A Review of Introductions of Exotic Oysters and Biological Planning for New Importations

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ABSTRACT—Importation and transplantation of exotic oysters has probably resulted in the introduction into new areas of more marine invertebrate species than any other of man's activities. Unintentional introductions have resulted from careless movements of oysters without planning or consideration of consequences. Diseases and parasites of marine invertebrates are poorly known and oysters cannot be adequately diagnosed or inspected for problems by biologists. The vigorous Pacific oyster, Crassostrea gigas, *was introduced to the Atlantic coast of western Europe in the past decade with serious effects on native oyster species. Some scientists propose to introduce it to the Atlantic coast of North America, primarily for culture in New England. If introduction is carried out properly, diseases and parasites may be excluded by breeding selected brood oysters in hatcheries under quarantine conditions. The progeny may then be tested in controlled natural environments for growth rates and reaction to native diseases and parasites. Selection of races, strains, and hybrids may be pursued in hatcheries to fit exotic oysters to new ecosystems. Introduction of an exotic species is a serious irreversible event which merits careful consideration of the reasons for culture of a new shellfish and the consequences to native biota and coastal ecosystems.*

Introduction

Oysters have been transported by mankind since Roman times because they are superbly adapted to withstand long journeys out of water. In this paper, the consequences of man's movement of oysters and the biological requirements for future introductions of oysters are reviewed.

Only one species of oyster, *Crassostrea gigas*, the Pacific oyster, has been introduced as a successful member of coastal communities around the world. In the temperate zone of the Northern Hemisphere only the Atlantic coast of North America does not now depend on this species for oyster production. *Crassostrea gigas* was successfully introduced to western North America, western European, and Australasian coasts. Most introductions began as casual unplanned events that were soon followed by deliberate ones on a larger scale. With the aid of man, the oysters spread on the coasts to the limit of their tolerances of climates and salinities.

Some scientists desire to culture *C. gigas* in New England. A major problem is keeping it confined to New England and away from large oyster fisheries of *C. virginica* to the south. *Crassostrea gigas* is a vigorous, fast-growing oyster that could compete advantageously with the native oyster, and possibly replace it, in the warm waters of Chesapeake Bay and Delaware Bay.

The famous European flat oyster, *Ostrea edulis*, has been tried on both coasts of North America and in Japanese waters with little success as a self-sustaining species. It is frequently grown in hatcheries in North America for experimental plantings. This favorite raw-bar oyster sustains a small industry in Maine by use of hatchery seed from acclimated broodstocks precariously established in Boothbay Harbor, Maine (Welch, 1966).

Extensive transplantation of native oysters along major coasts has long been used to sustain fisheries without regard for adaptations of local races to new environments. Transplantation of flat oysters from one country to another in Europe has a long history. It was instigated primarily because of failure of reproduction in the cold waters of northern countries such as France, Great Britain, the Netherlands, and Denmark (ICES, 1972). Crises such as continent-wide unexplained mortalities in 1920-21 and recent (1967-76) mortalities from diseases also caused extensive importations from the Adriatic Sea and Greece as well as Spain and Portugal. No consideration was given to racial traits of these diverse stocks for adaptation to various local climates (Andrews, 1979b). However, the Netherlands is trying to build up stocks of isolated native oysters which exhibit greater winter hardiness than imported French seed oysters now sustaining the industry (Drinkwaard, 1978). Transplantation between regions on a coast is a short-term marketing expedient that is not expected to contribute to rehabilitation of native stocks. However, it may result in genetic mixing and the spread of pests and diseases.

The impact of exotic marine species on endemic communities is difficult to predict until they are widespread in the new area and irrevocably established. Introductions of marine exotics are more difficult to isolate and to control than terrestrial ones because of rapid dispersion of larvae by currents.

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Inadequate monitoring and limited knowledge of identity, abundance, and distribution of native species may leave exotic species obscured for long periods. Often diseases of marine invertebrates become known only after mass mortalities of the host species (Sindermann, 1976). Seldom can such diseases be proven to be introduced. The strongest circumstantial evidence is that of timing when stocks were transplanted or imported immediately before an epizootic mortality.

Categories of Importations

The transport of endemic oysters of the same species along a coast is defined as transplantation (Mann, 1979). This is not the primary concern of this discussion. After hundreds of years of transplantation the potential for further damage may be minimal. However, care should be exercised in moving endemic oysters from regions of a coast that have been isolated by land barriers, ocean currents, or even temperature differences for many centuries. Exchanges between such areas on a coast carry the same dangers from diseases and pests as from importation of exotic oysters of a different species. Examples of isolated regions in North America include the Gulf of Mexico and the Gulf of St. Lawrence from which transplantings to and from the Middle Atlantic coast have been rare. The Mediterranean Sea and the Atlantic coast of Europe could also be hazardous regions for exchanges of oysters.

Importations of exotic species of oysters that result in establishment of new populations are called introductions to distinguish them from transplantations along a coast. Introductions from one continental coast to another are nearly always through the activities and agencies of man because wide land or ocean barriers preclude natural dispersal. These importations may be deliberate or accidental depending upon the role of man. They can be subdivided into several categories according to the purpose of the importation, agent of dispersal, and stage of the organism utilized (ICES, 1972). For purposes of discussion, casual importations of small lots of oysters without planning, supervision, or subsequent monitoring may be considered accidental. The risks and consequences are the same as for strictly accidental importations, i.e., inadvertent introductions. Most large-scale importations of oysters were preceded by accidental ones on a small scale. These accidental importations may prepare the way sociologically for subsequent large-scale deliberate ones. Imported oysters may exhibit excellent growth and survival while native species are destroyed by exotic diseases associated with the importation. This series of events occurred recently in France following importation of *C. gigas* in 1966 (Marteil, 1976).

Adaptations of Marine Organisms to Oceanic and Continental Climates

Continental air masses crossing large land masses exhibit the rapid heating and cooling attributes of the land with strong warming during summers and prolonged cooling from back-radiation in winters. Coastal waters on the eastern shores of continents share these extremes of atmospheric temperature with cold winter and warm summer temperatures. In contrast, coastal waters on western shores of continents, bathed by moderated oceanic air masses, receive mild weather, therefore, exhibit cool summers and mild winters. Hydroclimographs for estuaries on the eastern coast of North America show annual temperature ranges of 20°C or more inshore, whereas those for the western coast exhibit only about 10°C range (Andrews, 1971). These differences in maximal and minimal mean temperatures affect adaptations for summer breeding and winter survival of endemic species on the respective coasts.

The temperature effects on imported exotic species are most dramatic on maritime coasts which receive ocean-tempered air masses and currents that induce summer upwelling of deep, cold waters. The resulting moderated water temperatures and nutrient enrichment from upwelling ensure rapid growth in a continuous growing season for most organisms. Marine species native to continental-type climates with wide distributions and northern ranges are most likely to establish populations on coasts with oceanic climates. In contrast, organisms acclimated to mild oceanic climates are usually not able to survive either summer or winter extremes in severe climates of continental-type coasts. These adaptations to climates explain in large measure the numerous invasions of exotic species in the temperate zones on the western coasts of continents (Hanna, 1966) whereas introduced species are rare on eastern coasts. Tropical coasts are more easily invaded (Courtenay and Robins, 1973).

In general, *Ostrea* species are adapted to oceanic climates and *Crassostrea* to continental ones, although exceptions occur as waters along a coast become more tropical. Consequently, *Ostrea* species breed at lower summer temperatures (usually <20°C) and are more sensitive to low salinities and low winter temperatures. They will not withstand intertidal exposure to heat or cold. *Ostrea edulis* and *O. lurida* are the endemic species of western Europe and western North America, respectively; *Crassostrea virginica* and *C. gigas* are respective endemic commercial oysters of eastern shores of North America and Asia. These adaptations to respective climates should be considered before irreversible consequences of importations are incurred. Examples of serious alterations of biotic communities by importations of exotic oysters with their associated faunas are found on the maritime coasts of western Europe and western North America (Quayle, 1964; Hanna, 1966; Dundee, 1969; ICES, 1972).

Brief History of Major Introductions of Oysters

Crassostrea angulata From Portugal and Spain to France

Crassostrea angulata, the Portuguese oyster, is known to have thrived in southwestern Portugal and southern Spain for several hundred years (Korringa, 1970). The Sado and Tejo Rivers and the Gulf of Cadiz provide waters warm enough (>20°C) for reproduction of this subtropical oyster. The oysters were little used locally. When the natural public beds of *O. edulis* in southwest France and northern Spain were depleted about 1850, a famous report by Costé (1861) to Napoleon III initiated private culture. With a scarcity of *O. edulis* seed stocks, *C. angulata* was soon imported from Portugal's Sado River to stock private beds. The initial introduction of *C. angulata* to the French coast was attributed to the dumping of a shipload of spoiling oysters in the Gironde River in 1868 (Marteil, 1976). *Crassostrea angulata* proliferated in the Gironde and other areas of southwest France providing seed stocks for a hundred years. Eventually, in the 1960's, it produced five times as many oysters in France as *O. edulis* (Marteil, 1970). Cold summer temperatures prevented the Portuguese oyster from reproducing in Brittany and more northern countries; therefore it was transplanted annually to Great Britain for growth and marketing.

Although *C. angulata* was considered to have a less desirable taste than the European flat oyster, it provided in abundance relatively inexpensive oysters for Europe. It was a useful introduction to supplement production of the more temperature-sensitive *O. edulis* which is slower and more difficult to grow. The Portuguese oyster often sets and grows intertidally which offers cultural advantages of pest control and intensive visual farming at low tides. It is difficult to judge the extent of biological competition in France because *O. edulis* was grown primarily in Brittany and was overfished and depleted in southwest France before *C. angulata* was introduced. The Portuguese oyster certainly replaced the flat oyster in the warm waters of southern France where the latter was native.

Crassostrea gigas From Japan to France (1966)

A small importation of 900 kg of seed of the Pacific oyster was introduced to the Marennes area of France in March 1966 (ICES, 1972). The following fall (November 1966), a new disease was found in the gills of *C. angulata* by Trochon (Marteil, 1969, 1976). The disease spread widely in France and in the fall of 1967 an embargo was placed on further importations from Japan. However, the rapid decline in production of the Portuguese oyster from mortalities caused by the gill disease resulted in a decision to import *C. gigas* in commercial quantities in the early 1970's. In southwestern France, *C. gigas* reproduced prolifically permitting the cessation of commercial importations after 1975.

Another disease appeared in *O. edulis* in Brittany in Aber Wrach in 1968 where some Pacific oysters were being held. Aber Disease, caused by a protozoan, *Marteilia refringens*, caused extensive mortalities of flat oysters in Brittany. *Crassostrea gigas* was not appreciably affected by either of the new diseases. A shell malady of *C. gigas* has affected marketing somewhat (Marteil, 1976). *Crassostrea gigas* has completely replaced *C. angulata* in French waters south of Brittany and it has tended to breed farther north in Brittany and in the Netherlands in warm summers such as 1976 (23°C). Intensive spatfalls through 1976 in southern France reduced the growth rate by crowding.

Crassostrea virginica (1869) and *C. gigas* (1902) to Pacific Coast of North America

The native Olympia oyster, *Ostrea lurida*, of this coast is small, slow-growing, and difficult to culture (Korringa, 1976). Overfishing of natural beds caused depletion of most areas in the last half of the 19th century. A further decline occurred in the mid-1920's despite adoption of European cultural methods of diked parks to protect the cold- and heat-sensitive Olympia oysters from exposure to air temperatures. From 1928 to 1945, pulp-mill wastes were blamed for the decline in southern Puget Sound (McKernan et al., 1949). The species did not recover production appreciably after the pulp-mill was closed. Oyster planters turned their attention to *C. gigas* in the late 1920's. This species grew to marketable size in 2 years from imported Japanese seed whereas the Olympia oyster required about 4 years to attain its maximum size of 2 inches. *Ostrea lurida* did not fulfill the needs of a region with rich waters suitable for extensive oyster culture.

The first importations of the eastern oyster, *C. virginica*, began about 1869 to San Francisco Bay with completion of transcontinental railroads (Hanna, 1966). Shipments of oysters from New England continued to various rail points along the coast until about 1935. Growth was excellent in the early years but failure of reproduction from low summer temperatures required regular importations from the east coast. *Crassostrea virginica* is now rare on the Pacific Coast with one small persistent population in Boundary Bay, B.C. (Bourne, 1979). Importations over a period of 60 years failed to establish the species. The cool California current and accompanying upwelling kept coastal waters too cold for regular reproduction. Nevertheless, California permitted regular importation and planting of market-sized oysters from Long Island for raw-bar trade in the 1960's and 1970's. During this period, risks were high of introduction of new diseases prevalent on the east coast.

Crassostrea gigas has supported a growing industry along wide reaches of the Pacific Coast. The earliest importations were made by oriental residents about 1902 (Kincaid, 1951). Beginning in the late 1920's thousands of cases of spat on shells were shipped from Japan on decks of ships (Quayle, 1964). High prices and competition with air shipments to France greatly reduced Pacific Coast importations from Japan in the early 1970's. Fortunately, the industry has developed its own seed supply over the years. Two areas of regular spatfalls, Pendrell Sound, B.C., and Dabob Bay, Wash., supplement seed supplies for growing areas with irregular or no sets (Quayle, 1969; Bourne, 1979).

Crassostrea gigas From Japan to Australasia (1947-52)

Crassostrea gigas became established in Tasmania about 25 years ago. Five shipments from Japan to Australia were made between 1947 and 1952 (Thomson, 1952, 1959; Bourne, 1979). Three races of Pacific oysters (Miyagi, Kumamoto, and Hiroshima) were shipped as spat on shells and planted at two sites. Oysters planted at Pittwater on the southern shore of Tasmania survived well. Those exposed on the shores of southern West Australia died.

One recent shipment (1970) from Japan concluded the importations (Medcof and Wolf, 1975). Transplantations from Pittwater were made to Pt. Sorell on the northern shore of Tasmania where the species is now firmly established. Relative isolation at Pittwater provided a period for observation of growth and mortalities before native oysters were exposed. Unfortunately, all three races were planted in the same area and the surviving race of acclimated oysters is not known—probably Miyagi or Hiroshima oysters or a mixture.

Scattered individuals of *C. gigas* appeared in New South Wales in the 1970's where an important commercial fishery for *C. commercialis* is pursued (Medcof and Wolf, 1975). Some specimens were found on cultch sticks used to collect native oysters, implying that they were derived from larvae originating in the locality. The Pacific oyster outgrew the native oyster on these sticks suggesting that environmental conditions are favorable for growth. The location and source of brood oysters for spat found in New South Wales are unknown but probably they were derived from small accidental or illegal importations from Tasmania. Dispersal has been slow in Australasia providing opportunities to monitor population increases, and permitting industry adaptations if *C. gigas* replaces the native rock oysters. Four Australian states permit transplantings of *C. gigas* whereas New South Wales, with a valuable fishery based on *C. commercialis*, does not. *Crassostrea gigas* appeared suddenly in New Zealand in 1970 from unknown sources (Dinamani, 1974) and is increasing rapidly in abundance. Further spread of *C. gigas* in temperate zones of Australasia is to be expected.

Introduction of Exotic Invertebrate Species Associated With Oysters

Exotic Invertebrate Species in Western European Waters

The most serious introductions of foreign species accompanied importation of American oysters, *C. virginica*, to Great Britain. Reproduction did not occur in the cold waters, therefore they were relaid in British waters annually from the late 1800's to 1939 for growth and marketing (ICES, 1972). Among the exotic species introduced with oysters from North America was the predatory oyster drill, *Urosalpinx cinerea*, found in England in 1920. It is now well established on the southeastern and southern coasts. A gastropod competitor, *Crepidula fornicata*, which attaches to oysters in chains, exhibited fantastic populations in England on derelict beds called "mud and limpets" after its introduction about 1880 (Orton, 1937). It spread to the continent and is now distributed widely from Sweden to France. It has pelagic larvae but was probably spread mostly by man while attached to mussels and oysters. Other American species probably introduced with oysters, but exhibiting more subtle, noneconomic effects, include the bivalves *Petricola pholadiformis*, *Mya arenaria*, and a mud crab, *Rithropanopeus harrisi*, all now with wide distributions in northern Europe (ICES, 1972).

The introduction of *C. gigas* to France has added some oriental species to the fauna but their eventual status after importations ceased in 1975 remains to be determined (Gruet et al., 1976). The parasitic copepod *Mytilicola orientalis* may be the most destructive species introduced because it attacks both oysters and mussels. *Sargassum muticum*, an asiatic phaeophyte introduced with Pacific oysters, is established on the coasts of France and England (Maurin and LeDantec, 1979). It is spreading and interferes with the commercial species *Chondrus crispus*. Two other algal species have been introduced: *Undaria pinnafida* in the Mediterranean Sea and *Laminaria japonica* on the Atlantic coast of France. Five additional invertebrate species from the Orient have been collected in Brittany, including an annelid, a bivalve mollusk, an anthozoan, and two barnacle species (Gruet et al., 1976). The two oyster pathogens that appeared immediately after the first introductions of *C. gigas* are probably exotics from Japan also. The elimination of the Portuguese oyster from France and the serious reduction of production of the flat oyster are the most dramatic consequences of importation of *C. gigas*.

The importation of tropical *C. rhizophorae*, the mangrove oyster, from French Guyana to France defies explanation. Why this oyster should be expected to survive in the cold waters of the French Atlantic coast is not evident and its use in French oyster culture is obscure. Continued importations present the threat of introducing oyster diseases and parasites of the western Atlantic (Maurin and Gras, 1979).

Exotic Mollusks on the Pacific Coast of North America

A long list of exotic biota introduced from New England and Japan has been compiled by Hanna (1966) and Dundee (1969). The long periods of repeated oyster importations offered many opportunities for establishment of exotic species in this mild oceanic-type climate. Species capable of breeding at temperatures of 20°C or less, or finding warm niches, were successful colonizers. The introduced mollusks exemplify the opportunities provided immigrant species by man's importations. In the early years, no care was exercised in cleaning shipments of oysters from New England or Japan of unwanted aliens. Bonnot found 22 species of marine shells in 20 boxes of Japanese seed in 1930 (Hanna, 1966).

All three commercially important bivalves on the Atlantic coast of North America were imported early to the West Coast. *Mya arenaria*, apparently introduced accidentally with oyster transplantations, was immediately successful because of its adaptation for breeding at low temperatures. It is now distributed from Alaska to San Diego. The American oyster, *C. virginica*, and the hard clam, *Mercenaria mercenaria*, did not reproduce successfully which necessitated continued importations to produce crops. Both species can be grown commercially on the West Coast using hatchery seed.

Several western Atlantic mollusks closely associated with oysters for food or substrate achieved distributions on the West Coast in localized niches where oysters are grown. The oyster predator, *Urosalpinx cinerea*, is often found on oyster beds but not in all areas where salinities are favorable. All three species of *Crepidula* (*C. fornicata*, *C. convexa*, and *C. plana*) were introduced but only *C. fornicata* became established with a preference for the warm diked waters used for *O. lurida* culture. Many imported exotics were first observed with oysters in local seafood markets (Hanna, 1966). *Modiolus* (*Guekensia*) *demissus* was very common on the warm intertidal shores of San Francisco Bay during the years of oyster imports and was sometimes marketed. The common eastern mud snail, *Nassarius* (*Ilyanassa*) *obsoletus*, is now localized in warm bays where *C. virginica* was imported. Several small mollusks such as *Gemma gemma* from the East Coast and *Batillaria zonalis* from Japan are widely established in Puget Sound and California. Some mollusks, e.g., *Arca transversa* and *Busycon canaliculatus*, were present only as long as imports continued because they did not breed.

The most spectacular accidental invasion of West Coast ecosystems was made by the Japanese clam *Venerupis japonica*. It has a wide distribution and great abundance in Japan. It has been highly successful on the West Coast and has filled a warm intertidal niche not occupied by native clams (Quayle, 1964). It is widely accepted both ecologically and as a convenient shellfish for human food. Several species of *Venerupis* endemic to western Europe are also used for food, and are cultured there in hatcheries for commercial plantings. The Japanese oyster drill, *Ocenebra japonica*, is common on West Coast oyster beds from accidental importations.

Two nonmolluscan species introduced to the West Coast from Japan are serious parasites of oysters and mussels. The flatworm predator *Pseudostylochus ostreophagus* kills oyster spat in Puget Sound and is difficult to control. A macroscopic red copepod, *Mytilicola orientalis*, infests intestinal tracts of mollusks which affects their glycogen condition and saleability (Glude, 1975). This copepod genus is more serious as a parasite of mussels than of oysters. An extensive literature exists on *M. intestinalis*, the western European species (Marteil, 1976). Parasites and diseases have the advantage of often being able to attack new hosts when introduced to a new ecosystem, and they survive transportation easily in mollusk hosts.

The Role of Importations in Spreading Diseases and Parasites

Along any given continental coast there are marine communities, isolated for thousands of years by physical barriers, that had no opportunity to exchange fauna with neighboring areas until modern man and his transportation arrived. Many races of *C. virginica* occur along the North Atlantic coast of America (Stauber, 1950) and they appear to have retained their genetic traits despite much transplanting between regions. By transplanting oysters across these natural barriers, man has provided many opportunities for parasites and diseases to find susceptible hosts.

Malpeque Bay Disease in Canada (1914)

The most infamous mortality of oysters in North America was caused by Malpeque Bay Disease in the eastern Canadian provinces (Needler and Logie, 1947). Oysters from New England were imported into Malpeque Bay, Prince Edward Island, in 1914. This was to supplement reproduction which had become inadequate from overfishing and depletion of stocks (Needler, 1931). A severe mortality first occurred in 1915-16 and the epizootic continued until about 1930. The native oysters achieved resistance in a few generations, but over a long period due to infrequent spatfalls (Logie, 1956). The disease spread slowly around the bays of the Island and in 1952-55 it spread to tributaries of mainland New Brunswick in the Gulf of St. Lawrence. The causative organism has not been demonstrated although exposure of susceptible oysters from Bras d'Or Lakes shows that the pathogen is still present. Curiously, the disease has not been associated with mortalities in the New England area from which it was supposed to have originated.

Delaware Bay Disease On Mid-Atlantic Coast of North America (1957)

The oyster industry of the Mid-Atlantic Coast was crippled by the sporozoan pathogen *Minchinia nelsoni* which appeared in Delaware Bay in 1957 (Haskin et al., 1966), and in Chesapeake Bay in 1959 (Andrews and Wood, 1967). More than 90 percent of oysters growing in the two bays in waters >15‰ salinity were killed within 2 years.

The origin of this disease is unknown but imported oysters is a likely explanation (Rosenfield and Kern, 1979). Many small lots of exotic oysters have been planted along the East Coast from Louisiana to Maine (Dean, 1979). Often mature oysters were brought in secretly so that no records of the origins or the histories of importations exist. A few examples will illustrate the pattern of these careless importations.

Recently, *C. gigas* from the West Coast of North America was planted in Maryland waters by a seafood dealer which resulted in a specific law in that State prohibiting the species. The oysters were recovered as completely as possible by scuba diving. An oysterman from Delaware saw impressive specimens of *C. gigas* at the Seattle World's Fair in 1962 and he had some sent to his home state for planting. The oysters were confiscated by a biologist who held them in trays in open waters in Rehoboth Bay, Del., for several years without serious mortality or apparent successful reproduction. *Crassostrea gigas* was apparently resistant to Delaware Bay disease which at that time killed *C. virginica* in Rehoboth Bay.

A bushel of *C. gigas* was planted in Barnegat Bay, N.J., in the early 1930's. These oysters failed to grow, which is unusual for this species, and they died over a 2-year period. A shipment of *C. cucullata* (= *C. commercialis*) failed to survive air travel from Australia to New Jersey in the care of T. C. Roughley (Nelson, 1946). Two eminent scientists were involved which reflects the attitude toward importations at that time. None of these known incidents fits precisely the timing of arrival of the pathogen *M. nelsoni* in Delaware Bay.

For about 6 years prior to the appearance of Delaware Bay disease, seed oysters from the James River and Seaside of Eastern Shore, Virginia, had been transplanted to Delaware Bay in large quantities. It is now known that Seaside oysters are infected with an endemic pathogen, *Minchinia costalis*, which is closely related to *M. nelsoni* (Andrews, 1979a). Possibly by hybridization or mutation, a new virulent race of pathogens arose in Delaware Bay waters (Andrews, 1968). However, I believe it is more likely that the pathogen *M. nelsoni* was introduced from Asia.

Sacculinid Parasite of Mud Crabs Introduced From Gulf of Mexico (1962-63)

One last example can be documented of an oyster transplantation that greatly altered crab populations in Virginia. This event illustrates the complexity of such faunal changes. Disruption of oyster production in Virginia by Delaware Bay disease caused oystermen to search for new sources of supply. Live oysters were trucked from the Gulf of Mexico (Louisiana, Texas, and Florida) to Virginia for shucking at waterside plants where shells and wastes were discarded near native oyster beds.

A year or two after importations began (1962-63), two dominant species of mud crabs, *Eurypanopeus depressus* and *Rithropanopeus harrisi*, were found to be infested with a castrating sacculinid (cirripede) parasite (*Loxothylacus panopaei*) (Van Engel et al., 1966). These formerly dominant crab species, which were major scavengers of dead oysters, soon became scarce and have remained rare for 15 years to the present. A third crab species, *Neopanope texana sayi*, formerly rare on oyster beds in Chesapeake Bay, became abundant and is now the dominant mud crab. It is not susceptible to the parasite.

Fortunately, no new oyster diseases were introduced with these Gulf of Mexico transplantations. It is suspected that another disease caused by *Perkinsus marinus* (formerly *Dermocystidium marinum*) was introduced to Chesapeake Bay with seed oysters from South Carolina or the Gulf of Mexico prior to 1940 (Andrews and Hewatt, 1957).

Biological Planning for New Importations

The rationale for introducing new species of commercial organisms is usually economic and political, and not based on biological need. It could be argued that survival of the fittest is the most rational way to handle exotic oysters. Presumably, this could be justified by the success of *Crassostrea gigas*, the Pacific oyster, on the major oyster-growing coasts of the temperate zones of the world. It has succeeded biologically in western Europe, Tasmania, New Zealand, and the West Coast of North America as well as its native areas on eastern Asian coasts. It is vigorous, fast-growing, relatively disease resistant, and increasingly accepted as a raw-bar oyster due to rapidly changing economic and social mores (Bourne, 1979). Why not accept this superior oyster as the standard for temperate zone ostreid culture? *Crassostrea gigas* was also tried in tropical regions of the South Pacific with poor results (Bourne, 1979). Fortunately, most consultants and FAO officials are recommending use of native oysters in the tropics.

The French decision to introduce *C. gigas* has greatly altered oyster culture in Europe (Marteil, 1969, 1976). French oyster growers are adapting the technology of culture to *C. gigas* with new cultural methods and using new areas in Brittany where *C. angulata* was not grown. After excessive spatfalls occurred in the early 1970's, culminating in the hot summer of 1976, there have been spatfall failures. The effects of the parasitic copepod *Mytilicola orientalis* and introduced fouling organisms are yet to be determined. The rapid spread of gill disease resulted in elimination of *C. angulata*, the Portuguese oyster, from France, and Aber disease caused a severe decrease in *Ostrea edulis* production (Alderman, 1979).

Once introduced into southern France, it was probably inevitable that the Pacific oyster would spread rapidly in Europe. The economic and political decision to hasten the replacement of *C. angulata* by *C. gigas* involved additional risks, but sustained the French industry without serious reductions in total production (Maurin and LeDantec, 1979). The Atlantic coast of France was the major source of seed of *O. edulis* for Holland and some *C. angulata* for Great Britain. The cutoff of seed oysters encouraged development of hatcheries in Great Britain to produce *C. gigas* spat for England, Germany, and France. *Crassostrea gigas* is now established as wild stocks in Holland and also grown in the Adriatic Sea and the Mediterranean Sea (France).

The proponents of use of *C. gigas* in New England argue that land and cold water barriers would prevent larvae from spreading southward (Dean, 1979). But man is the problem. No laws or regulations will prevent the tourists in Maine from taking home to Chesapeake Bay waters live oysters sold for raw consumption. From Massachusetts southward the warm summers of our continental climate should permit *C. gigas* to reproduce successfully. The spatfalls could be excessive and cover all objects in the water as has occurred in the Arcachon area of France. *Crassostrea virginica* already exhibits this tendency in South Carolina, Georgia, and some areas of the Gulf of Mexico. It is not conducive to production of quality oysters (Hopkins, 1954).

The careful introduction of *C. gigas* into Maine through hatcheries and quarantine methods to avoid diseases and pests (Andrews, 1979) is most desirable in contrast to the French approach of mass importation. Yet elimination of many agents of biological control provides the exotic species with a contrived advantage in competition with the native oyster. Provided it does not encounter an endemic disease to which it is susceptible, the Pacific oyster should thrive on the Atlantic coast. This species is an intertidal oyster whose breeding populations escape many subtidal enemies. Miyagi oysters (northern race) also tend to reproduce and grow in slightly colder waters than comparable native races (Hickey, 1979). The argument that *C. gigas* has had opportunities to establish itself through careless importations is not persuasive because circumstances and conditions of importation were not known.

Attitudes and Rationales for New Introductions

It is no longer tolerable to permit the whims of individual citizens and scientists to determine the distribution of exotic species in an increasingly cosmopolitan manner. Courtenay and Robins (1973) described the minimal research and public review activities that should precede intentional introductions even for the best of rationales, such as biological control of established pests. It should not be necessary for each state or country to prohibit each species individually by specific laws. All marine importations should be made under appropriate licensing authority after public review and with clear obligations of control of organisms and responsibility for negative consequences. In the case of commercial species such as oysters, exportations should be subject to the same controls as importations. They should not remain private decisions of individuals or agencies whose motives may be profit or ego satisfaction.

The rationale or reasons for introducing a new oyster species must offer more advantages than just bringing a new competing species to a coastline. Importations may benefit one sector of a coast and endanger a commercial industry in another sector. It is important to determine how widely the new species will spread naturally and with man's help. Except for special niches (e.g., Pendrell Sound), *C. gigas* does not reproduce regularly on the Pacific Coast of North America, yet it spread widely during occasional warm years and persists without recruitment as breeding populations for many years (Quayle, 1969).

Ostrea edulis is now grown in Maine by hatchery reproduction from a small wild population adapted to the Gulf of Maine over a 30-year period (Welch, 1966). The flat oyster is a temperature-sensitive species that does not survive in the warm summer waters of Chesapeake Bay. It does not pose a threat in terms of growth and competition with the cultured native oyster south of New England. However, careless importations could introduce diseases and pests. The European shell disease prefers warm waters (Alderman and Jones, 1971). If imported, it could have disastrous effects on native oysters along our coast. It is reported to occur in flat oysters on Prince Edward Island in open waters after hatchery rearing in quarantine[1].

It is assumed that future importations of shellfish species will be made under quarantine conditions using hatcheries to produce disease-free and parasite-free progeny for testing and eventual release in open waters. This technique has proven to be feasible with oysters, and it overcomes the most serious problems of introductions in the past. However, this method is slow and has not been practiced in distributing *C. gigas* to Europe in recent years, except in Great Britain (Walne and Helm, 1979).

The times and quantities of recent French importations are not readily available in the literature despite the large volume of papers on the new diseases. No description of *C. gigas* importations is given in a comprehensive review of French shellfish culture (Marteil, 1976). An uninformed reader may not realize that the Pacific oyster is an exotic species in France. Ranson (1967) showed that the prodissoconchs or larval shells of *C. gigas* and *C. angulata* are indistinguishable and Menzel (1974) claimed they are the same species. Even if the oysters are accepted as cospecific, isolation from each other for several centuries is certain to have altered their immunities to diseases. Pathogens similar to those causing mass mortalities in eastern North America and western Europe have been found in Asiatic and Australian oysters (Kern, 1976; Sindermann, 1976; Perkins and Wolf, 1976). Trial introductions of shellfish into several countries of Europe are documented by ICES (1972).

[1]Drinnan, R. E., Fisheries and Environment Canada, Halifax, N.S., Canada. Personal commun., 1979.

Competition With Native Species

The most important aspect of competition is the ability of exotic oyster species to reproduce successfully in new environments. On oceanic-type coasts in the temperate zone, *C. gigas* is limited in its reproduction by low summer temperatures. However, it is successful to the point of severe crowding in southwestern France. Temperatures for breeding are no problem for *Crassostrea* species on coasts with continental-type climates. However, the races of *C. gigas* evolved in Japan with salinities near oceanic level may not tolerate the low salinities found in Chesapeake Bay and other southern estuaries during winter and spring.

The amount of competition between exotic and native species depends upon usage and relative adaptations of exotics to the new environments. In a region, such as northern Europe or New England, that depends on hatchery-produced seed oysters, there is no reproductive competition. Therefore, the most serious problem is eliminated. In the Netherlands, *C. gigas* has reproduced naturally in two recent years and competition with *O. edulis* may occur for space and food. However, *Crassostrea* species tend to set and survive most intensively in intertidal zones which reduces the competition for space. *Crassostrea gigas* grows faster than its native competitors in Australia (Medcof and Wolf, 1973), western Europe (Marteil, 1976) and eastern North American (Hickey, 1979).

Excessive reproduction of oysters in an area results in slow growth and stunting. This is characteristic of seed oyster areas. Accumulation of successive year classes of young oysters on growing stocks is particularly harmful when shellfish are intended for raw-bar trade, as in Europe where appearance is important.

When crowding of oysters encompasses most growing areas of a region, such as in Seaside Virginia, South Carolina and Georgia coasts, and many

Gulf of Mexico estuaries, harvesting may require steaming and shaking out meats for canned products. These canned oysters involve much waste of small oysters and they bring the lowest price of all shellfish preparations (Lunz, 1954). Excessive reproduction in an estuary or region inhibits efficient culture and is almost impossible to alleviate.

The potential effect of excessive populations of exotic oysters on other species in an ecosystem can only be surmised. Predators, diseases, parasites, and fouling organisms are likely to increase when excessive abundance of an exotic occurs from an irreversible introduction. The full consequences can only become apparent with time. The most desirable introduction would be one where reproduction of the species is limited by temperatures or isolated by hydrography to a few favorable seed areas. This now occurs in Delaware Bay and Chesapeake Bay with the native oyster *C. virginica*. A good example of a successful introduction of a species with limited reproduction areas is *C. gigas* on the West Coast of North America.

Importance of Races

There are many races of *C. virginica* along the Atlantic Coast of North America. These were first recognized because southern oysters failed to breed in New England waters (Stauber, 1950). Morphological traits of shell thickness and shape persist when oysters from several regions are grown in trays in Chesapeake Bay. Differences in susceptibility and resistance to diseases are exhibited by races not previously selected by the pathogens (Andrews, 1968). Isozyme characterization has shown regional genetic differences along the Atlantic Coast[2] despite much transplanting.

Experience has taught oystermen to use local seed oysters if available. Some disastrous losses occurred in oysters transplanted from other regions. Thin-shelled oysters from Seaside of Eastern Shore, Va., suffered severe drill predation when introduced to Delaware Bay in the 1950's. South Carolina oysters showed severe winter kills and remained poor when transplanted to Seaside of Virginia. The Malpeque Bay disease in Canada followed transplantation of New England oysters. It is the classical example of the consequences of mixing oyster races along a coast.

In Virginia, at least three races of oysters are known by growth habits, shape, and susceptibility to diseases and predators. Most distinctive are fast-growing thin-shelled Seaside oysters. Spatfall is excessive and predation intensive. Therefore, rapid growth and early harvesting are necessary. One might attribute all these traits to the environment, but the oysters fail to grow and survive well in low salinity waters within Chesapeake Bay. In contrast, Potomac River oysters are acclimated to low salinities, but are notable for their susceptibility to diseases, particularly *Minchinia nelsoni* (Andrews, 1968). They, too, exhibit vigorous growth and achieve larger sizes than Seaside oysters. The typical oyster of Chesapeake Bay is exemplified by James River seed oysters which Nelson[3] believed were genetically selected for slow growth by 100 years of tonging the largest ones for market. Their small mature size may be a consequence of early stunting in the unfavorable growing conditions of James River. These three races illustrate the genetic adaptations necessary to grow oysters in only one region of the Atlantic coast.

In Europe, winter hardiness of *Ostrea edulis* is a problem when seed oysters are transplanted from regions with warmer climates. Since the severe winter kill of natives in 1962-63, the Netherlands is dependent on seed oysters from Brittany. A culture of one warm-season is followed because the French race is less hardy than natives (Korringa, 1976). There is also the threat of Gill and Aber diseases from importing French oysters.

In eastern Canada, *Ostrea edulis* introduced from Conway, Wales, in 1957-59 did not survive the cold winters. A stock from Holland (Loosanoff, 1955) was found to be hardy in Prince Edward Island (Medcof, 1961) after nearly three decades of selection in the cold waters of the Gulf of Maine.

Even vigorous *C. gigas* may encounter difficulties in adaptation along the Atlantic coast from low salinities, warm climates, and diseases and predators. Depending upon the races introduced from Asia, the species could be limited to certain areas and hydrographic regimes. Since numerous races of *C. gigas* probably occur along the Asian coast, it would be advantageous to fit each new region with a race from a comparable climate on the coast of origin (Newkirk and Haley, 1977). Much needs to be learned about races with respect to diseases, climates, and genetic parameters of oysters before this is done. To learn by trial and error from hasty, unplanned imports has unacceptable risks for the industry and for the stability of present ecosystems.

The Role of Hatcheries in Importations

Most importations of exotic oysters in the past have been from natural sets of adult oysters or spat on shells grown in open waters. This made inspections for diseases and pests difficult if not impossible. The development of commercial and experimental hatcheries in most major oyster-growing areas of the world has made it possible to avoid these problems. Hatchery-reared spat of 2-5 mm may now be obtained a few weeks after setting without exposure to natural waters. Thousands of tiny live spat are shipped safely by air to distant countries at small cost. The subsequent handling of tiny spat in commercial numbers to prevent predation and smothering is tedious and costly, however.

To avoid these problems of early handling of cultchless spat (Andrews and Mason, 1969), many hatcheries have returned to the technique of setting on shells or shell fragments which facilitates early planting on oyster beds. These lots must soon be planted in open

[2]Anderson, W. W. University of Georgia, Athens, Ga. Personal commun.

[3]Nelson, T. C. Rutgers University, New Brunswick, N.J. (Deceased). Personal commun.

waters and hence carry the same risks as wild oysters for importations. In the decade between 1966 and 1975, the French imported 500 tons of adult oysters and 7,100 tons of spat on shells. All of these were wild oysters from British Columbia, Canada, and Japan, respectively.

Preimportation Studies Needed and Controls Required

The rationale for introduction of *C. gigas* is based on its vigor and fast growth. It appears to grow faster and during the cold season longer than native *C. virginica*. This applies only to the Miyagi race which is the only one tried in most new areas.

Crassostrea gigas presents the potential difficulties of: 1) Competition and hybridization with *C. virginica*, 2) probable susceptibility to some native diseases, and 3) some question as to its marketability as raw oysters in competition with the native oyster. It also may be expected to spread all along the North Atlantic coast and compete directly with native *C. virginica* for food and space in nearly all salinity regimes and environments. One must be prepared for replacement of the native oyster.

In the opinion of the author, *C. gigas* could be a useful species in New England where artificial reproduction in hatcheries can compensate for failure of natural spatfalls. However, based on hatchery seed, *O. edulis* and selected strains of *C. virginica* offer equal or better opportunities for culture of raw-bar oysters. *Crassostrea gigas* presents high risks in southern waters where it may be expected to reproduce naturally and to compete strongly and possibly interbreed with native oysters. These advantages and disadvantages of *C. gigas* will be discussed and contrasted for two large sectors of the coast, south and north of Long Island, N.Y.

The oyster-producing areas in the states south of Long Island generally have adequate spatfalls of *C. virginica* rather regularly, or they have the potential to yield large seed oyster crops if properly managed. The resurgence of Delaware Bay seed beds in the 1970's after severe losses to *Minchinia nelsoni* in the 1960's is evidence of this capacity. Moreover, the oyster industries in the south are much more productive than those in the north despite much lower market prices and greater problems of diseases and predators.

North of Long Island, the major oyster crop is raw-bar oysters which sell for high prices thus compensating for relatively low production. Supply of seed oysters is a constant problem in the north except in occasional years of intensive sets. Furthermore, slow growth in cold waters prolongs the cycle of marketable crops.

These factors provide a division of interests in use of exotic oysters and production of seed oysters in hatcheries. In the north, the cost of hatchery seed is not prohibitive where natural spatfalls do not occur, and the fast-growing *C. gigas* has an added appeal. Drinnan[4] reported that *C. gigas* outgrew *C. virginica* at Ellerslie, Prince Edward Island, 4 to 1 by dry meat weights over a period of 12 months in open waters. A recent report on tray-grown spat of the two species in a Massachusetts cove closed to a pond in the warm season also found faster growth in *C. gigas* (Hickey, 1979). Another commercial operation using *C. virginica* hatchery spat in trays is being conducted by Cotuit Oyster Co.[5] because of scarcity of natural seed in Massachusetts (Matthiessen, 1979). Biologists in Maine would like to replace native *C. virginica* with hatchery-grown *C. gigas*, along with hatchery seed of *O. edulis* already being grown in floats (Dean, 1979). The failure of *C. gigas* to reproduce in Massachusetts and Maine waters is a strong argument for use of hatchery seed in these northern waters. The risk of these exotic species spreading is thereby minimized.

In the southern sector of the North Atlantic coast, faster growth of *C. gigas* may be completely nullified by losses resulting from native diseases, slower growth in warm summer temperatures, and due to low salinities in seed areas. The fouling of native or exotic oysters on growing and fattening beds by heavy spatfalls of *C. gigas* would be disastrous to the Mid-Atlantic coast industry. Hatchery production of seed oysters in the south is not economically feasible yet. Unless *C. virginica* is replaced by *C. gigas*, the problem of separation for marketing of two easily distinguished species growing side by side may occur. Both quality of meats (fatness and taste) and differences in appearance of meats and shells will probably be noticeable to consumers. The proximity of *C. gigas* in New England would enhance the chances of accidental introduction in the south. Self-appointed "experimenters" could easily buy shell stock in Maine and transplant it to Chesapeake Bay for later "eating." Enactment and enforcement of laws to protect against this type of transplanting are not feasible. Canadian importations of both *C. gigas* and *O. edulis* are not discussed further since additional barriers of distance, cold waters, and a national boundary provide added protection.

Introduction of *C. gigas* cannot strictly be said to have occurred in New England until natural wild populations occur, although some oysters are being held in Maine and Massachusetts. In the south, where it is not needed, much additional information should be collected before releasing this species in open waters. The necessary tests are going to be difficult to conduct, control, and interpret within quarantine systems. Needed topics of study include the following items.

1) Characterization of major native seed-source populations in eastern Asia and along the North American Atlantic coast before mixing and hybridization occur. This involves isozyme tests of large wild breeding populations in genetic equilibrium (Hardy-Weinburg law). This procedure is costly and tedious, and depends upon how many enzyme systems need to be tested and the number of oysters required to characterize races.

2) Testing of races of exotic and native oysters for critical temperatures

[4]Drinnan, R. E. Fisheries and Environment Canada, Halifax, N.S., Canada. Personal commun., 1973.

[5]Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

and salinities that induce gonad maturation, spawning, and favorable growth of larvae. Tolerances to salinity regimes and reactions to temperature and salinity parameters in terms of survival and growth are needed for each species and its major races.

3) Long-term monitoring of exotic species in their native habitats for prevalences and effects of oyster diseases and parasites; and testing of exotic oysters for susceptibility to diseases native to proposed sites of importation. This involves coordination of research efforts in two widely separated regions or countries. Testing exotic species against native pests may prove difficult without exposure in open waters. Diseases may be unknown for certain regions and artificial infection techniques have not been developed for other pathogens and parasites.

4) Evaluation of comparative growth rates under various conditions of bottom types, intertidal exposure, depths, and phytoplankton regimes. The method of culture strongly influences growth rates and glycogen deposition. Oysters grow faster when suspended in the water, but currents, seasonal temperature regimes, duration of spawning season, and substrate type greatly influence growth and fattening.

5) Exploration of hybrids and selected strains for particular uses and adaptation to localities and needs. The availability of hatcheries provides great opportunities for hybridizing species and races and selection of superior strains to meet special conditions. Oysters resistant to sporozoan diseases have already been selected.

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