J., Jr. & D. S. Haven. 1988. Rehabilitation of the troubled oyster industry of the lower Chesapeake Bay. *J. Shellfish Res.* 7:271–279.

Haven, D. S., W. J. Hargis, Jr. & P. C. Kendall. 1978. The oyster industry of Virginia: Its status, problems and promise. VIMS Spec. Pap. Mar. Sci. No. 4. 1024 p.

Heral, M. & J. M. Deslous-Paoli. (1990). Oyster Culture in European Countries. In: Estuarine and Marine Bivalve Mollusc Culture. R. W. Menzel (Ed). CRC Press, Boca Raton, FL. pp 153–190.

Hedgecock, D. & N. B. Okazaki. 1984. Genetic diversity within and between populations of American oysters *(Crassostrea). Malacologia* 25(2):535–549.

His, E., R. Robert & A. Dinet. 1989. Combined effects of temperature and salinity on fed and starved larvae of the Mediterranean mussel *Mytilus galloprovincialis* and the Japanese oyster *Crassostrea gigas*. *Mar. Biol.* 100(4):455–463.

Hughes Games, W. L. (1977) Growing the Japanese oyster *(Crassostrea gigas)* in subtropical seawater fish ponds: 1. Growth rate, survival and quality index. *Aquaculture* 11(3):217–230.

Jhingran, V. G. & V. Gopalakrishnan. 1974. Catalogue of cultivated aquatic organisms. FAO Fisheris Technical Paper 130; 83 pp.

Johnson, P. T. 1984. Viral diseases of marine invertebrates. *Helgoländer Meeresunters.* 37:65–98.

Jones, S. 1970. The molluscan resources of India. Proceedings of the Symposium on Mollusca, Cochin, India, Part III:906–918.

Joseph, M. M. & M. N. Madhyastha. 1984. Annual reproductive cycle and sexuality of the oyster *Crassostrea madrasensis* (Preston). *Aquaculture* 40(3):223–231.

Kamara, A. B., K. B. McNeil & D. B. Quayle. 1976. Tropical oyster culture: problems and prospects. 344–348. *In* Pillay, T. V. R. & Dill, W. A. (eds.). Advances in Aquaculture: FAO Technical Conference on Aquaculture, Kyoto, Japan, 1976. Fishing News Books, Ltd., Surrey, England.

Katkansky, S. C. & R. W. Warner. 1970. Sporulation of a haplosporidan in a Pacific oyster (*Crassostrea gigas*) in Humboldt Bay, California. *J. Fish. Res. Bd. Canada* 27(7):1320–1321.

Kennedy, V. S. & L. L. Breisch. 1981. Maryland's oysters: research and management. Maryland Sea Grant, University of Maryland, College Park, MD. 286 p.

Kern, F. G. 1976. Sporulation of *Minchinia* sp. (Haplosporida, Haplosporidiidae) in the Pacific oyster *Crassostrea gigas* (Thunberg) from the Republic of Korea. *J. Protozool.* 23(4):498–500.

King, M. G. 1977. Cultivation of the Pacific oyster (*Crassostrea gigas*) in a non-tidal hypersaline pond. *Aquaculture* 11(2):123–136.

Kinne, O. (Ed.) 1983. Diseases of Marine Animals. Vol II, Introduction, Bivalvia to Scaphopoda. Biologische Anstalt Helgoland, Hamburg, 571 p.

Koganezawa, A. 1975. Present status of studies on the mass mortality of cultured oysters in Japan and its prevention. Proc. 3rd U.S.-Japan Meeting on Aquaculture, 1974:29–34.

Kong, C. P. & L. A. Luh. 1977. Notes on the efficiency of various materials tested as oyster spat collectors in Cowie Bay, Sabah. *Malaysian Agricult. Jour.* 50(4):462–479.

Kusuki, Y. (1990). Oyster culture in Japan and adjacent countries: *Crassostrea gigas* (Thunberg). In: Estuarine and Marine Bivalve Mollusc Culture. R. W. Menzel (Ed). CRC Press, Boca Raton, FL. pp. 227–244.

Le Gall, J. L. & O. Raillard. 1988. Influence de la temperature sur la physiologie de l'huitre *Crassostrea gigas*. *Oceanis* 14(5):603–608.

Loosanoff, V. L. 1958. Some aspects of behavior of oysters at different temperatures. *Biol. Bull.* 114(1):57–70.

Loosanoff, V. L. 1969. Maturation of gonads of oysters, *Crassostrea virginica*, of different geographical areas subjected to relatively low temperatures. *Veliger* 11(3):153–163.

Loosanoff, V. L. & H. C. Davis. 1952. Temperature requirements for maturation of gonads of northern oysters. *Biol. Bull.* 103(1):80–96.

Mane, U. H. 1978. Survival and behavior of oysters in water of low

salinities at Ratnagiri on the west coast of India. *J. Molluscan Studies* 44(2):243–249.

Mann, R. (Ed.). 1979. Exotic species in mariculture. The MIT Press. Cambridge, MA. 363 p.

Mann, R. 1981. The role of introduced bivalve mollusc species in mariculture. *J. World Maricult. Soc.* 14:546–559.

Meyers, J. A., E. M. Burreson, B. J. Barber & R. Mann. 1991. Susceptibility of diploid and triploid Pacific oysters, *Crassostrea gigas* in eastern oysters, *Crassostrea virginica,* to *Perkinsus marinus*. *J. Shellfish Res.* 10:433–437.

Menzel, R. W. 1974. Portuguese and Japanese oysters are the same species. Journal of the Fisheries Research Board of Canada 31(4):453–456.

Menzel, R. W. (Ed). 1990. Estuarine and Marine Bivalve Mollusc Culture. CRC Press, Boca Raton, FL. 361 pp.

Muranaka, M. S. & J. E. Lannan. 1984. Brookstock management of *Crassostrea gigas:* environmental influences on broodstock conditioning. *Aquaculture* 39(1–4):217–228.

Myhre, J. L. 1973. Levels of infection in spat of *Crassostrea virginica* and mechanisms of resistance to the haplosporidan parasite *Minchinia nelsoni*. M. S. Thesis. Rutgers University, New Brunswick. NJ. 102 p.

Nell, J. A. & J. E. Holliday. 1988. Effects of salinity on the growth and survival of Sydney rock oyster (*Saccostrea commercialis*) and Pacific oyster (*Crassostrea gigas*) larvae and spat. *Aquaculture* 68(1):39–44.

Newball, S. & M. R. Carriker. 1983. Systematic relationship of the oysters *Crassostrea rhizophorae* and *C. virginica:* a comparative ultrastructural study of the values. *American Malacological Bull.* 1:35–42.

Newell, R. I. E. 1985. Physiological effects of the MSX parasite *Haplosporidium nelsoni* (Haskin, Stauber & Mackin) on the American oyster *Crassostrea virginica* (Gmelin). *J. Shellfish Res.* 5:91–95.

Newell, R. I. E. 1989. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American Oyster (*Crassostrea virginica*)? in: Understanding the Estuary: Advances in Chesapeake Bay Research. Chesapeake Research Consortium Publication No. 129:536–546.

Pereya, W. T. 1964. Mortality of Pacific oysters, *Crassostrea gigas* (Thunberg), in various exposure situations in Washington. *Proc. Nat. Shellfish. Assoc.* 53:51–63.

Pollard, D. A. & P. A. Hutchings. 1990. A Review of Exotic Marine Organisms Introduced to the Australian Region. II. Invertebrates and Algae. *Asian Fisheries Science* 3:223–250.

Quayle, D. B. 1989. Pacific Oyster Culture in British Columbia. *Can. Bull. Fish. Aqua. Sci.* 218.

Rao, K. V. 1951. Observations on the probable effects of salinity on the spawning, development, and setting of the Indian backwater oyster, *Ostrea madrasensis* Preston. *Proc. Indian Acad. Sci.* 33:231–256.

Rao, K. V. & K. N. Nayor. 1956. Rate of growth in spat and yearlings of the Indian backwater oyster *Ostrea madrasensis* Preston. *Indian J. Fisheries* 3(2):231–260.

Reeb, C. A. & J. C. Avise. 1990. A genetic discontinuity in a continuously distributed species: mitochondrial DNA in the American oyster. *Genetics* 124:397–406.

Sandison, E. E. 1966. The effect of salinity fluctuations on the life cycle of *Gryphaea gasar* ((Adanson) Dautzenberg) in Lagos Harbor, Nigeria. *J. Animal Ecol.* 35(2):379–389.

Sandison, E. E. & M. B. Hill. 1966. The distribution of *Balanus pallidus stutsburi* Darwin, *Gryphaea gasar* ((Adanson) Dautzenberg), *Mercierella enigmatica* Fauvel and *Hydroides uncinata* (Philippi) in relation to salinity in Lagos Harbor and adjacent creeks. *J. Animal Ecol.* 35(1):235–250.

Shafee, M. S. & M. R. Sabatie. 1986. Croissance et Mortalite des Huitres dans la Lagune de Oualidia (Maroc). *Aquaculture* 53:201–214.

Sindermann, C. J. & D. V. Lightner. 1988. Disease diagnosis and control in North American marine aquaculture. Elsevier, New York. 431 p.

Stephen, D. 1980. The reproductive biology of the Indian oyster *Crassostrea madrasensis* (Preston): 1. Gametogenic patterns and salinity. *Aquaculture* 21(2):139–146.

Tebble, N. 1966. British Bivalve Seashells. British Museum of Natural History, London, England; 212 pp.

Torigoe, K. 1981. Oysters in Japan. J. Sci. Hiroshima University, 29B(2):291–419.

Wells, H. W. 1961. The fauna of oyster beds, with special reference to the salinity factor. *Ecological Monographs* 31(3):239–266.

Zenkevitch, L. 1963. Biology of the seas of the U.S.S.R. John Wiley & Sons, Inc., New York, NY; 955 pp.

Economics of Molluscan Introductions and Transfers: The Chesapeake Bay Dilemma

Douglas W. Lipton, Eileen F. Lavan, and Ivar E. Strand

INTRODUCTION

The major reason for introduction or transfer of molluscan species is economic gain. As Mann (1979) states, the economic incentive increases when an existing fishery becomes depleted or devastated due to overfishing, degradation of environmental quality, or disease. Also, even if there is no existing native fishery, great demand for a product may provide enough economic incentive for an introduction. Whether the introduction is intended to benefit a public or private fishery, the public sector's role is paramount in the decision to allow or disallow introductions. Economists have two interrelated roles in the public decision process regarding molluscan introductions. First, estimates of the net benefits (benefits minus costs) to the various groups affected by the introduction should be provided. This will involve estimating the net benefits to harvesters, processors and consumers but also might include benefits and costs external to these groups. An example is where introduction of filter feeders provides benefits of improved water quality (Newell 1988). The economists' role does not end at the provision of benefit-cost information, but includes, interpreting this information within the context of policy setting. This is particularly important in that exotic introductions have many uncertainties surrounding the benefits and costs of the action.

Our paper discusses both roles in the context of potential molluscan introductions and transfers. To illustrate, we use the potential introduction of *Crassostrea gigas* into the Chesapeake Bay to replace the devastated native *Crassostrea virginica*. To place the event in context, recent events in the Maryland oyster industry are reviewed. A review of molluscan introductions is then presented to provide a qualitative range of benefits and risks likely to be encountered in the Chesapeake Bay. Brief descriptions are provided of the effects of molluscan introductions into North America and other parts of the world. Although we made every attempt to document the market value of these introductions, these statistics are hard to come by, particularly when harvests are small relative to indigenous populations of fish and shellfish. These descriptions are followed by a theoretical discussion of measuring costs, benefits and associated risks of the contemplated introduction.

Paper presented at the Annual Meeting of The North American Shellfish Association, Williamsburg, VA. April 2–5, 1990. Revised 12/91, Final Version 10/92.

THE MARYLAND EXPERIENCE

Several useful and insightful histories of the Maryland oyster industry have been offered over the years (e.g. Power 1970, Wennersten 1978). The most recent and comprehensive is the Kennedy and Breisch (1983) work in which the dichotomy of the politics surrounding the oyster management and the science of oyster propagation is explained. The results of the mismanagement can be seen in the precipitous drop in Maryland oyster production between the late 1800's and late 1920's (Fig. 1). Landings apparently stabilized over the next 30 years to 1950. Although there are lessons to be learned from the early period, we focus on the post-war events.

In order to understand the current situation, the period from 1950 through 1989 is divided, from the point of view of landings, into an apparently stable period (1950–1980) and a declining period (1981–1989).

The oyster seasons from 1950[1] through 1981, while giving the impression of an unusually stable period, contains a major structural change. The 1950 season began the period with harvests of 2.16 million bushels and the 1981 season completed the period with landings of 2.10 million bushels (see Fig. 2). However, Maryland's oyster harvest declined by 50% from 1950 to 1962 and then exhibited an extraordinary revival. The resurgence in Maryland (1962–1981) is represented by an increase in production from 1.24 million bushels in 1962 to a period high of 3.01 million bushels in 1966. Events in the Maryland industry are best understood if we consider the complete East Coast oyster market. In 1950, there were three East Coast areas each with production in excess of 2 million bushels: the Mid-Atlantic (New York, New Jersey and Delaware), Maryland and Virginia. Possibly as a result of eutrophication, production from New York's waters dropped dramatically between 1950 and 1954. The decline in the Mid-Atlantic was exacerbated when MSX invaded the water of Delaware Bay in 1957. The effect of MSX on oysters is well-known, inflicting mortalities in adult oysters in the range of 50–90% (Haskins and Andrews, 1988). Total production in the Mid-Atlantic dropped from nearly three million bushels to 0.2 million during the decade. There was a corresponding drop in nominal

[1]The oyster season is referred to in terms of the year in which it began. Thus, the oyster season lasting from September of 1980 to March of 1981 is denoted as the 1980 oyster season.

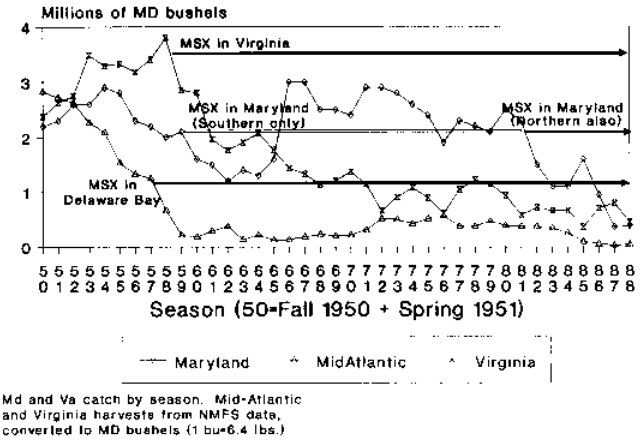


Figure 1. East coast oyster landings by region, 1950–1988.

value from $9.6 million in 1950 to $1.3 million in 1959. Production has remained at that magnitude until recently.

It is instructive to observe the effects in Maryland and Virginia from the decreases in Mid-Atlantic harvests. Ex-vessel prices rose nearly 15% in Maryland and 10% in Virginia. In response, the Chesapeake harvest in 1954 rose by nearly 50%. Maryland, which relies primarily on harvest from public grounds, had a spurt in production for approximately three years (1954–57), followed by a gradual decline in the harvest. At this point in time, the decision was implicitly made by the state not to increase expenditures to expand the industry. Budgetary constraints both at the state and private harvester level prevented it.

Virginia's production, on the other hand, was principally from grounds leased by private interests. The increase in price signalled greater profits to the private growers and they increased purchases of seed from Virginia's vast seed beds on the James River. Production rose from under three million bushels in 1950–1952 to around 3.5 million after 1954. The peak occurred in the 1959 season when nearly four million bushels were harvested in Virginia.

Whether the private growers and Virginia's seed resources could have sustained this production into the future became a moot point when MSX began to affect Virginia production around 1960. By 1964, Virginia production was one-half of the 1959 peak harvest. Growing areas in the southern portion of the Chesapeake Bay were devastated because, to a degree, the disease is confined to the higher salinity areas of the Bay. However, some sections of Maryland's Tangier Sound, Pocomoke and Fishing Bay were also affected.

Maryland was fortunate, however, as the disease did not move further north in Chesapeake Bay until much later, a fact which permitted actions which temporarily reversed the declining harvest. The key to the reversal was oyster shell. The nature of oyster reproduction is such that young larvae require a hard substrate on which to attach. The oyster shell provides such a substrate. However if the harvested shell is not replaced in the Bay by a suitable substrate, there is a strong likelihood that the future availability of oysters will be reduced. This relationship was recognized long ago and the Maryland legislature in 1927 passed a law providing funds for state shell-planting activity (Kennedy and Breisch). That legislation also required processors to make 10% of their shucked shell available for purchase by the state. These efforts were at least partially responsible for the upswing in oyster production from around 2 million bushels in the 1928–29 season to over 3 million a decade later. As the years passed, however, it became more expensive to use the shucked shell for the repletion program.

However, the discovery of pre-historic fossil shell sources and the development of a dredge to extract it provided a cheap[2] alternative to freshly shucked shell and fueled the resurgence observed in the 1962 to 1967 period. The use of inexpensive dredged shell momentarily changed the philosophy of oyster management from trying to sustain a collapsing industry to a philosophy of revitalizing a potentially valuable industry. In the process, the fundamentals of oyster production also changed. No longer would the watermen be solely dependent on the "recycling" of processed oyster shell, they would have a partial reprieve from the constraints of nature. Assuring a strong market with high prices was the new focus of attention.

In 1960, Maryland devoted substantial resources to the use of dredged shell for repletion of beds and enhancement of oyster production. There were 1.2 million bushels of fresh shell planted and 3.3 million bushels of dredged shell planted in that year. By 1966, fresh shell plantings had fallen to .5 million bushels whereas dredged shell plantings had risen to nearly 6 million bushels.

The results of the increased enhancement activity on Maryland's production are evident in Figure 2. In the period from 1960–1966, Maryland oyster production doubled, from around 1.5 million bushels to around 3 million, and nominal value increased from $7 million to $13 million. While the production stayed high through the 1967 season, it began to wane in the late 1960's and continued the trend throughout the 1970's.

Despite the trend, Maryland oyster production remained over 2 million bushels until 1981. The increase in importance of the repletion program relative to natural set transformed the oyster fishery from traditional natural resource gathering into a "put-and-take" state fishery. The constraining feature was no longer the natural reproduction but rather a belief that the market could not absorb, at an acceptable price, more than about 2.5 million bushels. The repletion program used this level of harvest as a target for its programs.

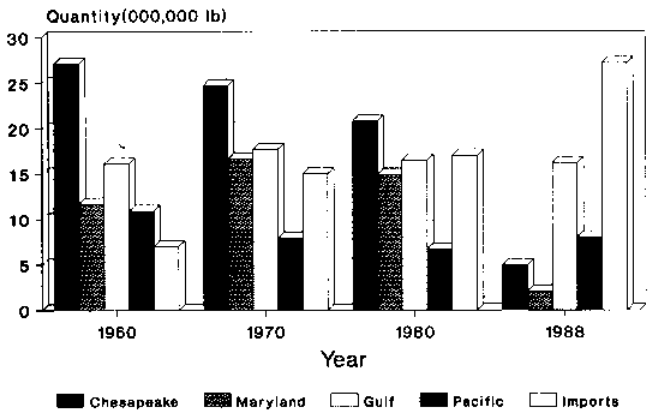


Figure 2. Oyster production and imports by region and selected years.

[2]Reasons for the shift relate both to costs of acquiring the shell and the relative productivity of the two types of shell. Although cost/bushel data for fresh shell does not extend back to 1960, there are records in 1970 showing that the cost of dredged shell was about $.15/bushel whereas the cost of fresh shell was around $.25/bushel. It has also been shown that a bushel of dredged shell has potentially greater effect on future oyster production than a bushel of fresh shell (Cabraal, 1978).

There was a reason for concern over the price in this period. The real price[3] obtained by Maryland watermen was greatest in the 1962 season when both Maryland and Virginia harvests were low. The near doubling of Maryland production in the 1966 season caused real prices to drop by nearly 20% in the short-run and by about 40% in the longer run. The lowest real price received by Maryland watermen occurred in the 1974 season.

The importance of the period is in the change in the role of the state in "managing" the industry. At the beginning of the period, the role was primarily to make it difficult for the industry to deplete the natural oyster beds. The discovery of an inexpensive alternative to provide seed created a different role for the State. The choice was made to increase production, rather than build up natural beds. Rather than being regulators, the State became the source of growth. However, the production was constrained by the market—production was not to surpass 2.5 million bushels.

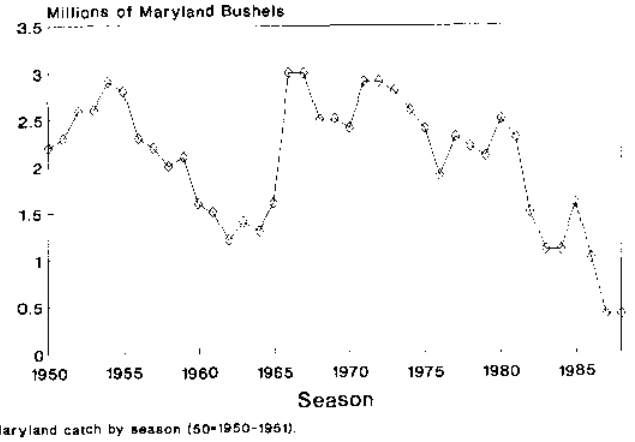


Figure 3. Maryland oyster harvest, by season, 1950–1988.

Diseased Waters 1981–1988

The dominant factor in the Maryland oyster industry after 1980 was the reappearance of the disease MSX and greater outbreaks of Dermo (*Perkinsus marinus*). Unlike the previous invasion in the 1960's which was limited to Maryland's portion of Tangier Sound, this invasion affected most of Maryland's major oyster bars from 1981–1983. There was a brief reprieve in disease-related mortality in 1984 and 1985, but a return of MSX in previously infected areas and an expansion into more areas followed in 1986–1988.

The trend in oyster harvests during the period parallels the course of MSX infection. Harvest declined from over 2.5 million bushels during the 1980–1981 season to just over a million bushels in the 1983 season. In the next two seasons, the catch increased to almost 1.6 million bushels. This brief revival did not last and production fell to around 0.4 million bushels in the 1987 and 1988 seasons.

The more than doubling of the real ex-vessel price of oysters from the 1980 ($8 per bushel) season to the 1987 ($20 per bushel) season did not offset the effect on watermen income of the decline in oyster harvest. As a result, gross revenues fell from over $20 million dollars to less than $8 million. The higher prices, however, did act to keep the level of effort (as measured in mandays) relatively constant even though the landings were declining. The number of individuals commercially harvesting and selling oysters declined by around 40%. The low resource abundance had the effect of removing most of the part-time fishermen and raising the level of effort of full-time fishermen.

The sporadic nature of the MSX infection made it difficult to develop a comprehensive strategy for the oyster repletion program. The amount and location of shell and seed plantings depended more on availability of seed and the location of disease than on any other factor. Initially during the period, seed oyster plantings closely followed the index of spat set in the previous year. With the 1983 and 1984 season being particularly poor for spatfall, seed plantings in 1984 and 1985 were extremely small even though they included several year classes of submarket oysters. Seed plantings increased steadily from 1985 and peaked in 1988, assisted by relatively good spat sets during the drought years from 1985 through 1987. In 1989, seed plantings were down 37% from 1988 but were still the second highest of the decade.

The pattern of decline in Maryland oyster landings over the period differs slightly from the pattern observed in other regions[4] (Fig. 3). Over the entire period (1980–1988), Maryland's decline in landings was 82%, while other regions declined only 37%. The Gulf states' oyster production increased to a record 29 million pounds of meats by 1983, but harvests declined continually to 16 million pounds in 1988. Only Pacific oyster production was greater in 1988 than it was in 1982, and that increase was only 600 thousand pounds.

Imports, which are principally low value canned or smoked oysters, increased from 27 million pounds of meats to a record 52 million pounds in 1987. Imports declined to 27.5 million pounds in 1990.

Interestingly, the source of production for the increased imports and West Coast production is the species, *Crassostrea gigas*. The reason is it has not been exposed to the levels of infestation of either MSX or Dermo that occur in Maryland, Virginia, Delaware and New Jersey. Thus, the obvious interest in importing it into Maryland, and Chesapeake Bay waters to test its hardiness against those diseases.

It is within the context of a devastated East Coast oyster industry that the introduction of *C. gigas* is being contemplated. In Maryland, harvesters have turned to an alternative resource, the softshell clam (*Mya arenaria*) for some economic relief. In Virginia harvest and culture of the hardshell clam (*Mercenaria mercenaria*) have helped cushion the impact of a declining oyster industry for some watermen. If *C. gigas* could be introduced, another possible source of income could make the difference between continuing to fish or having to leave fishing altogether.

EFFECTS OF RECENT MOLLUSCAN INTRODUCTIONS

Introductions of many aquatic species have taken place over the centuries. However, many attempts to establish populations have not been reported. The establishment of a reproducing population of the species is, presumably, the goal of an introduction. However, this goal is not always realized. As such, the examples we have are somewhat self-selecting; that is, many of the failures are not documented in the literature because researchers have little to

[3]Real prices are actual prices adjusted for the general level of inflation.

[4]Comparisons are made on a calendar year basis and in meat-weight rather than bushels because the available data are given in these terms.

report. Thus, our examples of introductions are those that have been mostly successful to date. France is the notable exception, the victim of many unfavorable experiences.

British Columbia

More than twelve known exotic species have been accidentally introduced in British Columbia (Quayle 1964). The introductions of *Crassostrea virginica* and *Crassostrea gigas*, however, were intentional

Ostrea lurida (the Olympia oyster) is the sole native oyster of British Columbia, and was the basis of the early oyster industry. Overfishing, and later, competition from introduced species led to its decline as a major fishery (Ketchen et al. 1983). Its diminutive size, slow growth, and high labor cost caused the industry to seek other species for commercial use (Bourne 1979).

Crassostrea virginica was first introduced to British Columbian waters in significant numbers in 1906, although minor introductions had occurred previously. Attempts ceased in 1936 due to limited natural spatfall and high mortality rates (Quayle 1964). Currently only a small population exists in Boundary Bay. Along with *C. virginica, Urosalpinx cinerea* (Eastern oyster drill), and *Nassarius obsoletus* (Eastern mud snail) were accidentally introduced. *U. cinerea* has the potential to cause severe damage to commercial shellfish populations. However, its population is apparently small and declining due to the limit of a suitable environment. *N. obsoletus* is well established in some areas, but apparently has not created any ecological harm.

Mya arenaria was planted in Puget Sound from Willapa Harbor, Washington, and water movement patterns distributed the species northward along the U.S. and British Columbian coasts (Quayle 1964). To date, the British Columbian and U.S. West Coast market for softshell clams has not developed to provide the incentive for significant commercial exploitation of the established *M. arenaria* population. A significant recreational fishery has developed. The lack of high fishing mortality has probably contributed to the successful establishment of the *M. arenaria* population.

Crassostrea gigas has been introduced to British Columbia on numerous occasions. The initial introductions are believed to have taken place in 1912 or 1913. The first significant official introduction occurred in 1926, with oysters from both Japan and the state of Washington (Quayle 1969). Reliable seed sources were a problem at the start of the industry as no local seed was available, and the imported seed had low survival (Im and Langmo 1977). It is too cold in most British Columbian waters for regular breeding, but Pendrall and Hotham Sounds have good breeding conditions, and now serve as the main sources of seed oysters. Imported seed has been completely displaced due to the natural set and the supply of domestic hatchery seed. *C. gigas* now constitutes the entire commercial oyster industry in British Columbia, at a catch of nearly 1800 tons in 1980 (Ketchen et al. 1983). Although the *C. gigas* introduction resulted in numerous accidental imports, as a whole, the introduction is viewed as a success.

Venerupis japonica (Manila clam) was accidently introduced with *C. gigas* (Quayle and Bourne 1972, Bourne 1982, Ketchen et al. 1983, Chew 1989). It is believed to have been included with oyster introductions on more than one occasion, establishing a strong population in the southern areas of the Province. Later intentional plantings in 1962 and 1969 in Northern British Columbia were unsuccessful. The *V. japonica* catch fluctuates greatly, and in good years comprises a significant portion of the local clam fishery. The landings have increased dramatically of late, from 700 metric tons in 1982 to approximately 1400 metric tons in 1989 (Chew 1990). Production figures demonstrate that although a species may require little effort to become established, its long-term success as a fishery requires good management.

Another accidental introduction, *Ceratostoma inornatum* (the Japanese oyster drill) was potentially threatening to the local oyster stocks. Fortunately, its lack of a pelagic larval stage resulted in negligible initial dispersal. When first observed, regulations were immediately enacted to prevent further spread. However, its presence has caused closing of some oyster beds (Quayle 1984). Another introduced oyster drill species, *Purpura clavigera*, does have a pelagic larval stage. Distribution appeared unavoidable, but a prompt, aggressive eradication program removed adults and egg capsules in the initial location area, and no others have been detected (Quayle 1964).

Other organisms accidentally introduced with the Japanese oyster include:

Batillaria zonalis—a somewhat common but innocuous gastropod.

Mytilicola orientalis—a parasitic copepod, also reasonably common in areas. Apparently the copepod does not cause harm to oysters, although it may pose a problem with mussels.

Limnoria tripunctata—the marine wood borer, responsible for significant damage to wood pilings in Southern British Columbia.

Pseudostylochus ostreophagus—a flatworm predator of small oysters, has not posed a serious problem in British Columbia, although it is a problem with oyster spat in Japan.

Sargassum muticum—a seaweed which has not posed any problems except as a nuisance to people using the shores for recreation.

Mikrocytos mackini—the Denman disease, an oyster ailment, was discovered after the introduction of the Japanese oyster. However, there is not conclusive evidence linking it to the Japanese oyster. The industry is said to have "learned to live with it" (Bourne 1979).

As previously noted, the introduction of *C. gigas* into British Columbia is considered successful, even though it was accompanied by accidental imports. *C. gigas* has prospered where the native oyster (*O. lurida*) failed. The accidentally introduced *V. japonica* is viewed as an important resource. Although serious biological and economic damage could have resulted from a few of the other accidental introductions, quick action and good fortune denied them any significance.

U.S. West Coast

California, Oregon, and Washington have followed similar routes in mollusc introductions. *O. lurida* is the native oyster species, currently comprising a small percentage of the commercial oyster catch. *C. virginica* was introduced in the late 1800's to northern California and Washington. As in British Columbia, its establishment as a commercial fishery failed, but its import was responsible for the introduction of *Nassarius obsoletus* and *Mya arenaria* (Quayle 1964). *Nassarius obsoletus*, although abundant, is apparently innocuous, as aforementioned. The success of *M. arenaria*, as in British Columbia, is limited by the lack of a strong market.

Crassostrea gigas was first introduced to the Northwestern states of the U.S. unsuccessfully in 1902 (Chew 1979). The first marginally successful introduction to Washington occurred in

1919. With subsequent introductions, commercial cultivation of *C. gigas* was realized by 1928. As in British Columbia, the *C. gigas* industry of the U.S. west coast at first relied upon seed imported from Japan. For some time, the Washington State Department of Fisheries monitored the concentration of oyster larvae in natural spawning areas (such as Dabob and Willapa Bays) and notified culturers, who then collected the pelagic larvae on cultch for their own leased beds. However, spat was not abundant enough to allow the industry to become independent from Japanese seed. Currently, culturists rely on purchasing larvae from hatcheries to sustain the industry and the dependence upon Japan for seed has lessened (Burrell 1985; Chew, personal communication). *C. gigas* does best in Washington; prolonged periods of relatively high water temperatures may be the reason for its limited success in California (Chew 1979). Regardless of the limitations of the natural set, *C. gigas* is the basis for the oyster industry in both states. Oregon harvests have never been significant. The 1988 commercial catch for the U.S. west coast totaled 7.97 million pounds, of which 6.6 million pounds originated in Washington. The ex-vessel value of the harvest in 1988 was $14.5 million. Although such a harvest may appear impressive, they represent a decline from the record 1946 harvest of 13.4 million pounds of meats. Expansion of the industry has probably been limited by the size of the market, competition from low cost imported oysters, and until recently, the availability of East and Gulf Coast oysters.

Other recognized accidental introductions with *C. gigas* to these states are *O. japonica*, *V. japonica*, and *P. ostreophagus*. *C. inornatum*, as in British Columbia, has limited distribution due to its lack of a pelagic larval stage. With regulations, further distribution has been avoided.

Venerupis japonica grows well in these areas, particularly in the slightly warmer waters. Harvests fluctuated somewhat in the early years, possibly due to the erratic nature of reproduction in small populations, but has increased greatly since 1975, and may be stabilizing. The 1980 harvest was second in pounds landed and economic value (at $1.1 million) to *Panopea generosa* (geoduck clam). In Washington, approximately 1.5 million pounds were landed in 1981, while the commercial harvests in California and Oregon are negligible. Ninety-five percent of the commercial catch is from natural set, but culturists are beginning to use hatchery seed on leased beds.

Ostrea edulis was introduced to northern California and Washington beginning in 1951. The oysters originated from the newly developing *O. edulis* population of Maine (Loosanoff 1955). There is no natural spawning in the west coast waters, and although a few hatcheries produce *O. edulis* seed, interest in culturing the European oyster in these areas is limited—the majority of interest remaining with *C. gigas* (Hulbrock, Chew, personal communication). There is no evidence of accidental introductions with the European oyster. There is a protozoan parasite (*Bonamia ostrea*) discovered in 1965, but it may be native to California and Washington waters (Katkansky et al. 1969). It attacks *O. edulis'* immune system, but apparently does not harm *C. gigas* or *C. virginica*. *O. edulis* populations in Washington, having been exposed to the disease, have been found to harbor the parasite while resisting damage (Elston et al. 1987).

Hawaii

Hawaiian molluscan shellfish introductions are unique in that according to state law, non-native organisms are prohibited from introduction to open waters. Therefore, all culturing of exotic species is done in landbased pond operations (Fassler, personal communication). The practice of purely landbased operations is costly. Consequently, only a smattering of exotic molluscan introductions have ensued. One (now bankrupt) oyster farm cultured *C. gigas*, *C. virginica*, and *O. edulis*, which all did very well from a biological standpoint. There was a slight problem with the mud worm (*Polydora* sp.), but placing the oyster in warmer water killed the worm. Although achieving biological success, the high costs of the operation precluded the possibility of economic success.

A recently opened oyster farm is anticipating its first harvest this year, 1991 (Archibald, personal communication). At present, only *O. edulis* is cultured for harvest. In order to approximate the oyster's natural habitat, salmon and kelp are also maintained in the ponds. Sea urchins and abalone are present to control the environment in the main kelp growing ponds. To minimize the possibility of introducing disease and other organisms, all eyed larvae are purchased from a single Maine hatchery. Each shipment is then kept in separate growing tanks. The company is optimistic about the economic success of the harvest; for there is promise of great demand for the product. It is now left to the market to determine if the introduction and culture of *O. edulis* in Hawaii under such costly conditions is economically feasible.

Maine

The native oyster of Maine is *C. virginica*. The present stock is sparse, with successful spawnings in only the warmest of years (Lewis, personal communication). As a result, Atlantic oyster production is erratic, yet it remains a significant component of the oyster industry. Reported commercial harvests of *C. virginica* were 2,510 bushels in 1988, and 3,715 bushels in 1989, worth $277 thousand.

Ostrea edulis was introduced in Maine in 1949 (Loosanoff 1955). Although oysters from Holland were brought to Connecticut for research purposes, a few bushels were held in reserve at the Boothbay Harbor Maine Laboratory where spawning occurred. Some spat survived and later reproduced, forming the foundations of a resident population. Thoughts turned to further introduction of the species in order to replace a then-failing softshell clam industry. Later introductions were made at various points along the coast from Boothbay Harbor to Merepoint Bay (Welch 1963). Although *O. edulis* is fairly well distributed, the populations are not very large, with the industry having just attained commercial significance in 1984. The 1988 harvest was 6,346 bushels, and in 1989: 14,435 bushels. No accidental introductions accompanying the *O. edulis* introduction have been discovered. The oyster is harvested from both natural and leased cultivation beds; leased beds utilizing both naturally produced spat and hatchery seed (Lewis, personal communication). The hope is for *O. edulis* to fill a market niche in the domestic market for gourmet oysters, and for possible export to Europe.

France

Ostrea edulis is the sole native oyster species of France. The oyster, considered an important component of French culture, has always been in high demand. The fishery, however, has a volatile history. Two distinct diseases caused production to fall in 1920 and 1950 (Goulletquer undated). In 1968, the protozoan parasite *Marteilia refringens* further reduced stocks. The origin of these

diseases and the protozoan is uncertain. *M. refringens* is limited to estuarine areas, between which it was transferred with the movement of oysters. (Goulletquer undated). In 1979 *Bonamia ostrea*, a protozoan that generates microcell disease, was introduced. The protozoan was introduced with *O. edulis* adults from Washington state, the progeny of infected Californian oyster stocks (Elston et al. 1987, Mann 1983). These oysters were intended to supplement the low French stocks. *B. ostrea* is considered by many the final blow to the industry, causing the flat oyster fishery in Brittany to fall from a harvest of 4,000 tons in 1978 to 2,000 tons in 1987.

Other oysters were introduced over the years to meet the high French demand and later, to compensate for the falling stocks of *O. edulis*. *Crassostrea angulata* (Portuguese oyster) was introduced in the 1860's without official regulation. The oysters thrived, with harvests reaching 85,000 mt in 1960 (Goulletquer and Héral 1991). However, *C. angulata* experienced high mortalities from an iridovirus damaging the labia and gills in 1964 and 1965 (Farley 1991), and again from 1970 to 1972 from damage to the blood by yet another iridovirus (Grizel and Héral 1991). The latter outbreak was estimated to cost the industry $90 million a year in revenues (Goulletquer and Héral 1991). The present *C. angulata* population is negligible.

Unofficial importations of *C. gigas* began in 1966 because of the oystermen's frustrations with the declines in *O. edulis* and *C. angulata*. Officials, alarmed by an increase in *C. angulata* mortalities, prevented further *C. gigas* introductions until studies in Japan cleared *C. gigas* of any responsibility for the *C. angulata* deaths. Official introductions of *C. gigas* from both Japanese and British Columbian waters ensued in 1971. *C. gigas*, as previously mentioned, is resistant to *Bonamia ostrea*. The resistance of the Pacific oyster to the diseases of the Portuguese oyster as well allowed the expansion of an otherwise failing oyster industry in France (Grizel and Héral 1991). Presently, *C. gigas* is the principal species in the French oyster industry, accounting for 92% of the 1990 landings which were a record 150,000 metric tons valued at $210 million (Goulletquer and Héral 1991). It will not reproduce in the northern waters of France, however, reproducing best in the warmer waters of southern France.

Accidental introductions did occur with the importation of *C. gigas*, although precautions were taken in the official introductions. A few of these species are still present, although in low numbers. These species include: *Balanus amprhitrite* and *B. albicostatus*, *Aiptasia pulchella*, *Anomia chinensis* (Grizel and Héral). The low numbers render the organisms of relatively little concern to the French, although the significance of any accidental introduction, harmful or not, should not be denied.

Currently, research is underway to seek out other oyster species with a resistance to *B. ostrea*. As mentioned, a strain of *O. edulis* in Washington state was found to carry, but not be highly damaged by the parasite. Also, breeding the immune *C. gigas* at the same time as *O. edulis* reduces the severity of the protozoan in *O. edulis*. Other species that have been studied in labs include *O. chiliensis* from Chile in quarantined system in 1981. Studies were abandoned due to lack of success (Mann 1983). *O. puelchana*, of Argentina, however, appeared insusceptible to the parasite in hatchery lab studies and was subsequently planted in northern Patagonia waters in 1988, the success of which is still to be determined (Goulletquer undated).

The French oyster industry has experienced what may be the most severe problem encountered thus far with the introduction of species, when *O. edulis* of America's West Coast brought new disease to a declining industry. The utilization of *C. gigas* has helped overcome that failure. *C. gigas* has eventually gained market acceptance as an alternative to *C. angulata*, although both are considered inferior to the native *O. edulis*. The French have presumably decided that an inferior oyster is better than no oyster. Further research on both of these species and others bring hope to the industry, which apparently has decided that one tragedy should not preclude further development.

Australia

The experience of Australia in regards to mollusk introductions depends on the state involved. In Tasmania and South Australia, *C. gigas* has been successfully introduced and is forming the basis for a cultured oyster industry. In 1989–1990, 3.5 million dozen oysters worth 13.7 M$Aus were harvested (Ayres 1991). In both these states there is no extant native oyster to compete with. However, in New South Wales there is an existing fishery based on the native rock oyster (*Saccostrea commercialis*). An unofficial or accidental introduction of *C. gigas* occurred in the seed production area of Port Stephens sometime prior to 1985. After several years of trying to eradicate *C. gigas*, because it interferes with the setting of *S. commercialis*, the government finally decided to allow the cultivation and sale of *C. gigas* from Port Stephens (Ayres 1991).

New Zealand

The native oyster in New Zealand is the rock oyster (*Saccostrea glomerata*) which was the basis of an oyster culture industry. *C. gigas* was accidently introduced to New Zealand waters in the 1960's and 1970's (Dinamani 1991). Distribution was aided by the traditional movement of *S. glomerata* seed in which was mixed *C. gigas* seed. In the course of about a decade, *C. gigas* went from a density on spat collectors of 1/1000 to 4/5. Harvests in 1985 reached 2000 mt. *C. gigas* is now the basis of the New Zealand cultured oyster industry.

NET BENEFITS OF MOLLUSCAN INTRODUCTIONS

Estimating Direct Net Benefits

In some ways, the estimation of net benefits for molluscan introductions is easier than most cost-benefit analysis. Many net benefits from environmental improvements arise from consumers' use of goods not sold in the marketplace. These non-market goods pose special difficulties in measurement. For example, improvements in water quality may improve recreational fishing opportunities, but because there is not a market with corresponding prices and quantities of fishing, there are unique problems in measuring the change in benefits to sportfishermen (Bockstael, Hanemann and Strand 1986). Fortunately, molluscs are market goods for which we can observe changes in prices and quantities, and thus, estimate supply, demand and corresponding welfare changes from introductions.

Although detailed data on the distribution of oysters in the marketplace are not available, it is common knowledge that the flow of West Coast *C. gigas* to the East Coast has increased since the collapse of the Chesapeake oyster fishery. It is not known to what extent consumers are aware or care about what oyster species they are consuming. In cases where a species is introduced to replace a depleted local species, and the two species are considered by the consumer to be close substitutes, demand studies based on a time series of prices and quantities of the depleted species may serve to estimate demand for the introduced species. Thus, in

France where there was an industry based on *C. angulata,* it is not surprising to expect similar demand for *C. gigas*. Of course, the reliability of forecasts from historical data are diminished the further out in time those forecasts must be made. Traditional consumer welfare measures (i.e., consumer surplus) can be made once the demand for the introduced oyster is determined.

The measurement of producer benefits, as in the case of consumers, must be measured net of costs. Total value of the harvest, probably the most often cited figure of success of an introduction, is not a measure of producer welfare unless culturing and harvesting are costless activities. Cost estimates can be made from current data on culturing, harvesting and processing costs to the extent these are available. Bosch and Shabman (1989) have developed such cost estimates for Virginia oyster growers, and these could be appropriately modified for the different species. In cases where data is not available, an economic-engineering approach can prove useful (Park and Jackson 1984). The opportunity cost of the producer's labor (i.e., what he could earn in the next best employment opportunity) should be included in the cost estimate. In areas where there are few alternative opportunities, the opportunity cost of labor tends to be low and results in higher producer benefits. Thus, in France, where there was a large oyster industry with few alternative opportunities, the benefits of the introduction of *C. gigas* are higher than in an area where there are several alternative fishing and culturing alternatives.

If the introduction is for purposes of restoring a public fishery, the net benefit to producers will depend on how the resource is managed. If an open access management regime is maintained, then net benefits to producers will be less than if a bottom leasing program or limited entry program on public grounds are producers will be less than if a bottom leasing program or limited entry program on public grounds are instituted. This is the well-known result of rent dissipation in common property fisheries (c.f., Gordon 1954, Copes 1972). Simply replacing one species with another does not necessarily eliminate the man-induced factors that caused the decline of the native species. One must still deal with the problem of overfishing, potential disease, and a decline in water quality.

Measuring "External" Costs of Mollusk Introductions

Although the direct net benefits of mollusk introductions may be many years off, the costs of these potential introductions are being incurred today mainly in the form of research dollars. Costs of general research on mollusk introductions that is applicable to a variety of species and variety of areas cannot fairly be assigned totally to the cost of introduction of one species in one area. However, as a specific introduction is contemplated, more of the research dollars are focused on determining the impact and likelihood of success for that given area.

The actual cost of performing the introduction or transfer, and monitoring and maintenance may be substantial. However, once it is determined what functions have to be performed, predicting the costs would not be an overwhelming task. For example, the magnitude of costs will be much greater when introducing a non-reproducing organism into an area for yearly harvest, as compared to an introduction of an organism that can successfully reproduce.

The most contentious issue regarding mollusk introductions and their costs is the potential that an introduction may be accompanied by deleterious effects to other resources in an area. These can include the case of an otherwise successful introduction of an organism that outcompetes native resources and causes a population decline of the native resource such as occurred in New Zealand. The introduction may also inadvertently introduce other undesirable species, disease organisms or parasites that can disrupt the ecosystem. The end result may simply be a nuisance or considered a disaster. The results may be either reversible or irreversible.

Uncertainty and the Use of Benefit-Cost Analysis

The fundamental issue surrounding introduction of molluscan species is the uncertainty of the effects. Even though the history of molluscan introductions, reviewed above, shows few disastrous external effects, the evidence is clear that molluscan introduction have resulted in inadvertent species being introduced with the mollusks. Some might say that it was a stroke of luck that no disasters occurred. A finite probability exists that an ecological and economic disaster can occur with an introduction of *C. gigas* into the Chesapeake Bay. How does one consider uncertainty within the benefit cost framework?

There are two primary ways it has been considered- through the use of expected net benefits and through a game-theoretic approach. When using expected net benefits, the distributions about the costs and benefits are used and the expected value of net benefits is calculated. In concept, this is a straightforward procedure but the distributions about net benefits are not easy to determine, especially the ones concerning future events. Often, higher discount is given to more risky choices.

The uncertainty involved in the decision on whether to allow an introduction can also be approached through game theory. Bishop (1978) applied this approach when examining extinction of a potentially valuable species due to building a dam. The game is depicted as follows:

	States		
Action	No Disaster	Disaster	Maximum Losses
Introduction	0	b	b
No introduction	a	a–b	a

Man has two choices, to allow or not allow an introduction. If he does not allow the introduction, the net benefits foregone are denoted as a. If the introduction is allowed and causes a disaster in existing populations this is denoted by b. The last column indicates the maximum losses under the introduction and no introduction scenario.

One strategy in playing this game is to adopt the minimax principle—chose the strategy that minimizes maximum possible losses (Ciriacy-Wantrup 1968). Thus, if we feel the damages from a potential disaster exceed the benefits from an introduction with no disaster, then under the minimax principle the decision would be not to allow the introduction.

Clearly, before any strategy is chosen, measures of the consequences of introductions and damages must be made. As discussed earlier, measuring a, the foregone benefits of not allowing the introduction has difficulties, but they are not insurmountable. Two issues will accompany this estimate: how should the stream of net benefits be discounted over time; and what are the characteristics of the uncertainty of these measurements.

It is entirely possible that the introduction of *C. gigas* into Chesapeake Bay will have negative net benefits. Given the nega-

tive publicity surrounding the health and safety aspects of eating molluscan shellfish, it is possible the demand for the product is highly inelastic so that a slight increase in the available quantity will be accompanied by a large decline in price. It may also be that the Chesapeake Bay has a comparative disadvantage relative to other areas for producing *gigas*. This may be due to natural environmental differences as well as production costs in this region.

Measuring b, the potential damages is much more problematic. Although it is probably not possible to predict all the potential consequences of introductions into an area, it may be possible to narrow the field of potential damages, and provide an estimate of maximum loss from this subset of damages. For example, at present in Maryland it would only take the destruction of three species, the blue crab, native oyster and soft clam, to virtually eliminate the Maryland bay fishery. These two species with an ex-vessel value of $31.2 million in 1988 make up approximately 60% of Maryland's Chesapeake Bay landings. The net loss to harvesters from a $31.2 million a year fishery would be significantly less because of the costs of harvesting. If this loss was irreversible or occurred over a long period, discounting would again be an important issue. The timing of when the disaster occurred would also be important, particularly when it is coupled with discounting.

In the case of uncertainty surrounding the benefit estimates, we probably have some intuition about what the probability distribution of net benefits looks like. In the case of the disaster our intuition about probabilities is severely diminished. If the probability distributions are known, it is possible to play the game with other standards. For example, one could compare the expected value of the introduction and no introduction scenarios, and choose the action with the greater expected value. Clearly, this is a much less conservative approach than the minimax principle. Policymakers may want to look at other moments of the probability distributions such as the variance to help in the decision process.

Finkel (1990) offers an excellent guide on how to represent the uncertainty present in an analysis, and how policymakers (risk managers) should use that information in making a decision. It will be necessary to assume some probability distribution for damages from an introduction. Monte carlo techniques are particularly useful in analyzing these types of problems when a number of different probability distributions must be combined.

CONCLUSIONS

Economics offers no perfect prescription for making decisions about molluscan introductions and similar types of environmental decisions. It, however, can aid, as Finkel (1990) states in "narrowing the riff between good decision processes and good outcomes". That is, one can ignore economic and risk analysis in the decision to make a species introduction, and by chance have a positive outcome anyway. This, however, does not validate the decision process. Our summary of the information on molluscan introductions to date seem to fall into the category of poor decision processes and good outcomes. Most of the introductions were done unofficially or unintentionally. Fortunately, the diseases and organisms that were introduced, for the most part have had minimal effects on the local ecology. The major exceptions are the introduction of oyster diseases in France, and the demise of the native rock oyster in New Zealand.

For the Chesapeake Bay, the magnitude of the potential benefits from an introduction of *C. gigas* will depend on the availability of alternative native species that will allow watermen and processors to continue to operate in their professions. For example, increases in striped bass populations, hard and soft clams, and other species would reduce the need for a renewed oyster fishery. Benefits will also depend greatly on the consumer perception of *C. gigas* as an alternative for *C. virginica*. If they are not considered substitutes, Chesapeake Bay production of *C. gigas* along with west coast production and imports will result in a substantially lower price, requiring fewer watermen, culturists and processors to handle larger quantities of product at low profit margins, in order to maintain profit levels. The potential cost from an introduction of *C. gigas* will depend on what is at risk. In terms of native oyster populations, there currently appears to be much less at risk in Virginia as compared to Maryland, because of the distribution of the oyster diseases MSX and Dermo. The economic magnitude of an ecological disaster resulting from the introduction would rise if other commercially important species were involved, such as blue crabs. Another possibility which would raise the impacts would be the introduction of a nuisance organism, such as a fouling organism like the zebra mussel. The good decision process requires the resource manager to weigh these factors in the decision of whether to allow an introduction.

ACKNOWLEDGMENTS

We wish to thank Dr. Aaron Rosenfield for urging us to write this paper and for his and Fred Kerns constructive comments in its preparation. Funding was provided by the Maryland Cooperative Extension Service and the Maryland Agricultural Experiment Station. MAES contribution #8579 and scientific article #A6393.

LITERATURE CITED

Archibald, Richard. Personal Communication.

Ayres, P. 1991. Introduced Pacific Oysters in Australia. Prepared for the Oyster Ecology Workshop, Maryland Sea Grant College, University of Maryland, College Park: 2–7.

Bishop, R. C. 1978. Endangered species and uncertainty: The economics of a safe minimum standard. *Amer. J. Agric. Econ.* 60(1):10–19.

Bockstael, N. E., W. M. Hanemann, and I. E. Strand. 1986. *Measuring the Benefits of Water Quality Improvements Using Recreation Demand Models*. Report on EPA contract No. CR-811043-01-0. 256 pp.

Bosch, D. J., and L. A. Shabman. 1989. The decline of private sector oyster culture in Virginia: Causes and remedial policies. *Mar. Res. Economics* 6:227–243.

Bourne, N. 1979. Pacific Oysters, *Crassostrea gigas* (Thunberg), in British Columbia and the South Pacific Islands. Mann, R., ed. *Exotic Species in Mariculture*: 1–53.

Bourne, N. 1982. Distribution, Reproduction, and Growth of Manila Clam, *Tapes philippinarum* (Adams and Reeves), in British Columbia. *Journal of Shellfish Research* 2(1):47–54.

Burrell, V. G., Jr. 1985. "Oyster Culture". Huner, J. V. and E. E. Brown, editors. In: *Crustacean and Mollusk Aquaculture in the United States*. pp. 235–274.

Cabraal, R. A. 1978. "Systems Analysis of the Maryland Oyster Fishery: Production, Management, and Economics." Ph.D. Dissertation. Department of Agricultural Engineering, University of Maryland. 309 pp.

Chew, K. K. 1979. The Pacific Oyster (*Crassostrea gigas*) in the West Coast of the United States. Mann, R., ed. *Exotic Species in Mariculture* 54–82.

Chew, K. K. 1989. "Manila Clam Biology and Fishery Development in Western North America." Manzi, J. J. and M. Castagna, editors. *Developments in Aquaculture and Fisheries Science*. 19:243–292.

Chew, K. K. Personal Communication.

Ciriacy-Wantrup, S. V. 1968. *Resource Conservation: Economics and Policies*. 3rd ed. Berkeley and Los Angeles: University of California Div. Agri. Sci., 395 pp.

Clime, Richard. Personal Communication.

Copes, P. 1972. Factor rents, sole ownership and the optimum level of fisheries exploitation. *Manchester School of Economics and Social Studies* 41:145–163.

Dinamani, P. 1991. Introduced Pacific Oysters in New Zealand. Prepared for the Oyster Ecology Workshop, Maryland Sea Grant College, University of Maryland, College Park: 8–11.

Elston, R. A., M. L. Kent and M. T. Wilkinson. 1987. Resistance of *Ostrea edulis* to *Bonamia ostrea* Infection. *Aquaculture* 64:237–242.

Farley, C. A. 1991. Mass Mortalities and Infectious Lethal Diseases in Bivalve Mollusks and Associations with Geographic Transfers of Populations. In: *Dispersal of Living Organisms into Aquatic Ecosystems* (Rosenfield, A. and R. Mann, editors). University of Maryland Press. pp. 1–15.

Fassler, Richard. Personal Communication.

Finkel, A. M. 1990. *Confronting Uncertainty in Risk Management*. Resources for the Future, 68 pp.

Gordon, H. S. 1954. The economic theory of a common-property resource: The fishery. *J. Polit. Econ.* pp. 124–142.

Goulletquer, P. Oyster Production and Management in France, Summary. Undated mimeo.

Goulletquer, P. and M. Héral. 1991. Aquaculture of *Crassostrea gigas* in France. Prepared for the Oyster Ecology Workshop, Maryland Sea Grant College, University of Maryland, College Park: 8–11.

Grizel, H. and Héral, M. 1991. Introduction into France of the Japanese Oyster (*Crassostrea gigas*). *J. Cons. int. Explor. Mer.* 47:399–403.

Hulbrock, R. Personal Communication.

Im, K. H. and D. Langmo. 1977. Economic Analysis of Producing Pacific Oyster Seed in Hatcheries. *Proceed. Nat. Shellfish. Assoc.* 67:17–28.

Katkansky, S. C., W. A. Dahlstrom and R. W. Warner. 1969. Observations on Survival and Growth of the European Flat Oyster, *Ostrea edulis*, in California. *Calif. Fish. and Game*. 55(1):69–74.

Ketchen, K. S., N. Bourne, and T. H. Butler. 1983. History and present status of fisheries for marine fishes and invertebrates in the Strait of Georgia, British Columbia. *Can. J. Fish. Aquat. Sci.* 40:1095–1119.

Kennedy, V. S. and L. L. Breisch. 1981. "Maryland's Oysters: Research and Management." Maryland Sea Grant, University of Maryland, College Park, Maryland. 286 pp.

Kennedy, V. S. and L. L. Breisch. 1983. "Sixteen Decades of Political Management of the Oyster Fishery in Maryland's Chesapeake Bay." *Journal of Environment Management* 16:153–171.

Lewis, Robert. Personal Communication.

Loosanoff, V. L. 1955. The European Oyster in American Waters. *Science*. 121:119–121.

Mann, R. 1979. Exotic Species in Aquaculture: An Overview of When Why and How. In: *Exotic Species in Mariculture* (Mann, R., ed.). pp. 331–354.

Mann, R. 1983. The Role of Introduced Bivalve Mollusc Species in Mariculture. *J. World Maricul. Soc.* 14:546–559.

Maryland Department of Natural Resource (DNR). 1987. *Maryland's Oyster resource: Status and Trends*.

Newell, R. I. E. "Ecological Changes in Chesapeake Bay: Are They the Result of Overharvesting the American Oyster, *Crassostrea virginica*? In *Understanding the Estuary: Advances in Chesapeake Bay Research*. Proceedings of a Conference. 29–31. Chesapeake Research Consortium Publication 129. March 1988.

Park, W. R. and D. E. Jackson. 1984. *Cost Engineering Analysis*. John Wiley & Sons, New York, 335 pp.

Power, G. H. 1970. "Everything You Ever Wanted to Know About Oyster and More." Maryland Law Review, 50:44–76.

Quayle, D. B. 1964. Distribution of Introduced Marine Mollusca in British Columbia Waters. *J. Fish. Res. Bd. Canada*. 21(5):1155–1181.

Quayle, D. B. 1969. Pacific Oyster Culture in British Columbia. *Bull. Fish. Res. Board Can.* 169. 193 pp.

Quayle, D. B. and N. Bourne. 1972. The Clam Fisheries of British Columbia. *Fish. Res. Board Can. Bull.* 179.

Welch, W. R. 1963. The European Oyster, *Ostrea edulis*, in Maine. *Proceed. Nat. Shellfish. Assoc.* 54:7–23.

Wennersten, J. R. 1978. "The Almighty Oyster: A Saga of Old Somerset and the Eastern Shore, 1850–1920." Maryland Historical Magazine, 74(1):80–94.

Public Health Aspects of Transferring Mollusks

Cameron Ray Hackney, Marylin B. Kilgen and Howard Kator

ABSTRACT This paper discusses microorganisms associated with molluscan shellfish borne illness, their growth after harvesting, transportation and storage, and their response to depuration and relaying. Organisms of public health concern are categorized as to whether they originated in the natural environment or are present as the result of pollution. The organisms of concern and their significance were determined by examining the North East Technical Services Unit of the Food and Drug Administration and Centers for Disease Control data bases over a 15–17 year period. Enteric viruses accounted for most of the illness, followed by naturally occurring marine vibrios. Other microorganisms accounted relative few incidences of illness. Vibrios and certain indicator bacteria will increase in number during storage and transportation. Furthermore, vibrios are resistant to depuration. Relaying will cause reduction in enteric bacteria and viruses but not marine vibrios.

KEY WORDS: pathogens, shellfish, public health

INTRODUCTION

This paper will discuss microorganisms associated with molluscan shellfish borne illness and their growth after harvesting and during transportation and storage. Also, their response to depuration and relaying will be discussed. Organisms of public health concern can be divided by their source. They may originate in the natural environment or be present as the result of pollution. The organisms of concern and their significance can be estimated by examining the data bases of the North East Technical Services Unit of the U.S. Food and Drug Administration (NETSU) and the Centers for Disease Control (CDC) over a 15–17 year period (Tables 1 and 2). These data bases do not agree because of their nature. The CDC data base is a summary of foodborne outbreaks reported by the states. It is possible that an outbreak will be published in the CDC publication Mortality and Morbidity Weekly and yet, not appear in the data base because the outbreaks form was not submitted by the state. On the other hand, the NETSU data base is a summary of outbreaks and cases reported in the literature and includes personal communications. Thus, it is more complete but at the same time less precise. The NETSU data includes individual cases that were not reported as outbreaks. The CDC defines an outbreak as two or more persons becoming ill after consuming a common food at the same time. Illness that only affects specific individuals will not be reported in the CDC data base. For example, the NETSU data base lists several cases of *Vibrio vulnificus*, but because this bacterium only affects individuals in high risk categories, no outbreaks (two or more individuals having a similar illness after consuming the same food), have been reported. Thus, illnesses from this organism do not appear in the CDC data base. Finally, the definition of shellfish used by the data bases is different. The NETSU data base includes only bi-valve mollusks, whereas CDC defines shellfish to include bi-valves, uni-valves and crustacea.

The information in tables 1 and 2 is useful for estimating the risk from microbial contaminants. Most of the illnesses associated with molluscan shellfish have been associated with either enteric viruses or naturally occurring marine organisms of the family Vibrionaceae. Other microorganisms account for far fewer illnesses. The first section will deal with agents associated with pollution followed by a section on pathogens associated with the environment.

The effect of depuration (controlled purification) and relaying on various microorganisms will be discussed. Controlled purification and relaying is a process whereby shellfish are allowed to purge themselves of contaminants, either in a natural setting or in land based facilities (Richards 1988). Controlled purification is usually a land based process, where the shellfish are put into tanks with purification systems for the water. Relaying is the process of transferring the mollusks from polluted water to areas approved for shellfish harvesting. The process of controlled purification is based on reduction of indicator (fecal coliforms) counts, whereas relaying depends upon a specified time. The time for controlled purification is usually far shorter than that of relaying, 2–3 days versus 14 days. It is important to have an understanding of the relationship between indicator microorganisms and the various types of pathogens in these systems. For example, the time required for depuration of indicator bacteria and enteric bacterial pathogens is similar. However, rates vary greatly between indicator bacteria and some enteric viruses. In addition, the depuration of naturally occurring vibrios is quite different than that of indicator bacteria (Richards 1988). With respect to relaying, the numbers of naturally occurring bacteria such as vibrios are increased or at least stay the same. This is because *Vibrios* are indigenous to the

TABLE 1.

Illness Associated with Naturally Occurring Pathogens in Shellfish: Summary of CDC and NETSU Data, 1973–1987.[1,2]

	Reported By		
	CDC[3]		NETSU[3]
	Cases	Outbreaks	Cases
	No. %	No. %	No. %
Pathogens			
Aeromonas	0	0	7 (0.1)
Bacillus cereus	6 (0.7)	2 (4.3)	—
Plesiomonas	0	0	18 (0.3)
Vibrio cholerae 01	16 (1.8)	3 (6.4)	7 (0.1)
V. cholerae non-01	11 (1.2)	2 (4.3)	125 (2.3)
V. fluvialis	0	0	3 (0.1)
V. hollisae	0	0	5 (0.1)
V. mimicus	0	0	6 (0.1)
V. parahaemolyticus	298 (32.9)	18 (38.3)	98 (1.8)
V. vulnificus	0	0	104 (1.9)
Total	331	25	373

[1] No illnesses associated with parasites or *C. botulinum*, were reported in these data bases.

[2] The number in parentheses is the % of total illness of Tables 1 and 2 combined.

[3] The term shellfish in the CDC data base includes all molluscan and crustacean shellfish. In the NETSU data base only bivalve shellfish are considered.

marine environment and their numbers are not affected by pollution. Of course waters used for relaying are classified by pollution, not by absence of naturally occurring pathogens.

AGENTS ASSOCIATED WITH POLLUTION

Agents associated with pollution include certain enteric viruses and bacteria. As mentioned earlier, enteric viruses are agents most often associated with shellfish borne illness. Of the enteric bacteria only salmonellae, *Campylobacter jejuni* and *Shigella* have been associated with illness from molluscan shellfish in the United States. Pathogenic *Escherichia coli* has been implicated with shellfish borne illness in other countries, such as Japan. Many other pathogens have been isolated from molluscan shellfish but have not been implicated in illnesses associated with mollusks. These include *Yersinia enterocolitica* and *Listeria monocytogenes*. In this discussion, only organisms that have caused documented illness are discussed.

Human Enteric Viruses

Human enteric viruses are of concern in seafood products, especially in raw molluscan shellfish that may have been harvested from fecally polluted waters. Viruses are inert in food systems and are only active inside the host; therefore, they will not multiply during storage after harvesting. Only a few viruses can be transmitted through food. These are usually transmitted by the fecal oral route which includes contamination from human sewage. Enteric virus infections are limited mostly to the intestine. However, when the infection goes past the intestine, a more serious illness such as hepatitis may result. When a person becomes infected they shed viruses in their feces which may in turn contaminate seafood through pollution or poor personal hygiene habits. Most of the reported outbreaks of viral illness associated with seafood have involved fecally contaminated bi-valve shellfish; however, viruses have the potential to contaminate seafood during processing. This has happened with other food products.

More than 100 enteric viruses can be found in human feces. Picornaviruses make up the largest of all virus families with nearly 200 host-specific picornaviruses having been identified in man. Of these, 69 enteroviruses inhabit the enteric tract (White and Fenner 1986, Gerba 1988). These viruses have a naked icosahedral capsid 25–30 nm in diameter, appear as smooth and round in outline, are constructed from 60 protomers, and replicate in the cytoplasm. Each protomer is comprised of a single molecule of four polypeptides, VP 1, 2, 3 and 4, or 1D, 1B, 1C and 1A respectively. The genome is a single stranded RNA linear molecule of positive polarity with a M.W. of 2.5×10^6. The molecule is polyadenylated at its 3′ end with the protein VP_g covalently linked to its 5′ end.

Enteroviruses have been subdivided into the species group Polioviruses (PV), Coxsackie viruses, Echoviruses and Enteroviruses. While polioviruses are frequently isolated from bi-valve shellfish, they are mostly vaccine strains and are not a cause of concern with respect to public health. Hepatitis type A (HAV) is the picornavirus of most concern in shellfish.

Enteric viruses are obligate parasites and of course do not multiply in shellfish. They do however, survive quite well. For example, in oysters polioviruses survive more than 30 days in shucked product stored under refrigeration.

Hepatitis Type A (HAV) (Enterovirus Type 72)

The onset of HAV is associated with the clinical symptoms of fever, malaise, anorexia, nausea and lethargy. Symptoms also include dark urine, jaundice and an enlarged, tender, palpable liver. In children, most infections are anicteric; however, the se-

TABLE 2.

Illness Associated with Contamination of Shellfish by Fecal Pollution: Summary of CDC and NETSU Data, 1973–1987.[1,2,3]

	Reported By		
	CDC[3]		NETSU[3]
	Cases	Outbreaks	Cases
	No. %	No. %	No. %
Salmonellae (non-typhi)	80 (8.8)	3 (6.4)	—
Salmonella typhi	—		—
Hepatitis A	335 (36.9)	9 (19.2)	356 (6.6)
Hepatitis (unspecified)			4479 (82.9)
Norwalk and similar viruses	42 (4.6)	2 (4.3)	82 (1.5)
Shigella	77 (8.5)	4 (8.5)	93 (1.7)
Staphylococcus aureus	14 (1.5)	2 (4.3)	5 (0.1)
Campylobacter	—	—	16 (0.3)
Clostridium perfringens	28 (3.1)	2 (4.3)	—
Total	907 (100)	47 (100)	5404 (100)

[1] No illnesses associated with parasites, *C. botulinum*, enterococci, or *S. typhi* were reported in these data bases.

[2] The number in parentheses is the % of total illness of Tables 1 and 2 combined.

[3] The term shellfish in the CDC data base includes all molluscan and crustacean shellfish. In the NETSU data base only bivalve molluscan shellfish are considered.

verity of the disease increases with age (Overby et al. 1983, Bryan 1986, White and Fenner 1986, Cliver 1988).

When HAV is ingested it multiplies primarily in the intestinal epithelium. Secondary infection of the parenchymal cells of the liver is through the blood stream. The virus is found in the feces approximately one week prior to the clinical signs. It may also be found in the blood approximately one week prior to the appearance of the main clinical sign of dark urine. It disappears after serum transaminase levels reach their peak. The onset time for symptoms is normally four weeks, but may range from 2–6 weeks. Infection with HAV results in permanent immunity.

HAV is spread by the fecal-oral route. It is hyperendemic in countries which are overcrowded, have inadequate sanitation and poor hygiene. Most infections in these communities occur in childhood and are subclinical. In more developed countries the disease is seen most often between the ages of 15 and 30.

Contaminated food and water and person to person contact are the main routes of transmission of HAV. Each year 20,000 to 30,000 cases are reported to the Centers for Disease Control (CDC). Of these cases, approximately 140 are due to foods (0.5% of the total). Most of these food-borne outbreaks are due to mishandling of foods by infected individuals (Cliver 1988). Outbreaks can also occur due to inadequate cooking of contaminated foods and by human sewage contamination of drinking water supplies, swimming waters and shellfish growing waters.

In the 1950's the first documented case of shellfish-associated HAV occurred in Sweden. The first case was documented in the U.S. in the 1960's (Richards 1985, Cliver 1988, Gerba 1988). Richards (1985) reported approximately 1400 cases of molluscan shellfish-associated HAV since 1961. The Centers for Disease Control reported 335 cases of shellfish-related HAV from 1973 to 1987. The North East Technical Services Unit of the U.S. Food and Drug Administration reported approximately 438 cases of shellfish-associated HAV from 1973 to 1990 (CDC 1973–1986, Rippey 1991).

Prevention and control of HAV can be accomplished at several levels. Municipal sewage systems should be properly functioning to prevent contamination of public water supplies and shellfish producing waters. Also, proper classification of shellfish growing areas and restricting shellfish harvest only to approved areas is important in preventing HAV contamination from untreated human sewage.

Considerable research has been conducted on the fate of enteric viruses, including HAV, during depuration and relaying. This research was hampered until recently because cell cultures were not available to propagate HAV virus. HAV viruses seems to be resistant to depuration in comparison to indicator bacteria and many other enteric viruses (Richards 1991). Sobsey (cited by Richards 1991) examined the depuration of poliovirus, *E. coli*, enterococci, the bacteriophage MS-2 and HAV. The organisms were taken up naturally by feeding in contaminated water in laboratory tanks. Each organism depurated at a different rate, with poliovirus being depurated the quickest, followed by *E. coli*, enterococci, the bacteriophage MS-2 and HAV. HAV remained in the oyster for more than five days after being exposed to clean water at various temperatures and salinities. This implies that commercial depuration would not eliminate HAV from shellfish.

Non-A, Non-B Enteral Hepatitis; Hepatitis E

The disease caused by Hepatitis E Virus (HEV) is called hepatitis E, or enterically-transmitted non-A non-B hepatitis (ET-NANBH). Other names include fecal-oral non-A non-B hepatitis, and A-like non-A non-B hepatitis. It should not be confused with hepatitis C, also called parenterally transmitted non-A non-B hepatitis (PT-NANBH), or B-like non-Anon-B hepatitis, which is a common cause of hepatitis in the U.S. (Gouvea 1991).

HEV has a particle diameter of 32–34 nm, a buoyant density of 1.29 g/ml in KTar/Gly gradient, and is very labile. Serologically related smaller (27–30 nm) particles are often found in feces of patients with Hepatitis E and are presumed to represent degraded viral particles. HEV has a single stranded polyadenylated RNA genome of approximately 8 kb (Gouvea 1991). Enteral HEV can be more severe than HAV with a high incidence of cholestasis. The incubation period for hepatitis E varies from 2 to 9 weeks. Disease usually is mild and resolved in 2 weeks leaving no sequelae. The fatality rate is 0.1–1% except in pregnant women. This group is reported to have a fatality rate approaching 20%. The highest attack rate is in young adults, especially pregnant women in the third trimester (Gouvea 1991). The incidence of chronic active hepatitis is extremely low in HEV (Overby et al. 1983, White and Fenner 1986).

Enteral HEV is transmitted mainly by sewage contaminated water in epidemics. It is also transmitted sporadically by person to person contact. In the middle East and Africa, it appears to be endemic (Overby et al. 1983). Cliver (1988) noted water-associated outbreaks have been reported for years from India, Africa, the USSR, and most recently, Mexico. Cases have been associated with consuming raw shellfish (Rippey 1990). No research has been conducted on the fate of HEV in shellfish during depuration or relaying. This work is needed as the potential for spread in the U.S. is great.

Unclassified Viruses

These include the non-specific agents of gastroenteritis including Norwalk and Norwalk-like agents, Snow Mountain agent, and Small Round Viruses (SRV's). The Norwalk group is 25–32 nm in diameter, while the SRV's are 27–40 nm. The SRV's have been identified in the feces of infants with diarrhea using Immune Electron Microscopy (IEM). The incubation period for the Norwalk agent is from 24 to 72 hours. Infection results in the sloughing of intestinal villi followed by rapid regeneration. Clinical symptoms include diarrhea, nausea, vomiting, abdominal cramps, and in some cases, headache, myalgia and low grade fever. Symptoms are more serious in adults. Immunity following an infection with Norwalk virus is only temporary, lasting approximately one year. This may be one of the reasons for the very high attack rate in at risk individuals of 50–90% (Cliver 1988).

Outbreaks of viral gastroenteritis due to the Norwalk agent has been associated with swimming in waters contaminated with human sewage, fecal contamination of food or drinking water and consumption of uncooked or partially cooked shellfish harvested from estuaries contaminated with human sewage. The first documented shellfish-associated outbreak of gastroenteritis involving Norwalk virus was in 1979 in Australia, where more than 2000 people were involved. Since this time, there have been many documented outbreaks in the U.S. Norwalk virus illness associated with shellfish is a continuing problem and has increased with the last decade while HAV infections have decreased. Between 1973 and 1990, the USFDA NETSU reported 176 shellfish-related outbreaks of Norwalk gastroenteritis, 71 outbreaks of Snow Mountain agent, and 5924 cases of gastroenteritis of unknown etiology,

many of which may have been caused by Norwalk like viruses (Rippey 1991). The Centers for Disease Control reported 3524 shellfish-related cases of unknown etiology from 1973 to 1987 and 42 cases from Norwalk virus (CDC 1973–1987). Richards (1985) reported over 6,000 cases of shellfish-associated gastroenteritis over the past 50 years. It is presumed that many of these are of viral etiology, possibly Norwalk or Norwalk-related agents. Over 75% of these cases have been reported since 1980, which shows increased awareness and reporting practices in regards to shellfish illnesses.

Good personal hygiene and good manufacturing practices, proper classification of recreational and shellfishing waters and prevention of sewage contamination in drinking, swimming, or shellfish growing waters are the most effective preventive measures for the Norwalk and related gastroenteritis viruses since they are found only in human sewage.

Because these agents do not grow in tissue culture, very little information is available on their fate during transfer. Outbreaks have been associated with depurated clams imported to the U.S. from the United Kingdom. However, these clams were most likely depurated in contaminated water.

ENTERIC BACTERIA ASSOCIATED WITH POLLUTION

Salmonella

From a historical perspective, *S. typhi* is a bacterium of concern; however, no cases have been associated with shellfish since the 1950s. The food poisoning type has been associated with shellfish. The food poisoning syndrome develops after ingestion of a food that contains a sufficient number of Salmonella cells to cause infection, usually between 100,000 and 100,000,000 cells. (The infective dose can be much lower in certain high fat foods such as cheese or chocolate.) The symptoms usually develop 12–14 hours after ingestion of the food, although incubation times of greater than 24 hours are not uncommon. Symptoms consist of mainly diarrhea along with nausea, vomiting, abdominal pain, headaches and chills. The symptoms are often accompanied by prostration, muscle weakness, moderate fever and drowsiness. Symptoms usually last only 2–3 days. The death rate is less than 0.2% (Jay 1987).

Raw foods, particularly those of animal origin, are the major vehicles of salmonellosis (Cox and Bailey 1987, Allred et al. 1967). The five most common food vehicles for *Salmonella* in the United States are beef, turkey, homemade ice cream (containing eggs), pork and chicken (Jay 1987, Cox and Bailey 1987). Turkey is the most common vehicle in Canada. However, many other foods have been involved in salmonellosis. For example, in 1985, the largest outbreak ever reported (18,000 cases) was traced to pasteurized milk produced in Illinois.

In the United States most outbreaks of salmonellosis are traced to contaminated products of terrestrial animals. However, vehicles for sporadic salmonellosis are rarely identified. While CDC and NETSU foodborne surveillance data indicate that seafood is a much less common vehicle for *Salmonella* than are other foods such as chicken and red meat, fish and shellfish may be responsible for at least a small proportion of the total number of *Salmonella* cases that occur each year in the United States. However, current data are inadequate to make any attempt at estimating attributable risk. Seafood has been infrequently incriminated as a vehicle of foodborne salmonellosis.

When examining the importance of salmonellae in seafood, it is useful to examine the overall incidence reported to CDC. CDC tracks disease incidence by several mechanisms, including laboratory-based *Salmonella* Surveillance system and the Morbidity and Mortality Weekly Report (MMWR). These systems do not agree and data in one system often is not included in the other systems. When examining the annual foodborne disease incidence data for the 14 year period from 1973 to 1986, an average of 55 foodborne outbreaks of non-typhoidal *Salmonella* infections affecting a total of 3944 persons were reported each year to CDC. During this same time frame, only 6 seafood borne outbreaks involving 147 cases were reported. Two of these outbreaks involving 40 cases were shellfish-associated (Chapter 8). Examining the other surveillance systems; during the 14 year period from 1973 to 1987, an annual average of 32,957 and 35,490 *Salmonella* cases were reported through the laboratory-based *Salmonella* Surveillance system and the Morbidity and Mortality Weekly Report (MMWR), respectively.

The NETSU data base, which attempts to document all cases of shellfish borne disease outbreaks from 1894 to 1990, reported only two shellfish associated outbreaks of confirmed non-typhoidal salmonellosis between 1894 and 1973 (Rippey 1991). A 100-case outbreak that occurred in Florida in 1947 was traced to contaminated oysters. The other outbreak occurred in New York in 1967 and involved 22 cases. This outbreak was associated with oysters imported from England (Rippey and Verber 1988). No cases of *Salmonella* infections from shellfish were reported to the NETSU between 1973 and 1988. However, several sporadic cases of salmonellosis associated with shellfish occurred in 1989 and 1990 (Rippey 1991). In September, 1989, three cases of salmonellosis were associated with mussels harvested in Maine and consumed in Connecticut. *S. infantis* was isolated in two of the cases. In October and December, 1989 oyster associated cases were reported in Florida. In 1990, four separate oyster associated cases were reported in Florida (Rippey 1991).

In other countries outbreaks of salmonellosis have been associated with shellfish. For example, an outbreak of salmonellosis associated with clams (*Venus verrucosa*) was reported in Italy (Cantoni et al. 1985). In this outbreak fifty people were affected. The causative agents were *S. typhimurium* and *S. mbandaka*. The estimated count per clam was 400–800 cells which implies that the infective dose was low. The NETSU data base on shellfish associated outbreaks—Foreign Reports, did not report outbreaks due to *Salmonella* during the period from 1973–1990.

Isolations of salmonellae from shellfish is not uncommon. Fraiser and Koburger (1984) examined various seafoods including clams and oysters from the east and west coasts of Florida for the presence of *Salmonella*. The highest incidence of *Salmonella* was from clams harvested from the Gulf (west) coast of Florida. The shellfish were analyzed very quickly after harvest and the authors felt that quick analysis greatly increased recovery of salmonellae. In addition, individual animals were analyzed instead of using composite samples. The authors felt this increased the probability of isolating different sero-types of *Salmonella*. In this study 43% of the clams tested were positive for *Salmonella*. This is one of the few studies that report the numbers of *Salmonella* present in the samples. In analysis of oyster meats the levels of *Salmonella* isolated was 2.2 per 100 grams of tissue. It was noted that this level of salmonellae would be unlikely to cause illness in most consumers. Eleven different sero-types of *Salmonella* were isolated, with as many as six sero-types being isolated from the same group of samples. The authors went on to theorize that salmonellae might be part of the free living micro-flora of shellfish.

Andrews et al. (1974) examined the coliforms as indicators of

Salmonella in oysters and clams. Over an 18 month period 263 oyster and 96 clam samples were tested for coliforms, fecal coliforms and the presence of *Salmonella*. Thirty-nine of the oyster and 5 of the clam samples were positive for *Salmonella*. It was observed that the indicators did give an indication of the presence of *Salmonella*. However, high numbers of indicators did not necessarily mean that the pathogen was present.

In later work this same group examined the comparative validity of members of the total and fecal coliforms groups for indicating the presence of *Salmonella* in the eastern oyster (*Crassostrea virginica*). In this study 539 oyster samples and corresponding harvest water samples were analyzed. Occurrence of *Salmonella* more closely paralleled increases in fecal coliform counts compared to total coliform counts. More *Salmonella* was isolated from water, meeting the total coliform standard compared to the fecal coliform standard. *Salmonella* was not isolated from samples that met both the sanitary survey and fecal coliform standard. This study points out the importance of using both the sanitary survey in conjunction with microbial analysis to insure safety.

Andrews et al. (1976) studied the validity of members of the total coliforms and fecal coliform groups for indicating the presence of *Salmonella* in hard clam (also called quahaug). In this study 214 samples were tested over a two year period. The harvesting waters were tested for coliforms and fecal coliforms and classified as to whether it met either the total coliform standard of less than or equal to 70 coliforms per 100 mLs or less than or equal to 14 fecal coliforms per 100 mLs. The clams were further classified as to whether they met the market guideline of 230 fecal coliforms per 100 grams of tissues. None of the clams harvested from waters meeting either standard contained *Salmonella*. Furthermore, *Salmonella* was not isolated from any meat sample meeting the market guideline. *Salmonella* was isolated from some of the samples which exceeded the National Shellfish Sanitation Program's standards. From this work the investigators concluded that fecal coliforms were adequate indicators of shellfish safety, with respect to *Salmonella*.

Timoney and Abston (1984), studied the contamination and elimination of *E. coli* and *S. typhimurium* in the hard clam, *Mercenaria mercenaria*. The bacteria were eliminated at similar rates; however, *E. coli* levels declined more rapidly than salmonellae. The organisms were eliminated from the clams becoming associated (non-ionicly bound) with feces and pseudo-feces particulate matter. Most of the test organisms were eliminated between six and twenty-four hours. This study indicates that *E. coli* is a good indicator with respect to salmonellae.

Hood et al. (1983), examined the relationship among fecal coliforms, *E. coli* and *Salmonella* species in freshly harvested, Gulf of Mexico coast oysters and clams. *Salmonella* was only found in samples which exceeded the National Shellfish Sanitation Program's market guideline of 230 fecal coliforms per 100 grams of product. These investigators reported that low levels of fecal coliforms and *E. coli* were good indicators of the absence of *Salmonella*. However, high levels of these indicators did not necessarily indicate the presence of *Salmonella*.

Elimination of Salmonellae and *E. coli* from Shellfish

It is interesting that there are species differences in depuration rates of species of *Salmonella*. For example, Cook and Ellender (1986) examined the depuration of *S. typhimurium*, *S. montevideo* and poliovirus in Gulf oysters. *S. montevideo* persisted longer than *S. typhimurium*.

Matev et al. compared the depuration of *S. typhimurium* and *S. enteritidis* to that of *E. coli* and *Staphylococcus aureus* in artificially contaminated Black Sea mussels. *E. coli* was recovered for six days compared to four days for the *Salmonella* and two days for *S. aureus*. Rowse and Fleet (1982) observed that both *Salmonella* and *E. coli* survived in oyster feces and could be released in the overlying waters. Survival depended on water temperature. In later studies Rowse and Fleet (1984a,b) studied the effects of water temperature and salinity on the depuration of *S. charity* and *E. coli* from the Sidney Rock oyster. In this study the organism was eliminated at similar rates. For this species, elimination was most rapid at 18–22°C and salinities of 3.2–4.7‰. Higher or lower temperatures and lower salinities slowed depuration. Eyles and Davey (1988) observed that isolation of *Salmonella* from the Sidney rock oyster was correlated to rainfall and to a lesser extent low salinity waters. The presence of salmonellae in this study was related to high *E. coli* counts.

Campylobacter jejuni and Other Species

Campylobacter are curved, spiral Gram-negative rods that are nonsporeforming and microaerophilic (Simbert 1984). Campylobacters grow between 25 and 43°C, are motile, oxidase positive and do not ferment or oxidize carbohydrates (Stein et al. 1992, Franco 1988). The campylobacters can be broadly placed into two groups on the basis of the catalase test. The catalase-positive campylobacters are most frequently associated with human disease.

Campylobacteriosis may be the first or second leading cause of food poisoning in Western countries including the United States (Seattle-King County Depart. Pub. Hlth. 1984, Totten 1987, Franco 1988). Only recently has its importance been realized because methodology to detect the organism in food and feces was not available (Doyle 1981).

Campylobacter species were once thought to be primarily important to veterinary medicine. Prior to 1974 these bacteria were placed in the genus *Vibrio* because of their shape (Blaser 1981, Doyle 1981). The organism, now known as *C. jejuni* was grouped with *V. fetus*. In the 1974 edition of Bergey's Manual the genus *Campylobacter* was created. The genus *Campylobacter* currently consists of at least 18 species, subspecies, and biovars, with 17 names officially recognized by the International Committee on Systematic Bacteriology (Franco 1988, Stern et al. 1992).

Human illness is associated with three species of *Campylobacter*, *C. jejuni*, *C. coli* and *C. laridis*. These organisms are carried in the intestinal tract of animals and therefore, may contaminate foods of animal origin. In addition, fecal contamination of harvesting waters may allow shellfish to be a vehicle for the pathogens (Rippey 1991). *C. jejuni* is recognized as a leading cause of acute bacterial gastroenteritis. It is recognized as both a food and water borne pathogen. Foodborne illness is usually associated with the consumption of products of animal origin. In addition, *C. coli* and *C. laridis* are also recognized causes of gastroenteritis, but less frequently than *C. jejuni*. These three species are collectively referred to as the *C. jejuni* group.

Campylobacteriosis Associated with Shellfish Consumption

NETSU reported 1 domestic shellfish-associated outbreak of campylobacteriosis between 1894 and 1988, an outbreak of 16 cases due to contaminated hard clams that occurred in New Jersey in 1980. In addition, *Campylobacter* was suspected in several outbreaks reported to the NETSU where the etiological agent was

listed as unknown (Rippey and Verber 1988). In the 1991 update of the NETSU data base several outbreaks and cases of *Campylobacter* associated with shellfish were reported. Most of these illnesses were reported in the state of Florida. In one outbreak in 1989 two people became ill three days after consuming oysters. *C. jejuni, Vibrio paraheamolyticus* and *V. vulnificus* were all isolated from the individuals. In another incident, a single case of confirmed *Campylobacter* infection was reported in Lee County, Florida. That same year in December, four separate cases of confirmed *Campylobacter* were reported (Rippey 1991). In 1990 six separate cases of illness from *Campylobacter* were reported in Florida. Five of the incidents involved oysters and clams were implicated in the other case. The age of the victims ranged from 23 to 70 years of age. In addition another case of *Campylobacter* illness from oysters was suspected in Alabama in 1989 (Rippey 1991).

Isolation from Shellfish

Arumugaswamy and Proudford (1987) reported the isolation of *C. jejuni* and *C. coli* from the Sidney Rock oyster. These investigators were able to detect these organisms in 17 of 79 samples. This work is interesting, because the Sidney Rock oyster is usually harvested from water of fairly high salinity. *Campylobacter* species are reported to be very sensitive to environmental conditions; however, in the Sidney Rock oyster, survival was reported during refrigeration and freezing. Arumugaswamy et al. (1988) allowed the oysters to feed in waters containing approximately 10,000 cells of *C. jejuni* and *C. coli* per mL. The oysters were then subjected to depuration. They were depurated within the 48 hour period usualty allowed for depuration systems. These investigators also investigated survival of the organisms during storage as shellstock at 20 and 30°C, on the half shell during refrigeration, shucked and bottled, stored refrigerated and frozen. The organisms failed to multiply during room temperature storage, but did survive for 2–9 days. At 3 or 10°C the organism survived 8–14 days. Survival was better at the lower temperature and in the shucked product. The organisms survive for months during frozen storage at −20–24°C. Another *Campylobacter* species linked to illness is *C. laridis*. This organism has been isolated from mussels (Owen et al. 1988).

Shigella

Shigella are Gram-negative, non-motile, non-sporeforming rods-shaped bacteria. The illness caused by *Shigella* (shigellosis) accounts for less than 10% of the reported outbreaks of foodborne illness in this country. *Shigella* rarely occurs in animals; principally, a disease of humans except other primates such as monkeys and chimpanzees. The organism is frequently found in water polluted with human feces.

Symptoms of the illness include: abdominal pain; cramps; diarrhea; fever; vomiting; blood, pus, or mucus in stools; tenesmus. The on-set time is 12 to 50 hours. The infective dose is very low and can be as few as 10 cells depending on age and condition of host. The disease is caused when virulent *Shigella* organisms attach to, and penetrate, epithelial cells of the intestinal mucosa. After invasion, they multiply intracellularly, and spread to contiguous epithelial cells resulting in tissue destruction.

Association with Shellfish

Sewage pollution has been associated with outbreaks of shigellosis from shellfish. The number of cases are limited. The organism does not survive well and illness is most often the result of contamination by a handler. Cantori et al. (1980) reported an outbreak of shigellosis from mussels (*Mytilus galloprovincialis*). The report was written in Italian and only the abstract was in English. The outbreak occurred in Milan in 1978 and approximately 100 people were affected. Studies of the mussels revealed the presence of *S. dysenteriae* and *S. boydii*.

Taylor and Nakamura (1964) reported that *S. sonnei* and *S. flexneri* could survive at 25°C in clams for more than 50 days and in oysters for more than 30 days.

As is the case for the salmonellae, 3 surveillance systems for shigellosis exist at CDC. For the years 1978–1987, an average of 7 foodborne outbreaks affecting a total of 573 persons were reported each year to the foodborne disease surveillance system (CDC 1989). Seven outbreaks involving 137 cases were seafood borne. Four of the 7 outbreaks, involving 77 cases, were shellfish associated (Chapter 8). During the same period an annual average of 14,460 and 18,498 total foodborne cases were reported through the laboratory-based *Shigella* Surveillance system and the MMWR, respectively. NETSU (Rippey and Verber 1988) reported 4 shellfish-associated outbreaks involving a total of 93 cases of shigellosis in the United States between 1894 and 1988. Nine persons were reported ill in Massachusetts in 1977, 11 in California and 26 in Arizona in 1979, and 47 in Texas in 1986. Between 1978–1987 NETSU reported 84 cases of shellfish-associated shigellosis (Rippey and Verba 1989).

In 1989 and 1990 additional cases of shigellosis from the consumption of oysters were confirmed or suspected (Rippey 1991). The cases were for the most part sporadic and only two outbreaks occurred. All the cases were reported in the state of Florida. The two outbreaks where *Shigella* was suspected as the causative agent occurred in October 1989. In both incidences, four people became ill after consuming oysters. In the first outbreak four of nine people became ill one day after eating the oysters. *S. sonnei* and/or *Vibrio parahaemolyticus* and *V. fuluvialis* were suspected. In the other suspected outbreak four of four people became ill. Again either *Shigella* or a *Vibrio* was suspected. One case of *Shigella* in a two year old girl was reported in November of the same year. In 1990, four separate cases of shigellosis were reported. Three of the victims were female and the other was a male. Oysters were the vehicle in all cases.

Pathogenic Escherichia coli

E. coli is often thought of as an indicator of fecal pollution. In 1887, Escherich observed the ubiquity of what we now designate as *Escherichia coli* in human stools. Shardinger, in 1892, suggested that members of this species be used as an index of fecal pollution because they could be recovered more easily than *Salmonella* species (Kator and Rhodes 1991, Banwart 1989). Pathogenic strains fall into four categories; enterotoxigenic, enteropathogenic, enteroinvasive and hemorrhagic (Medallion 1987, Mehlman 1982, Frank 1988). The first three are usually associated with human fecal contamination, whereas, hemorrhagic strains are most often associated with farm animals.

Association with Shellfish

Much of the research on isolation and incidence of pathogenic *E. coli* in shellfish has been done in Japan. Sato (1971) was perhaps the first person to report on the isolation of enteropathogenic *E. coli* from oysters. From July 1969 to February 1971, this author examined 160 commercial samples of foods including 66 ground

pork samples, 34 chicken samples and 60 oyster samples. Nineteen of the 60 oyster samples were positive for enteropathogenic *E. coli*. The author lists the serotypes of the strains isolated; however, only the abstract was in English and this reviewer could not determine which serotypes were specifically associated with the oyster isolates. Other work published in Japan include an article by Kokubo (1978) that describes a study where 405 oyster samples were examined for the presence of *E. coli* and a portion of the isolates were tested for pathogenic strains of *E. coli*. Only four pathogenic strains were isolated. One strain produced only heat labile enterotoxin, while the other three strains produced only heat stable enterotoxin. Ogawa et al. (1980) studied the incidence of enteropathogenic *E. coli* in sea water, oysters, river water, and sediment samples over a 10 year period. In this extensive study enteropathogenic *E. coli* was isolated from 14.4% of the sea water samples, 14% of the oyster samples, 15.3% of the river water samples and 3.7% of the sediment samples. The relationship between *E. coli* levels and enteropathogenic *E. coli* levels was excellent. As the numbers of *E. coli* increased, the frequency of isolation of the pathogenic strains increased. Perez Martinez et al. (1981) investigated the incidence of enteropathogenic *E. coli* in raw oysters obtained from supermarkets in Mexico using inoculation of suckling mice to evaluate for toxin. Only 3.7% of the isolates produced heat-stable toxin. Stephen et al. (1975) reported the isolation of both enteropathogenic and enterotoxigenic *E. coli* from mussels in India.

There are currently no data to indicate that any seafood, including shellfish, is an important source for diarrheagenic *E. coli* infections in this country. Neither the CDC annual summaries (from 1973 through 1987) or the NETSU data base (Rippey 1991) report any shellfish borne illness associated with pathogenic *E. coli*.

NATURALLY OCCURRING BACTERIA

Vibrionacae

The members of the family vibrionacae of concern include *V. cholerae* 01 and non 01, *V. parahaemolyticus*, *V. vulnificus*, *V. mimicus*, *V. hollisae*, *V. fluvalis*, *Pleisomonas shigelloides*, and *Aeromonas*. A brief description of these organisms is presented below. For the most part, these organisms are associated with the marine environment, show a definite seasonal variation, and are easily killed during heating.

V. cholerae is usually divided into two groups, serotype 01 and non-01 *V. cholerae*. Those groups can be further subdivided as toxigenic and non-toxigenic. Toxigenic strains are capable of producing cholera toxin or a very similar toxin.

Toxigenic *V. cholerae* 01 is the causative agent of endemic or asiatic cholera. The 01 serotype contains two biotypes; classical and El tor, both of which may contain toxigenic and non-toxigenic strains. The biotypes are differentiated by sensitivity to polymyxin B and Murkee's group four phage and by the ability to agglutinate chicken red blood cells (Sakazaki 1979). The classical biotype predominated worldwide until the 1960's. The El tor biotype is currently predominant world wide and is the biotype associated with recent cases in the U.S. and South America (Blake et al. 1980, Levine 1981, Morris and Black 1985, CDC 1986).

Symptoms of *V. cholerae* 01 infection can range from asymptomatic or mild diarrhea to severe cases (cholera gravis). In severe cases, *V. cholerae* 01 can cause profuse watery diarrhea, dehydration and death if not promptly treated. The incubation period varies from 6 hours to five days. Initially, the stool is brown with fecal material but it quickly assumes the classic "rice water" appearance. Enormous amounts of fluids are passed effortlessly, resulting in dehydration and circulatory collapse. The stool is rich in potassium and bicarbonate. Renal function is suppressed and the patient suffers from severe thirst, leg cramps, hoarse speech, weakness and rapid pulse (Morris and Black 1985, Blake et al. 1980, Sakazaki 1979). Fortunately, cholera gravis is relatively uncommon. Cholera gravis results in only 1 in 25–100 infections from the El tor biotype and in 1 in 5–10 infections by the classical biotype. People with type O blood are more susceptible to the severe disease (Sakazaki 1979).

The infective dose for *V. cholerae* is estimated to be approximately one billion cells; however, consumption of antacids or medication to lower gastric acidity markedly lowers the infective dose (Blake 1987). *V. cholerae* 01 induces illness by elaborating cholera toxin which stimulates the production of cyclic AMP (Holmgien 1981). Therefore, only toxigenic strains can cause cholera. Non-toxigenic strains of *V. cholerae* can cause diarrhea but not cholera and have also been implicated in wound infections.

Cholera in the United States is relatively rare. The U.S. has been spared any identified cholera outbreak from 1911 until 1973, then a single unexplained case occurred in Texas. A second cholera outbreak occurred during August, September and October of 1978 when 11 people were infected with *V. cholerae* 01 El Tor from recontaminated cooked crabs (Blake et al. 1980). In 1981, there were two cases of cholera involving residents of the Texas Gulf Coast and 17 additional cases on an oil rig in the Gulf (Morris and Blake 1985). Thirteen cases of domestically acquired cholera occurred in 1986; 12 in Louisiana and one in Florida (CDC 1986). Inadequate cooking or improper handling of crustaceans seems to have been the vehicle in this outbreak. Ten of the patients had severe diarrhea and 7 required hospitalization. The *V. cholerae* 01 was of the El Tor biotype. Of course, an epidemic of cholera is currently under way in certain South American countries. Poor sanitation and consumption of raw fecally contaminated seafood is responsible for many of the cases. It is not believed that this outbreak is a threat to the U.S. because of better sanitation and sewage disposal.

V. cholerae 01 is widely distributed and is probably part of the indigenous bacterial flora in estuarine waters (APHA 1985, Colwell 1984). There is evidence of seasonal variation and most cases of domestically acquired cholera have occurred during the late summer and fall; with August being the primary month for infection (Madden et al. 1982).

Non 01 V. cholerae

At least 70 other groups of *V. cholerae* are known to exist. They are referred collectively as non-01 *V. cholerae* or non-agglutinable (NAG) *V. cholerae*. The majority of the strains isolated from seafood and patients are non-toxigenic strains; less than 5% of the non-01 strains from human sources in the United States produce cholera toxin. The non-toxigenic strains are principally associated with gastrointestinal illness; but in the U.S. about ⅓ of the human isolates are from extra-intestinal sources, including wound infection, ear infection and primary and secondary septicemia (Morris and Black 1985). Associated symptoms of gastroenteritis have included diarrhea (100% of cases; 25% have bloody stools), abdominal cramps (93%) and fever (71%). Nausea and vomiting occurs in 21% of the victims. The diarrhea may occa-

sionally be severe; with as many as 20–30 watery stools per day (Morris and Black 1985). Almost all of the cases of non-01 *V. cholerae* infections in the U.S. have been associated with eating raw oysters.

Considering the relative frequency of isolates from seafood, the incidence of illness is very low. There is evidence that victims often have an underlying liver disease, which might be a host factor for the disease. Also, in most cases the disease may not be severe enough to warrant medical attention and therefore, the incidence may be unreported. However, it can be observed from Table 1 that non 01 *V. cholerae* accounted for a large percentage of the cases associated with the naturally occurring vibrios.

Non-01 *V. cholerae* strains are widely distributed in the environment of the United States, Asia and Europe. They occur most frequently in bays and estuaries with salinity in the area of 0.4–1.7% (Colwell and Kaper 1978); but have also been found in rivers and brackish inland lakes of salinity levels as low as 0.01%. Their presence in oysters and water samples does show a seasonal variation with the highest numbers being isolated June–August (Madden et al. 1982). Non-01 *V. cholerae* are free living organisms and are part of the autochatonous flora.

Vibrio parahaemolyticus

V. parahaemolyticus was first associated with food poisoning in 1950 in Osaka, Japan (Fujino et al. 1974). Since its discovery, *V. parahaemolyticus* is implicated in greater than 1,000 outbreaks per year in Japan and accounts for 45–70% of that country's bacterial food poisonings. Food poisoning in Japan is usually related to the consumption of raw seafood during the warm months. Typical symptoms include diarrhea (sometimes bloody), abdominal cramps, nausea, vomiting, headaches, fever and chills (Fujino et al. 1974). The infective dose for humans is between 10^5 and 10^7 viable cells; however, a decrease in stomach acidity may decrease infective dose. The time for onset of symptoms is usually 9–25 hours and the duration of the illness is usually 2.5–3 days. No deaths have been reported in the United States, but a death rate of 0.04% is reported for Japan. In Japan, raw seafood is the usual vehicle for the organism, but in the U.S. most of the foods implicated in *V. parahaemolyticus* outbreaks are cooked seafoods that have been recontaminated; although raw oysters and raw crabs have been implicated in some outbreaks (Barker 1974, Blake 1980, Spite et al. 1978). CDC data indicates that it is the agent most responsible for illness associated with molluscan shellfish. The NETSU data base indicates that it ranks sixth as a leading cause of illness. In any case, it is a significant cause of illness in shellfish.

V. parahaemolyticus is widely distributed in nature and has been isolated from coastal waters worldwide. Its presence has been documented in virtually all the marine coastal environs of the United States from the coast of Maine, south to the Gulf of Mexico, all along the west coast and from the coastal waters of Hawaii (Fujino 1974, Blake 1980), It is not considered to be a microorganism of the open sea because of its sensitivity to cool temperatures and high hydrostatic pressure (Kaneko and Colwell 1978, Colwell 1984, Schwarz and Colwell 1974). Its presence in estuarine environments and in the seafood harvested from these environments usually shows a seasonal variation, being present in the highest numbers during the summer months (Kenako and Colwell 1978, Hackney et al. 1980). Thompson and Vanderzant (1976) did not observe a positive correlation between numbers and season in the waters of the Gulf of Mexico off the Texas coast. However, Paille et al. (1987) observed seasonal variation in numbers of *V. parahaemolyticus* in oysters and waters of Louisiana.

While *V. parahaemolyticus* is a common contaminant of seafood, often present in high numbers, almost none of the isolates from seafood are capable of causing gastroenteritis in man (Fujino et al. 1974, Blake 1980, Hackney 1981). The test most widely used to differentiate between virulent and avirulent strains is the Kanagawa reaction, which tests a strain's ability to produce a heat stable hemolysin in an agar medium containing 7% NaCl, mannitol and fresh human or rabbit red blood cells. The heat stable hemolysin is the main virulence determinant for *V. parahaemolyticus*. Isolates from the marine environment and seafood are predominantly Kanagawa negative. Thompson and Vanderzant (1976) reported only 0.18% of the isolates from water, shellfish and sediments of the Gulf of Mexico were Kanagawa positive. In Japan 99% of the sea and fish isolates are Kanagawa negative (Sakazaki 1979). Food poisoning victims usually only excrete Kanagawa positive isolates. Studies have demonstrated that isolates do not change in the intestines and that Kanagawa positive types are probably part of marine *V. parahaemolyticus* populations, but present in low numbers.

Vibrio vulnificus

V. vulnificus has been called the new "terror of the deep" and is one of the most invasive species ever described (Oliver 1985). It has been identified as a halophilic "lactose-positive" marine vibrio. Foodborne infection may result after consuming contaminated, raw or undercooked seafood, particularly oysters and clams, with illness usually starting 16–48 hours after ingestion. The organism penetrates the intestinal tract and produces a primary septicemia. The illness usually begins with malaise, followed by chills, fever, and prostration. Vomiting and diarrhea are uncommon, but sometimes occur shortly after chills and fever. Hypotension (systolic blood pressure $\geq$80 mmHg) is present in approximately 33% of the cases (Blake et al. 1979). The fulminating infection progresses rapidly and may cause death in 40–60% of the patients (Oliver 1985). Primary septicemia by *V. vulnificus* is NOT OBSERVED in normal healthy people and is ONLY associated with certain risk factors including: liver disease, gastric disease, malignancy, hemochromatosis and chronic renal insufficiency (Oliver 1985, Blake et al. 1979). Healthy individuals can develop a gastroenteritis from this bacterium. The most common vehicle for the organism is raw oysters.

V. vulnificus is wide spread in the environment and has been isolated from estuarine waters of most coastal states. Infection via the intestinal tract is most often associated with the consumption of raw oysters, but it is sometimes difficult to isolate from the mollusks. Oliver (1981) demonstrated that antimicrobial factors in oysters could be lethal to *V. vulnificus* when the oysters were homogenized for analysis. Kelly and Dinuzzo (1985) demonstrated that the presence of *V. vulnificus* in oysters was probably due to filtration of the bacterium from sea water rather than active multiplication in oysters.

The presence of *V. vulnificus* in water and shellfish is seasonal being most prevalent when the water temperature is high (>20°C). Low salinity (0.5–1.6%) also favors the presence of *V. vulnificus* in seawater (Kelly 1982). Some strains of *V. vulnificus* show bioluminescence and these strains may also be pathogenic (Oliver 1986). Environmental isolates are phenotypically indistinguish-

able from clinical isolates and produce virulence factors identical to clinical isolates (Tison and Kelly 1986).

It is interesting that *V. vulnificus* is not listed in the CDC data base. This is because this data base only lists outbreaks and not individual cases. Since this organism only affects comprised individuals no outbreaks have been reported, just individual cases. This organism is causing concern. For example, in Louisiana, warning labels are now required on sacks of oysters. Also, in California, oyster from the Gulf coast must have a warning label. The warning suggests that individuals who have a compromised immune system or have other risk factors described above, should not eat raw oysters.

V. mimicus

V. mimicus is biochemically similar to *V. cholerae*, with the exception that the strains are sucrose negative. In earlier publications, they were listed as *V. cholerae* of the Hieberg group 5; however, DNA homology studies demonstrated that may of the sucrose negative strains were a separate species and in 1981 the name *mimicus* was proposed because of their similarity to *V. cholerae* (Shandera et al. 1983, Colwell 1984). Both toxigenic and non-toxigenic strains have been isolated, however, the food poisoning cases have been mostly from the non-toxigenic strains. Symptoms of the illness have included diarrhea in most cases, but approximately 67% of the cases had nausea, vomiting and abdominal cramps. Diarrhea may be bloody and will last 1 to 6 days.

Raw oysters and boiled crawfish (crayfish) have been implicated as vehicles for the organism. *V. mimicus* is widely distributed in nature and can be found in fresh as well as brackish waters. It does show seasonal variation, being present in highest numbers in the warmer months (Bockemuhl et al. 1986, Colwell 1984).

V. hollisae

V. hollisae (formerly EF 13) has been implicated in approximately 36 cases of food poisoning. Symptoms have included diarrhea and in approximately half the cases vomiting and fever. Seafood was implicated as the vehicle for *V. hollisae*, including raw oysters, clams and shrimp (Morris et al. 1982).

The ecology of *V. hollisae* is not well understood because it grows poorly or fails to grow in TCBS, the medium most used in isolation of members of the genus *Vibrio*.

V. furnissi and *Vibrio fluvialis*

V. furnissi was previously classified as biovar II of *V. fluvialis*. *V. furnissi* has been implicated in food borne illness (Brenner et al. 1983). It produces gas from glucose, which is an unusual characteristic among *Vibrio* species. Symptoms of illness include diarrhea, abdominal cramps, and sometimes nausea and vomiting. Most of the cases listed by NETSU are probably *V. furnissi*.

Pleisomonas shigelloides

P. shigelloides (formerly *Aeromonas shigelloides*) has been implicated in human gastroenteritis for 40 years (Miller and Koberger 1985). *P. shigelloides* is widespread in nature, being mostly associated with fresh surface water, but may also be found in seawater. It shows a seasonal variation in its isolation similar to that of marine vibrios; being more often isolated during the warmer months (Miller and Koburger 1985).

Foods implicated as vehicles for *P. shigelloides* include cuttle fish salad, salt mackerel, raw oysters and undercooked oysters. In the U.S. raw oysters are probably the most implicated food.

According to the NETSU data base, *P. shigelloides* has only been implicated in 18 cases during the 15 year period from 1973–1987. This accounted for less than 0.5% of the cases of illness associated with molluscan shellfish.

Miller and Koburger (1985) reviewed infections by *P. shigelloides* and reported by the percent of people experiencing symptoms which included diarrhea (94%), abdominal pain (74%), nausea (74%), chills (49%), fever (37%), headache (34%), and vomiting (33%). The onset of symptoms usually occurred 24–50 hours after ingestion of the food. The illness was self limiting and usually lasted 24–48 hours.

Most strains of *P. shigelloides* have a minimum growth temperature of 8°C, but at least one strain has been reported to grow at 0°C. They seem to survive well in shellstock oysters held at refrigeration temperatures. The organism is sensitive to pH of <4 and salt concentrate of $>5\%$ (Miller and Koburger 1986). In addition, being a member of the family Vibrioneae, it should be killed by relatively mild cooking temperatures.

Aeromonas

Aeromonas hydrophilia is listed as a cause of diarrheal illness by the NETSU data base. However, there is some question as to whether it is truly a pathogen.

Other agents that have caused illness from consuming molluscan shellfish that are of natural origin include *Clostridium perfringens* and *Bacillus cereus*. There is some question as to whether these organisms caused illness from consuming raw shellfish or were contaminants of cooked products that were temperature abused. The data bases do not make this clear. *B. cereus* was most likely associated with cooked products or products that were stored for a long period of time. On the other hand, it is probable that *C. perfringens* was in some outbreaks associated with raw products.

Clostridium perfringens

Clostridium perfringens has been associated with human disease, mostly gas gangrene, for over 90 years. However, it was not until the 1940's that it was first associated with food poisoning. *C. perfringens* food poisoning is associated with proteinaceous food products. The bacterium has exacting growth requirements, requiring thirteen amino acids and six vitamins. Foods of animal origin are more likely to provide these needed growth requirements. Meat and poultry products account for most of the reported illness with seafood products only accounting for approximately 2% of the reported outbreaks (Banwart 1989).

Most of the outbreaks of *C. perfringens* food poisoning have been associated with food service establishments. Cooking of foods contaminated with *C. perfringens* will kill vegetative cells of the organism, but the spores will survive. Cooking tends to lower the oxidation/reduction potential of foods and heat shocks the spores into activation, creating ideal conditions for growth of the organisms. Time-temperature abuse of the cooked food allows the organism to grow to high numbers. *C. perfringens* grows very quickly, with a generation time of as low as 8.5 minutes reported in some foods (Willardsen et al. 1979). Growth can occur at temperatures as high as 50–52.3°C (Shoemaker and Pierson 1976). Thus, if warming trays in food service establishments are not kept at proper temperatures, growth can occur. Time-temperature abuse of cooked products is usually a critical factor in most food poi-

sonings of *C. perfringens* origin. The number of organisms normally found in foods is usually low compared to the high number required to induce illness. The critical number needed to induce illness has been estimated at between $10^6 - 5 \times 10^8$ (Labbe, 1988 and Hatheway et al. 1980).

The source of the *C. perfringens* can be from soil, dust, water, spices, or the food itself. Type A is the strain mostly associated with food poisoning. It is considered to be part of the microflora of soil. Virtually all soils examined have contained type A *C. perfringens* at levels between log 3–4 per gram (Labbe, 1989). Also, it is associated with the intestinal contents of most animals being present at levels of log 3–5. This level is usually observed in infants after 6 months of age (Labbe 1988). This bacterium has also been isolated from the intestinal contents and surface of fish but at considerably lower levels. In addition, it is often isolated at low levels from shellfish and has been suggested as an indicator of fecal pollution.

The presence of *C. perfringens* in shellfish has been documented worldwide. Burow (1974) reported that 56% of mussel samples were positive for the organism. Inal et al. (1974) also reported the isolation of *C. perfringens* from mussels in Turkey. Ayres (1975) reported the organisms isolation from a number of shellfish including the European flat oyster, mussels, and hard clams. Fruin (1978) reported that most of the *C. perfringens* isolated from foods including clams were type A. Saito (1990) reported high incidence of *C. perfringens* in oysters in Japan. Furthermore 12% of the isolates from oysters were positive for enterotoxin production. This compared to six percent of the isolates from food handlers, 2% of isolates from dogs, and 10% of water isolates being positive for enterotoxin production.

Tia Son and Fleet (1980) observed that oysters (Crassostrea *commercialis*) were commonly contaminated with low levels of *C. perfringens* and *Bacillus cereus*. These organisms could be removed by depuration or relaying to clean water. Their depuration rates were similar to that of enteric bacteria such as *Escherichia coli*. They further observe that in artificially contaminated oysters that *C. perfringens* rapidly died off during storage, whereas counts of *B. cereus* remained stable to refrigeration.

Examination of CDC (Chapter 8 of this report) data shows that *C. perfringens* accounted for 5.4% of the outbreaks and 16.6% of the cases of illness associated with fish over the 15 year period from 1973–1987. Additionally, it was responsible for 4.3% and 3.1% of the outbreaks and cases associated with shellfish respectively during the same period. Since the illness associated with *C. perfringens* is usually mild, the number of cases are probably much higher.

The NETSU data base did not report any cases of shellfish born illness since 1894. Since the CDC data base includes crustaceans in its classification of shellfish, it is possible that the shellfish borne illness caused by *C. perfringens* reported by CDC may not have involved molluscan shellfish.

Analysis of the incidence of seafood borne illness caused by *C. perfringens*, indicates that *C. perfringens* is of little importance as a seafood borne pathogen. The number of outbreaks are low and most likely due to contamination and temperature abuse. It may be of greater importance as an indicator of pollution than as a pathogen. Madden et al. recommends that *C. perfringens* be the indicator of choice for depuration systems. These workers noted that *C. perfringens* was far more likely to be present in polluted shellfish than *Escherichia coli* because the spores survive well in the environment. Yet, they are depurated from shellfish at similar rates. By using *C. perfringens* as an indicator of depuration the public could be assured that the shellfish were indeed depurated. In addition, enumeration of the organism is easier.

The symptoms of *C. perfringens* food poisoning include severe abdominal cramps and a pronounced diarrhea. Nausea and vomiting are rare and headache and fever are usually absent. The on-set of symptoms is usually 8–12 hours after ingestion of the food and the illness usually does not persist for more than 24 hours. The illness is caused by sporulation of the vegetative cells in the intestine accompanied by production of an intracellular enterotoxin. The enterotoxin can be produced in food during sporulation but it has not been proven that illness has resulted from preformed toxin in foods (Labbe and Harmon, 1992).

Bacillus cereus

Bacillus cereus is a Gram-positive, facultatively aerobic spore-forming rod. The cells are large and the spores do not swell the sporangium. These and other characteristics including biochemical features are used to differentiate and confirm the presence *B. cereus* although these characteristics are shared with *B. cereus* var. mycoides, *B. thuringiensis* and *B. anthracis*. Differentiation of these organisms depends upon determination of motility (most *B. cereus* are motile), presence of toxin crystals (*B. thuringiensis*), hemolytic activity (*B. cereus* and others are beta hemolytic while *B. anthracis* is usually non-hemolytic) and rhizoid growth which is characteristic of *B. cereus* var. mycoides (Harmon et al. 1992).

Bacillus cereus food poisoning is the general description although, two types of illness are recognized which are caused by two distinct metabolites. The diarrheal type of illness is caused by a large molecular weight heat labile protein while the vomiting (emetic) type of illness is believed to be caused by a low molecular weight, heat-stable peptide.

The symptoms of *B. cereus* diarrheal type food poisoning mimic those of *Clostridium perfringens* food poisoning. The onset of watery diarrhea, abdominal cramps and pain occurs 6–15 h following consumption of contaminated food. Nausea may accompany diarrhea, but vomiting (emesis) rarely occurs. Symptoms persist for 24 h in most instances. The emetic type of food poisoning is characterized by nausea and vomiting within 0.5 to 6 h after consumption of contaminated foods. Occasionally, abdominal cramps and/or diarrhea may also occur. Duration of symptoms is generally less than 24 h. The symptoms of this type of food poisoning parallel those caused by *Staphylococcus aureus* foodborne intoxication.

The type most likely associated with shellfish is the diarrheal type. The emetic type has almost exclusively been associated with rice and starchy products. The presence of large numbers of *B. cereus* (greater than 10^6 organisms/g) in a food is indicative of active growth and proliferation of the organism and is consistent with a potential hazard to health. These high numbers could be reached during prolong storage out of water, or during transport to other states.

THE EFFECT OF HARVESTING, TRANSPORTATION AND STORAGE ON THE NUMBERS OF MICROORGANISMS IN SHELLFISH

This section will only be concerned with bacteria since enteric viruses do not multiply in shellfish.

Only a few studies have addressed the fate of pathogens and indicators during transportation and storage. In our laboratories we have examined the fate of indicators during transportation from Louisiana to Florida and Virginia. Non *E. coli* fecal coliforms

increased much faster than *E. coli* and often reach extremely high counts by the end of the trip. The oysters were harvested from waters meeting the fecal coliform standard of 14 or less per 100 mLs. The oysters were harvested and put into sacks on the boats. The first oysters were harvested before 6 AM and the boat arrived at the dock at approximately 4 PM. Approximately 425 sacks were loaded onto a refrigerated truck. The refrigeration was turned on after loading and the oysters were transported to Virginia over a period of 27 hours. Both *E. coli* and fecal coliform counts were <18/100 g for samples taken dockside. During the trip fecal coliform levels increased to levels of greater than 400 per 100 grams. *E. coli* levels remained very low. The fecal coliforms were identified to be *Klebsiella* species. In other studies, oysters were monitored in route from Louisiana to Apalachicola Bay, Florida. These studies were conducted in the months of July and August. In these studies the results were far more dramatic. The initial fecal coliform counts averaged 13,000 per 100 grams when the oysters reached the dock. *E. coli* only accounted for a small fraction of the fecal coliform count. In one trip the *E. coli* MPN was 50 per 100 g and in the other study the MPN was 20 per 100 grams. Four hundred sacks of oysters were loaded onto a truck and during the 15 hour trip the fecal coliform counts increased from 13,000/100 grams to 240,000/100 gm. The *E. coli* counts increased from 50 to 70/100 gms. In other studies from our laboratories, oyster samples were taken dockside as the harvesting boats landed and at the wholesale market during June and July. A total of 53 samples were taken dockside and 30 samples were taken at the wholesale level. Fecal coliform counts averaged 1112/100 grams dockside and 10,000/100 grams at the wholesale market. This data clearly shows that fecal coliforms increase in numbers during storage and transportation of shellfish harvest during the summer from the Gulf coast.

Cook and Ruple (1989), also examined the fate of fecal coliforms and *E. coli* during the trip from the harvest area to the plant. In general *E. coli* increased only during the time on the boat. Non *E. coli* fecal coliforms increase at all stages of transportation and during the summer months dominated the fecal coliform population. These studies clearly indicated that fecal coliforms are not adequate indicators of fecal contamination in shell stock oysters. Similar studies with soft shell clams have demonstrated that fecal coliforms are not good indicators of fecal contamination during the summer.

Cook and Ruple (1989) also studied the effect of transport on levels of vibrios in oysters. Many of the vibrios including *V. vulnificus* and *V. parahaemolyticus* increased by 3–4 orders of magnitude during time from harvest to the plant.

Marine vibrios do not depurate at the same rate as enteric bacteria and may be present far longer than indicators. This observation, coupled with the growth of vibrios demonstrated by Cook and Ruple may indicate that immunocompromised individuals should not assume that depurated shellfish are safe to consume. A significant reduction in bacterial counts is observed during depuration (not relaying); however, a certain bacteria of the normal microflora are resistant to depuration. These include vibrio species (Richards 1991). *V. parahaemolyticus* counts of naturally contaminated oysters were unchanged during depuration. Likewise, depuration does not significantly affect counts of *V. vulnificus* or *V. cholerae*. These pathogens could increase in numbers during storage and transportation.

LITERATURE CITED

Allred, J. N., J. W. Walker, V. C. Beal, Jr. & F. W. Germaine. 1967. A survey to determine the *Salmonella* contamination rate in livestock and poultry feeds. *J. Am. Vet. Med. Assoc.* 151:1857–1861.

American Public Health Association. 1985. M. L. Speck, Ed. Compendium of methods for the microbiological examination of foods. APHA, Washington, DC.

Andrews, W. H., C. D. Diggs, J. J. Miescier, C. R. Wilson, W. N. Adams, S. A. Furfari & J. F. Musselman. 1976. Validity of members of the total coliform and fecal coliform groups for indicating the presence of Salmonella in the quahaug, Mercenaria mercenaria. *Journal of Milk and Food Technology* 39:322–324.

Andrews, W. H., C. D. Diggs, M. W. Presnell, J. J. Miescier, C. R. Wilson, C. P. Goodwin, W. N. Adams, S. A. Furfari & J. F. Musselman. 1975. Comparative validity of members of the total coliform and fecal coliform groups for indicating the presence of Salmonella in the Eastern oyster, Crassostrea virginica. *Journal of Milk and Food Technology* 38:453–456.

Arumugaswamy, R. K. & R. W. Proudford. 1987. The occurrence of Campylobacter jejuni and Campylobacter coli in Sydney Rock oyster (Crassostrea commercialis). *International Journal of Food Microbiology* 4:101–104.

Arumugaswamy, R. K., R. W. Proudford & M. J. Eyles. 1988. The response of Campylobacter jejuni and Campylobacter coli in the Sydney Rock oyster (Crassostrea commercialis), during depuration and storage. *International Journal of Food Microbiology* 7:173–183.

Aserkoff, B., S. A. Schroeder & P. S. Brachman. 1970. Salmonellosis in the United States—a five-year review. *American. J. Epidemiol.* 92: 13–24.

Balachandran, K. K. & P. K. Surendran. 1985. Purification of live clams for processing. *Seafood Export Journal* 17:5–9.

Banwart, G. 1989. "Basic Food Microbiology." Van Nostrand Reinhold Co. New York, NY.

Barker, W. H. 1974. *Vibrio parahaemolyticus* outbreaks in the United States. *Lancet* 10:551–554.

Blake, P., D. T. Allegra, J. D. Snyder, T. J. Barrett, L. McFarland, C. T. Caraway, J. C. Feeley, J. P. Craig, J. V. Lee, N. D. Puhr & R. A. Feldman. 1980. Cholera—A possible endemic focus in the United States. *New Eng. J. Med.* 302:305.

Blake. 1980. Diseases of humans (other than cholera) caused by *Vibrios*. *Ann. Rev. Microbiol.* 34:341–352.

Bockemühl, J., K. Roch, B. Wohler, S. Aleksia & R. Wokatsch. 1986. Seasonal distribution of facultative enteropathogenic vibrios (*Vibrio cholerae, Vibrio mimicus, Vibrio parahaemolyticus*) in the freshwater of the Elbe river at Hamburg. *J. Appl. Bact.* 60:435–439.

Bryan, F. L. 1988. Risks associated with vehicles of foodborne pathogens and toxins. *Journal of Food Protection* 51:498–508.

Bryan, F. L. 1986. Seafood-transmitted infections and intoxications in recent years. In: *Seafood Quality Determination*. pp. 319–337. Eds. D. E. Kramer and J. Liston. Elsevier Science Publishers B.V., Amsterdam.

Cantoni, C., S. D'Aubert & G. Soncini. 1985. Food poisoning outbreak caused by salmonellae. *Aechivio Veterinario Italiano* 36:74–75.

Castro, K., I. Gonzalez, C. Espeleta & J. Carrera. 1990. Presence of Salmonella in oysters, Cuba, 1985–1988. Dep. Nacional de Higiene de los Alimentos y Nutr., Min. de Salud Publica., Havana, Cuba. *Revista Cubana de Higiene y Epidemiologia* 28:88–93.

Castro, K., I. Gonzalez, C. Espeleta & J. Carrera. 1990. Presence of Salmonella in oysters, Cuba, 1985–1988. Dep. Nacional de Higiene de los Alimentos y Nutr., Min. de Salud Publica., Havana, Cuba. *Revista Cubana de Higiene y Epidemiologia* 28:88–93.

Centers for Disease Control. 1986. Cholera in Louisiana—Update. MMWR. Dept. Hlth. and Human Ser. Atlanta, GA.

Centers for Disease Control. 1986. Toxigenic *Vibrio cholerae* 01 Infec-

tion—Louisiana and Florida. MMWR. Dept. Hlth. and Human Ser. Atlanta, GA.

Centers for Disease Control, Foodborne Surveillance Data for all Pathogens in Fish/Shellfish for years 1973–1987. Issued December, 1989.

Centers for Disease Control, Foodborne Disease Outbreaks. Annual Summaries 1973–1982, USDHHS Publication (CDC).

Cliver, D. O. 1988. Virus transmission via foods. A Scientific Status Summary by the Institute of Food Technologists' Expert Panel on Food Safety and Nutrition. *Food Tech.* 42(10):241–247.

Cole, M. T., M. B. Kilgen, L. A. Reily & C. R. Hackney. 1986. Detection of enteroviruses and bacterial indicators and pathogens in Louisiana oysters and their overlying waters. *Journal of Food Protection* 49(8):596–601.

Colwell, R. 1984. "Vibrios in the Environment." John Wiley & Sons. NY, NY.

Colwell, R. & J. Kaper. 1978. *Vibrio cholerae, Vibrio parahaemolyticus* and other vibrios: occurrence and distribution in Chesapeake Bay. *Science* 198:394–397.

Cook, D. W. & A. D. Ruple. 1989. Indicator bacteria and Vibrionaceae multiplication in post-harvest shellstock oysters. *Journal of Food Protection* 52:343–349.

Cook, D. W. & R. D. Ellender. Relaying to decrease the concentration of oyster-associated pathogens. *Journal of Food Protection* 49:196–202.

Corradini, L. & F. Paesanti. 1984. Microbiological survey on edible shellfish—results of four years of control. Atti della Societa Italiana delle Scienze Veterinaire 1983, publ. 37:626–628.

Cox, N. & J. Bailey. 1987. Pathogens associated with processed poultry. In Microbiology of Poultry Meat Products. F. Cunningham & N. A. Cox ed. Academic Press, Orlando, FL.

Doyle, M. 1981. *Campylobacter fetus* subsp. *Jejuni*—an old pathogen of new concern. *J. Food Protect.* 44.

Elliot, E. L. & R. R. Colwell. 1985. Indicator organisms for estuarine and marine waters. *FEMS Micro. Rev.* 32:61–79.

Eyles, M. 1986. Microbiological hazards associated with fishery products. *CSIRO Food Res. Q.* 46:8–17.

Eyles, M. J. & G. R. Davey. 1984. Microbiology of commercial depuration of the Sydney rock oyster. 1984. *Journal of Food Protection* 47:703–706, 712.

Eyles, M. J. & G. R. Davey. 1983. Vibrio cholerae and enteric bacteria in oyster-producing areas of two urban estuaries in Australia. *International Journal of Food Microbiology* 6:207–218.

Fraiser, M. B. & J. A. Koburger. 1984. Incidence of salmonellae in clams, oysters, crabs and mullet. *Journal of Food Protection* 47:343–345.

Francis, D. W. & R. M. Twedt. 1975. A rapid method for the detection and enumeration of fecal coliforms in shellfish. *Abstracts of the Annual Meeting of the American Society for Microbiology* 75, 201.

Franco, D. A. 1988. *Campylobacter* species: Considerations for controlling a foodborne pathogen. J. Food Protect. 51:145–153.

Franco, A., L. Toti, R. Gabrieli, L. Croci, D. de Medici & A. Pana. 1990. Depuration of Mytilus galloprovincialis experimentally contaminated with hepatitis A virus. *International Journal of Food Microbiology* 11(3/4):321–327.

Fujino, T., G. Sakaguchi, R. Sakazaki & Y. Takeda. 1974. International symposium on *Vibrio parahaemolyticus*. Saikon Pub. Co. Tokyo, Japan.

Galassi, D., D. Quercetti & G. Simonella. 1976. Bacteriological studies on clams (Venus gallina) caught in the Adriatic Sea. Instituto Zooprofilattico Sperimentale, 64100 Teramo, Italy. *Atti della Societa Italiana delle Scienze Veterinarie* 30, 564–567.

Gangarosa, E. J. 1978. What have we learned from 15 years of *Salmonella* surveillance? In "National Salmonellosis Seminar." Washington, DC.

Garrett, E. S. 1988. Microbiological standards, guidelines, and specifications and inspection of seafood products. *Food Technology* 42:90–93.

George, C. 1974. Technological aspects of preservation and processing of edible shell fishes. *Fishery Technology* 11:22–27.

Gerba, C. P. 1988. Viral disease transmission by seafoods. *Food Technology* 42(3):99–103.

Gopalakrishna Iyer, T. S. & P. R. G. Varma. 1987. Isolation of Salmonella braenderup (6.7:e, h:e, n, Z15) from mussel meat. *Fishery Technology* 24(2):138.

Gouvea, V. 1991. Hepatitis E virus. In. Center for Food Safety and Applied Nutrition, Foodborne pathogenic microorganisms and natural toxins. U.S. Food and Drug Admin. Washington, D.C.

Greenberg, E. P., M. Duboise & B. Palhof. 1982. The survival of marine vibrios in Mercenaria mercenaria, the hardshell clam. *Journal of Food Safety* 4:113–123.

Hackney, C. R., B. Ray & M. L. Speck. 1980. Incidence of *Vibrio parahaemolyticus* in and the microbiology quality of seafoods in North Carolina. *J. Food Prot.* 43:769–772.

Hackney, C. R. & A. Dicharry. 1988. Seafood-borne bacterial pathogens of marine origin. *Food Technol.* 42:104–109.

Harmon, S. M., J. M. Goepfert, and R. W. Bennett. 1992. *Bacillus cereus. In* Vanderzant, C. and D. F. Splittstoesser (Eds.) Compendium of Methods for the Microbiological Examination of Foods. American Public Health Assoc. Washington, DC.

Heffernan, W. P. & V. J. Cabelli. Elimination of bacteria by the northern quahaug (Mercenaria mercenaria): environmental parameters significant to the process. *Journal of the Fisheries Research Board of Canada* 27:1569–1577.

Holmgien, J. 1981. Actions of cholera toxin and the prevention and treatment of cholera. *Nature* 292:413.

Hood, M. A., G. E. Ness & N. J. Blake. 1983. Relationship among fecal coliforms, *Escherichia coli*, and *Salmonella spp.* in shellfish. *Applied and Environmental Microbiology* 45:122–126.

Jay, J. M. 1986. "Modern Food Microbiology." Van Nostrand Reinhold Co. New York, NY.

Kai, A., T. Itoh, K. Saito, Y. Yanagawa, M. Inaga, M. Takahashim, S. Matsushita, Y. Kudoh, S. Sakai & T. Shinohara. 1983. Two outbreaks of oyster-associated food poisoning due to enterotoxigenic Escherichia coli 027:H7. *Annual Report of Tokyo Metropolitan Research Laboratory of Public Health* 34:121–124.

Kaneko, T. & R. Colwell. 1978. The annual cycle of *Vibrio parahaemolyticus* in Chesapeake Bay. *Microbiol. Ecol.* 4:135.

J. Kaper, J. Nataro, N. Roberts, R. Seibeling & H. Bradford. 1986. Molecular epidemiology of non-01 *Vibrio cholerae* and *Vibrio mimicus* in U.S. Gulf coast regions. *J. Clin. Microbiol.* 23:652.

Kawano, J., A. Shimizu, K. Fujii, S. Takeuchi & S. Kimura. 1987. Characterization of Bacillus cereus: haemolysis pattern, cytotoxicity and vascular permeability factory activity. Japan Science Reports of Faculty of Agriculture, Kobe University. *Journal Article* 17:273–281.

Kilgen, M. B., M. T. Cole & C. R. Hackney. 1988. Shellfish sanitation studies in Louisiana. *J. of Shellfish Research* 7:527–530.

Kilgen, M. B. 1989. Final Report on the Current National Status of the Relationships of Indicators, Human Enteric Pathogens and Potential Health Risks within a Total Environmental Assessment. Grant No. 37-01-79000/37500.

Kobubo, Y., S. Matsushita, A. Kai, M. Yamada & H. Konuma. 1978. Incidence of Escherichia coli in raw oyster and enterotoxin producibility of the isolates. *Journal of the Food Hygienic Society of Japan* (Shokuhin Eiseigaku Zasshi) 19(1):117–121.

Kolvin, J. & D. Roberts. 1982. Studies on the growth of *Vibrio cholerae* biotype eltor and biotype classical in foods. *J. Hyg. Camb.* 89:243.

Labbe, R. G., and S. M. Harmon. 1992. *Clostridium perfringens. In* Vanderzant, C. and D. F. Splittstoesser (Eds.) Compendium of Methods for the Microbiological Examination of Foods. American Public Health Assoc. Washington, DC.

Labbe, R. 1989. *Clostridium perfringens. In:* (M. P. Doyle ed). Foodborne Bacterial Pathogens. p. 191–234. Marcel Dekker, Inc., NY, NY.

Levine, M. M., E. J. Bergquist, D. R. Nalin, D. H. Waterman, R. B. Hornick, C. R. Young, S. Sotman & B. Rowe. 1978. Escherichia coli strains that cause diarrhea but do not produce heat-labile or heat-stable enterotoxins and are non-invasive. *Lancet* i:1119–1122.

Levine, M. 1981. Cholera in Louisiana: old problem, new light. *New Eng. J. Med.* 302:345.

Madden, J., I. McCardell & R. Read. 1982. *Vibrio cholerae* in shellfish from U.S. coastal waters. *Food Technol.* 36:93.

Matches, J. R. & C. Abeyta. 1983. Indicator organisms in fish and shellfish. *J. Food Prot.* 37:114–117.

Matev, I., Z. Dimitrova & V. Stafanov. 1987. Survival of some pathogenic microorganisms in Black Sea mussels after experimental infection. Vissh Inst. po Zootekhnika i Vet. Med., Sofia, Bulgaria. *Veterinarnomeditsinski Nauki* 24:87–90.

Medallion Laboratories. 1987. Food Microbiology—Examining the greater risk. Anlyl. Progress. Vol. 4. No. 1.

Melnick, J. L., C. P. Gerba & C. Wallis. 1978. Viruses in water. *Bull. Wld. Hlth. Org.* 56:499–504.

Moreno Garcia, B., M. E. Escacho Perez & V. Diez Fernandez. 1976. Coliform bacteria in non-purified mussels (Mytilus edulis). *Anales de la Facultad de Veterinaria de Leon* 22:315–324.

Morris, J. & R. Black. 1985. Cholera and other vibrioses in the United States. *New Eng. J. Med.* 15:1–10.

Ogawa, H., H. Tokuno, M. Sasaki & T. Kishimoto. 1980. Distribution of enteropathogenic E. coli in oyster farm areas. *Journal of the Food Hygienic Society of Japan* (Shokuhin Eiseigaku Zasshi) 21:5–12.

Overby, L. R., F. Deinhardt & J. Deinhardt, Eds. 1983. Viral Hepatitis: Second International Max von Pettenkofer Symposium. Marcel Dekker, Inc., New York.

Owen, R. J., M. Costas, L. Sloss & F. J. Bolton. 1988. Numerical analysis of electrophoretic protein patterns of Campylobacter laridis and allied thermophilic campylobacters from the natural environment. *Journal of Applied Bacteriology* 65(1):69–78.

Paille, D., C. Hackney, L. Reily, M. Cole & M. Kilgen. 1987. Seasonal variation in the fecal coliform population of Louisiana oysters and its relationship to microbiological quality. *J. Food Prot.* 50:545–549.

Perez Martinez, J. A., A. L. Roma Garcia, Y. Almanza Marquez, I. Rose Perez & A. Yela Miranda. 1988. Determination of entero-toxigenicity of Escherichia coli isolated from oysters, by means of inoculation of suckling mice. Beterinaria, Mexico 19(1):9–13.

Power, U. F. & J. K. Collins. 1990. Tissue distribution of a coliphage and Escherichia coli in mussels after contamination and depuration. *Applied and Environmental Microbiology* 56:803–807.

Power, U. F. & J. K. Collins. 1990. Elimination of coliphages and Escherichia coli and mussels during depuration under varying conditions of temperature, salinity, and food availability. *Journal of Food Protection* 53:208–212, 226.

Power, U. F. & J. K. Collins. 1989. Differential depuration of poliovirus, Escherichia coli, and a coliphage by the common mussel, Mytilus edulis. *Applied and Environmental Microbiology* 55:1386–1390.

Rajagopalan, K. & P. M. Sivalingam. 1978. Bacterial flora of a green mussel (Mytilus viridis Linnaeus) and a naturally occurring rock oyster (Crassostrea cuculata). *Malaysian Applied Biology* 7:43–47.

Richards, G. P. 1988. Microbial purification of shellfish: A review of depuration and relaying. *J. Food Prot.* 51:218–251.

Richards, G. P. 1985. Outbreaks of shellfish-associated enteric virus illness in the United States: requisite for development of viral guidelines. *J. Food Prot.* 48:815–823.

Richards, G. P. 1987. Shellfish-associated enteric virus illness in the United States, 1934–1984. *Estuaries* 10:84–85.

Rippey, S. R. & J. L. Verber. 1988. Shellfish borne disease outbreaks. Department of Health and Human Services, Public Health Service, Food and Drug Administration, Shellfish Sanitation Branch. NETSU, Davisville, RI.

Rippey, S. R. 1991. Shellfish borne disease outbreaks. Department of Health and Human Services, Public Health Service, Food and Drug Administration, Shellfish Sanitation Branch. NETSU, Davisville, RI.

Rowse, A. J. & G. H. Fleet. 1984a. Effects of water temperature and salinity on elimination of Salmonella charity and Escherichia coli from Sydney Rock oysters (Crassostrea commercialis). *Applied and Environmental Microbiology* 48:1061–1063.

Rowse, A. J. & G. H. Fleet. 1984b. Temperature, salinity important in oyster purification. *Australian Fisheries* 43:26–28.

Rowse, A. J. & G. H. Fleet. 1982. Viability and release of Salmonella charity and Escherichia coli from oyster feces. *Applied and Environmental Microbiology* 44:544–548.

Sakazaki, R. 1979. Vibrio infections, *In* (H. Rieman F. Bryan, F. Ed). Food-borne infections and intoxications. Academic Press NY NY.

Samadpour, M., J. Liston, J. E. Ongerth & P. I. Tarr. 1990. Evaluation of DNA probes for detection of Shiga-like-toxin producing Escherichia coli in food and calf fecal samples. *Applied and Environmental Microbiology* 56:1212–1215.

Sato, A. 1971. Enteropathogenic Escherichia coli in commercial foods. I. *Journal of the Food Hygienic Society of Japan* (Shokuhin Eiseigaku Zasshi) 12:473–477.

Sato, A. 1972. Distribution of enteropathogenic Escherichia coli in commercial foods. II. Drug resistance and R factors in strains of enteropathogenic E. coli isolated from commercial fresh meats and oysters. *Journal of the Food Hygienic Society of Japan* (Shokuhin Eiseigaku Zasshi) 13(5):388–391.

Shah, D. B. & U. S. Rhea. 1986. Foodborne enterotoxigenic Escherichia coli: identification and enumeration on nitrocellulose membrane by enzyme immunoassay. *International Journal of Food Microbiology* 3:79–87.

Shultz, L., J. Rutledge, R. Grodner & S. Biede. 1984. Determination of the thermal death time of *Vibrio cholerae* in blue crabs (*Callinectis sapidus*). *J. Food Prot.* 47:4.

Sobsey, M. D., C. R. Hackney, R. J. Carrick, B. Ray & M. C. Speck. 1980. Occurrence of enteric bacteria and viruses in oysters. *J. Food Prot.* 43:111–128.

Spite, G., D. Brown & R. Twedt. 1978. Isolation of one enteropathogenic, Kanagawa-positive strain of *Vibrio parahaemolyticus* from seafood implicated in acute gastroenteritis. *Appl. Environ. Microbiol.* 35:1226.

Stephen, S., R. Indrani, M. Kotian & K. N. A. Rao. 1975. Isolation of enteropathic Escherichia coli from sea fish and fresh water mussels. *Indian Journal of Microbiology* 15:64–67.

Stern, N. J., C. M. Patton, M. P. Doyle, C. E. Park, B. A. McCardell. 1992. *Campylobacter*. *In* Vanderzant, C. and D. F. Splittstoesser (Eds.) Compendium of Methods for the Microbiological Examination of Foods. American Public Health Assoc. Washington, DC.

Thi Son, N. & G. H. Fleet. 1980. Behavior of pathogenic bacteria in the oyster, Crassostrea commercialis, during depuration, re-laying, and storage. *Applied and Environmental Microbiology* 40:994–1002.

Thompson, C. & C. Vanderzant. 1976. Serological and hemolytic characteristics of *Vibrio parahaemolyticus* from marine sources. *J. Food Sci.* 41:204.

Thompson, C. A. & C. Vanderzant. 1976. Relationship of *Vibrio parahaemolyticus* in oysters, water and sediment and bacteriological and environmental indices. *J. Food Sci.* 41:117.

Timoney, J. F. & A. Abston. 1984. Accumulation and elimination of Escherichia coli and Salmonellae typhimurium by hard clams in an in vitro system. *Appl. Environ. Microbiol.* 47:986–988.

Todorov, I. 1968. Microflora of the Black Sea mussel Mytilus Galloprovincialis (L). *Veterinarnomedicinski Nauki* 5:49–55.

U.S. Department of Health and Human Services, Food and Drug Administration. 1988 revision. Sanitation of shellfish growing areas. National Shellfish Sanitation Program Manual of Operations Part I.

U.S. Department of Health and Human Services, Food and Drug Administration. 1988 revision. Sanitation of the harvesting, processing and distribution of shellfish. National Shellfish Sanitation Program Manual of Operations Part II.

Venkateswaran, K., H. Nakano, H. Kawakami & H. Hashimoto. 1988. Microbiological aspects and recovery of Salmonella in retailed foods. *Journal of the Faculty of Applied Biological Science*, Hiroshima University 27(1):33–39.

Volterra, L., F. A. Aulicino, E. Tosti & M. Zicarelli. 1980. Microbiological monitoring of pollution in shellfish from the Neapolitan area. *Progress in Water Technology* 12(4):553–577.

Wells, G. C. & R. A. Edwards. 1969. A survey of sewage pollution in Georges River oysters. *Food Technology in Australia* 21(12):616–617.

West, P. A. & S. V. Wipat. 1988. Detection of bacteriophage tracers in bivalve molluscan shellfish. *Letters in Applied Microbiology* 7(4):95–98.

White, D. O. & F. Fenner. 1986. Medical Virology, 3rd. Ed. Academic Press, Inc.

Genetic Aspects of Introduction and Transfer of Molluscs

Patrick M. Gaffney and Standish K. Allen, Jr.

ABSTRACT Attempts to predict the biological impact of an introduction have traditionally focused on the ecological dynamics of competition and predation, or the concomitant introduction of parasites or disease organisms. We focus here on a subject that has received less attention: the genetic effects of introductions on native populations. These may be broadly defined as direct or indirect changes in the genetic composition of an endemic population attributable to the arrival and establishment of a non-native population. Direct effects occur when the gene pool of the native population is open to the introgression of genes from the introduced population. Indirect effects occur when hybridization between the native and introduced populations is not possible, but alterations in gene frequencies result from ecological interactions with the introduced organism.

A transfer is defined here as the movement of individuals of a given species to another area within the current geographic range of that species. An introduction is defined as the importation of individuals of a given species into an area where it is not endemic. The nature and extent of genetic effects are determined primarily by the degree of reproductive isolation between the introduced and resident populations, the nature of the isolating mechanisms (pre- vs. postzygotic), and the relative sizes of the two populations.

We consider the introduction of the Pacific oyster *Crassostrea gigas* to mid-Atlantic waters and conclude that the genetic impacts of such an introduction are likely to be indirect only. The magnitude of such impacts will depend on ecological factors affecting the success of the introduction and cannot be accurately predicted at present.

KEY WORDS: introductions, hybridization, oyster, *Crassostrea*

Attempts to predict the biological impact of an introduction have traditionally focused on the ecological dynamics of competition and predation, or the concomitant introduction of parasites or disease organisms. We focus here on a subject that has received less attention, the genetic effects of introductions and transfers on native populations. These may be broadly defined as direct or indirect changes in the genetic composition of an endemic population attributable to the arrival and establishment of a non-native population. Direct effects occur when the gene pool of the native population is open to the introgression of genes from the introduced population. Indirect effects occur when hybridization between the native and introduced populations is not possible; alterations in gene frequencies result from ecological interactions with the introduced organism.

Three considerations are important for assessing the genetic impacts of introductions and transfers: time scale, the ameliorating role of natural selection, and the meaning of fitness. Immediate genetic effects—those evident in the first few generations following an introduction—may differ substantially from long-term effects. This is because natural selection continually acts to remove less adapted genotypes from a population. For example, the interbreeding of an introduced population with natives may at first lead to the production of poorly adapted hybrid progeny, thus lowering mean population fitness. Over time, however, natural selection will act to improve the mean fitness of the population, either by eliminating the alleles responsible for hybrid inferiority, or by favoring the development of reproductive isolation between the native and introduced populations. Finally, attributes that enhance biological fitness, the ability of an individual to survive and transmit its genes to the next generation, may not be desirable attributes from a human perspective. For example, genetic changes resulting in earlier reproduction or smaller adult size may increase fitness, to the chagrin of the human consumer.

In order to estimate the genetic effects of a particular introduction, we must consider two factors: 1) the strength of the barrier, if any, to gene flow between the native and introduced populations, and 2) the degree of genetic differentiation between them (Figure 1). We will consider three cases along this spectrum.

TRANSFERS

At one end of the spectrum are "transfers," which we define as admixtures of native and introduced populations belonging to the same biological species. Although the two populations may differ to some extent genetically, they readily interbreed. The genetic consequences of interbreeding will depend on the degree to which the introduced population differs from the native population.

If the species is characterized by the existence of locally adapted stocks or populations, the immediate result of introgression will be the disruption of coadapted gene complexes and a consequent reduction of fitness in the descendants of hybrid matings. Only when the number of animals introduced is large relative to the native population will this transient effect be noticeable. Following the transfer, natural selection will act to restore mean population fitness and form new coadapted gene complexes. After the winnowing action of natural selection, the native population may even reach a higher "adaptive peak" as favorable new genes contributed by the introduced population increase in frequency.

When the endemic population is small and locally adapted, as may commonly occur in terrestrial or island populations of organisms with restricted dispersal capacities, transfers may destroy the unique phenotype of the local population, even if overall population fitness is not compromised. The homogenizing effect of indiscriminate transfers is popularly labelled "genetic pollution," and results in the loss of interpopulation diversity and distinct local phenotypes. This concept is most appropriately applied to rare or

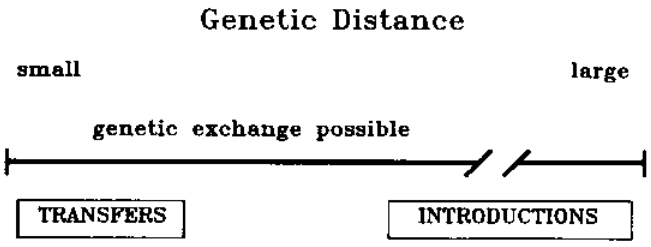


Figure 1. The continuum of genetic difference between populations in relation to reproductive isolation. Transfers involve freely interbreeding conspecific populations; introductions involve distinct species between which varying amounts of gene flow are possible.

endangered terrestrial vertebrates restricted to small isolated populations; it is not particularly apropos in the case of shellfish populations, which are typically very large and characterized by extensive gene flow between geographic regions.

In cases where the native population does not represent the pinnacle of adaptedness—for example, where rapid environmental change has outstripped the capacity of the population to respond genetically—the introgression of new genes may result in immediate benefits. Similarly, when the population possesses commercially undesirable characteristics, the influx of genes conferring a more desirable phenotype may be beneficial from the human perspective. Moav et al. (1978) demonstrated how the introduction of selected populations may be used for the genetic improvement of commercially exploited wild fish populations.

Perhaps the most important factor affecting the immediate genetic impact of a transfer is the size of the introduced population relative to the native population. In most cases, involving commercial shellfish, the transferred population is infinitesimal compared to the resident population, with the result that any immediate genetic impact, negative or positive, will be difficult to detect. However, if the transfer introduces beneficial genes to the native population, these will increase in frequency over time and a long-term positive effect may result from even a small transfer.

Transfers have been a regular practice in commercial shellfish populations for over a century (e.g., Ingersoll 1881, cited in Haven et al. 1978); indeed, Elton (1958) considered oyster culture to be "the greatest agency of all that spreads marine animals to new quarters of the world." Unfortunately, no clear evidence on the genetic impact of such transfers is available. Interpopulation crossing of *C. virginica* produced negligible or positive effects on larval survival (Newkirk 1978) or reduced larval survival (Mallet and Haley 1984). Juvenile growth (Mallet and Haley 1983) and survival (Mallet and Haley 1984) were higher in the progeny of interpopulation crosses than in the progeny of intrapopulation crosses. These limited results suggest that both immediate and long-term genetic effects of transfers will range from negligible to positive. However, as these authors noted, environment typically plays a larger role than genetics in overall performance, and genotype-environment interactions are common. The effect of a particular transfer is thus difficult to predict accurately without detailed information on the resident and introduced populations and their performance at the site of introduction.

INTRODUCTIONS: DIRECT GENETIC EFFECTS

An introduction is defined here as the importation of a species into an area where it is not endemic. The genetic effects of an introduction on an endemic species will be determined largely by the permeability of the barriers to interspecific hybridization. Although the classical biological species concept of Mayr (1963) defines species on the basis of reproductive isolation, there are many cases where good biological species produce hybrids, even under natural conditions. Contemporary species concepts (reviewed by Templeton 1989) more readily accommodate situations where reproductive isolation is less than absolute yet species nevertheless behave as distinct, cohesive evolutionary lineages.

When interspecific hybridization is possible, we must ask whether it is probable. This requires a careful consideration of the biology of the native and introduced species, and the nature of the mechanisms that effect reproductive isolation. Reproductive isolating mechanisms (RIMs) are conveniently categorized as pre- and postzygotic. Examples of the prezygotic RIMs range from behavioral differences that prevent interspecific mating (e.g., time of spawning) to gametic incompatibility. Postzygotic reproductive isolation occurs when hybrids are formed, but are less viable or sterile.

If the primary barrier to hybridization is prezygotic, direct genetic effects will occur when occasional breaches result in gene flow between the two species. The immediate results may range from detrimental to beneficial, while long-term effects—from the perspective of the organism, not the human consumer—may range from negligible to positive. As discussed above, the size of the introduced population and the extent of gene flow play key roles in determining the magnitude of short- and long-term genetic impacts.

If on the other hand the primary barrier to hybridization is postzygotic, then the mere presence of one species may impose a burden on the other. This occurs when the two species readily cross-fertilize, but the progeny show reduced viability or sterility, effectively resulting in gametic wastage. The possibility of wasted gametes becomes important when the introduction is massive, or if the introduced species is able to become established and attain high density. In this case, both species will lose gametes to the formation of interspecific hybrids. If the two species occupy the same niche and have no prezygotic RIMs, then the loss of gametes becomes critical, and one species may drive the other to extinction. This situation is analogous to the use of sterility induced by chromosomal rearrangements in insect population control (Foster et al. 1972). Which species wins the competition will depend on the population sizes and reproductive outputs of the two species. In practice, it is unlikely that two distinct species will occupy precisely the same niche; this, coupled with the widespread larval dispersal typical of shellfish, would likely lead to the stable coexistence of the two species in some areas, with other habitats supporting one or the other species only.

When interspecific hybridization does occur, the evolutionary dynamics of the hybrid and parental populations can be complex (e.g., references in Levin 1979). The fate of an introgressed gene depends not only on its fitness on the new genetic background, but also on the fitness of alleles at linked loci, and the rate of recombination between it and linked loci (Barton and Bengtsson 1986). Consequently, it is very difficult to predict the nature and extent of genetic changes in a recipient population due to the introgression of heterospecific genes.

INTRODUCTIONS: INDIRECT GENETIC EFFECTS

In the event the barrier to hybridization cannot be breached, the only genetic effects the introduced species may exert on the native species will be indirect, and will depend on the nature of interactions between the two species. Two different scenarios may be outlined: 1) The alien has only marginal success in becoming established. Its genetic effect on the native species is negligible. 2)

The alien becomes well-established, occupying a niche that overlaps partially with the native species. Ecological interaction in areas of sympatry will drive genetic changes in both species. The effects of such changes on the two gene pools will depend on the relative abundance and reproductive output of sympatric vs. allopatric populations, and on the amount of gene flow among populations of each species.

A Concrete Example: Crassostrea virginica *and* Crassostrea gigas

The continued decline of the American oyster (*C. virginica*) fishery in the mid-Atlantic region has raised the prospect of introducing the Pacific oyster (*C. gigas*) to areas which no longer support commercial harvests of the former (Mann 1979, Virginia Sea Grant 1990). At the same time, this notion is strongly opposed by those who fear dire biological impacts, in the form of introduced parasites or disease organisms, competitive exclusion or even "genetic pollution" of the American oyster. We leave the question of parasites, diseases and ecological impacts to others in this symposium, and address here the potential genetic effects of the introduction of *C. gigas* to the mid-Atlantic region.

The first issue to be resolved is whether any direct genetic effects are likely, i.e., what RIMs exist between the two species? Both eggs and sperm from one species are effective at stimulating spawning by the other species in the laboratory (Galtsoff and Smith 1932). Cross-fertilization also appears to occur readily in both directions (reviews in Menzel 1987, Gaffney and Allen in prep.). We have found no published data on the interspecific competitive abilities of sperm, but preliminary evidence indicates that the schedule of meiotic events is not altered in either species by heterospecific fertilization (Bernat and Gaffney unpubl., Scarpa, Allen and Gaffney unpubl.). Overall, it appears that prezygotic RIMs between the two species are very weak.

The question of postzygotic RIMs between the two species is problematic. The literature (see Menzel 1987 for review) is inadequate to settle this question, because hybridization experiments have rarely been followed by genetic verification (Gaffney and Allen 1991). Recent experimental data confirm the view that hybrids do not survive to metamorphosis (Allen and Gaffney 1991). Therefore it seems likely that introduced *C. gigas* would be capable of cross-fertilizing native oysters, and that the hybrids so formed would represent wasted gametes. In places where native oysters vastly outnumbered the introduced species, the loss of gametes would seriously hinder the spread of the latter. Any *C. gigas* zygotes formed during a mass spawning of the two species would probably be spread so thin after larval dispersal that they would be incapable of propagating a second generation by homospecific mating. In areas devoid of indigenous oysters, on the other hand, if ecological conditions were favorable and minimum critical densities were attained, an introduced species such as *C. gigas* might stand a good change of becoming established. Such areas could act as reservoirs from which larvae would be dispersed to sites where growth and survival were satisfactory, but reproduction effectively undermined by gametic wastage.

The Pacific oyster has been introduced repeatedly into eastern waters, including Maine (Dean 1979), Massachusetts (Galtsoff et al. 1950, Dean 1979, Hickey 1979), Long Island Sound (Dean 1979), the Chesapeake Bay (Cranston Morgan, pers. comm.) and several southern states (Galtsoff et al. 1950). Its failure to become established in these localities may be the result of the "gametic warfare" described above, rather than an inhospital environment, as it has been successfully introduced to a wide range of environmental regimes (Mann 1983).

Where the American oyster has been introduced to exotic waters, it has sometimes succeeded in establishing small but stable populations. Examples include Pearl Harbor, Hawaii (Brock 1960) and Boundary Bay, British Columbia (Elsey 1933, Quayle 1964). In Hawaii, there appears to have been no indigenous oyster adapted to the relatively limited estuarine habitat present there, and the establishment of *C. virginica* followed the planting of almost 40,000 oysters at the end of the nineteenth century (Brock 1960). This population persists today (John Ewart, pers. comm.). In British Columbia, the only indigenous oyster is *Ostrea lurida;* oysters of the genus *Ostrea* are generally incapable of cross-fertilizing *Crassostrea* species (Davis 1950, Menzel 1987). In any case, by the time *C. virginica* was introduced there, the native oyster population was severely depleted. Repeated introductions beginning at the turn of the century eventually resulted in the establishment of extensive American oyster beds in two small tributaries of Boundary Bay (Elsey 1933). It is possible that the introduction of the Pacific oyster at about the same time may have limited the subsequent spread of the American oyster on the west coast of North America, by either genetic (i.e., "gametic warfare") or ecological interactions. The apparent persistence of *C. virginica* populations as discrete entities coexisting with sympatric populations of *C. gigas* (Bourne 1979) is further evidence against the likelihood of successful hybridization in nature.

In conclusion, we believe on the basis of presently available data that the introduction of *C. gigas* to mid-Atlantic waters is unlikely to have any direct genetic effects on native oyster populations. Indirect genetic effects might occur if the Pacific oyster succeeded in becoming established; the magnitude of such effects could range from negligible to extensive, depending on the nature of ecological interactions between the species. Our current understanding of the ecology of bivalve introductions does not allow us to predict confidently the nature or extent of any such indirect genetic effects.

ACKNOWLEDGMENTS

We thank our colleagues for frank and stimulating discussions during the workshop on "Genetic Impacts of Introducing Non-Native Oyster Species in the Mid-atlantic Region" held at Rutgers Shellfish Research Laboratory, March 15–16, 1990. This is New Jersey Agriculture Experiment Station Publication No. D-32001-3-90 and Contribution 92-53 of the Institute of Marine and Coastal Sciences.

LITERATURE CITED

Allen, S. K., Jr. & P. M. Gaffney. 1991. Hybridization among three species of *Crassostrea*. *Journal of Shellfish Research* 10:301. (Abstract).

Barton, N. & B. O. Bengtsson. 1986. The barrier to genetic exchange between hybridising populations. *Heredity* 56:357–376.

Bourne, N. 1979. Pacific oysters, *Crassostrea gigas* Thunberg, in British Columbia and the South Pacific islands. Pages 1–53 *in* R. Mann, editor. Exotic Species in Mariculture. MIT Press, Cambridge.

Brock, V. E. 1960. The introduction of aquatic animals into Hawaiian waters. *Internationale Revue der gesamten Hydrobiologie* 45:463–480.

Davis, H. C. 1950. On interspecific hybridization in *Ostrea*. *Science* 111: 522.

Dean, D. 1979. Introduced species and the Maine situation. Pages 149–164 *in* R. Mann, editor. Exotic Species in Mariculture. MIT Press, Cambridge.

Elsey, C. R. 1933. Oysters in British Columbia. *Bulletin of the Biological Board of Canada* 34:1–34.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen and Co. Ltd., London.

Foster, G. G., M. J. Whitten, T. Prout & R. Gill. 1972. Chromosome rearrangements for the control of insect pests. *Science* 176:875–880.

Gaffney, P. M. & S. K. Allen Jr. 1991. Hybridization in *Crassostrea:* a critical review. *Journal of Shellfish Research* 10:303. (Abstract).

Galtsoff, P. S. & R. O. Smith. 1932. Stimulation of spawning and cross-fertilization between American and Japanese oysters. *Science* 76:371–372.

Haven, D. S., W. J. Hargis Jr. & P. O. Kendall. 1978. The Oyster Industry of Virginia: Its Status, Problems and Promise. Virginia Institute of Marine Science, Gloucester Point, Virginia. (VIMS Special Papers in Marine Science No. 4).

Hickey, J. M. 1979. Culture of the Pacific oyster, *Crassostrea gigas*, in Massachusetts waters. Pages 129–148 *in* R. Mann, editor. Exotic Species in Mariculture. MIT Press, Cambridge.

Levin, D. A., editor. 1979. Hybridization An Evolutionary Perspective. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania. (Benchmark Papers in Genetics, Volume 11.)

Mallet, A. L. & L. E. Haley. 1983. Growth rate and survival in pure population matings and crosses of the oyster *Crassostrea virginica*. *Canadian Journal of Fisheries and Aquatic Sciences* 40:948–954.

———. 1984. General and specific combining abilities of larval and juvenile growth and viability estimated from natural oyster populations. *Marine Biology* 81:53–59.

Mann, R. 1983. The role of introduced bivalve mollusc species in mariculture. *Journal of the World Mariculture Society* 14:546–559.

Mayr, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge.

Menzel, W. 1987. Hybridization of oysters and clams. Pages 47–59 *in* K. Tiews, editor. Selection, Hybridization, and Genetic Engineering in Aquaculture. Volume 2. Heenemann, Berlin.

Moav, R., T. Brody & G. Hulata. 1978. Genetic improvement of wild fish populations. *Science* 201:1090–1094.

Newkirk, G. 1978. Interaction of genotype and salinity in larvae of the oyster *Crassostrea virginica*. *Marine Biology* 48:227–234.

Quayle, D. B. 1964. Distribution of introduced marine Mollusca in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 21:1155–1181.

Templeton, A. R. 1989. The meaning of species and speciation: a genetic perspective. Pages 3–27 *in* D. Otte and J. A. Endler, editors. Speciation and Its Consequences. Sinauer Associates, Inc., Sunderland, Massachusetts.

Avoiding the Transmission of Disease in Commercial Culture of Molluscs, with Special Reference to *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX)

Susan E. Ford

ABSTRACT Epizootic mortalities of oysters in the United States and Europe over the last several decades have stimulated a great deal of concern over the potential spread of disease-causing agents by introduction or transfer of molluscs in commerce. Whereas there is good evidence for the spread of some pathogens in this manner, especially those that are demonstrably contagious, evidence for others is purely circumstantial. When making decisions concerning shipments of stocks, shellfish regulators, managers, biologists, and industry members must critically evaluate such evidence, and add to it all other available information about the disease and its causative agent. Rational decision-making should consider biological information on life cycles and transmission of the pathogens, their distribution patterns in enzootic waters, environmental limits to their spread or survival, and a knowledge of the history of the animals to be shipped. In the United States, two major oyster pathogens, exhibiting distinctly different biological characteristics, are used to illustrate problems and to provide advice, concerning potential transfer of disease agents. *Perkinsus marinus*, cause of Dermo disease, is a highly contagious pathogen with a documented history of spread through movement of oysters. Until 1990, it had not become epizootic in northern estuaries (Delaware Bay and north) despite repeated large scale introductions from southern areas (Chesapeake Bay and south). Coincident with abnormally high winter temperatures from 1990 through 1992, *P. marinus* was reported as far north as Cape Cod, and caused an epizootic in Delaware Bay, underscoring the probable influence of temperature in control of this parasite. *Haplosporidium nelsoni*, cause of MSX disease, has not been demonstrated to be contagious and oysters can become parasitized in the absence of nearby infected oysters. Its spread has not been convincingly linked to transfers of oysters. Decision-makers are urged not to dwell solely on the "unknowns" in molluscan disease situations, but to make full use of what *is* known about the diseases, their causes and controls.

KEY WORDS: disease, introduction, mollusc, oyster, *Haplosporidium nelsoni*, *Perkinsus marinus*

INTRODUCTION

The documented, suspected, and potential transfers of disease-causing organisms in transplantations and introductions of commercially valuable molluscs have received considerable attention over the past two decades (Mann 1979, Rosenfield and Kern 1979, Andrews 1980, Elston et al. 1986). Since the middle of the twentieth century, concern over possible introduction of disease has been stimulated by epizootic mortalities associated with previously undescribed pathogens in several species of oysters on the east coast of the United States and in western Europe (Andrews 1980).

In response to these and other disease problems in marine species, the Working Group on Disease of the International Council for the Exploration of the Seas (ICES) established criteria for the introduction of exotic species, which are designed to limit the spread of disease (Sindermann and Lightner 1988). The guidelines specify that broodstock must be quarantined prior to and during spawning, and subsequently destroyed. First generation progeny can be transplanted to the natural environment if no diseases or parasites become evident in quarantine. When an introduced or transferred species is part of current commercial practice, ICES recommends periodic inspection of material (including microscopic examination) by the receiving country prior to mass transplantation. Each shipment must be inspected upon arrival and quarantined or disinfected whenever possible or appropriate. Importation must be immediately discontinued if inspection reveals any introducible pests or diseases.

In the United States, several conferences have considered the overall problems surrounding the introduction of exotic species and the movements of shellfish in commerce, and have attempted to standardize regulations of the various states affected. Austin Farley and Fredrick Kern of the U.S. National Marine Fisheries Service have proposed the establishment of shellfish management zones and embargo areas based on the known distribution of infectious diseases, parasites, predators, pests, and competitors (Proceedings of a Shellfish Relocation Conference, Marine Biological Laboratory, Woods Hole, MA. February 3–4, 1982). Movement of species between zones would require approval by a "controlling authority" and transfers between embargoed areas would, in addition, be permitted only after thorough assessment of the proposed transfer, including a review of the biology of the species and associated organisms, and compliance with the ICES recommendations, including inspection by a certified laboratory.

Despite efforts to establish uniform regulations for the transfer of native species, shellfish are commonly shipped between areas of the United States without concern for potential disease transfers—as they have been for centuries. In other instances, it may be impractical to follow ICES recommendations because of the expense and time required to provide the needed information. For example, movement of seed stocks from areas of high natural setting to other areas for growth and conditioning, or relays from condemned to clean water, are rarely accompanied by inspection for disease agents. Some states have no regulations and many that do are lax in enforcement. Some shellfish growers are unaware of the potential risks or willfully ignore the rules. Managers and regulators are often caught between the desire to foster shellfish industries that rely on transfer of animals and fear of allowing

Contribution No. 90-10 from the Institute of Marine and Coastal Sciences, Rutgers University.

introduction of a pest or pathogen that could result in catastrophe. They almost always are forced to make decisions with too little information.

A decade ago, Matthiessen (1979) stated that "many decisions made by regulatory authorities relating to the importation of shellfish inevitably will be made on the basis of best guess rather than fact." This statement is true today. Some of the guess work is because we don't completely understand the biology of the parasites and their hosts, but some is because individuals making decisions (whether regulator or industry member) are not aware of what *is* known about them. In this situation, the scientist can be most helpful by evaluating available information as accurately as feasible, by presenting it as clearly as possible, and by taking pains to distinguish between fact and speculation (Bowden 1979, Mann 1979).

Evidence implicating shipments of molluscs in the spread of disease is convincing in some cases. For instance, the spread of *Bonamia ostrea,* a parasite of the flat oyster *Ostrea edulis* (Linnaeus, 1970) (Grizel et al. 1988), can be followed along a documented path tracing introductions of host and parasite from the east coast of the United States to the west coast and then to Europe (Elston et al. 1986, Farley et al. 1988). The linkage, however, is not in itself sufficient evidence. What fortifies this argument is the fact that *B. ostrea* can be transmitted directly from oyster to oyster (Poder et al. 1982).

Much of the evidence for transmission of disease along with movement of molluscs, however, is circumstantial. The outbreak of Malpeque Bay disease of oysters, *Crassostrea virginica* (Gmelin, 1791), in Prince Edward Island in 1914–15 was preceded by transplantation of oysters from New England, which first took place on a large scale just before the mortalities occurred (Needler and Logie 1947). Nevertheless, Fraser (1938) reported that direct inoculation of material from sick to healthy oysters failed to cause disease symptoms, and the disease was unknown in New England, although the oysters there may have been resistant.

Two diseases of oysters appeared in France shortly after the introduction of Pacific oyster, *Crassostrea gigas,* (Thunberg 1793) seed. Gill disease of the Portuguese oyster, *Crassostrea angulata* appeared in late 1966 in an area of southwestern France where *C. gigas* had been introduced at approximately the same time (Grizel and Héral 1991). The disease, caused by a virus, almost completely destroyed *C. angulata* culture in France. Aber disease, caused by the protozoan *Marteilia refringens* (Alderman 1979, Balouet 1979), appeared in Brittany in 1968, in an area where Pacific oysters were being held, and subsequently caused extensive losses of the flat oyster, *Ostrea edulis* (Andrews 1980). *Marteilia* sp. has been found occasionally in *C. gigas,* (Cahour 1979), but experimental transmission (between or within the two oyster species), has never been successful (Balouet et al. 1979, Figueras and Montes 1988).

Two important protozoan parasites of oysters have been responsible for catastrophic mortalities of *C. virginica* on the Gulf and East Coasts of the United States over the past forty to fifty years. The recognition of *Perkinsus marinus* (Mackin, Owen, Collier 1950) as the cause of Dermo disease in southern estuaries and *Haplosporidium nelsoni* (Haskin, Stauber, Mackin 1966) as the cause of MSX disease in the mid-Atlantic estuaries has spurred most of the concern over the spread of shellfish disease in the United States. Many of the greatest worries of industry members, state regulatory officials, and biologists in the United States center on the very real and immediate problems caused by these two pathogens. To illustrate some problems commonly faced by these individuals, I'd like to cite some specific concerns about potential spread and control of MSX and Dermo diseases. The questions are of immediate practical importance and they illustrate what we do and do not know concerning these diseases as they impact movement of the shellfish:

1. What is the evidence for introduction of *Perkinsus marinus* and *Haplosporidium nelsoni* by oyster transport?
2. Can the pathogens be transmitted in hatchery-produced larvae or small seed?
3. Can the pathogens be spread through overboard disposal of contaminated meats, shells, or other wastes by processors, dealers, restaurants, or consumers?
4. Can the pathogens be transmitted to and from other species?
5. Are there methods for treating small lots of oysters (broodstock, larvae, small seed) to eliminate pathogens?

EXAMPLES

1. What is the Evidence for Introduction of Perkinsus marinus and Haplosporidium nelsoni by Oyster Transport?

One of the well-documented, but unpublished, instances of transmission of a disease-causing organism affecting molluscs occurred in the early and mid 1950s in Delaware Bay. Because the supply of native seed was low during this period, many Delaware Bay planters bought "seed" oysters from private leases in the Hampton Roads area and other higher salinity regions of Chesapeake Bay where *P. marinus* was present and causing heavy losses (Andrews 1988). Infected oysters were brought by the shipload for planting in Delaware Bay (H. Haskin, Haskin Shellfish Research Laboratory, personal communication, 1989).

A survey conducted by Rutgers University in 1955 and 1956 found evidence that the disease had spread from the imported to native oysters (Christensen 1956). The highest prevalences of *P. marinus* were in the oysters brought from Virginia and in the native oysters growing close to them. Prevalences were negligible on the seed beds and on the eastern edge of the planting grounds. Prevalences and intensities of infection were low compared to those in fully epizootic areas of Virginia and the Gulf of Mexico (Andrews and Hewatt 1957, Mackin 1962) and there were no reports of heavy mortalities in Delaware Bay (Christensen 1956).

Although the proximity of imported oysters to infected native oysters was highly suggestive of transmission, lack of monitoring for the period before introduction precluded a clear assessment of the origin of *P. marinus* in native stocks. Within two years of this survey (spring 1957), however, the epizootic caused by *H. nelsoni* (MSX) had begun (Haskin et al. 1966) and all imports and exports into and out of Delaware Bay were embargoed. Intensive monitoring in 1958 and 1959 to determine the cause of the epizootic failed to show significant presence of *P. marinus* (unpublished records of this laboratory).

We interpreted these observations as evidence that *P. marinus* was introduced into Delaware Bay and sustained by importations of infected oysters from lower Chesapeake Bay, but was unable to maintain itself once that source was stopped (Ford and Haskin 1982). Andrews (1988) pointed out that *P. marinus* also disappeared from major planting areas in the lower Chesapeake after the MSX epizootic of 1959–1960 killed most of the oysters there. The

same occurrence in Delaware Bay between 1957 and 1959 undoubtedly contributed to the elimination of *P. marinus* in that estuary, but in contrast to Chesapeake Bay, *P. marinus* never reappeared to cause problems in Delaware Bay, even after intensive plantings of native seed resumed in the late 1960s and 1970s (Haskin and Ford 1983). Rather, low temperature was considered to be the controlling factor in the failure of *P. marinus* to persist in Delaware Bay or to become epizootic north of Chesapeake Bay (Christensen 1956, Andrews and Hewatt 1957).

In the summer of 1990, *P. marinus* was found in oysters at a number of sites in Delaware Bay (Ford, unpublished) where it caused localized epizootics. In 1991, the disease intensified causing severe mortalities over much of the New Jersey portion of the Bay. Coincidentally, temperatures in the Delaware Bay area during 1990 and 1991 were among the highest on record (U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Climatological Data for New Jersey). The 1990–91 epizootic was not linked with large-scale transplants of infected oysters and, in fact, an apparent focus of infection appeared on the New Jersey seed beds where oysters would never have been introduced. At the same time, infected oysters were found at several locations on the Atlantic coast of New Jersey, including Raritan and Manasquan Bays (W. J. Canzonier, Maurice River Oyster Culture Foundation, personal communication) where oyster industries have not existed for many years. Our current interpretation of these data is that pre-existing non-lethal infections in a few native oysters, or introductions by transient ships or overboard disposal (see below), were stimulated to proliferate and spread by unusually warm temperatures. It is significant that the previous incursion of *P. marinus* into Delaware Bay in the 1950s, which occurred during a more typical temperature regime, never caused epizootic mortalities and disappeared after importation of infected seed was stopped. We expect that a return to more normal temperatures will attenuate the cycle of parasite proliferation, host death (releasing infective forms), and reinfection of new hosts, but its effective disappearance (not causing mortalities or being detectable through routine sampling) will probably require unusually low temperatures. It is not yet clear, however, whether the critical controlling temperatures occur in the winter or summer, or both (Ford and Tripp 1992).

It is much more difficult to evaluate evidence of possible introduction of MSX disease because the complete life cycle and means of transmission of its etiologic agent, *Haplosporidium nelsoni*, are not known. Nevertheless, there is information available of use to those making decisions about possible introduction of this disease into non endemic areas.

After the first outbreaks of MSX disease in Delaware and Chesapeake Bays in the late 1950s, considerable effort was put into elucidating the life cycle of *H. nelsoni* and in trying to transmit the parasite experimentally. None of these experiments resulted in transmission, but most of them have involved the plasmodial stage of the parasite (Canzonier 1968, 1974). Few have used the spore stage (Andrews 1979), which is most likely involved in transmission, but which has been reported only rarely in oysters. Most researchers have concluded that another host may be involved in the life cycle (Farley 1965, Andrews 1968, Ford and Haskin 1982, Haskin and Andrews 1988). Recently, Barber et al. (1991) have found that sporulation may occur regularly in spat (oysters under a year of age) if infections reach the advanced stage. Andrews (1979) also reported heavy spore production in a single group of spat in Virginia in 1976. These observations have led us to consider the possibility that direct transmission from oyster to oyster may indeed occur, with the source of infective stages being very young oysters in which spores are produced.

For several years before the first MSX epizootic in 1975, Delaware Bay planters had been importing large quantities of seed oysters from the seaside bays on the eastern shore of Virginia (N. Jeffries Sr., personal communication), as well as from the lower Chesapeake. When the first oyster disease survey was initiated in that region in mid-1959, *H. nelsoni* was found, although a newly discovered, related species, *H. costale* (Woods and Andrews 1962) (cause of SSO disease), was more prevalent in these high salinity waters (Andrews et al. 1962, H. Haskin, personal communication). Andrews (1968) speculated that a new and virulent "race" of *H. nelsoni* may have developed by "interbreeding" of *H. costale* and *H. nelsoni* when the imported oysters were moved into the lower salinity waters of Delaware Bay. A simpler hypothesis also presupposes that *H. nelsoni* was enzootic to the seaside of Virginia, but was masked by the better adapted (to high salinity) *H. costale*. If spores of *H. nelsoni* were present in the huge numbers of young, rapidly growing oysters moved into the Delaware Bay, then they, rather than a hybrid strain, might have initiated the epizootic once *H. nelsoni* was in a more favorable salinity.

Outbreaks of MSX disease in at least two areas on Cape Cod have followed importation of seed oysters from areas where *H. nelsoni* was present (Krantz et al. 1972, Haskin and Andrews 1988), but it is equally significant that other outbreaks have occurred in the absence of any known importations. Notable among these was the initial epizootic in Chesapeake Bay in 1959, which occurred in the midst of "native [James River] transplants no different from beds in surrounding areas [which did not experience mortalities]" (Andrews 1968). Seed oysters were not moved into this area from seaside bays (J. D. Andrews, Virginia Institute of Marine Science, personal communication). Mortalities caused in 1983–85 by MSX in Oyster Bay, Long Island, a location totally controlled by one company, were not associated with imports (D. Relyea, F. M. Flower and Son Oyster Co., personal communication to H. Haskin) nor were outbreaks in North Carolina in 1988 (M. Marshall, North Carolina Division of Marine Fisheries, personal communication, 1989). Also relevant is that grounds on the Delaware side of Delaware Bay, heavily planted with Chincoteague Bay seed between 1953 and 1957, did not experience losses due to MSX disease until the spring of 1958, a full year after epizootic mortalities had begun on the New Jersey side (N. Jeffries, Sr., personal communication, 1989).

The link between movement of infected oysters and outbreaks of MSX disease is thus quite tenuous compared to that for *P. marinus*. In addition to its introduction into Delaware Bay in the 1950s, the latter has been spread around Chesapeake Bay by transplants of infected seed (E. Burreson, personal communication in (Andrews 1988)). In contrast, there are as many examples of *H. nelsoni* appearing in areas with no known history of introductions or transfers as there are cases with connections, although many undocumented transfers of oysters are undoubtedly made.

2. Can the Pathogens be Transmitted in Hatchery-produced Larvae or Small Seed?

The ICES measures designed to reduce risk of disease introduction involve the quarantine of broodstock. A recent report sug-

gested that a parasite of bay scallops, *Argopecten irradians*, which was identified as *P. karlssoni* and was reported to occur in scallop eggs, might undergo vertical transmission (McGladdery et al. 1991). *Perkinsus marinus* has never been reported to occur in oyster eggs, although it does survive intracellularly in hemocytes. Greater concern exists that larvae could become infected by the adults during spawning in a hatchery. Although there is no absolute reason that larvae could not become infected by *P. marinus* in this manner, it has never been reported and there are a number of biological reasons why it is unlikely. The presumed site of infection by *P. marinus* is the digestive tract (Mackin 1951) and the spawning stock would normally be removed from contact with the embryos long before the latter developed into veligers (18–24 hr) with the capacity to feed. If viable infective particles were discharged during spawning and survived in sufficient numbers until the larvae were capable of ingesting them, the larvae theoretically could become infected. There is, however, no reason to believe that lightly infected oysters would discharge *P. marinus* cells during spawning, and heavily infected individuals will not spawn because they do not produce gametes (Mackin 1962). Thus, the chances of larval contamination, although possible, are extremely slight. Hatchery operators could minimize the possibility by thoroughly cleaning the shells of parent stock, including placing the oysters in dilute (0.3%) hypochlorite solution for 15–20 minutes to kill epibionts that might harbor *P. marinus* cells and removing parent oysters from spawning containers as soon as they have spawned. As a further safeguard, broodstock could be screened for systemic *P. marinus* by non-destructive blood diagnosis (A. Farley, Oxford Cooperative Laboratory, personal communication 1989; Gauthier and Fisher 1990) before selecting spawners.

Because of the life cycle and transmission considerations already discussed, there is no danger that larvae could acquire *H. nelsoni* from infected broodstock. The parasite has never been observed in eggs and, as a matter of fact, is typically extracellular. Spat, which might be carrying spores capable of producing infective stages, are hardly likely to be chosen as broodstock, and oyster-to-oyster infection does not occur from plasmodia. As with *P. marinus*, cleaning of shells (to remove potential alternate or intermediate hosts) and screening for the presence of systemic *H. nelsoni*, would be added safety measures.

Juvenile oysters (spat) can become infected with either pathogen, but because they "pump" much smaller volumes of water than do adult oysters, their chances of encountering either of these water-borne parasites is considerably reduced. If the juveniles are maintained in an on-shore nursery where water flow is restricted compared to the field, their chances of becoming infected would be further reduced. The potential for seed being infected is thus a combination of their size, the length of time they have been "exposed," and the concentration of infective particles in the water surrounding them. We cannot presently measure the abundance of either pathogen in water samples, but inferences as to relative abundance can be made based on the history of infections in the immediate area.

3. Can the Pathogens be Spread through Overboard Disposal of Contaminated Meats, Shells, or Other Wastes by Processors, Dealers, Restaurants, or Consumers?

There is no conclusive evidence of which I am aware that any molluscan disease-causing organism has been transmitted through shucking wastes or shell transplants; however, Andrews (1980) cites a case involving the presumed introduction of a sacculinid parasite (*Loxothylacus panopaei*) into Chesapeake Bay. This parasite, which devastated two species of mud crab in the mid 1960s, may have been introduced in shipments of oysters from the Gulf of Mexico brought "to Virginia for shucking at waterside plants where shells and wastes were discarded near native oyster beds."

We do know that *P. marinus* can be very easily transmitted in a laboratory simply by water splashing from a tank holding infected animals (W. J. Canzonier, personal communication, 1989) and that any stage is infective (Andrews 1988). We also know that oysters with high levels of *P. marinus* appear glassy and emaciated, and might well be discarded (overboard) by shuckers, as would infected gapers (dead oysters). On the other hand, injection experiments with measured numbers of *P. marinus* cells indicate that a threshold inoculum is required to initiate infection and cause mortality (Mackin 1962). In the laboratory, a relatively small number of infective cells may initiate an epizootic because of the limited volume of water and the high density of oysters involved making the chance that each infective particle will come into contact with an oyster very high. If wastes are disposed of in an areas with restricted circulation where oysters are present nearby (within several hundred yards) in relatively large numbers, the chance of transmission is high. That possibility would be reduced if infective stages from wastes were diluted before they contact a host, either because of flushing patterns or distances of oysters from the disposal site. Andrews (1988) found that isolation of oysters by as little as 15 m substantially delayed the transmission of *P. marinus*, although transmission over longer distances is possible.

Between 1986 and 1989, when local oysters were scarce, several shucking plants bordering the Maurice River, a New Jersey tributary of Delaware Bay, processed oysters from the Gulf of Mexico and the Chesapeake Bay, where *P. marinus* was enzootic. During the initial stages of the 1990 epizootic in Delaware Bay, very high prevalences of *P. marinus* were found in oysters growing in the river adjacent to the shucking houses. We do not think that *P. marinus* was necessarily re-introduced into Delaware Bay by this means because of other apparent infection foci in the Bay and along the New Jersey Atlantic coast (see above), but the intensity of the early outbreak near the shucking houses suggests that a combination of waste disposal and suitable temperature may have stimulated a localized epizootic in the river.

The proximity of processing plants to oyster populations and the characteristics of the water into which they are discharging wastes should be considered in assessing the potential for transmission of *P. marinus* in this manner, but because of the extremely contagious nature of this disease, processors should be encouraged not to dispose of fresh shucking wastes overboard in non-enzootic areas if oyster populations exist nearby. Additionally, appropriate means for treating *P. marinus*-contaminated wastes should be investigated (Goggin et al. 1990).

Transmission of *P. marinus* via the movement of shells from shucked infected oysters is less likely, but probably not impossible. Andrews and Hewatt (1957) reported survival of *P. marinus* (i.e., it could be cultured in fluid thioglycollate) after infected tissues had been frozen or dried, although the authors did not attempt transmission with material that had been subjected to freezing or drying. Also to be considered is the possibility that carriers such as the parasitic snail *Boonea impressa* (White et al. 1987), crabs, oyster drills, polychaetes, etc. (Table 1) might survive for extended periods in the interior of shell piles, particularly during cool weather, and infect oysters when reintroduced into the

TABLE 1.

Organisms in which *Perkinsus marinus*, or *Perkinsus*-like cells culturable in fluid thioglycollate, have been identified.

Transmission to Oysters Demonstrated	Cells Found in/on Scavengers	Perkinsus-Like Cells in Bivalves
Boonea impressa[W]	*Opsanus tau*[H]	*Mercenaria mercenaria*[A]
Gobiosoma bosci[H]	*Chasmodes bosquianus*[H]	*Macoma balthica*[A]
Ostrea lurida[(U)R]	*Urosalpinx cinerea*[H,C]	*M. phenax*[A]
	Neopanope texana[H]	*M. tenta*[A]
	Rhithropanopeus harrisii[H]	*Tagelus plebeius*[A]
	Nereid worms[C]	*Mya arenaria*[A]
		Mulinia lateralis[A]
		Anomia simplex[A]
		Anadara transversa[A]
		Laevicardium mortoni[A]
		Ensis minor[A]
		Lyonsia hyalina[A]
		Ostrea frons[R]
		O. equestris[R]
		Crepidula fornicata[R]
		Argopecten irradians[R,M]

[A] (Andrews 1955)
[C] (Christensen 1956)
[H] (Hoese 1963)
[M] (McGladdery et al. 1991)
[R] (Ray 1954)
[(U)R] (Ray 1954)
[W] (White et al. 1987)

water. It is unlikely that more than a few organism would survive for long in this environment and, further, Andrews (1988) considers that scavengers do not carry sufficient infective stages of *P. marinus* to make "major contribution to the high dosage necessary to produce infections."

The concerns discussed above apply also to overboard disposal of infected oysters, or their remains, by restaurants, seafood markets, or consumers. Such disposal is practically impossible to prevent except by education, but is likely to introduce only a small amount of infective material.

Transmission of *H. nelsoni* by this means is far less likely than for *P. marinus*. As mentioned already, *H. nelsoni* has proved impossible to transmit in the laboratory, whereas special care must be taken to prevent contamination by *P. marinus*. We are confident that plasmodial stages of *H. nelsoni*, even when injected or transplanted into recipient oysters, cannot initiate infections (Canzonier 1968, 1974; Ford unpublished). Thus overboard disposal of whole animals or tissues infected with only this stage (which is by far the most common form in oysters) could not be a source of infective stages for oysters. The fact that most processors, distributors, and consumers would not be dealing with spat minimizes the potential for distributing spore stages from young oysters; on the other hand, shuckers would not open spat on shells of market-sized oysters and they might be discarded overboard.

4. Can the Pathogens be Transmitted to and from Other Species

Perkinsus-like organisms (i.e., those that culture in fluid thioglycollate) have been found in many North American species other than oysters (Table 1). Some of these species, like the gastropod *Boonea impressa*, carry *P. marinus* that can infect oysters (Hoese 1963, White et al. 1987). Most, however, appear to carry related, but not identical, organisms. Ray (1954) and Andrews (1955) reported finding them in many species, but always in very low abundance. Attempts at cross-species transmission between oysters and *Mercenaria mercenaria* (Linnaeus, 1758) *Macoma balthica* (Linnaeus, 1758), and *Mya arenaria* (Linnaeus, 1758), by direct inoculation or feeding, failed in nearly all cases (Ray 1954, Andrews and Hewatt 1957). The same techniques easily transmit the parasite between oysters. Apparent invasion of *M. mercenaria* tissues did occur at the site of injection, but no parasites spread from there. Several *M. arenaria* did become infected when injected with material from infected oysters (Ray 1954). Presently available evidence indicates that the chances are remote of transmitting the oyster parasite by moving other commercially important bivalves, such as clams, in which thioglycollate-culturable organisms have been found.

Although *H. nelsoni* has never been found in any species other than the eastern oyster, members of the family Haplosporidiidae parasitize a variety of marine invertebrates. Until the complete life cycle of *H. nelsoni* is known, the possibility that the pathogen exists in, and is spread by, another host must be considered very real.

5. Are There Methods for Treating Small Lots of Oysters (Broodstock, Larvae, Small Seed) to Eliminate Pathogens?

Both *P. marinus* and *H. nelsoni* are found primarily in the higher salinity portions of estuaries, where salinities are between 15 and 30 parts per thousand (ppt). At temperatures of 20°C or more it has been shown that *H. nelsoni* can be eliminated from infected oysters if they are submerged for two weeks at salinities below 10 ppt (Ford 1985). The use of low-salinity immersion to clear *H. nelsoni* infections from broodstock or seed would appear to be a very inexpensive and practical means for reducing the risk of transmitting this parasite through aquacultural practices. Additional research is needed, however, to pinpoint the exact time-temperature-salinity requirements needed to assure complete elimination of the parasite.

P. marinus cannot be cleared under similar conditions as it is much more tolerant of low salinity than is *H. nelsoni* (Andrews and Ray 1988). There are currently no anti-protozoal agents known to be effective and practical in ridding oysters of *P. marinus*. Ray (1966) demonstrated that exposure of infected oysters to cycloheximide reduced disease levels, but when the "treatment" was stopped, even after 164 days, the parasite recovered and again started causing deaths.

SUMMARY AND RECOMMENDATIONS

Catastrophic losses caused by oyster pathogens over the last several decades have justifiably frightened persons concerned with shellfish transfers. In attempting to prevent the spread of disease, most individuals, particularly regulators, are extremely conservative. While caution is appropriate, over-reactions, sometimes approaching paranoia, can result if those responsible are ignorant of, or are reluctant to emphasize, biological knowledge in their decision-making.

It is not sufficient to conclude that a disease agent has been introduced through transfer of the host species simply because it has been newly discovered in a particular location (or something resembling a known pathogen has been found in tissue sections or culture media). Even when mortalities associated with a parasite

occur suddenly after transfer of host species, there may be alternate explanations. For instance, review of the vast numbers of species moved about the world in ballast water or on the bottom of ships (Carleton, this volume?) suggests that some potential introductions may be well out of the immediate control of shellfish regulators! A good example is the recent finding of *P. marinus* in native oysters in Raritan Bay (see above). Because of water pollution, an oyster industry has not existed for more than half a century (H. Haskin, personal communication, 1989) and it is difficult to believe that oysters would have been imported into this area by commercial shellfish growers, but there is heavy boat traffic through the area.

Alternatively, a parasite may have existed in limited numbers, and gone undetected, in areas where environmental or culture conditions prevented its development to epizootic proportions. If those conditions change, even temporarily, the parasite may multiply to a critical threshold that results in an epizootic. Further, parasites, like their hosts, experience unexplained long-term natural cycles in abundance. A host species may be harvested for the first time when it is at peak abundance, at which time the abundance cycle of a major pest or parasite is at an ebb. Later, when the pest or parasite becomes abundant enough to detect (usually when it causes mortalities), it may be considered "new."

In addition to a critical evaluation of these kinds of observations, rational decision making will take into account all available information on the diseases and their etiological agents. These include:

1. What is known of the life cycle and method of transmission of disease agents? For instance, it would be unwise to introduce animals from areas known enzootic for contagious pathogens such as *Perkinsus marinus* or *Bonamia ostrea*. There is somewhat less cause for concern in the case of agents that are not contagious (i.e., host species do not require proximity to infected individuals of the same species to become infected) such as *Haplosporidium nelsoni* and *Marteilia refringens*. In cases where direct transmission has not been demonstrated, much greater attention should be paid to possible introductions of other hosts in shipments of wild seed. Our recent findings concerning spores of *H. nelsoni* in oyster spat do, however, dictate caution in transferring young oysters (which are precisely the ones most likely to be shipped) from regions where MSX disease is enzootic.
2. What information is available about the distribution of the disease agents in known enzootic water? For instance, *H. nelsoni* is distributed fairly evenly over wide areas and can move miles up estuary during a drought (without concurrent transplant of oysters). It thus makes little sense to ban movement of oysters within an estuary, or even between subunits of the same general water system, to prevent the spread of *H. nelsoni* in an area where it already exists. The presumed infective stage of this parasite is a spore, which may last for years outside the host and be transported great distances in the water or in vectors. In contrast, *P. marinus* may take several years to move naturally from one location in an estuary to another. For instance, certain regions of Delaware Bay remain free of the disease. If the disease persists, experience from other areas indicates that it will eventually spread to all oyster-growing areas of the lower estuary, but moving infected oysters would only hasten this process and might introduce it to areas that would remain disease free until the return of more normal temperatures, which should inhibit its further spread.
3. What is known about environmental constraints, especially salinity and temperature? Is it likely that the pathogen could survive and/or cause damage in the new environment? *Perkinsus marinus* was introduced in tremendous quantities into Delaware Bay over several years, yet failed to cause serious problems at the time and effectively disappeared after importation of diseased oysters ceased. Historically, southern oysters, presumably carrying the same pathogen, were repeatedly shipped to New England without introducing detectable levels of *P. marinus* (Andrews 1988). It is probable that low temperature prevented the development and spread of the parasite in these areas, but some low-level parasitism may have persisted over many years and provided a source of infective material that caused the recent outbreaks in New Jersey when environmental temperatures became favorable for the parasite. A similar origin can be argued for the *P. marinus* recently found in several Cape Cod estuaries (E. J. Lewis, Oxford Cooperative Laboratory, personal communication, 1991) where it was previously undetected and where there are stringent prohibitions against introductions of southern oysters.
4. What is known about the history of the animals to be moved and the area from which they originate? Histological examination is often a prerequisite to such shipments, and is reasonable, but it should be clearly understood that **it is impossible to "certify" them as being "disease or pathogen free."** A "negative" rating simply means that in that particular sample of animals collected at a certain place and time, and in the subsample of tissues examined, no recognizable pathogens were found by the diagnostic method(s) used. Subpatent infections are common in certain seasons and in resistant or tolerant animals. Thus, it is critical that the histological examination be accompanied by a background profile of the animals to be shipped.

Clearly, indiscriminate shipment of molluscs, particularly large quantities of wild stocks, is unwise if not downright foolish. Long distance shipment of commercial species is currently more likely to be to or from a hatchery than from the wild, so that ICES guidelines can be followed to a much greater extent than previously. Further, the costs of hatchery produced seed and the relatively large investment in the shellfish as they are grown under intensive culture makes the aquaculturist much more wary of possible disease problems than were earlier planters who had vast reserves of plentiful and cheap natural seed.

Even after taking into account all possible known factors, we will still be faced with unanticipated or unknown elements that could confound our best judgement. Yet, we should avoid making decisions based solely on what might conceivably happen if our worst fears come true. Rather, we should decide using the best available information, while assessing potential risks and benefits. Above all, we should dwell less on the "unknowns," and make more rational and complete use of what we do know.

ACKNOWLEDGMENTS

I thank H. H. Haskin and W. J. Canzonier for reviewing the manuscript. The unpublished data cited herein, including those in the manuscript by Greta Christensen, were collected under grants to H. H. Haskin from the New Jersey Department of Environmental Protection and the U.S. National Marine Fisheries Service, and their predecessors. This is New Jersey Agricultural Experiment Station Publication No. F-32405-1-90, supported by state funds.

LITERATURE CITED

Alderman, D. J. 1979. Epizootiology of *Marteilia refringens* in Europe. *Mar. Fish. Rev.* 41(1–2):67–69.

Andrews, J. D. 1955. Notes on fungus parasites of bivalve mollusks in Chesapeake Bay. *Proc. Natl. Shellfish. Assoc.* 45:157–163.

Andrews, J. D. 1968. Oyster mortality studies in Virginia. VII. Review of epizootiology and origin of *Minchinia nelsoni*. *Proc. Natl. Shellfish. Assoc.* 58:23–36.

Andrews, J. D. 1979. Oyster diseases in Chesapeake Bay. *Mar. Fish. Rev.* 41(1–2):45–53.

Andrews, J. D. 1980. A review of introductions of exotic oysters and biological planning for new importations. *Mar. Fish. Rev.* 42(12):1–11.

Andrews, J. D. 1988. Epizootiology of the disease caused by the oyster pathogen *Perkinsus marinus* and its effects on the oyster industry. In: W. S. Fisher, (ed). Disease Processes in Marine Bivalve Molluscs, American Fisheries Society, Bethesda, MD. pp. 47–63.

Andrews, J. D. & W. G. Hewatt. 1957. Oyster mortality studies in Virginia II. The fungus disease caused by *Dermocystidium marinum* in oysters of Chesapeake Bay. *Ecolog. Monogr.* 27:1–26.

Andrews, J. D. & S. M. Ray. 1988. Management strategies to control the disease caused by *Perkinsus marinus*. In: W. S. Fisher, (ed). Disease Processes in Marine Bivalve Molluscs, American Fisheries Society, Bethesda, MD. pp. 257–265.

Andrews, J. D., J. L. Wood & H. D. Hoese. 1962. Oyster mortality studies in Virginia III. Epizootiology of a disease caused by *Haplosporidium costale*, Wood and Andrews. *J. Insect Pathol.* 4:327–343.

Balouet, G. 1979. *Marteilia refringens:* Considerations of the life cycle and development of Aber disease in *Ostrea edulis*. *Mar. Fish. Rev.* 41(1–2):105–109.

Balouet, G., C. Chastel, A. Cahour, A. Quillard & M. Poder. 1979. Étude épidémiologique et pathologique de la maladie de l'hûitre plate en Bretagne. *Science et Peche, Bulletin Peches Maritimes* 289:13–25.

Barber, R. D., S. A. Kanaley & S. E. Ford. 1991. Evidence for regular sporulation by *Haplosporidium nelsoni* (MSX) (Ascetospora: Haplosporidiidae) in spat of the American oyster, *Crassostrea virginica*. *J. Protozool.* 38(4):305–306.

Bowden, G. 1979. Law, politics and biology: aquaculture in the primordial ooze. In: R. Mann, (ed). Exotic Species in Mariculture, MIT Press, Cambridge, MA and London, England. pp. 306–330.

Cahour, A. 1979. *Marteilia refringens* and *Crassostrea gigas*. *Mar. Fish. Rev.* 41(1–2):19–20.

Canzonier, W. J. 1968. Present status of attempts to transmit *Minchinia nelsoni* under controlled conditions. *Proc. Natl. Shellfish. Assoc.* 58:1.

Canzonier, W. J. 1974. Tissue grafts in the American oyster, *Crassostrea virginica*. *Proc. Natl. Shellfish. Assoc.* 64:92–101.

Christensen, G. 1956. The occurrence of *Dermocystidium marinum* (Mackin, Owen and Collier) in Delaware Bay. Unpublished manuscript. Haskin Shellfish Research Laboratory, Rutgers University, Port Norris, NJ, USA. 30 p.

Elston, R. A., C. A. Farley & M. L. Kent. 1986. Occurrence and significance of bonamiasis in European flat oysters *Ostrea edulis* in North America. *Dis. Aquat. Org.* 2:49–54.

Farley, C. A. 1965. Acid-fast staining of haplosporidian spores in relation to oyster pathology. *J. Invertebr. Pathol.* 7:144–147.

Farley, C. A., P. H. Wolf & R. A. Elston. 1988. A long term study of "Microcell" Disease in oysters with a description of a new genus—*Mikrocytos* (g.n.) and two new species—*Mikrocytos mackini* (sp. n.) and *Mikrocytos roughleyi* (sp. n.). *Fish. Bull.* 86(3):581–593.

Figueras, A. J. & J. Montes. 1988. Aber disease of edible oysters caused by *Marteilia refringens*. In: W. S. Fisher, (ed). Disease Processes in Marine Bivalve Molluscs, American Fisheries Society, Bethesda, MD. pp. 38–46.

Ford, S. E. 1985. Effects of salinity on survival of the MSX parasite *Haplosporidium nelsoni* (Haskin, Stauber, and Mackin) in oysters. *J. Shellfish Res.* 2:85–90.

Ford, S. E. & H. H. Haskin. 1982. History and epizootiology of *Haplosporidium nelsoni* (MSX), an oyster pathogen, in Delaware Bay, 1957–1980. *J. Invertebr. Pathol.* 40:118–141.

Ford, S. E. & M. R. Tripp. 1993. Diseases and defense mechanisms. In: A. F. Eble, V. S. Kennedy and R. I. E. Newell, (eds). The Eastern Oyster *Crassostrea virginica*. Maryland Sea Grant, (in press).

Fraser, R. 1938. Pathological studies of Malpeque disease. MS Report of the Biological Station. Fisheries Research Board of Canada. 40 p.

Gauthier, J. D. & W. S. Fisher. 1990. Hemolymph assay for diagnosis of *Perkinsus marinus* in oysters *Crassostrea virginica* (Gmelin, 1791). *J. Shellfish Res.* 9(2):367–372.

Goggin, C. L., K. B. Sewell & R. J. G. Lester. 1990. Tolerances of *Perkinsus* spp. (Protozoa, Apicomplexa) to temperature, chlorine and salinity. *J. Shellfish Res.* 9(1):145–148.

Grizel, H. & M. Héral. 1991. Introduction into France of the Japanese oyster (*Crassostrea gigas*). *J. Conseil Int. Expl. Mer* 47:399–403.

Grizel, H., E. Mialhe, D. Chagot, V. Boulo & E. Bachère. 1988. Bonamiasis: a model study of disease in marine molluscs. In: W. S. Fisher, (ed). Disease Processes in Marine Bivalve Molluscs, American Fisheries Society, Bethesda, MD. pp. 1–4.

Haskin, H. H. & J. D. Andrews. 1988. Uncertainties and speculations about the life cycle of the eastern oyster pathogen *Haplosporidium nelsoni* (MSX). In: W. S. Fisher, (ed). Disease Processes in Marine Bivalve Molluscs, American Fisheries Society, Bethesda, MD. pp. 5–22.

Haskin, H. H. & S. E. Ford. 1983. Quantitative effects of MSX disease (*Haplosporidium nelsoni*) on production of the New Jersey oyster beds in Delaware Bay, USA. ICES. CM 1983/Gen:7/Mini-Symp. Goteborg, Sweden. October, 1983. 20 pp.

Haskin, H. H., L. A. Stauber & J. A. Mackin. 1966. *Minchinia nelsoni* n. sp. (Haplosporida, Haplosproidiidae): causative agent of the Delaware Bay oyster epizootic. *Science* 153:1414–1416.

Hoese, H. D. 1963. Studies on oyster scavengers and their relation to the fungus *Dermocystidium marinum*. *Proc. Natl. Shellfish. Assoc.* 53: 161–174.

Krantz, E. L., L. R. Buchanan, C. A. Farley & A. H. Carr. 1972. *Minchinia nelsoni* in oysters from Massachusetts waters. *Proc. Natl. Shellfish. Assoc.* 62:83–88.

Mackin, J. G. 1951. Histopathology of infection of *Crassostrea virginica* (Gmelin) by *Dermocystidium marinum* Mackin, Owen, and Collier. *Bull. Mar. Sci. Gulf Carib.* 1:72–87.

Mackin, J. G. 1962. Oyster diseases caused by *Dermocystidium marinum* and other microorganisms in Louisiana. In: J. G. Mackin and S. H. Hopkins, (eds). Studies on Oysters in Relation to the Oil Industry, *Publications of the Institute of Marine Science* 7:132–299.

Mann, R. 1979. Exotic species in aquaculture: an overview of when, why and how. In: R. Mann, (ed). Exotic Species in Mariculture, MIT Press, Cambridge, MA and London, England. pp. 331–359.

Matthiessen, C. 1979. The oyster industry of Massachusetts and the introduction of exotic species. In: R. Mann, (ed). Exotic Species in Mariculture, MIT Press, Cambridge, MA and London, England. pp. 212–225.

McGladdery, S. E., R. J. Cawthorn & B. C. Bradford. 1991. *Perkinsus karlssoni* n. sp. (Apicomplexa) in bay scallops *Argopecten irradians*. *Dis. Aquat. Org.* 10(2):127–137.

Needler, A. W. H. & R. R. Logie. 1947. Serious mortalities in Prince Edward Island oysters caused by a contagious disease. *Trans. Royal Soc. Can., Ser. III* 4(V):73–89.

Poder, M., A. Cahour & G. Balouet. 1982. Études histologiques et ultrastructurales des lésions de parasitose hémocytaire chez *O. edulis:* contaminations expérimentales. *107e Congrès nat. Soc. sav. Brest, 1982, sciences, fasc. II*:175–186.

Ray, S. M. 1954. Biological studies of *Dermocystidium marinum*, a fungus parasite of oysters. Rice Institute, Houston, TX. 114 pp.

Ray, S.M. 1966. Cycloheximide: Inhibitor of *Dermocystidium marinum* in laboratory stocks of oysters. *Proc. Natl. Shellfish. Assoc.* 56: 31-36.

Rosenfield, A. & F. G. Kern. 1979. Molluscan imports and the potential for introduction of disease organisms. In: R. Mann. (ed). Exotic Species in Mariculture, MIT Press, Cambridge, MA and London, England. pp. 165-191.

Sindermann, C. J. & D. V. Lightner. 1988. Disease diagnosis and control in North American Marine Aquaculture. Elsevier, New York. 431 pp.

White, M. E., E. N. Powell, S. M. Ray & E. A. Wilson. 1987. Host-to-host transmission of *Perkinsus marinus* in oyster *Crassostrea virginica* populations by the ectoparasitic snail *Boonea impressa* (Pyramidellidae). *J. Shellfish Res* 6:1-5.

Wood, J. L. & J. D. Andrews. 1962. *Haplosporidium costale* (Sporozoa) associated with a disease of Virginia oysters. *Sciences* 136:710-711.