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Russian roulette with oysters : a review of exotic introductions and information needed for planning new ones

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RUSSIAN ROULETTE WITH OYSTERS - A REVIEW OF EXOTIC INTRODUCTIONS AND INFORMATION NEEDED FOR PLANNING NEW ONES

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ABSTRACT

Importation and transplantation of exotic oysters has probably resulted in introduction 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 are often unknown and oysters cannot be adequately diagnosed or inspected for problems by biologists. After small plantings in 1966, The vigorous Pacific oyster Crassostrea gigas has invaded the Atlantic Coast of Western Europe in the past decade with serious consequences for native oyster industries. It is now proposed to introduce it to the Atlantic Coast of North America, primarily for culture in New England. 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 and reaction to native diseases and parasites. Selection of races, strains and hybrids may be pursued in hatcheries to fit exotic oysters to new environments. Introduction of an exotic species is a serious irreversible event that merits careful consideration of the reasons for culture of a new shellfish and of the consequences to native biota and coastal environments.

TABLE OF CONTENTS

Russian Roulette with Oysters

Page

Introduction..1

Categories of Introductions.........................4

History of Major Introductions and their Consequences......7

1. C. angulata to France............................7

2. C. virginica and C. gigas to Pacific Coast of NA....8

3. C. gigas from Japan to Australasia...............10

Adaptations of Organisms to Oceanic and Continental Climates.........12

Consequences of Importation of Exotic Species Associated with Oysters..........13

1. Introduction of Exotic Species to Western European Waters..........13

2. Introduction of Exotic Mollusca to Pacific Coast of N.A..........15

3. Consequences of Transplantation along a Continental Coast..........19

Biological Planning for New Importations............24

1. The Role of Hatcheries in Importations...........24

2. Competition with Native Species..................27

3. Attitudes and Rationales for New Introductions.....30

4. The Importance of Races..........................32

5. Preimportation Studies Needed and Controls Required..........35

References..40

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INTRODUCTION

Since World War II, human population growth with its numerous effects on environments, and the consequences of rapidly accelerating technology have placed fisheries for marine molluscs in jeopardy around the earth. Overfishing with increasingly larger fleets and more efficient gears has depleted shellfish in many areas or forced drastic changes in harvesting and cultural patterns to maintain seafood supplies. The surf clam fishery off the Atlantic Coast of North America is an example of an industry that has depleted one area after another [by pulse fishing]. Inshore, oyster fisheries along the Middle Atlantic Coast declined severely after 1958 as the result of a disease (Delaware Bay Disease) the origin of which is unknown (Andrews, 1979). New pesticides and chemicals released from factories or washed from land surfaces have further complicated shellfish culture and marketing (e.g. Kepone in Virginia, Schimmel & Wilson, 1977).

"Pulse fishing" may puzzle readers, & sentence complete without it

Among the cures that have been attempted for shellfish problems are introduction of exotic species and use of hatcheries for rearing seed oysters. Extensive transplantation of endemic stocks along continental coasts has long been utilized to sustain fisheries, and numerous non-endemic bivalve species have been imported for trial as replacements for depleted stocks (ICES Report, 1972). Hatcheries facilitate this cosmopolitan distribution of bivalves around the earth by providing tiny spat of many species that may be easily shipped long distances. Control of shipments of small hatchery-reared spat is difficult at best. There is a temptation for the grower to try every species available from a hatchery.

Many species of exotic plants and animals have been introduced into terrestial communities where their ecological roles have been documented (Elton, 1958). Most introductions have been accidental through man's activities. Even deliberate importations often go awry of expectations as illustrated by grass carp in America (Courtenay, 1972). The failure of insecticides to control scale insects and mites led recently to introduction of parasitic insects for biological control of these pests (Huffaker, 1971). The complexity of ecosystem interactions is shown in pest control management. ~~by the need~~ It is necessary to consider timing of activities, food supply, and abundance of several predator species and the prey simultaneously in orchards, grain fields and cotton plantings.

Marine exotics are more difficult to study and to control than terrestial ones because of rapid dispersion of larvae by currents. Inadequate knowledge of identity, abundance and distribution of native species may leave exotics obscured for long periods. Often diseases of marine invertebrates become known only after mass mortalities of host species (Sindermann 1976). Seldom can such diseases be proven to be introduced. The only evidence is that of circumstantial timing when stocks were transplanted or imported immediately before an epizootic. One must conclude that it is difficult to predict the impact of exotic marine species on endemic communities until they are established and widespread in the new area.

In this paper, the consequences of transplantations, importations, and introductions on native oyster fisheries and their ecosystems will be examined. Emphasis is placed on two oysters (*Crassostrea gigas* and *Ostrea edulis*) that have been repeatedly imported on a small scale to the Atlantic Coast of North America. *C. gigas* was successfully introduced to Western North American, Western European and Australasian coasts. Several case histories are given of exotic oysters that became established in new areas. Most began as casual importations that were soon followed by deliberate ones on a larger scale. Man was responsible for all the introductions although the oysters usually spread on the new coasts to the limit of their temperature and salinity tolerances.

After the case histories are described, with successes and failures noted, the biological requirements for planning future introductions of oysters are given. This planning envisages the use of carefully selected brood stocks in hatcheries to prevent introduction of exotic diseases, predators, and associated species in the new ecosystems. The emphasis, therefore, is on fitting the chosen oyster species to the new environment. The uses and objectives of importations of new species must be clearly defined to avoid catastrophes of excessive reproduction, too-wide dispersion, and vulnerability to native diseases, parasites, and physical extremes of the environment. Lastly, the kinds of information and studies needed to satisfy these requirements are reviewed.

CATEGORIES OF INTRODUCTIONS

Oysters have been transported by man since Roman times, and they are superbly constructed to withstand long journeys out of water. Transplantation of endemic species of oysters along a given coast has occurred frequently in the past. Usually oysters were transplanted from southern to northern regions to utilize excellent spatfalls in the warmer climes. Millions of bushels of Chesapeake Bay oysters were transplanted to New England waters in the last third of the 19th century (Ingersoll, 1881). Yet the racial integrity of local oysters seems to have been preserved, presumably through specific reproductive traits such as breeding temperatures.

Transplantation of flat oysters (*Ostrea edulis*) from one country to another in Europe has a long history. It was instigated primarily by failure of reproduction in the cold waters of northern countries such as Great Britain, Netherlands, and Denmark (ICES Report, 1972). Crises induced extensive transplantation at times, such as after continent-wide mortalities in 1920-21.

These movements of endemic oysters of the same species along a coast are defined as transplantations. They are not, however, the primary concern of this discussion, for most of the potential for damage has been done presumably in the past. However, care should be exercised in moving endemic oysters from regions of a coast that have been isolated by land barriers, ocean currents, and even temperature differences for many centuries. Exchanges between such areas on a coast carry the same dangers from diseases and pests as importing ~~from~~ exotic oysters of a different species. Examples of isolated regions include the Gulf of Mexico and the Gulf of St. Lawrence on the Western Atlantic Coast. The Mediterranean Sea and the Atlantic Coast of Europe could be hazardous regions for exchanges of oysters.

The importations of exotic species of oysters that may result in established populations are called introductions to distinguish them from transplantations. These importations may be deliberate or accidental and can be subdivided into several categories according to purpose of the introduction, agent of dispersal, and stage of the organism utilized (ICES Report, 1972). Introductions from one continental coast to another are almost always through the activities and agencies of man although subsequent spread of new species along the coast is often by natural means. For purposes of discussion, deliberate 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 were preceded by accidental ones on a small scale.

Only rarely have importers utilized hatcheries to eliminate the dangers of exotic diseases, predators, and other species being introduced accidentally. Careful selection of broodstock oysters, spawning under quarantine conditions in a hatchery, and production of F_1 progeny for release in open waters are highly feasible mariculture activities now. It is presumed that this will be the method by which all future deliberate introductions will be made.

HISTORY OF MAJOR INTRODUCTIONS AND THEIR CONSEQUENCES

1. Crassostrea angulata from Portugal and Spain to France.

When the natural beds of O. edulis in northern Spain and the southwest coast of France were depleted about 1850, private culture was initiated following a famous report by Coste to Napoleon III. Soon C. angulata was imported from Ria Sado in Portugal to stock private beds. C. angulata, the Portugese 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 provided waters warm enough (>20°C) for reproduction of this subtropical oyster. The introduction to the South Atlantic Coast of France is attributed to the dumping of a shipload of spoiling oysters in the Gironde River where a vessel sought refuge from a storm in 1868.

C. angulata proliferated in the Gironde estuary which provided seed stocks for a hundred years. This introduced species produced five times as many oysters as O. edulis in France in the 1960's (Marteil, 1970). Cold summer temperatures prevented the Portugese oyster from reproducing in Brittany and more northern countries although it was transplanted annually to Great Britain for growth and marketing.

C. angulata was considered less desirable in taste than the European flat oyster, but it provided in relative abundance inexpensive oysters for Europe. It was a desirable importation to supplement the more temperature-sensitive O. edulis that is more difficult to grow. It is difficult to judge the extent of biological competition because *O. edulis* was overfished and depleted before *C. angulata* was introduced. The Portugese oyster certainly replaced the flat oyster in the warm waters of southern France where the latter was native.

In November 1966, a disease of the gills (Franc and Arvey, 1970) appeared in *C. angulata* which caused it to virtually disappear by the mid-1970's (Marteil, 1976). It was replaced in the 1970's by *C. gigas*, the Pacific oyster, which was first imported in March 1966 (ICES Report, 1972). Another pathogen, a protozoan named *Marteilia refringens*, appeared in *O. edulis* in 1968 in Brittany, France. This disease (Aber Disease) has caused extensive mortalities in flat oysters in some areas of Brittany but not in the Netherlands where French seed oysters are planted annually. As may be expected of a possible carrier host, *C. gigas* was not appreciably affected by either of the two new diseases, although there are indications that an undescribed new shell malady may become a problem in French waters (Marteil, 1976).

The Pacific oyster replaced *C. angulata* in nearly the same warm areas of French waters south of Brittany which the latter occupied for a century. Very intensive spatfalls of *C. gigas* in southern France have reduced the growth rate by crowding.

2. *C. virginica* and *C. gigas* to Pacific Coast of North America

The small, slow-growing, native oyster, *Ostrea lurida*, of this coast is excellent in taste but unsatisfactory in growth and difficult to culture (Hanna, 1966). The first

2. C. virginica and C. gigas to Pacific Coast of North America

The native Oympia oyster of this coast, Ostrea lurida, 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 1920s despite adoption of European cultural methods of diked parks to protect the cold and heat sensitive Olympia oysters. From 1928 to 1945, pulpmill wastes were blamed for the decline in southern Puget Sound (McKernan, et al., 1949). The species did not recover production appreciably after the pulpmill was closed. Oyster planters had turned their attention to C. gigas in the 1920s. 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. O. lurida does not fulfill the needs of a region with rich waters suitable for extensive oyster culture.

The first importations of eastern oysters (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 required regular importations from the east coast. C. virginica is now rare on the Pacific Coast. Importations over 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 rawbar trade in the 1960s and 1970s. During this period risks of importation of new diseases prevalent on the east coast were high.

C. 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 1920s thousands of cases of spat on shells were shipped from Japan on decks of ships (Quayle, 1964). In the early 1970s, high prices and competition with air shipments to France greatly reduced importations from Japan. Fortunately, the industry has developed its own seed supply over the years. Two areas of regular spatfalls, Pendrell Sound, British Columbia, and Dabob Bay, Washington, supplement growing areas with irregular or no sets.

3. C. gigas from Japan to Australasia

C. gigas became established in Tasmania about 25 years ago. Five shipments from Japan to Australia were made between 1947 and 1952 (Thomson, 1952 and 1959). Three strains of Pacific oysters shipped as spat on shells were planted at two sites. Oysters planted at Pittwater on the southern shore of Tasmania survived well. Those exposed to 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 threee strains were planted in the same area and the surviving race of acclimated oysters is not known - probably Miyagi or Hiroshima oysters or a mixture.

The appearance of scattered individuals of *C. gigas* in New South Wales in the 1970s where an important commercial fishery for *C. commercialis* is pursued has raised concern among oystermen. Some of the specimens were found on cultch sticks used to collect native oysters, implying that they were derived from larvae ~~growing~~ produced or originating in the locality. The Pacific oyster outgrew the native oyster on these sticks suggesting that conditions were favorable for it. 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 giving time to permit industry adaptations in the event *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. *C. gigas* appeared suddenly in New Zealand in 1970 from unknown sources (Dinamani, 1974).

to the one in France that kills O. edulis was found in native oysters of New South Wales (Wolf, 1972; Perkins and Wolf, 1976).

ADAPTATIONS OF 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 radiation in winters. Coastal waters on the eastern shores of continents share these extremes of atmospheric temperature with cold winters and warm summers. In contrast, coastal waters on western shores of continents, bathed by oceanic air masses, receive moderated weather, therefore exhibit cool summers and mild winters. Hydroclimographs for estuaries on the eastern coast of North American show annual temperature ranges of 20°C or more inshore, whereas those for the western coast exhibit only about 10°C range (Andrews, 1969). These differences in maximal and minimal mean temperatures affect summer breeding and winter survival adaptations 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 upwelling of deep cold waters. The resulting moderated water temperatures, and nutrient enrichment from upwelling, insure 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 succeed on oceanic-type coasts when introduced. In contrast, organisms acclimated to mild oceanic-type coasts are usually not able to survive either summer or winter extremes on severe continental-type coasts. These adaptations to climates explain in large measure the numerous invasions of exotic species on the western coasts of continents whereas introduced species are rare on eastern coasts.

In general, Ostrea species are adapted to maritime temperate climates and Crassostrea to continental ones, although exceptions occur as waters along a coast become more tropical. Consequently, Ostrea breeds at lower summer temperatures (usually <20°C) and is more sensitive to low salinities and low winter temperatures. It 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.

CONSEQUENCES OF IMPORTATIONS OF EXOTIC SPECIES ASSOCIATED WITH OYSTERS

1. Introduction of Exotic Species to Western European Waters

The most serious introductions of foreign species into Western European waters followed importation of American oysters to Britain. Since reproduction did not occur, C. virginica was relaid annually in British waters from the late 1800's until 1939 for growth and marketing (ICES Report, 1972). The predatory oyster drill, Urosalpinx cinerea, was found in England in 1920. It is now well established on the south eastern 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 mostly by man.

Other American species probably introduced with oysters, but exhibiting more subtle, non-economic effects, include Petricola pholadiformis, Mya arenaria, and Rithropanopeus harrisi (a mud crab), all now with wide distributions in northern Europe (ICES Report, 1972).

When C. gigas was imported to France over the decade 1966 to 1975, both the French and their suppliers (Japanese mostly) were well aware of the potential for unintentional, perhaps dangerous, introductions of other exotic species. Importations have ceased, following the explosive reproduction of Pacific oysters in southwestern France, but it is still too early to assess the extent and consequences of accidental introductions of associated exotic species. The asiatic parasitic copepod, Mytilicola orientalis is known to be introduced in France (Marteil, 1976).

The most serious consequence of importation of C. gigas to Europe may be the spread of previously unknown diseases, including the gill disease of C. angulata and Aber disease of O. edulis. The place of origin of these diseases will probably always be ~~ambiguous~~ uncertain. The timing of importations provides only circumstantial evidence of source. The disappearance of susceptible oysters (*C. angulata*) from France, and the cessation of importations from Portugal, where the disease is also established, may cause gill disease to decline to a low level of activity. Aber disease has not caused mortalities in the Netherlands even though infected seed oysters have been imported from France (Van Banning, pers. comm., 1978).

Shell disease of oysters, caused by the fungus, *Ostracoblabe implexa*, attacks young oysters and spat in western Europe. It causes serious shell malformations and eventually deaths. This endemic disease organism grows best at 30°C, therefore could become a serious pest in countries with warm temperatures as pointed out by Alderman and Jones (1971). Shell disease is prevalent in England, Holland, and France, but has not been reported from North America despite several shipments of *O. edulis* to New England and Canada.

2. Introductions of Exotic Mollusks to Pacific Coast of North America

A wide variety of plants and animals were introduced to the maritime coast of western North America through imports of oysters from New England and Japan. Mostly exotic mollusks will be discussed to exemplify the invasions of oceanic-type coastal ecosystems. Many mollusks have been imported to the West Coast of North America in attempts to establish and maintain an oyster industry there (Hanna, 1966). Except for one or two commercial species, the marine mollusks were brought in as accidental importations in oyster shipments.

These immigrants were probably small individuals or spat, which tended to limit introduction of diseases and parasites. The opportunities for foreign species to accompany oyster shipments is illustrated by Bonnot who in 1930 found 22 species of marine shells in 20 boxes of Japanese seed oysters (Hanna, 1966). Fortunately, this era of carelessness is over. Boxes of seed oysters were inspected for pests on both ends of recent shipments and importations have declined.

The most successful commercial bivalve from the East Coast is _Mya arenaria_ which breeds at temperatures below 20°C. Introduced accidentally with oysters it is now found from Alaska to San Diego. The American oyster, _C. virginica_ and the hard clam, _Mercenaria mercenaria_ did not breed successfully in cold western waters which necessitated continued importations to produce crops. Use of more northerly races of these bivalves might have increased their breeding potential although knowledge of races was lacking before 1930. It was known that races of southern oysters from Virginia remained plump throughout the summer in New England waters but did not usually spawn. Both _C. virginica_ and _M. mercenaria_ are found very rarely on the West Coast now although experiments with hatchery-reared clams continued into the 1960s. Both species can be grown on this coast by use of hatchery seed. The continuous importations of market-sized American oysters insured that their endemic diseases would be offered many chances of becoming established in the west. The State of California has continued to allow importation of small truckload lots for relaying during the last two decades.

Several eastern mollusks closely dependent upon oysters for substrate or food achieved rather wide distributions in localized niches on the west coast. The oyster predator, Urosalpinx cinerea, is often found on oyster beds but not in all areas where salinities are favorable. The southern rough tingle, Eupleura caudata, was not transplanted to the West Coast with Chesapeake Bay oysters because most commercial importations of oysters were from the Long Island Sound area north of its range. Eupleura is another oyster predator that depends upon man to spread from one estuary to another. San Francisco Bay with its relatively warm tidal arms was a favorable site for survival of imported exotics, hence many unusual specimens were first observed with oysters in local seafood markets (Hanna, 1966). Among these were exotic mussels, conchs and snails.

All three species of eastern coast boat shells or slipper limpets were introduced to the West Coast (Crepidula fornicata, C. convexa and C. plana). Only C. fornicata became established with a preference for the warm diked waters of intertidal pools used for O. lurida culture. 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 in the city. The common mud snail, Nassarius (Ilyanassa) obsoletus, is now localized in warm bays where C. virginica was imported. Some small mollusks such as Batillaria zonalis from Japan and Gemma gemma from the East Coast of North America are widely established in Puget Sound and California without causing known ecological harm. Many other live mollusks found growing with imported oysters were collected and specimens deposited in museums, but they never became established species (Hanna, 1966). *Busycon canaliculatus* is an example of a very large conch transplanted into western waters accidentally, probably as juveniles among oysters, but did not establish itself. Another is *Arca transversa*, a blood clam that disappeared after imports of *C. virginica* were discontinued.

The most spectacular invasion of West Coast ecosystems was made by the Japanese clam *Venerupis japonica*. It has a wide distribution and great abundance in Japan. It was highly successful on the West Coast and it 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 occasionally cultured in hatcheries for experimental plantings. The Japanese oyster drill, *Ocenebra japonica* is common on West Coast oyster beds from accidental importations.

Two non-molluscan species introduced to the West Coast from Japan are serious pests 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~~ and affects their condition

(Glude, 1975)
and saleability. This copepod genus is more serious as a parasite of mussels than of oysters. An extensive literature exists on the western European species M. *intestinalis* (Marteil, 1976). Parasites and diseases have the advantage of being able often to attack new hosts when introduced to a new ecosystem, and they survive transmission in marine waters better than mollusk larvae that must have food.

3. Consequences of Transplantations along a Continental Coast

Along any given continental coast there are marine communities , isolated for thousands of years by physical barriers, that have had no opportunity to exchange fauna with neighboring groups north or south of them. Man seems always willing to experiment carelessly with nature. Why *O. edulis* from the Adriatic Sea should be expected to breed in France and England, or stocks from northern Europe survive in the warm southern waters of Chesapeake Bay is not evident, but this species has been introduced many places around the earth.

Many races of *C. virginica* occur along the North Atlantic Coast of America (Stauber, 1950). There is little evidence that transplantings, usually from south to north, have resulted in any useful improvement of local breeding stocks or caused harmful genetic mixing. The local races seem to retain their phenotypic traits. The detrimental effects of such transfers are also difficult to document although a few conspicuous examples are well known.

The most famous mortality of oysters in North America was the one caused by Malpeque Bay Disease in Eastern

Canadian provinces (Needler and Logie, 1947). In 1914, oysters from the high-salinity waters of New England were imported into Malpeque Bay, Prince Edward Island, Canada, to supplement inadequate reproduction resulting from overfishing and depletion of stocks (Needler, 1931). A severe mortality occurred in 1915-16 and the epizootic continued until about 1930. Finally native oysters achieved resistance to the disease, probably [illegible] in fewer generations than may be assumed due to irregular setting in the area. The disease spread slowly around the bays of the Island, presumably ~~spread~~ carried by oystering activities. In 1952-55, it spread to widely-spaced New Brunswick tributaries of the Gulf of St. Lawrence (Logie, 1956). The causative organism has not been demonstrated although exposure of susceptible oysters from Bra d'Or Lakes shows that the pathogen is still present.

Another more important disease crisis for an oyster industry was the advent of the sporozoan pathogen, <u>Minchinia nelsoni</u> to Delaware Bay in 1957 (Haskin et al., 1966), and to Chesapeake Bay in 1959 (Andrews and Wood, 1967). Upwards of 90% of all oysters in the two bays growing in waters with salinities above about 15 o/oo were killed within two years after mortalities began. The mid-Atlantic oyster industry was crippled! No proof of the geographic origin of the pathogen is likely, but one can offer several possible explanations.

The importation of Delaware Bay disease with foreign oysters is a likely explanation. There have been many small lots of exotic oysters planted along the East Coast from Louisiana to Maine. Often large oysters were brought in secretly so that no records of their origins or histories exist. A few examples will illustrate the patterns of these importations. Recently, *C. gigas* from the West Coast of North America was planted in Maryland waters by a seafood dealer. ~~which~~ This resulted in a specific law in that state prohibiting the species. The oysters were recovered as completely as possible by SCUBA diving. In 1962, an oysterman from Delaware saw impressive specimens of *C. gigas* at the Seattle World's Fair 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, Delaware for several years without serious mortality or known successful reproduction. *C. gigas* was apparently resistant to Delaware Bay disease which killed *C. virginica* in Rehoboth Bay. In the early 1930's, a bushel of *C. gigas* was planted in Barnegat Bay, New Jersey. These oysters failed to grow, which is unusual for this species, and they died over a two-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). None of these known incidents fits precisely the timing of *M. nelsoni* in Delaware Bay.

Another sequence of events involving transplantings of oysters along the mid-Atlantic coast does fit the timing of *M. nelsoni* disease in Delaware Bay. Overfishing had impaired oyster setting on the seed beds by the late 1940's. For a period of about six years prior to 1957, seed oysters from the James River and Seaside of Eastern Shore, Virginia had been transported to Delaware Bay in large quantities. It is now known that these Seaside oysters are infected each year with an endemic organism, Minchinia costalis, closely related to M. nelsoni (Andrews, 1978). In fact, for several years it was argued that they were the same organism responding to different environmental conditions (Stauber, pers. comm.). With Virginia oysters comprising over half the planted oysters in Delaware Bay, the new disease appeared in 1957. Seaside was suspected, therefore as the source of M. nelsoni. If this pathogen was not imported in exotic oysters, it had to arise as a virulent race by mutation, or possibly hybridization of the two Minchinia species in Delaware Bay waters. There is evidence that M. nelsoni was present in Chesapeake Bay in the early 1950s but it was benign and caused few deaths (Andrews, 1968). Presumably, transplantation of large quantities of oysters could have provided the interactions of pathogens, oysters and environment to initiate a virulent race of disease organisms.

The traffic in seed oysters and shells between Delaware Bay and Seaside was expected to expand the distribution of M. nelsoni to Seaside; however, the disease may have moved the other way. A large mortality of oysters in Chincoteague Bay in the cold summer of 1958 was attributed to smothering by mats of macroscopic algae (Sieling, pers. comm, 1959). It may actually have been caused by M. nelsoni which was found there in late 1958.

One last example can be given of an oyster transplantation that drastically altered important species of the oyster communities in Chesapeake Bay, and which illustrates the complexity of such changes. Disruption of oyster production in Virginia by Delaware Bay disease caused oystermen to search for new sources of supply. Much needed production was obtained in Maryland from low-salinity public grounds where the disease did not occur. Live oysters were also trucked from the Gulf of Mexico, particularly Louisiana, Texas, and Florida, for shucking. Shucking was done at waterside plants where shells and wastes went overboard near native oyster beds. Some imported southern oysters were planted for later use.

A year or two after oyster importations began from the Gulf of Mexico, two dominant species of mud crabs (*Eurypanopeus depressus* and *Rithropanopeus harrisi*) which are major scavengers of dead oysters were found to be infested with a sacculinid (cirripede) parasite (*Loxothylacus panopaei*) that stunts and sterilizes the crabs (Van Engel et al., 1966). These formerly abundant crabs soon became scarce and remained rare for 15 years to the present. A third crab species, *Neopanope sayi*, formerly rare on oyster beds became abundant. It is not susceptible to the cirripede parasite. These mud crabs are also alternate hosts with oysters for a protozoan parasite called *Nematopsis ostrearum*.

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

BIOLOGICAL PLANNING FOR NEW IMPORTATIONS

1. The Role of Hatcheries in Importations

Commercial and experimental hatcheries are available in most of the major oyster-growing regions . Hatcheries are in operation on two coasts of the United States, but in the Gulf of Mexico natural setting is usually adequate. France and England also have shellfish hatcheries. Japan abandoned oyster hatcheries years ago although the facilities are used for culture of other mollusks such as abalones. Adequate quarantine facilities to handle exotic species are less common. Great risks of introduction are often taken moving exotic oysters in or out of "closed" aquaria to avoid open water spawning.

The development of commercial shellfish hatcheries has occurred mostly in the last decade (Hidu et al., 1969; Landers, 1968; and Matthiessen, 1970). Their success depends upon isolation and culture of suitable algal species as food for larvae, or use of centrifuged natural waters that yield satisfactory mass nannoplankton cultures in greenhouses. The cost of growing artifically-reared food stocks has limited the financial success of hatcheries.

Another major problem in hatcheries is handling spat on bulky cultch (shells, tiles, plastic, or wood frames) until they can be safely planted on natural bottoms. In 1968 a method for production of free or cultchless spat was developed in a hatchery at Pigeon Point, California by Pacific Mariculture Inc. (Andrews and Mason, 1969). This development revolutionized the dispersal of oysters by man.

Thousands of tiny live spat are now shipped safely by air to distant countries at little cost. The handling of 2 to 3 mm spat in commercial numbers to prevent predation and smothering before planting in open waters is, however, tedious and costly. Some hatcheries have therefore returned to the use of shells or shell fragments as cultch to prevent such losses. Thousands of cases (about 2 bushels each) of broken shells bearing spat set naturally were shipped from Japan to France by air when C. gigas was imported to Europe in quantity in the early 1970's.

Hatcheries may be used to produce seed oysters free of exotic diseases, parasites and other pests. It is impossible to effectively inspect large shipments or even a few brood oysters from natural waters for diseases and parasites. However, sampling the population at its origin for microscopic examination of fixed and stained tissues is desirable. Quarantine of relatively small groups of brood stocks with treatment and containment of effluents adds greatly to the safety of importations. Production of F_1 progeny in the hatchery eliminates all but transovarian diseases and provides a period of observation and testing before release into open waters. The small number of brood oysters needed to satisfy genetic requirements of gene pool diversity makes importation of hatchery-grown selected stocks a possibility.

Another important reason to use hatchery-reared stocks of exotic species for release in open waters is for selection of genetic attributes that fit the new environment. Technology is available in experimental hatcheries to produce a wide variety of race and species crosses. Geneticists are only beginning to characterize native populations by serological methods (isozyme alleles, isolation tests). Biologists are only vaguely aware of the extent of racial segregation of bivalve species along a coast of varying environments. Also, hatcheries have permitted selection of strains or races with special attributes such as disease resistance and fast growth (Andrews, 1968 and Haskin, 1972). Hybrids of _C_. _gigas_ and _C_. _virginica_ produced at the Virginia Institute of Marine Science, Gloucester Point, Va. were shipped to Washington State for growth trials (Dupuy, pers. comm., 1978).

There are some dangers associated with the rearing of seed oysters in hatcheries. Some hatcheries are advertising the availability of spat of several species for sale. It is almost inevitable that some hatchery seed may become adulterated with unwanted species. This has already occurred with a shipment of _C_. _virginica_ to Maine containing some _C_. _gigas_ (Dean, pers. comm., 1978). Also seed oysters from a hatchery may be derived from a small number (even a pair) of unselected brood oysters of unknown genetic traits. Oysters with such a restricted gene pool would be undesirable for introduction. One advantage of introduction through hatcheries is to avoid the dangers of repeated importations. However, breeding of several races may be needed before a stock selection meets genetic and environmental requirements.

In cold regions where a species is prevented from reproducing, an industry may be sustained by hatchery production of seed oysters. New England is an area where high market prices, intensive off-bottom culture techniques and scarcity of native seed oysters make this feasible. The State of Maine already has a small production of *O. edulis* depending on a hatchery supply of seed oysters (Hidu and Richmond 1974). Selection of brood-stocks and genetic manipulation of stocks may permit use of strains of either native or exotic species or both in some areas. Once a species or strain is successfully used in a region, only potential for genetic improvement by controlled laboratory breeding could justify additional importations. Neither shortage of seed oysters nor the desire for rapid expansion of production should be adequate reasons for further importations.

2. Competition with Native Species

The amount of competition between exotic and native species depends upon usage and relative adaptations in the new environments. The introduction of *C. gigas* to Southern France resulted in large breeding populations that quickly replaced *C. angulata* already depleted by "Gill Disease" (Franc and Arvy, 1970). It is curious that these two oyster species are reported to be almost indistinguishable, cross breed easily, and are believed by some to be the same species (Menzel, 1974). ~~Irrespective of whether they,~~ C. gigas and C. angulata may have been separated in Asia and Western Europe respectively for hundreds of thousands of years (Stenzel, 1971), but after introduction *C. gigas* survived in Southern France because it exhibited a physiological trait of high resistance to gill disease to which C. angulata succumbed. Summer temperatures are usually too low for *C. gigas* to reproduce in Brittany, or in the Oosterschelde in Holland

(Andrews, 1971). It can therefore be grown alongside *O. edulis* without the severe impact on ecosystems that occurred in Southern France from excessive spatfall. One should be cognizant, however that the Pacific oyster achieved most of its wide distribution in British Columbia in three or four warm seasons scattered over a period of 30 years after significant importations were first made in 1926 (Quayle, 1969). There may be occasional warm years of widespread setting of *C. gigas* in Western Europe depending on temperatures and current regimes, and some localized niches may prove suitable for permanent colonization. ~~Thus~~ *C. gigas* ~~may impinge on~~ is grown widely in *O. edulis* culture al areas. New Zealand experienced a rapid build-up of *C. gigas* although the origin of introduced stocks is unknown (Medcof and Wolf, 1975). Scattered individuals of *C. gigas* set on cultch sticks in the *C. commercialis* fishery of New South Wales, Australia. These are suspected to have originated from brood stocks in neighboring Victoria, or Tasmania where the Pacific oyster was introduced. *C. gigas* did not reproduce successfully in Victoria, however. The fate of the native oyster fishery in New South Wales remains uncertain with the known invasive tendencies of *C. gigas* (Medcof and Wolf, 1975).

Excessive reproduction of oysters in an area results in slow growth and stunting. This is characteristic of seed oyster areas. Accumulation of successive yearclasses 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 occurs 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). Overcrowding has occurred in Southern France with *C. gigas*, a condition for which there is no easy remedy.

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

One might have expected reproductive success on the western North American coast to be similar to that on the western European coast, but in the latter area the geography and the climate are different from the former with wider drainage areas and greater runoff into numerous river estuaries. These estuarine areas provide temperatures and salinities favorable for oyster reproduction.

3. Attitudes and Rationales for New Introductions

Present attitudes and current activities in North America can only lead to accidental introductions of exotic oysters on the western Atlantic Coast without awareness or knowledge of the consequences. This will follow in the tradition of first importations of C. angulata to France in 1868 (Marteil, 1970) and of C. gigas to the Pacific Coast of North America about 1905 (Hopkins, 1946). Because the consequences are similar, I consider small, unplanned, unsupervised importations as equivalent to accidental ones.

The times and quantities of recent French importations are not readily available in the literature despite the volume of papers on new diseases. No description of C. gigas importations are given in a comprehensive review of French shellfish culture (Marteil, 1976). An uninformed reader would not realize that the Pacific oyster was an exotic species in France from this extensive review of oyster culture. Perhaps Ranson's (1967) studies, showing that the prodissoconchs or larval shells of C. gigas and C. angulata are indistinguishable, are accepted as proof of identity of the species, and therefore, the Pacific oyster is not considered to be an exotic species by the French (Marteil, 1976). British importations of C. gigas began in 1964, but were restricted to small numbers of oysters for breeding in hatcheries. Hatchery-reared progeny were planted in open waters with reliance on cold waters to prevent natural reproduction. A small importation of C. gigas seed from Japan was laid in open waters in the Netherlands in 1963 (ICES Report, 1972).

Unplanned introductions on the Atlantic Coast of North America that fall in the category of accidental are numerous. The potential consequences of importations were not fully realized even by prominent biologists in earlier eras. It is not surprising, therefore, that many small importations were made by laymen with no history of the results and consequences.

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) describe 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 to prohibit each species individually by specific laws. ~~However, rarity and uniqueness are the main attributes of animals sought by man in pet and zoo importations.~~ All marine importations for purposes of introductions should be made under Federal licenses after public review and with clear obligations of control of organisms and responsibility for 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.

?) Word seems used in a sense that I can't find in big dictionary

It is assumed in this context that future importations of shellfish species will be made under quarantine conditions using hatcheries to produce progeny free of diseases and parasites ~~free progeny~~ for testing and eventual release in open waters. This technique has proven to be feasible with oysters and it overcomes some of the most serious problems of introductions in the past.

The rationale or reasons for introducing a new oyster species must offer more advantages than just bringing a new competing species to a coastline. ~~It~~ Importations may benefit one sector of the coast and endanger a commercial industry in another sector. It is important to determine how widely the new species will spread naturally or with man's support. Ostrea edulis is already grown in Maine by hatchery reproduction from a small adapted wild population in the Gulf of Maine. O. edulis is a temperature sensitive species that did not survive well in Chesapeake Bay waters. It does not pose a threat to the oyster industry of the southern North western Atlantic Coast in terms of growth and competition with the native oyster. However, if European shell disease (Alderman, 1971) were to be imported, it could have disastrous effects on native oysters in warm waters.

4. The Importance of Races

There are many races of C. virginica along the Atlantic and Gulf of Mexico Coasts of North American (Anderson, pers. comm., 1976). ~~This is true of A~~ Other races of different species occur along Asian and European coasts too. One could argue at length with advocates of exotic introductions about the necessity for adaptive races for local climates and hydrographic conditions, but they are interested mainly in current economics and how well imported species survive and grow in rather casual trials. Planned introductions of Ostrea edulis from Conway, Wales in 1957-59 did not survive the cold winters in Eastern Canada. A stock from Holland that survived in the Gulf of Maine (Loosanoff, 1955), was found to be winter hardy at Prince Edward Island, Canada (Medcof, 1961). Since the severe winter kill of 1962-63, Holland is dependent on seed oysters from Brittany. The French race is less hardy than natives (Korringa, 1976) and is obtained from areas where threatening diseases (Gill and Aber diseases) occur. Lacking seed oysters, Holland chose to risk importations of seed from France. Probably most of the risk had been incurred through shipments of seed oysters before the new diseases were generally recognized. Gill disease spread rapidly and widely in western Europe in the late 1960's.

Along the western Atlantic Coast, oysters from Chesapeake Bay are winter hardy and grow well in New England but do not reproduce usually. Yet experience has taught oystermen to use local seed oysters if available. Some disastrous losses occurred in transplants from other regions. Thin-shelled Seaside oysters from Virginia suffered severe drill predation when introduced to Delaware Bay. South Carolina oysters showed severe winter kills and remained poor when transplanted to Seaside of Virginia. The Malpeque Bay disaster in Canada followed transplantation of New England oysters. It is the classical example of the consequences of mixing oyster races.

In Virginia, at least three races of oysters are known by growth habits and susceptibility to diseases and predators.

Most distinctive are fast-growing, thin-shelled Seaside oysters. Spatfall is usually 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 survive well within Chesapeake Bay for unknown reasons. Potomac River oysters, acclimated to low salinities, are noted for their susceptibility to diseases, particularly *Minchinia nelsoni*, and for their vigorous growth and large size. The typical oyster of Chesapeake Bay is represented by James River seed oysters which Nelson (pers. comm.) believed were selected for slow growth by one hundred years of tonging the largest ones. Perhaps their small final size is a consequence of early stunting in the unfavorable growing conditions of James River. These three races, whether genetic or environmental in origin, illustrate the adaptations that are necessary to grow oysters in only one region of the Atlantic Coast.

Even the vigorous *C. gigas* may encounter adaptive difficulties along the Atlantic Coast, and like *C. virginica*, races could be limited to certain areas and hydrographic regimes. It seems absurd to expect one race (Miyagi Prefecture) of *C. gigas* to fill all these varied niches without multiple problems. How much better it would be to utilize the numerous races that must exist along the Pacific Coast of Asia by fitting them to particular environments. Much needs to be learned before this can be done. To learn by trial and error from hasty imports, as past experiences exemplify in Europe, western North America and Australia, has unacceptable risks for the industry and for the stability of present ecosystems.

5. Pre-importation 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 tested in most new areas. *C. 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 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 spawning. However, *O. edulis* and selected strains of *C. virginica*, based on hatchery seed, offer equal or better opportunities for culture of rawbar oysters. *C. gigas* presents high risks in southern waters where it may be expected to reproduce naturally and to compete and 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, New York.

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 1970s after severe losses to *Minchinia nelsoni* in the 1960s 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, if natural spatfalls do not occur, and the fast-growing *C. gigas* has an added appeal. Drinnan (pers. comm. 1973) reported that *C. gigas* outgrew *C. virginica* at Ellerslie, Prince Edward Island, Canada 4 to 1 by dry meat weight over 12 months in open waters. A recent report of 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, Woods Hole, Massachusetts Symposium 1978). Another commercial operation using *C. virginica* hatchery spat in trays is being conducted by Cotuit Oyster Co. because of scarcity of natural seed in Massachusetts (Matthiessen, ibid.

Symposium, 1978). Biologists in Maine would like to replace native *C. virginica* with hatchery-grown *C. gigas*, along with *O. edulis* already being grown in floats using hatchery seed. (Dean, ibid. Symposium, 1978). 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 the 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, and by slower growth in warm summer temperatures and ~~due to~~ in low salinities. ~~in seed areas.~~ Hatchery production of seed 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 appearance of meats and shells will probably differ noticeably 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 transport 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 are being held in Maine and Massachusetts.

In the south, where ~~it~~ C. gigas 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 closed systems. Needed topics of study include:

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 populations in genetic equilibrium (Hardy-Weinburg law). ~~It~~ This procedure is costly and tedious, and depends upon how many enzyme systems need to be tested and the number of oysters required to document races.

2) Testing of races of seed oysters for critical temperatures 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 oyster diseases and parasites for prevalence and effects in native habitats of exotic species; 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 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. Oysters grow faster when suspended in the water, but currents, seasonal temperature regimes, duration of spawning season, and substrate type greatly influence growth.

5) Exploration of hybrids and selected strains for particular uses and localities.

   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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