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THE DECLINE OF THE VIRGINIA OYSTER FISHERY IN CHESAPEAKE BAY: CONSIDERATIONS FOR INTRODUCTION OF A NON-ENDEMIC SPECIES, *CRASSOSTREA GIGAS* (THUNBERG, 1793)[1]

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

KEY WORDS: *Crassostrea gigas*, oyster, introductions

INTRODUCTION

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

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

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

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

Developing the Rationale: Historical Perspective and Current Situation

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

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

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

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

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

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

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

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

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

Selection of Species for Introduction: Why Crassostrea gigas?

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

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

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

TABLE 1.

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

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

TABLE 2.

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

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

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

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

The native northern European oysters *Ostrea edulis* and *Crassostrea angulata* were decimated by disease in the mid 1970s. Production of the former fell from 15,000 tons to the present day level of 2,500 tons per year. Production of the latter fell from 60,000 tons per year to zero. The industry was saved from economic extinction by the introduction of *C. gigas*. European *C. gigas* production (including French) now employs over 20,000 people and produces approximately 140,000 tons of oysters per year, this representing over 80% of the total production. Further, *C. gigas* appears resistant to challenge by both *Bonamia ostreae* and *Marteilia refringens*, diseases that continue to decimate native European oysters. The analogies with Chesapeake Bay are painfully obvious.

TABLE 3.

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

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

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

Risk Analysis for Introduction of Diseases with Crassostrea gigas

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

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

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

1. Diseases of Unknown Etiology.

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

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

2. Viral Diseases.

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

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

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

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

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

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

3. Bacterial Diseases.

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

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

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

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

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

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

4. Protozoan Diseases.

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

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

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

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

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

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

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

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

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

5. Metazoan Parasites.

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

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

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

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

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

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

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

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

The Dilemma: Where to Now?

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

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

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

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

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

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

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

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LITERATURE CITED

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

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

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

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

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

Barber, B. J., S. E. Ford & H. H. Haskin. 1988a. Effects of the parasite MSX (*Haplosporidium nelsoni*) on oyster (*Crassostrea virginica*) energy metabolism. 1. Condition index and relative fecundity. *J. Shellfish Res.* 7:25–31.

Barber, B. J., S. E. Ford & H. H. Haskin. 1988b. Effects of the parasite MSX (*Haplosporidium nelsoni*) on oyster (*Crassostrea virginica*) energy metabolism. 11. Tissue biochemical composition. *Comp. Biochem. Physiol.* 91A:603–608.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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