Journal of Shellfish Research, Vol. 16, No. 2, 463–477, 1997.

CONSIDERATIONS REGARDING THE POSSIBLE INTRODUCTION OF THE PACIFIC OYSTER (*CRASSOSTREA GIGAS*) TO THE GULF OF MAINE: A REVIEW OF GLOBAL EXPERIENCE

GREG SHATKIN,[1] SANDRA E. SHUMWAY,[2]* AND ROBERT HAWES[1]

[1]*Animal Veterinary and Aquatic Sciences*
University of Maine
Orono, Maine 04469-5735
[2]*Natural Science Division*
Southampton College of Long Island University
Southampton, New York 11968

ABSTRACT This report was prepared in response to an interest among representatives of the Maine oyster culture industry in potentially introducing the nonendemic species *Crassostrea gigas* into the Gulf of Maine for culture purposes. The manuscript was originally written for the members of the shellfisheries subcommittee of the Maine Aquaculture Association. Topics reviewed include: the history of oyster culture in Maine, the rationale behind the interest in introduction of the Pacific oyster, a history of *C. gigas* introduction around the world, the legal aspects of nonendemic introduction, diseases associated with the Pacific oyster, methods of inhibiting reproduction of the nonendemic species, the ecological implications of introducing *C. gigas,* and production of the Pacific oyster in Maine. The article is a compilation of both published material and information contributed through personal communications with regional specialists. The authors do not assert conclusions but offer the material assembled below as a source of information to those involved in the decision-making processes concerning proposed introductions in Maine and other geographic regions.

KEY WORDS: Pacific oyster, *Crassostrea gigas,* introduction, nonendemic, aquaculture, Maine, reproduction, interaction, ecology

INTRODUCTION

This article addresses a recurring interest among representatives of the Maine aquaculture industry in the introduction of the nonendemic species *Crassostrea gigas* into the Gulf of Maine for culture purposes. What follows is an objective review of issues that are pertinent to any proposed introduction including means of circumventing associated potential problems. The relevant information is arranged categorically, and much of the material assembled here was derived from literary sources. Additional information was contributed verbally and in writing through personal communications with many individuals. No conclusions are offered. Rather, it is expected that the members of the shellfisheries subcommittee of the Maine Aquaculture Association, for whom this article was prepared, will take into account the facts presented here when drawing their own conclusions. Further, it is hoped that presentation of these data will provide the necessary facts on which reasonable and sensible management decisions will be made.

THE HISTORY OF OYSTERS IN MAINE

The history of oysters along the Maine coast may be traced back to the earliest records of the region. Points adjacent to the Gulf of Maine where shell heaps and underwater deposits serve as vestiges to the once flourishing eastern oyster beds include: the George River, the Damariscotta River, the Sheepscot River, Casco Bay, Scarborough headlands, and the Piscataqua River (Baird and Goode 1881). The largest aboriginal accumulations of oyster shells in the world (98% *Crassostrea virginica,* the remaining 2% composed of Ensis, Mya, *Mytilus, Mercenaria,* and *Littorina*) are located at the head of the Damariscotta River (Myers 1965). These middens have been estimated to include 14 million m^3 of shell (Castner 1950), and specimens taken from 1 foot above the pile's base have been radiocarbon dated to approximately 2,100 y before present (Russell 1979).

The northern coast of New England has not been able to support an oyster industry reliant on an endemic, wild fishery since the early 1800s because eastern oysters (*C. virginica*) have gradually become less plentiful in Maine (with the exception of limited, isolated oyster beds in the Sheepscot and Piscataqua Rivers) (Ruge 1879). The demise of *C. virginica* in Maine began during the 18th and 19th centuries when mills, built by European immigrants, released sawdust waste into many estuaries, smothering and poisoning adult animals, while effectively eliminating suitable substrate for larval settlement (Myers 1965). In addition, the waters of the Gulf of Maine have become cooler over the last few millennia (Dunham and Bray 1974). Resulting temperature regimens no longer favr the propagation and larval survival of Transhatteran species, including *Mercenaria mercenaria* and *C. virginica,* north of Cape Cod because the relative rise in sea level, permitting greater tidal mixing and less stratification, has resulted in cooler water temperatures in the Gulf of Maine (McAlice 1981).

THE HISTORY OF OYSTER CULTURE IN MAINE

Eastern Oysters

The culture of eastern oysters in Maine using intensive methods was initiated in the 1970s by a few small, pilot-commercial ventures in the warm, upper reaches of bays and estuaries in the midcoastal portion of the state. Before this era, the only documented aquaculture efforts were the extensive practices of the Wawenocks, natives to the Abenaki State and the region now known as Maine. These native people are believed to have dived in the Damariscotta River for oysters (Russel 1979) which they traded and planted in the Sheepscot and George Rivers to maintain

*Author to whom all correspondence should be addressed.

continued and convenient supplies (Baird and Goode 1881). Currently, two hatcheries produce *C. virginica* seed in this region, and the five companies that grow this seed to market size in Maine are all located on the Damariscotta River.

European Oysters

Populations of *Ostrea edulis* have been successfully introduced to Maine waters in two locations. European oysters were introduced from Holland between 1949 and 1961 by the Maine Department of Sea and Shore Fisheries in cooperation with the Fish and Wildlife Service (Dow 1970). These oysters survived, spawned, and successfully set below mean low water in Boothbay Harbor and Casco Bay (Welch 1963). In the hatchery, however, where culture of *O. edulis* has been attempted in Maine for nearly 20 y, the species has not proven hearty and exhibits inconsistent and unpredictable larval survival (Clime personal communication, Mook personal communication). The wild European oyster fisheries, which even at peak production from 1983 to 1987 produced only one-half million individuals for market, have been decimated by overfishing, lack of management, and possibly the protozoan pathogen, *Bonamia ostreae,* which was recently discovered in *O. edulis* from the Damariscotta River (Friedman and Perkins 1994, Zabaleta and Barber 1996) and other sites in Maine (Barber and Davis 1994). In France, where native beds of *O. edulis* were extensive before 1979, no populations of European oysters are reported to have recovered after decimation by *B. ostrea* (Bol personal communication). Production of European oysters in France, which was 15,000 tons in 1973, had been reduced to 1,800 tons by 1991 because of disease (Heral and Deslous-Paoli 1991).

Pacific Oysters

C. gigas represents the third and final species of oyster that has been cultured in Maine waters. In April 1949, 5 bushels of Pacific oyster seed was imported from Seattle, WA, by John Glude of the Maine Bureau of Commercial Fisheries and planted in a salt pond at Blue Hill-Sedgwick below mean low tide (Dow 1970). Those animals that survived pollution by sawdust debris reached market size of 75 mm in two growing seasons. Although gonadal development and apparent maturation occurred, surviving spat were never located (Dow and Wallace 1971). *C. gigas* were not cultured again until the early 1970s, when representatives of the species were incidentally introduced to Goose Pond at Cape Rosier, Middle Salt Pond in Blue Hill, and both Seal and Long Coves on the Damariscotta River, with shipments of *O. edulis* and *C. virginica* seed from Pacific Mariculture, Inc., Pascadero, CA (Hidu personal communication). *C. gigas* were also experimentally cultured at three locations on the Damariscotta River by researchers at the Darling Marine Center during 1972 (Packie et al. 1975).

THE RATIONALE BEHIND THE CURRENT INTEREST IN INTRODUCTION OF THE PACIFIC OYSTER

Economics

The current interest in investigating the possibility of introducing the Pacific oyster to the Gulf of Maine for culture purposes originates in part from a belief by some that this species could enhance the economic development of Maine's commercial marine resources. The economies of northern Maine's rural, coastal towns, primarily located in Washington County, require stimulation via new industry (Bassano personal communication). Oyster farming is culturally consistent with the skills and resources of those currently employed in the diminishing traditional fisheries. An oyster culture industry in Downeast Maine would provide employment to growers and processors and could be a means of circumventing the loss of communities and coastal heritage by providing an economic alternative to immigration to the cities. The governments of Denmark and Germany made the decision to introduce *C. gigas* for culture purposes after observing successful introductions of the species elsewhere in northern Europe, in an effort to provide alternative employment to coastal communities hit hard by the decline of the fishing industry (Helm personal communication). "Expanding the oyster culture industry offers the potential for improving the standard of living in rural Maine while building upon a traditional marine resource" (Beyea personal communication).

Existing Markets

Before any production of Pacific oysters in Maine, marketing and distribution of the final product should be carefully planned by targeting markets and determining their specific desires (e.g., size and form). Per capita oyster consumption has been falling steadily in the United States since before 1950 (Dunham and Bray 1974) and is continuing to decline (Kirkley personal communication). According to data compiled on food consumption by the U.S.D.A., the number of households purchasing oysters in stores, restaurants, and raw bars on a weekly basis decreased by 50% between 1978 and 1988 (Lipton personal communication). The broad market for oysters initially declined because of improved transportation, which eliminated the requirement for long shelf life of fresh products and made available alternative seafoods that required less preparation. More recently, health concerns fueled by negative press made the market for oysters even more narrow (Shapman personal communication). Contemporary markets for the commodity are very specific and can be best developed by promoting a name-brand product, cultured in the safe waters of Maine (Kirkley personal communication).

There are currently several existing markets for Maine-raised oysters that could accommodate the Pacific oyster if it were introduced. *C. gigas* production could be used to supplement the half-shell trade, currently occupied by *C. virginica.* In Virginia, Pacific oysters, imported from Washington State, are served as a raw, gourmet substitute for eastern oysters during the early spring when no eastern oysters of appropriate size are available (Castagna personal communication). Some contend that the East Coast species is superior in appearance and flavor. According to the Western Regional Aquaculture Center, the prospect for oyster culture on the West Coast is great because of the demand for Pacific oysters on the East and Gulf coasts of the United States (Chew and Toba 1991). Nearby Canada represents an additional market opportunity for Maine growers because the wholesale price of half-shell oysters in Montreal is 50% higher than that in the United States; tariffs only amount to 7.5% of the wholesale price (Ehrbar 1975). *C. gigas* presently constitutes between 30 and 40% of the oysters consumed in the United States (Smith personal communication).

The exotic species could also represent a new market product. The colorful, fluted shell of the Pacific oyster may contribute to its appeal on the half-shell. Jon Shalpack (personal communication), general manager of Legal Seafoods in Boston, MA, who purchases 30 to 40 tons of shellfish per week "would be interested in exclusive rights to such a unique shellfish product which originated from clean, cold waters."

Pacific oysters produced in Maine could also supplement the large existing market for shucked oysters, which are stewed and fried by restaurants across the United States. Maine's existing clam-shucking industry is currently underused because of lack of *Mya arenaria* abundance (Beal personal communication). *C. gigas* could be used to expand this industry (Walker personal communication).

Finally, the possibility exists that *C. gigas* production could be expanded vertically to include processed products. The United States is a net oyster importer. Imports of canned products, predominantly from Korea, more than doubled between 1970 and 1988 from 9.5 to 21 million kg (National Sea Grant 1990). Fresh smoked oysters are the only processed oyster product for which market demand is currently growing (Lipton personal communication).

Habitat Suitability

Interest in the oceanic *C. gigas* also stems from the fact that suitable habitat for *C. virginica,* an estuarine species, is very limited in Maine, because of the primarily marine coastline. Eastern oyster growth is optimal at water temperatures ranging from 20 to 30°C (Galtsoff 1964) and a salinity range of 10 to 28 ppt (Loosanoff 1965). Pacific oysters, in contrast, live and grow in water with temperatures of 4–24°C, displaying high growth rates at 15–19°C (Walne 1979) and optimal water transport at 20°C and 25–35 ppt (Quayle 1969a). As of March 1990, only 3.25 km^2 of Maine's 3,225 km^2 of coastal waters were leased for aquaculture purposes (Maine Aquaculture Innovation Center 1990). *C. gigas* could potentially be bottom cultured in many high-salinity, cold-water areas of the coast where the Transhatteran eastern oyster grows too slowly to be of commercial value.

Biological Performance

C. virginica requires three growing seasons to develop from seed to market size in the upper reaches of the Damariscotta River. During this comparatively long growth cycle, approximately 50% of the mariculture crop is lost to mortality and predation (Scully personal communication). Culture of a faster growing species could result in an increase in survival, which would reduce investment time and labor costs.

Pacific oyster seed, averaging 7 mm in length, was grown in floating trays on the Damariscotta River between July and October 1972. Although this was a comparatively poor growth year for oysters, the animals grew to mean lengths ranging from 53 to 70 mm, with a relatively small size differential between warm- and cool-water sites (Packie et al. 1975). *C. gigas* were observed pumping water at 2°C and grew through a wire mesh of overwintering tray between November and April (Chapman personal communication). ''*C. gigas* have quite a high filtration even when temperature is at 5°C. *C. gigas* is more tolerant of low temperatures, and when the level of food is high enough, winter growth occurs'' (Heral and Deslous-Paoli 1991).

Water temperatures ranged from −1.8 to 25°C and salinities ranged from 20 to 32 ppt at all Maine locations where Pacific oysters were grown during the 1970s. The *C. gigas* seed, received as a contaminant species in shipments of American and European oyster seed, reached market size in a maximum of two growing seasons (Mant personal communication, Richmond personal communication, Shalfont personal communication). *C. gigas* represents a very robust species that is apparently not greatly affected by disease (Pauley et al. 1988). Although no histological analyses were made, no disease presence was observed macroscopically in any Pacific oysters cultured in Maine (Chapman personal communication, Dow and Wallace 1971, Hidu personal communication, Mant personal communication, Richmond personal communication, Shalfont personal communication).

INTRODUCTIONS OF THE PACIFIC OYSTER AROUND THE WORLD

The Pacific oyster is now established on all major coasts of the Northern Hemisphere, with the exception of the Atlantic Coast of North America, making the species the most ubiquitous oyster in the world; apparently, it can adapt to a wide range of environmental and hydrographic conditions. Harvest of *C. gigas* represents 80% of the total world production of edible oysters (Ayres 1991, Holliday and Nell 1987). The primary stimuli for the introduction of nonendemic species include economic pressures in the presence of diminishing wild fisheries resources, destruction of a fishery because of disease, and the original nonexistence of a native fishery (Mann 1979). Regarding the introduction of *C. gigas* to the mid-Atlantic region of the East Coast, European oysters have provided the basis for an important oyster fishery. The pages that follow contain characterizations of the individual introductions of *C. gigas* to several nations. In addition to a historical perspective, each description emphasizes culture methods, ecological implications, economic information, and marketing techniques that may be relevant to the proposed introduction to Maine.

Australia

Hundreds of cases containing *C. gigas* spat from Hiroshima, Kumamoto, and Miyagi, Japan, were shipped and flown to Western Australia, Southern Australia, and Tasmania between 1947 and 1952 by the Commonwealth Scientific and Industrial Research Organization, a federal government agency (Ayres 1991). Although no Pacific oysters survived in the west, these introductions marked the establishment of an oyster industry where none had previously existed in the state of South Australia and on the island of Tasmania (Thomson 1952). In Tasmania, successful spawning and recruitment occurred during the late 1950s (Thomson 1959). During the 1960s, spat was collected by members of the industry in the Tasma River, northern Tasmania, for distribution around the island as well as to South Australia (Dix 1991). Erratic spatfalls inspired the construction of a pilot-scale, commercial, Pacific oyster hatchery by the Tasmanian government and prospective farmers in 1977 (Ayres 1991). The growers established their own hatchery in 1980, and two additional facilities followed in 1985 (Dix 1991). The present industry is totally reliant on hatchery-produced seed from Tasmania (Ayres 1991).

The majority of Pacific oyster production in Australia today takes place in Tasmania, with limited growout on several leases in South Australia. Cultchless seed, grown in nursery upwelling systems to 3–4 mm, is transferred to floating upwellers and grown to 10–15 mm (Dix 1991). Growth to harvest size occurs on intertidal racks or longlines on which *C. gigas* become marketable in approximately 18 mo (Chew 1990). Their short survival time out of water dictates that the oysters be refrigerated soon after harvest (Ayres 1991, Pollard and Hutchings 1990). Pacific oysters are most frequently supplied ''opened on the halfshell,'' fresh or frozen to Australian restaurants where they are consumed raw (Dix 1991). In 1987, the combined *C. gigas* production of South Australia and Tasmania was 48 million oysters valued at $10 million U.S. (Pollard and Hutchings 1990). Despite the imprudent nature of initial introductions from Japan, there exists no recorded incidence of disease on Tasmanian, Pacific oyster farms, where the low mortality rates that do occur result from predation by flatworms and fish (Dix 1991).

The introduction has not, however, been entirely without controversy. In the state of New South Wales, the Pacific oyster is considered undesirable by many who view *C. gigas* as a potentially serious ecological, social, and regulatory problem because its presence threatens a century-old industry based on the indigenous Sydney rock oyster (*Saccostrea commercialis*). In 1985, Pacific oyster spat began setting on commercial rock oyster leases in Port Stephens, 160 km north of Sydney, in locations with water temperatures ranging from 13 to 27°C and salinities of 10–35 ppt. Evidence suggests the deliberate introduction of Tasmanian spat between 1982 and 1983. Subsequent movement of Port Stephens stock has led to *C. gigas* establishment in many other estuaries on the East Coast of Australia, sometimes reaching nuisance proportions because of excessive spatfalls (Ayres 1991). Because Pacific oysters grow faster than Sydney rock oysters, they interfere with stick culture of the native oyster by outgrowing them. In 1985, the New South Wales Agriculture and Fisheries Department declared the Pacific oyster a noxious fish, making culture and presence of the oyster on leases a legal offense. In hopes of limiting the distribution of *C. gigas* and curtailing the problem of juvenile settlement on existing crops, which results in increased culling operations for spat removal, all Pacific oysters on a lease must be destroyed before any Sydney rock oysters may be removed (Pollard and Hutchings 1990).

New Zealand

C. gigas spat of Miyagi prefecture were first discovered on the North Island of New Zealand in 1970 (Andrews 1980); however, old shell specimens have been dated back as far as 1958 (Pollard and Hutchings 1990). The four proposed sources of this accidental introduction include: spawn from Pacific oysters clutched on the hulls of Japanese and Korean squid vessels, discarded individuals that subsequently spawned, larvae released in ship ballast discharge, and larval drift across the Tasman Sea from Australia (Bourne 1979, Parameswar 1991). *C. gigas* has made rapid gains, establishing itself alongside the native *S. commercialis* in most rocky, intertidal inlets and mangrove areas, where water temperatures range from 14 to 22°C and salinities vary between 16 and 35.5 ppt (Dinamani 1991). Although the two animals coexist, the Pacific oyster has become the farmer's species of choice over the rock oyster because, even though both have a similar market value, *C. gigas* reaches harvest size in 15–18 mo (Pollard and Hutchings 1990) as opposed to *S. commercialis,* which requires 2–3 y growout time (Parameswar 1991). *C. gigas* has recently been found among the valuable green mussel beds of Marlborough Sound, New Zealand (Chew 1990).

C. gigas cultivation has represented a significant business in New Zealand. The industry employed 150 individuals in 1990. *C. gigas* were cultured on 350 ha of intertidal shoreline where wild, collected spat were grown on racks. Two thousand tons of Pacific oysters valued between $2.7 million and $3.2 million U.S. were produced in 1985 (Dinamani 1991).

Researchers at the Food and Technology Department of Massey University, New Zealand, found that *C. gigas* require prompt chilling in order to prevent bacterial growth that resulted in deterioration of organoleptic qualities including flavor, odor, and texture. Pacific oysters maintained at an ambient temperature of approximately 11°C could be held for only 6 days; at 2–3°C, shelf life extended to 13 days, whereas oysters kept at 0°C were stored for at least 17 days with no quality depreciation. Local growers chilled *C. gigas* in a freshwater-ice slurry at the time of harvest and stored the oysters in cardboard cartons at 0°C on land (Boyd et al. 1980).

France

The introduction of *C. gigas* to France resulted in the establishment of a new industry while contributing to the decimation of oyster fisheries already in existence. The relatively small importation of 900 kg of Pacific oyster seed from Japan by French oyster farmers in March 1966 was followed by the outbreak of a viral gill disease known as gill necrosis virus (GNV), which plagued local beds of *Crassostrea angulata* (Andrews 1979). The malady had been previously diagnosed and described by Ferreira and Dias (1973) in Portugal as causing the gills of *C. angulata* to become notched with separation of filaments and discoloration occurring as tissues became abscessed and necrotic. Rapid spread of the gill disease resulted in a French government embargo on further importations of *C. gigas* (Andrews 1980). Between 1970 and 1972, a second syndrome, hemocytic infection virus (HIV), caused by another iridovirus and characterized by invasion of the connective tissue by blood cells and an increase in the number of brown cells, resulted in the complete disappearance of Portuguese oysters from French waters (Goulletquer and Heral 1991). According to Henri Grizel, IFREMER, France, both viruses were present in France before any *C. gigas* introductions. Because no attempt was made to isolate the viruses at that time, the truth will remain uncertain (Maurin and LeDantec 1979).

The elimination of *C. angulata* from France and the coincident termination of an industry that produced 65,000 tons of oysters annually (Grizel and Heral 1991) resulted in an official government decision to import *C. gigas* in commercial quantities to the West Coast for culture purposes (Andrews 1980). Between 1971 and 1975, 562 tons of mature Pacific oysters was introduced from British Columbia, while 10,015 tons of spat was imported from Japan between 1971 and 1977 (Grizel 1988). After these extensive introductions, two haplosporidians were found in the endemic *O. edulis* including *Marteilia refringens* (Aber disease), which inhabits the digestive tract, and *Minchinia armoricana,* a protozoan similar to *M. castalis,* a pathogen of *C. virginica* (Andrews 1979). Although further imports of *C. gigas* were banned by the French government in 1982 after the discovery of these haplosporidia in supposedly disease-free Japanese seed, Pacific oysters reproduced so prolifically on the southwest coast of France that further imports were not necessary to sustain the industry (Mann 1983). The exotic species that accompanied *C. gigas* introductions despite inspection and immersion in freshwater include the onidarian *Aiptasia pulchella,* the cirripeds *Balanus amphitrite* and *Balanus albicostatus,* and the macroalgae *Laminaria japonica* and *Undaria pinnatifida* (Goulletquer and Heral 1991).

Prodigious Pacific oyster settlement has resulted in colonization of all sites formerly occupied by *C. angulata* and some areas including Arcachon, Brittany, and Southern Normandy, where Portuguese oysters did not exist. Spawning occurred where both water temperature (>22°C) and salinity (34–35 ppt) were high

(Maurin and LeDantec 1979). Commercial oyster landings by French farmers in 1990 were recorded at 150,000 metric tons, valued at $210 million U.S., of which *C. gigas* accounted for 92% (Grizel and Heral 1991). The present industry employs 35,000 individuals and occupies 2,000 ha of state leasing ground. Consumer acceptance has increased with production, and 97% of the crop is sold domestically, primarily in the shell to be consumed on the half-shell (Heral and Deslous-Paoli, 1991).

The industry is extensive in nature, and production is almost entirely dependent on natural spatfall (Goulletquer and Heral 1991). Oysters are cultured on intertidal racks, on hanging ropes, and on bottom. Bottom culture, which produced 20 tons of mature oysters for every ton of seed sown, resulted in the highest mean yields but also required the largest capital investment, primarily in dredging boats used for harvesting and to turn the oysters regularly with forks. *C. gigas* are grown below 1–3 m of water, at densities of 5 kg of oysters m^{-2} of leasing ground for ''pregrowing'' and 7 kg oysters m^{-2} of bottom space for ''maturing phase'' (Heral and Deslous-Paoli 1991). The gradual reduction in growth rate of Pacific oysters since 1972, when a market size of 70 g was reached in 18–20 mo, has been attributed to overcrowding via intensive spatfalls, resulting in a growth period of 2–5 y from seed to harvest (Maurin and LeDantec 1979). Oyster overstocking has also induced sedimentation of vast quantities of biodeposits, causing deterioration of shellfish grounds (Goulletquer and Heral 1991).

The Netherlands

O. edulis has been cultured on lease grounds in southwestern Holland since 1875 (Bol personal communication). A disastrous flood in 1953 in the same region prompted construction of barriers between the North Sea and the two estuaries that represented the major center of oyster and mussel culture in the Netherlands. The Storm Surge Barrier in the Oosterschelde (eastern Scheldt) has caused a reduction in tidal volume of 35%, whereas the Grevelingen estuary, to the north, has been completely embayed by a dam. The absence of tidal exchange in Lake Grevelingen resulted in high water temperatures (above 20°C for several weeks almost every summer) and favorable conditions for settlement. The lake was consequently used to produce *O. edulis* seed, which were grown to market size in the Oosterschelde where high current speeds and relatively low summer temperatures were favorable for fattening (Dijkema 1988). However, since 1981, *B. ostreae* has caused high mortality in European oysters, predominantly in yearlings of approximately 50 g (Bol personal communication).

After an extreme winter in 1962–1963 damaged 95% of the Dutch, European oyster crop, Dr. P. Korringa with the assistance of Mr. J. Bol (personal communication) of the Netherlands Institute for Fishery Investigations introduced *C. gigas* on an experimental scale to test the oyster's performance in Dutch waters. Small amounts of 10-mm *C. gigas* spat of Kumamoto and Miyagi strains were imported from Japan to the Oosterschelde and stocked in a shallow lease site. These oysters reached market size (100 g) in two growing seasons, and a decision was made to introduce *C. gigas* to the Oosterschelde on a commercial scale under the assumption that summer water temperatures would be too low for successful recruitment (Dijkema personal communication).

C. gigas has been imported to Holland regularly from France since 1964, yet not until the unusually hot summer of 1976 did natural spat recruitment occur (Mann 1983). Spawning and spatfall in subsequent, warm summers have been profuse, resulting in the establishment of wild, reeflike oyster banks on the sandflats of the intertidal zone and on the slopes of the flood barrier dikes (Bol personal communication, Dijkema personal communication). Sustained summer water temperatures of 21–22°C have resulted in extensive expansion of Pacific oysters in the Oosterschelde (Bol personal communication), and since 1986, *C. gigas* has been found incidentally in the Westerschelde to the south and Lake Grevelingen to the north (Dijkema personal communication). No diseases are known to have been introduced with Pacific oysters (Bol personal communication).

Although *O. edulis* is marketed at four to five times the price, devastation by *Bonamia* has resulted in the predominance of *C. gigas* cultivation, which is more labor intensive (Bol personal communication). Mussel shell, used as cultch, is dredged after spatfall, broken into shell pieces, and seeded for bottom culture below the mean low-water mark in the tidal area and also in deeper plots. Water temperatures of the Oosterschelde range from −3 to 24°C, and salinities vary between 28 and 30 ppt (Dijkema personal communication). A small commercial nursery has recently raised imported French, Pacific oyster seed to 10 mm in an upwelling system and to 35 mm (5 g) in suspended trays. These animals have not survived their final growth phase on bottom because their shells, which were thin compared with those of naturally recruited seed, made these hatchery-produced oysters more vulnerable to predation by starfish (Bol personal communication). Between 700 and 1,000 tons of *C. gigas* is produced each year by the Netherlands and sold primarily to Belgium and Germany but also to France (Dijkema personal communication).

The Pacific Northwest, United States

C. gigas was first introduced to the West Coast of the United States to supplement dwindling stocks of *Ostrea lurida,* the Olympic oyster, native to Washington. The decline of this fishery has been attributed to overharvesting, poor management, disease, and adverse winter weather (Chew 1979). At its peak in 1890, harvest of wild *O. lurida* produced in excess of 130,000 bushels before its subsequent, and rapid, decline (Clark and Langmo 1970). Olympic oysters required 4 y to reach their maximum size of only 50 mm and probably could not have fulfilled the needs of the Pacific Northwest, a region encompassing vast areas suitable for extensive oyster culture (Andrews 1980). Whether or not the introduction of Pacific oysters contributed to this native's decline is a matter of debate (Beattie 1983). *C. gigas* is more resistant to some environmental stresses and diseases, possibly enabling the exotic to outcompete Olympic oysters for space (Dinamani 1981). The hypothesis that chemicals released by *C. gigas* inhibit the setting of *O. lurida* has also been proposed (Chew 1979).

Adult *C. gigas* from Japan were first imported to Puget Sound, WA, by companies (Clark and Langmo 1970) and Japanese-American residents (Kincaid 1951) in 1902 after several attempts to introduce *C. virginica* between 1900 and 1902 proved unsuccessful (Chew 1979). Although these Pacific oysters suffered high mortality during transport, spat cultched to their shells survived well (Chew 1990). Large-scale culture of *C. gigas* in Washington was consequently established via imports of seed from Miyagi and Kumamoto prefectures (Chew 1979). In 1928, 40 cases were relayed to Willapa Bay, representing the first Japanese seed to be planted in U.S. waters. Willapa Bay received a subsequent shipment of 3,000 cases in 1929. Plantings in British Columbia, Oregon, and California soon followed (Chew 1987). By 1940, the production of shucked meats from Willapa Bay exceeded 3.8 million L (Sparks and Chew 1961).

During the 1970s, shipments of Japanese seed diminished because of the increased cost of shipping and the higher price of seed itself. In addition, the presence of naturalized, spawning populations of *C. gigas* in northern Hood Canal and southern Willapa Bay (Chew 1979) provided a local seed source as a consequence of the many years of introductions (Chew 1990). The industry in Washington has become almost entirely hatchery based (Chew 1991) because commercially feasible wild sets were obtained in only 7 of 10 y (Chew 1979). Private hatcheries produced larvae of Miyagi strain, which they set and dispersed as seed or sold directly to growers, who transferred the larvae to their own setting tanks. Remote setting of eyed larvae has been very successful in Washington, where in excess of 100,000 cases of seed were produced each year by this method in the late 1980s. Oyster larvae were well suited to distribution by shipment and could be set with a high rate of success by the experienced grower (Chew 1990).

Pacific oysters cultured on bottom was the chosen method in Washington, whereas off-bottom methods using rafts, racks, and stakes were tested and rejected because of increased costs. The high tidal range of 7–20 feet on the Pacific Coast exposes large areas of intertidal ground at low tide, many of which have proved suitable for culture (Glude and Chew 1980). *C. gigas* has been grown where water temperatures ranged from 8 to 22°C and salinities normally varied between 24 and 28 ppt but occasionally dropped to 5 ppt during periods of heavy rainfall. The species survived such reduced salinities for up to 2 wk with no signs of adverse affects (Chew personal communication). Larvae were remote set on shell clutch in plastic mesh bags that were opened at planting time when shells were spread on bottom and oysters were grown, extensively, to market size (Donaldson, personal communication) Growout time to market size varied between 2 and 4 y (Chew 1979). Common predators included starfish, crabs, birds, the oyster drill *Ceratostoma inornatum,* and the flatworm *Pseudostylochus ostreophagus,* introduced with *C. gigas* (Beattie 1983). Three methods have been used for harvest of the market-sized product including: removal of oysters by hand at low tide and use of drag (bag) dredges and hydraulic (escalator) dredges, both at high tide (Glude and Chew 1980).

C. gigas accounted for 98% of Washington's oyster production, which totaled 4.5 million kg, representing a market value of $28 million in 1991. The remaining 2% was shared by *O. lurida* and *O. edulis* (Chew personal communication). The vast majority of Pacific oysters were shucked, sorted into several size categories, and sold either fresh or frozen. The 5% that remained were marketed whole for consumption on the half-shell (Smith personal communication). *C. gigas* produced for the half-shell trade were grown on hard bottom, resulting in a milder flavor compared with those cultured on a muddy substrate (Glude and Chew 1980). Approximately 60% of the commodity has been marketed on the West Coast through the major distribution centers of Seattle, Portland, San Francisco, and Los Angeles. The remainder has been distributed across the United States and Canada (Smith personal communication).

The introduction of Japanese oysters to the Pacific Northwest of the United States has been relatively trouble-free in light of the extensive early shipments of both seed and adults. The pests transferred with these animals include the Japanese oyster drill *C. inornatum,* the turbellarian flatworm *P. ostreophagus,* and the macrophyte algae *Sargassum muticum* (Quayle 1969b). All of these organisms have negatively affected bivalve mollusks (Chew 1990).

During the 1960s and 1970s, major *C. gigas* mortalities occurred during the later summer months, resulting in a loss of 60–80% of the oysters on some beds. Particularly affected were those animals in their second year of growth, located in areas with poor circulation and temperatures that exceeded the normal range (Chew 1991) of 10–15°C (Smith personal communication). Extensive sampling followed by histological studies revealed no disease organisms, and physiological stress associated with spawning was initially blamed for the oyster losses (Chew personal communication, Perdue et al. 1981). *C. gigas* is an extremely fecund species of bivalve in which more than 50% of the body volume may be composed of gonad during the breeding season (Quayle 1988). However, more recently, nocardiosis, caused by the actinomycete bacterium *Nocardia* and resulting in raised green and yellow nodules on the mantle before fatality, was determined to be at least partially responsible for these recurring mortalities (Chew personal communication, Mann et al. 1991).

The United Kingdom

The introduction of *C. gigas* to the waters of the United Kingdom was made in a comparatively responsible manner and may serve as a model for introductions and transfers of aquatic species elsewhere. The first shipment of 76 adults from Pendrell Sound and Seymour Inlet, British Columbia, to the Ministry of Agriculture, Fisheries and Food (M.A.F.F.), Conwy, North Wales (Edwards, personal communication), was supplied by the Pacific Biological Station's Fisheries Research Board of Nanaimo, Canada, in June 1965 (Walne and Helm 1979): 16–18°C during summer (Helm personal communication). Additional broodstock was imported to the Conway Laboratory (Mann 1983) from the source cited above in 1972 and from Oregon in 1979 (Utting and Spencer 1992). The laboratory has been attempting to overcome the problems associated with a limited gene pool by regularly introducing new stocks. Shipments have consisted primarily of Miyagi strain, but Pacific oysters of Kumamoto prefecture, reputed to be slower growing while producing deeper shells, are being evaluated for potentially improved meat content. Although *C. gigas* grow, fatten, and undergo gonad development in British waters, natural recruitment is very limited because of low temperatures (Walne and Helm 1979).

The hatcheries of Great Britain have minimized the risk of introducing unwanted, accompanying species while producing Pacific oyster seed, the natural recruitment of which has been limited to sheltered bodies of water on England's southern coast. "No alien pathogens or parasites appear to have been associated with the introduction in contrast with the situation in France where seed and adults of foreign origin were directly relayed in coastal waters without prior quarantine" (Helm personal communication). During exceptionally warm summers, including those of 1989 through 1991, small numbers of naturally recruited spat occurred in shallow, embayed areas (Helm unpublished data; Utting and Spencer, 1992) like Emsworth Harbor, where water temperatures reached 23–24°C (Helm personal communication). These limited spatfalls have caused some concern regarding ecological implications (Edwards personal communication). The situation demands particularly close attention in an era of global warming (Helm personal communication).

Stringent legislation has significantly contributed to the precautionary nature of the introduction of *C. gigas* to Britain. The Molluscan Shellfish (Control of Deposit) Order of 1965, strengthened in 1974 and further amended in 1983, has prohibited the deposit, in any waters adjacent to England and Wales, of molluscan shellfish without a license granted by the M.A.F.F. (Helm unpubl.). Introduction of nonindigenous species for evaluation of culture potential has been permitted only through the quarantine facilities of the M.A.F.F. Fisheries Laboratory, Conwy (Utting and Spencer 1992).

The procedure followed by the M.A.F.F. Laboratory for introduction of non-native species has been quite involved. Imported broodstock were thoroughly cleaned and held in quarantine tanks, the effluent of which was collected in large-volume, outdoor, concrete tanks where it was sterilized by adding powdered sodium hypochlorite at a rate yielding 100 ppm free-chlorine. The treated water was held for a minimum of 24 h before being discharged into the sea (Spencer et al. 1977). Subsequent to spawning, the parent stock were destroyed by boiling and were buried on land (Utting and Spencer 1992). The Conwy Lab held F_1 juveniles in quarantine for 8 mo, during which time 200 animals were randomly sampled on four dates for histopathological examination. In the absence of adverse findings, the progeny were transferred to open waters for test culture by the M.A.F.F. A final sample was examined to reconfirm the population's health 4 mo later.

No shellfish were released for commercial culture until the M.A.F.F. staff was satisfied that the species had local culture potential and presented little or no risk of negatively affecting the environment (Helm unpubl.). Samples of commercially cultivated species have been periodically checked for diseases and parasites by British government staff. The adoption of these rigorous procedures has resulted in the production of only healthy *C. gigas* seed, which has been grown out within the United Kingdom and also distributed to Denmark and Germany (Helm personal communication).

The British *C. gigas* industry has been based on production by two hatcheries: Seasalter Shellfish in Kent and Guernsey Sea Farms in the Channel Islands (Helm personal communication), which have sold seed ranging in size from 2 to 20 mm (Spencer 1990). Seed were transferred from the hatchery to land-based or floating, upwelling, nursery systems and grown to 3–4 mm (0.01 g). Pacific oysters required some form of protection from wave action, siltation, and predation by crabs, whelks, and starfish until they reached a refuge size of 45 mm (10 g), at which time they could withstand the rigors of transplantation to unprotected bottom grounds. Floating trays were used to cultivate *C. gigas* through their first year of growth. Oysters smaller than 5 mm were stocked at densities of 0.02–0.2 g/cm^2 or 2.5 oysters/cm^2, whereas animals larger than 5 mm were maintained at densities not in excess of 0.5–1.0 g/cm^2 (Spencer 1990).

Growout took place primarily in plastic mesh bags fastened with rubber bands to intertidal trestles of steel or timber, but bottom culture has also been used (Edwards personal communication). *C. gigas* should be completely immersed during growout because Spencer et al. (1978) found that an inverse relationship existed between percentage of time exposed to air and percentage of growth increment, with growth ceasing when animals were exposed to air for 34% of the time. Pacific oysters have been successfully overwintered in deep seawater (Helm personal communication) or underground pits (Walne 1979). Market size of 90 mm (75 g) was attained in 2–4 y, depending on water temperature (Walne and Helm 1979). Temperature varied with location and season from 3 to 22°C, with some shallow areas experiencing 25°C. Salinities ranging from 25 to 35 ppt were common, with decreases to 15 ppt after heavy rainfalls (Edwards personal communication, Helm personal communication). Growers have expected 70% survival of first-year crops and subsequent *C. gigas* survival of 90% to market size (Spencer 1990).

The introduction of *C. gigas,* now the primary species of oyster cultured in the United Kingdom (Edwards personal communication), has resulted in a stable industry because of the excellent survival, relative ease of culture, and good marketability of the species (Helm personal communication). Commercial hatcheries produced over 100 million juvenile Pacific oysters in 1989 (Spencer 1990). Small and medium-sized growers have included individuals from all walks of life, many of whom have no background in fisheries' work (Helm personal communication). Producers have sold their oysters directly to outlets including restaurants, shellfish bars, hotels, and public houses (Spencer 1990). Helm (personal communication) called the production of approximately 1,000 tons of *C. gigas* per year "small," and Edwards (personal communication), who estimated the value of 1 year's harvest at $2 million U.S., added "but demand is growing."

Ireland

C. gigas was introduced to Ireland in 1969 from the quarantined stocks at the M.A.F.F. Laboratory in Conwy, North Wales, where the oysters were certified disease free. No foreign organisms (i.e., disease, pests, or parasites) have appeared subsequent to the introduction. All seed grown in Ireland has been hatchery produced by Seasalter Shellfish in Kent, South England, Guernsey Sea Farms in the Channel Islands, and two major hatcheries on the West Coast of Ireland. Growout techniques have mimicked those used in the United Kingdom, and the environmental conditions of Irish waters (temperature range, 3–33°C; salinity range, 17–34 ppt) were also similar. Pacific oysters reached a market size of approximately 100 g in three summer growing seasons, yet some growth occurred during the winter in milder areas. Spawning without consequent spatfall has occurred during hot summers. Although recruitment did not occur, the spawning of oysters negatively affected their marketability. However, the previously unprecedented event of natural *C. gigas* spat settlement was observed recently in a shallow, well-enclosed bay on the northwest coast. The establishment of a breeding population of Pacific oysters in Ireland is generally considered unlikely (Minchin personal communication).

The Irish Pacific oyster industry has continued to develop slowly, with an annual production in 1991 of approximately 1,500 tons (Minchin personal communication). However, a major challenge recently facing the producers has been the development of new markets (Aquaculture Ireland 1991, Grizel and Bailly 1991, Quaestus and BIM 1991). The predominant market for Irish *C. gigas* has been the United Kingdom, where demand for other species was very limited (Aquaculture Ireland 1991). The Board Iascaigh Mhara (BIM) (the Irish Seafisheries Board) recently commissioned Quaestus Ltd. to develop a market-oriented strategic perspective of the industry. Quaestus and BIM (1991) advised the Irish Pacific oyster growers to concentrate efforts on the domination of two segments of the U.K. market, including the catering business and the second-level (moderately priced) hotels and restaurants. In addition, the report advised the establishment of Irish-owned depuration, handling, and packaging facilities in England, along with a quality guarantee program to support promotional campaigns. Such campaigns would educate caterers and consumers on the handling, storage, opening, and presentation of the shellfish, while promoting oysters as a safe product of high quality by providing literature, samples, and press coverage incorporating a slogan for Irish oysters. BIM plans to follow up this report by providing advice and financial assistance to growers toward these goals (Quaestus and BIM 1991).

THE LEGAL ASPECTS OF NONENDEMIC INTRODUCTIONS

There exist both federal and state laws pertaining to introductions. The U.S. Federal Law that addresses the introduction of nonendemic species into the United States and across state lines is contained in the Lacey Act Amendments of 1981, Public Law 97–79. This law essentially requires compliance with state legislation and permitting requirements. Section 6071 of Title 12 of the Maine Revised Statutes Annotated (M.R.S.A.) authorizes the Commissioner of the Maine Department of Marine Resources (M.D.M.R.) to issue permits for ''possession, importation and introduction of organisms which will not endanger the indigenous marine life or its environment.'' Before granting a permit allowing the introduction of a species that has not previously been introduced under a M.D.M.R. permit, the Commissioner is required to hold a hearing.

The M.D.M.R. Regulation 24 stipulates that anyone who wishes to introduce shellfish or finfish must apply for a permit from and on forms supplied by the Commissioner. All of the East Coast of North America, south of New York state, as well as Willapa Bay, WA, and many other regions are considered quarantine zones for all species of shellfish, and all such species from these areas are presumed to carry infectious diseases, pests, or parasites unless the applicant demonstrates that the shellfish have been reared in a disease-free, closed system. Any permitted broodstock must be held in quarantine, within a hatchery, the effluent from which must be treated with chlorine at a free concentration of at least 50 ppm, at least 2 h after application before discharge. Daily records of chlorination procedures must be kept.

I.C.E.S. GUIDELINES FOR NONENDEMIC INTRODUCTIONS

The introduction of a nonendemic marine species to Maine could affect the waters of other states, as well as the Atlantic Provinces of Canada. Although neither the federal nor the state laws cited above require consultation with bordering nations or states, an international policy concerning introductions has been endorsed by member nations, including countries bordering the North Atlantic. The International Council for Exploration of the Seas (I.C.E.S.) has developed a ''Code of Practice'' for the introduction of marine species.

The essence of the Code may be summarized as follows: ''The species proposed for introduction should be studied in its native habitat. The study should include known diseases, pests and predators, food habits, and biotic potential. To be included would be consideration of pathological, environmental, and genetic implications of the introduction. The study should extend over several years, and the results should be examined by a committee of specialists. If a decision is made to proceed, then a brood stock should be established in quarantine in the recipient country. Only the F_1 generation should be introduced to open waters, provided that no problems emerge.'' (Sinderman et al. 1992).

REDUCING THE ECOLOGICAL RISKS OF INTRODUCTION OF *C. GIGAS* TO MAINE

Inhibition of Reproduction Through Geographic Location

One means of reducing the risk that a nonendemic species will reproduce and establish a resident population is to introduce the animal only in locations where, historically, environmental conditions have never been compatible with those required for procreation. *C. gigas* was reported to spawn at water temperatures ranging from 16 to 30°C and salinities of 10–30 ppt. However, Pacific oyster larval survival required sustained temperatures of 18°C or above and salinities of at least 19 ppt (Mann et al. 1991). These environmental conditions had to be maintained for at least 2 wk before the pelagic larvae completed metamorphosis and became sessile animals. This relatively high required water temperature may have been the reason that no successful *C. gigas* larval recruitment has been reported in Maine, despite numerous introductions over many years. However, in those instances where Pacific oysters were introduced incidentally with other seed varieties, the fact that *C. gigas* were reared at extremely low densities may have been responsible for inhibiting the synchronized release of gametes among males and females (Clime personal communication).

Coastal water temperature charts are produced on a weekly basis by the U.S. National Oceanic and Atmospheric Administration (N.O.A.A.). Such charts, specific to the coastline of the northeastern United States for the months of June, July, August, and September in 1989, 1990, and 1991, were obtained and referred to in writing this report. According to these charts, temperatures in the Gulf of Maine between Belfast and Eastport never reached the critical minimum of 18°C, although water temperatures did rise to 17°C at several locations including Englishman Bay (8/21/90), Frenchman Bay (8/14/90 and 8/28/90), Penobscot Bay (7/15/89), and Pleasant Bay (9/12/89). In addition, water temperatures of shallow, protected inlets were probably higher than water temperatures in the locations documented. However, the fact that these temperatures were measured at the surface, whereas *C. gigas,* if introduced, would be cultured on bottom where cooler conditions usually prevail, should be noted.

TABLE 1.

Temperature and salinity ranges of adults of *Crassostrea* species.

	Temperature (°C)		Salinity (ppt)	
Species	Growth	Spawning	Spawning	Growth
C. virginica	5–34 (28–32)	18–25 (23)	>5 (12–27)	>8
C. gigas	3–35 (11–34)	16–34 (20–25)	10–42 (35)	10–30 (20–30)

Optimal ranges given in parentheses. From Mann et al. 1991.

Technical Methods of Inhibiting Reproduction

Triploidy

Triploidy is a genetic state produced artificially in cultured finfish and shellfish resulting in three sets of chromosomes instead of the normal two contained within the nucleus of each of the animal's cells. This odd number of chromosome sets prevents triploids from accomplishing normal meiosis, making them functionally sterile (Purdom 1983). The consequent reduced gonadal development in triploid oysters is advantageous to aquaculturists when fecundity affects survival, growth, or product quality in a negative way. Increases in mortality may be correlated with the summer spawning season when oysters, particularly the extremely fecund *C. gigas,* invest the majority of their energy budget in gamete production (Allen and Downing 1986). This energy is no longer available to support somatic growth, which is thus reduced during the summer when environmental conditions are most conducive to growth. Stored glycogen, which increases the palatability of the oyster, is replaced by gonad, ramifying throughout the somatic tissue and rendering the oysters less marketable at the time of year when demand is often highest. Allen and Downing (1991) demonstrated that both consumers and growers preferred the flavor, texture, and overall quality of firm, glycogen-rich triploids over softer, gravid diploids in blind taste tests ($p < 0.001$). The primary advantage of triploidy to the Maine eastern oyster industry appears to be summer marketability because of reduced gonadic development (Shatkin 1992) and an implicit increase in meat yield (Walker personal communication).

In this context, triploidy could be used to reduce the number of reproductively competent Pacific oysters introduced to the Gulf of Maine to a minimum. The hatchery-based oyster culture industry of Maine is suited to the production of triploids. Triploid *C. gigas* account for approximately 10% of the oysters produced in the Pacific Northwest (Woog 1991). Over 50% of the oysters being planted by Coast Seafoods, Washington, in 1993 were triploid (Donaldson personal communication). Meiosis of fertilized oyster eggs may be inhibited in the hatchery through chemical shock with the cytostatic chemical cytochalasin B (CB). Because this fungal metabolite is hydrophobic, it is dissolved in dimethyl sulfoxide (DMSO) as a carrier solution before treatment (Allen 1987).

To produce triploids, eggs are treated with CB after fertilization. Fertilized eggs were sampled continuously to monitor development microscopically, and treatment was begun when approximately 50% of the developing eggs exhibited first polar bodies (Allen and Bushek 1992, Barber et al. 1992), thus exposing most eggs to CB during the extrusion of polar body II. Fertilized eggs were exposed to concentrations of 0.5–1.0 mg CB/L for 10–20 min in filtered seawater held at a constant temperature. After treatment, eggs were screened onto an appropriate sized mesh and resuspended in 0.01–0.1% DMSO to remove residual CB; then, larvae were hatchery reared in a normal fashion (Allen et al. 1989). CB has been approved by the U.S. Food and Drug Administration for the production of triploid oysters according to the protocol established by Allen and Downing (1986).

The results of a given CB treatment—the percentage of triploidy in a batch of oysters—may be assessed by several different techniques, including flow cytometry, which has proved to be both fast and accurate (Allen et al. 1989). The cells of both hemolymph and tissue, taken from spat and adult oysters, have been used for flow cytometric assessment of ploidy level in mollusks (Allen 1983). Straight hinge larvae (48 h old) may also be assayed via flow cytometry (Allen and Bushek 1992). Such early determination of treatment success allows hatcheries to avoid wasting time and space rearing batches of oyster larvae with low yields of triploids (Beaumont and Fairbrother 1991). Flow cytometry of larvae often yields a higher initial assessment of percent triploidy than the actual proportion of polyploids among the spat (e.g., triploidy in larvae—75% percent, triploidy in spat—60%) (Allen personal communication).

Treatment of *C. gigas* eggs with CB has repeatedly yielded triploidy in spat determined to be 100% via flow cytometry (Allen et al. 1989, Allen and Downing 1986). However, the possibility remains that fertile diploid animals exist within a group of oysters assessed to be 100% triploid, yet merely escaped sampling for assay of ploidy level. Although 100% triploidy may be verified in experimental trials by assaying every individual oyster, such complete analysis is simply not realistic for commercial purposes (Allen personal communication). Commercial hatcheries in the Pacific Northwest obtain 90% triploidy on average from a given CB treatment (Donaldson personal communication).

In June 1993, after more than 2 y of controversy, an experiment using triploid *C. gigas* was initiated by the Virginia Institute of Marine Science (VIMS) in the York River, VA, with a permit from the Virginia Marine Resources Commission. Researchers intended to determine whether Pacific oysters were resistant to MSX and dermo, two parasitic diseases that have decimated the native populations of *C. virginica* (Blankenship 1994). If *C. gigas* were found to be disease resistant, perhaps information concerning how they survived could be used to increase disease resistance in native populations of American oysters.

On June 29, 1993, trays containing 200 Pacific oysters and 400 American Oysters were placed in the York River. All *C. gigas* were treated with CB at Rutgers University's Haskin Shellfish Research Laboratory to induce triploidy and presumed sterility. Before the experiments, the triploid status of each Pacific oyster used was confirmed by flow cytometric assay of blood samples at the Rutgers Laboratory. Oysters were periodically removed from the York River during the study for disease as well as ploidy analysis. In October 1993, one individual *C. gigas* tested was found to be diploid. Examination of the remaining 85 oysters revealed that 20% were mosaics, i.e., contained both triploid and diploid cells. These results suggested that the animals were in the process of reverting to diploidy. Although the water in the York River was too cold to stimulate reproduction at the time that the reversion took place, the experiment was terminated by the researchers (Blankenship 1994). VIMS "does not support the introduction of non-native species as an alternative to restoration of natural populations of *C. virginica,* or as a substitute in the public fishery" (Taylor unpublished data).

As of January 1996, VIMS researchers were seeking permission from the state of Virginia to resume experiments with foreign oysters in the Chesapeake Bay. A 4-y project has been proposed using all four strains of Pacific oysters to determine which would be best suited for the Chesapeake. The "controlled experiments" would examine growth, reproduction, and disease resistance under a variety of environmental conditions (Aquaculture News 1996).

Tetraploidy

Chromosome set manipulation technologies similar to those used to induce triploidy have recently been applied to the investigation of molluscan tetraploid production. Viable, female, tetraploid oysters would spawn diploid eggs, which when fertilized with normal sperm, would yield 100% triploid progeny. Guo (1991) has attempted to induce tetraploidy in *C. gigas* using four approaches: meiosis I blocking, polar body I blocking, cell fusion, and gynogenetic egg activation. All of these methodologies produced tetraploids; however, none of the tetraploids survived past larval stage. The inviability of the induced tetraploids could not be satisfactorily explained by defects caused by induction treatments, and the hypothesis was proposed that inviability may be caused by a cell deficiency. Further studies are necessary to determine conclusively that tetraploidy is lethal in Pacific oysters.

Although molluscan tetraploidy research is not currently ongoing, Dr. Ximing Guo (personal communication) believes that two methods of producing tetraploids, using gynogenesis (all chromosomes obtained from the mother) and triploid eggs, deserve further investigation. Gynogenetic tetraploids may be produced by inhibiting both polar bodies I and II in developing eggs. These eggs could metamorphose into tetraploid animals if fertilized with sperm that has been treated with ultraviolet light, which destroys the DNA contributed by the male gamete. Further research is required in order to perfect this ultraviolet irradiation treatment technique. Additional research should also focus on the production of tetraploids by fertilizing triploid eggs with normal, haploid sperm, followed by the blocking of polar body I extrusion.

Biotechnology

Biotechnology might offer the prospect of establishing 100% sterility among desired populations of mollusks in the future. Normally, genes are transcribed or copied from one strand of a section of double-stranded DNA as a plus or sense strand of messenger RNA. This mRNA is in turn translated into a functional protein within the organism. One possible approach to assuring molluscan sterility is manipulation of the genetic material that codes for a particular protein. Through gene splicing, a piece of DNA could be inserted in the reverse orientation, which would be transcribed as antisense RNA. This minus strand would be complementary to the messenger but would not code for any gene product or protein. The antisense would form a complementary complex with the plus strand of mRNA, preventing translation of the messenger into a protein (Shatkin personal communication). This technique would be particularly applicable in the case of protein hormones required for gametogenesis (Allen personal communication).

Hormones responsible for the stimulation of gametogenesis and the genes that code for these neuropeptides in *Mollusca* are currently under investigation. Genes encoding for egg-laying hormones and the neurons that control egg laying have been identified in gastropod mollusks among both the *Aplysiidae* and the *Lymnaeidae* (Van Minnen et al. 1992). The egg-laying hormone gene is expressed in the neuroendocrine bag cells of the central nervous system in the marine mollusc *Aplysia.* Egg laying is induced and coordinated in this snail by peptide products of the egg-laying hormone (Painter et al. 1989). The neuroendocrine caudodorsal cells of the freshwater snail *Lymnaea stagnalis* control egg laying and associated behaviors (Jansen et al. 1985) by releasing at least nine neuropeptides encoded by a small multigene (Van Minnen et al. 1989), including the ovulation hormone (Schmidt and Roubos 1989). When this pond snail is parasitized by *Trichobiharzia ocellata,* a peptidergic factor called schistosomin (Hordijk et al. 1991b), released from the central nervous system, counteracts the bioactivity of a number of gonadotropic hormones causing inhibition of the reproduction activities in infected snails (Hordijk et al. 1991a). In the bivalve *M. edulis,* progesterone levels have been correlated with regulation of gametogenesis in both males and females (Reis-Henriques and Coimbra 1990).

The possibility exists that an aquaculture industry could use gene-splicing technology in the future to produce sterile shellfish. A gene that codes for a specific protein hormone necessary for gametogenesis would be identified and inserted in a reverse orientation into the genome of the broodstock. In addition, the normal gene signal sequence or promoter for gene expression would be replaced with a promoter inducible by a particular compound such as a simple sugar. In the absence of this inducer or sugar, the reverse gene would be silent and the animals would reproduce. However, after treatment with the inducer, the minus strand would be made and prevent production of the necessary hormone, resulting in sterility (Shatkin, personal communication). Thus, the broodstock would be fertile, whereas the progeny, after treatment, would be 100% sterile.

RATIONALE AGAINST INTRODUCTION OF C. GIGAS TO MAINE

The Ecological Implications of Introducing the Pacific Oyster

The culture of exclusively putative triploid Pacific oysters, restricted to Maine waters that have historically never reached critical minimum temperatures required for spawning and successful recruitment, is not a guarantee that successful reproduction would not occur. If spawning and successful recruitment were to occur, the establishment of a resident population of Pacific oysters in the Gulf of Maine could potentially result in serious effects to marine ecology and established fisheries on the coast of Maine and ultimately elsewhere. In a worse-case scenario, Pacific oysters could find a niche in hard-bottom subtidal and rocky intertidal areas and establish reefs, displacing habitat and disrupting endemic ecology in these zones. *C. gigas* could also outcompete *C. virginica, M. arenaria,* and *M. edulis* for space, building reefs where these native species existed and resulting in depletion of available planktonic food for consumption by these commercially important filter feeders. Finally, Pacific oyster spat could settle on and foul the shells of eastern oysters, soft-shelled clams, blue mussels, and European oysters, reducing the market value of these crops.

Diseases Associated With the Pacific Oyster

Mann et al. (1991) have provided a complete description of organisms associated with the Pacific oyster that represent actual or potential agents of disease in bivalve mollusks. The researchers summarized their characterizations with the following: "quarantine of broodstock in a hatchery and the use of first generation offspring for any field studies, that is compliance with I.C.E.S. 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." The viruses and bacteria that may serve as vertical vectors of disease transfer are briefly described below, along with any reported methods of diagnosis.

Viral Diseases

Viral diseases reported from *C. gigas* include oyster velar virus disease (OVVD), HIV, and GNV. OVVD has occurred in Willapa

Bay and Puget Sound in Washington, affecting Pacific oyster larvae greater than 150 Êm in shell height (Elston and Wilkinson 1985) and resulting in hatchery mortalities (Leibovitz et al. 1978). The virus has developed in the cytoplasm of epithelial cells of the velum, causing lesions (Comps 1988). Light or electron microscopic observation revealed detached, necrotic velum and copious mucus being regurgitated. General necrosis of the velum and mantle preceded necrosis of other soft tissues (Johnson 1984). Both HIV and GNV were implicated in the mass mortalities of *C. angulata* in France during the 1970s, discussed earlier in this report. GNV caused ulceration of the gills, resulting in inflammation, whereas HIV induced cytoplasmic lesions in the hemocytes and injured interstitial tissues (Comps 1988). No techniques for diagnosing these viruses have been established, but the development of cell cultures could allow for their isolation and provide large quantities of virus for the determination of immunological parameters (Ford personal communication).

Bacterial Diseases

The reported bacterial diseases associated with Pacific oysters were bacillary necrosis, Pacific oyster nocardiosis, and rickettsiae. Bacillary necrosis was caused by opportunistic pathogens known as vibrios, which were free living, requiring conditions favorable to their proliferation in order to cause vibriosis in both larval and juvenile mollusks (Elston 1984). These bacteria are naturally present in seawater, so no danger of introduction exists (Mann unpubl.). Signs of bacillary necrosis in larvae including reduction in motility, extension of foot or velum, and swarming have been observed macroscopically (Lauckner 1983). Staining with trypan blue revealed detachment of mantle epithelial cells (Elston et al. 1982). Affected juvenile oysters displayed liquefaction of the ligament and growth of bacteria into the mantle, when examined histopathologically. Disease presence in juvenile cultures was also recognized by a reduction in growth rate and a loss of coloration (Elston 1984).

Nocardiosis, characterized earlier in this report, has resulted in gaping or weak shell closure in affected animals. The mantle was slightly discolored or contained yellow, green, or brown raised nodules. Characteristic histopathological changes included an infiltration of hemocytes, surrounding aggregates of Gram-positive bacteria of the genus *Nocardia* (Friedman et al. 1991). Rickettsiae have been identified as obligate intracellular parasites found in the cytoplasm of digestive diverticula epithelial cells of many bivalve mollusks (Lauckner 1983). They have not been known to cause mortality (Mann et al. 1991). This procaryotic organism has been found repeatedly in the eastern oysters, blue mussels, and soft-shelled clams of Maine and has been observed in stained histological sections as dark, irregular masses located in the epithelial cells of the digestive diverticula (Sherburne personal communication).

Potential Interaction With the Eastern Oyster

Intergeneric interactions between *C. gigas* and all of the species listed above, with the exception of *C. virginica,* have been documented in locations where Pacific oysters have been introduced. Pacific oysters grow faster than eastern oysters (Hickey 1979) and would probably outcompete *C. virginica* if the two species were to overlap geographically (Sutherland and Osman 1991). *C. gigas* would not pose a genetic threat to *C. virginica* because all attempts to produce hybrid adults have been unsuccessful. The reproductive potential of both species may be reduced because gametes of the two species do combine to produce nonviable progeny (Allen et al. in press).

Potential Interaction With the Soft Shelled Clam

Mya arenaria represents an important wild fishery in Maine. In 1991, 1,702 commercial shellfish licenses were sold to diggers of soft-shelled clams (Lewis personal communication). In Washington, *M. arenaria* was introduced incidentally with *C. virginica* around 1900 and has established itself in Hood Canal and Puget Sound. However, despite the fact that *M. arenaria* successfully reproduces at water temperatures between 12 and 15°C (Laursen 1966), establishing itself earlier in the season than *C. gigas,* competition with *C. gigas* limits the clam to only the very softest substrates where Pacific oysters cannot survive. In areas where hard bottom coincides with water temperatures high enough for *C. gigas* larval recruitment, Pacific oysters create a ''carpet'' of spat, outcompeting *M. arenaria* for food and space (Bonacker personal communication).

Potential Interaction With the Blue Mussel

The annual value of the total landings of cultured and captured blue mussels in Maine, averaged over the years 1984 through 1991, was $1.6 million (Morril personal communication). These harvests represented 86% of the mussels landed in the United States during the 7-y period (Hurst, personal communication). On the North Island of New Zealand (Dinamani 1991) and in Washington (Bonacker personal communication), *M. edulis* is considered a fouling organism by individuals who culture *C. gigas.* However, in the Oosterschelde, Holland, Pacific oysters are considered a pest by mussel growers. Fouling of *M. edulis* by *C. gigas* in the Netherlands reduces market value of the mussels and has resulted in restricted transfer of mussels to the North Sea (Dijkema personal communication).

Potential Interaction With the European Oyster

When the two species simultaneously occupy a body of water, Pacific oysters are generally not considered a competitive threat to the subtidal European oyster. *C. gigas* and *O. edulis* are cultured side by side in England (Helm personal communication) and Ireland (Minchin personal communication), where spawning of Pacific oysters is a rare event, and no interaction between the genera are reported. However, in the Netherlands, Pacific oysters threaten cultivated beds of European oysters and must be actively removed from these culture areas (Mann 1983).

Predators

The abundance of the Pacific oyster, if introduced to Maine, would probably be controlled by many of the same animals that prey on eastern oysters. Spat of *C. gigas* were reported to have softer shells than *C. virginica* by Sutherland and Osman (1991) and, consequently, could suffer higher mortality via predation. Glude (1971) reported a 40% mortality in cultured Pacific oysters in Maine as the result of predation by starfish. The species that would be likely to act as agents of biological control of *C. gigas* in Maine include the seastars *Asterias forbesi* and *Asterias vulgaris* in the intertidal zone, the green crab *Carcinus maenas* in the intertidal and subtidal zones, the rock crab *Cancer irroratus,* benthic feeding fish, and lobsters in the subtidal zone, as well as black ducks, eider ducks, and wading birds (Beal personal communication).

Glude, J. 1971. Recent developments in shellfish culture on the U.S. West coast. *Proc. 1st U.S.-Japan Meeting Aquacult.* 388:89–96.

Glude, J. & K. Chew. 1980. Shellfish aquaculture in the Pacific Northwest. Proceedings of the North Pacific Aquaculture Symposium pp. 291–304.

Goulletquer P. & M. Heral. 1991. Aquaculture of *Crassostrea gigas* in France. pp. 13–19. *In:* J. Sutherland and R. Osman (ed.). The Ecology of Crassostrea gigas in Australia, New Zealand, France and Washington State. Maryland Sea Grant College, MD.

Grizel, H. 1988. Introduction en France de l'huitre creuse *Crassostrea gigas* ICES Mini 4:8 pp.

Grizel, H. & D. Bailly. 1991. A biological and economic assessment of the Pacific oyster industry in Carlingford Lough. Special Report of the Carlingford Lough Aquaculture Association Limited 59 pp.

Grizel, H. & M. Heral. 1991. Introduction into France of the Japanese oyster (*Crassostrea gigas*). *J. Conseil* 47:399–403.

Guo, X. 1991. Studies in tetraploid induction in the Pacific oyster *Crassostrea gigas* (Thunberg). Ph.D. Thesis, University of Washington, Seattle, WA. 168 pp.

Heral, M. & J. Deslous-Paoli. 1991. Oyster culture in European countries. pp. 153–190. *In:* W. Menzel (ed.). Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Inc. Boca Raton, FL.

Hickey, J. 1979. Culture of the Pacific oyster, *Crassostrea gigas,* in Massachusetts waters. pp. 129–148. *In:* R. Mann (ed). Exotic Species in Mariculture. The MIT Press, Cambridge, MA.

Holliday, J. & J. Nell. 1987. The Pacific oyster in New South Wales. Dept. of Ag., New South Wales. Agfact F2.1.3:4 pp.

Hordijk, P., R. Ebbernik, M. DeJong-Brink & J. Joosse. 1991a. Hormones in a freshwater snail. *Eur. J. Biochem.* 195:131–136.

Hordijk, P., H. Schallig, R. Ebberink, M. DeJong-Brink & J. Joosse. 1991b. Primary structure and origin of schistosomin and anti-gonadotropic neuropeptide of the pond snail *Lymnaea stagnalis. Biochem. J.* 279: 837–842.

Imai, T. & S. Sakai. 1961. Study of breeding Japanese oyster *Crassostrea gigas. Tohoku J. Agricult. Res.* 12:125–171.

Jansen, R., A. Maat & N. Bos. 1985. Membrane mechanism of neurocrine caudodorsal cell inhibition by the ring neuron in the pond snail *Lymnaea stagnalis. J. Neurobiol.* 16:15–26.

Johnson, P. 1984. Viral diseases of marine invertebrates. *Helgolander wissenschaffliche Meeresuntersuchungen* 37:65–98.

Kincaid, T. 1951. The oyster industry of Willapa Bay, Washington. The Tribute, Ilwaco, Washington. 45 pp.

Lauckner, G. 1983. Diseases of mollusca: bivalvia. pp. 477–879. *In:* O. Kinne (ed.). Disease of Marine Animals Volume II. Biologische Anstalt. Helgoland, Hamburg, Germany.

Laursen, D. 1966. The genus *Mya* in the Arctic Region. *Malacologia* 3:399–418.

Leibovitz, L., R. Elston, V. Lipovsky & J. Donaldson. 1978. A new disease of larval Pacific oysters (*Crassostrea gigas*). pp. 603–615. Proceedings of the 9th Annual Meeting World Mariculture Society, Atlanta, GA.

Loosanoff, V. 1965. The American or eastern oyster. United States Fish and Wildlife Service Circular 205:36 pp.

Maine Aquaculture Innovation Center. 1990. An aquaculture development strategy for the state of Maine. 16 pp.

Mann, R. 1979. Exotic species in aquaculture: an overview of when, why and how. pp. 331–354. *In:* R. Mann (ed.). Exotic Species in Mariculture. The MIT Press, Cambridge, MA.

Mann, R. 1983. The role of introduced bivalve mollusc species in mariculture. *J. World Maricult. Soc.* 14:546–559.

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

Maurin, C. & J. LeDantec. 1979. The culture of *Crassostrea gigas* in France. pp. 106–122. *In:* R. Mann (ed). Exotic Species in Mariculture. The MIT Press, Cambridge, MA.

McAlice, B. 1981. On the Post-glacial History of *Acartia tonsa* (Copepoda: Calanoida) in the Gulf of Maine and the Gulf of St. Lawrence. *Mar. Biol.* 64:267–272.

Myers, A. 1965. The Damariscotta oyster shell heaps: some further considerations. B.A. Thesis, Princeton University, Princeton, NJ. 34 pp.

National Sea Grant College Program, NOAA. 1990. A plan addressing the restoration of the American oyster industry. Sea Grant Publication VSG-90-02. 22 pp.

Packie, R., H. Hidu & M. Richmond. 1975. The suitability of Maine waters for culturing American and European oysters. Maine Sea Grant Technical Report 10:30 pp.

Painter, S., A. Gustavson, V. Kalman, G. Nagle & J. Blankenship. 1989. The excitatory effects of freshly deposited egg cordons. *Behav. Neural Biol.* 51:222–236.

Parameswar, D. 1991. Introduced Pacific oysters in New Zealand. pp. 9–11. *In:* J. Sutherland and R. Osman (eds.). The Ecology of *Crassostrea gigas* in Australia, New Zealand, France and Washington State. Maryland Sea Grant College, MD.

Pauley, G., B. VanDerRaay & D. Troutt. 1988. Pacific oyster. United States Fish and Wildlife Service Biological Report 82:29 pp.

Perdue, J., J. Beattie & K. Chew. 1981. Some relationships between gametogenic cycle and summer mortality phenomenon in the Pacific oyster (*Crassostrea gigas*) in Washington state. *J. Shellfish Res.* 1: 9–16.

Pollard, D. & P. Hutchings. 1990. A review of exotic marine organisms introduced to the Australian region. II. invertebrates and algae. *Asian Fish. Sci.* 3:223–250.

Purdom, C. 1983. Genetic engineering by the manipulation of chromosomes. *Aquaculture.* 3:287–300.

Quaestus Ltd. and Board Iascaigh Mhara (BIM). 1991. A strategy for the development of the Irish Pacific oyster industry. BIM Report. 121 pp.

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

Quayle, D. 1969a. Pacific oyster culture in British Columbia. *Fish. Res. Bd. Can. Bull.* 168:68 pp.

Quayle, D. 1969b. Pacific oysters culture in British Columbia. *Fish. Res. Bd. Can. Bull.* 169:193 pp.

Quayle, D. 1988. Pacific oyster culture in British Columbia. *Can. Bull. Fish. Aquatic Sci.* 218:241 pp.

Reis-Henriques, M. & J. Coimbra. 1990. Progesterone levels in *Mytilus edulis. Comp. Biochem. Physiol.* 95A:343–348.

Ruge, J. 1879. The oyster and oyster beds of Florida. *Bull. U.S. Fish. Commiss.* 561:289 pp.

Russell, J. 1979. The Damariscotta River: oysters and aquaculture. Damariscotta-Newcastle Rotary Club, Damariscotta, ME. 32 pp.

Schmidt, E. & E. Roubos. 1989. Quantitative immunoelectron microscopy and tannic acid study of dynamics of neurohemal and non-synaptic peptide release by the caudodorsal cells of *Lymnaea stagnalis. Brain Res.* 489:325–337.

Shatkin, G. 1992. Production and growth of yearling triploid American oysters (*Crassostrea virginica*). M.S. Thesis, University of Maine, Orono, ME. 95 pp.

Sinderman, C., B. Steinmetz & W. Hershberger. 1992. Introductions and transfers of aquatic species: introduction. *Int. Council Expl. Sea Mar. Sci. Symp.* 194:1–2.

Sparks, K. & K. Chew. 1961. Preliminary report on growth and survival of the Pacific oyster in Washington waters. University of Washington, College of Fisheries, Seattle. 8 pp.

Spencer, B. 1990. Cultivation of Pacific oysters. Laboratory Leaflet 63. M.A.F.F., Lowestoft, England. 47 pp.

Spencer, B., Helm & P. Dare. 1977. Recommended quarantine measures for marine molluscs. Tech. Rep. M.A.F.F. Direct. Fish. Res. Lowestoft, England 32:7 pp.

Spencer, B., D. Key, P. Millican & M. Thomas. 1978. The effect of intertidal exposure on the growth and survival of hatchery-reared Pacific oysters (*Crassostrea gigas* Thunberg) kept in trays during their first ongrowing season. *Aquaculture.* 13:191–203.

Sutherland, J. & R. Osman, 1991. Synopsis of the oyster ecology workshop: *Crassostrea gigas*. Maryland Sea Grant College, MD. 8 pp.

Thomson, J. 1952. The acclimatization and growth of the Pacific oyster *Cryphaea gigas* in Australia. *Aust. J. Mar. Freshwater Res.* 3:64–73.

Thomson, J. 1959. The naturalization of the Pacific oyster in Australia. *Aust. J. Mar. Freshwater Res.* 10:144–149.

Townsend, D. 1991. Influences of oceanographic processes on the biological productivity of the Gulf of Maine. *Rev. Aquat. Sci.* 5:211–230.

Utting, S. & B. Spencer. 1992. Introductions of marine bivalve molluscs into the United Kingdom for commercial culture-case histories. *Int. Council Expl. Sea Mar. Sci. Symp.* 194:84–91.

Van Minnen, J., R. Dirks, E. Vreugdenhil & J. VanDiepen. 1989. Expression of the egg-laying hormone genes in peripheral neurons and exocrine cells in the reproductive tract of the mollusc *Lymnaea stagnalis*. *Neuroscience*. 33:35–46.

Van Minnen, J., H. Schallig & M. Ramkema. 1992. Identification of putative egg-laying hormone containing neuronal systems in gastropod molluscs. *Gen. Compar. Endocrinol.* 86:96–102.

Walne, P. 1979. Culture of bivalve molluscs: 50 years experience in Conwy. Fishing News Books, Ltd. Surrey, England. 189 pp.

Walne, P. & M. Helm. 1979. Introduction of *Crassostrea gigas* into the United Kingdom. pp. 83–105. *In:* R. Mann (ed.). Exotic Species in Mariculture. The MIT Press, Cambridge, MA.

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

Westley, R. 1956. Retention of Pacific oyster larvae in an inlet with stratified waters. *Fish. Res. Papers Wash. Dept. Fish.* 1:25–31.

Woog, A. 1991. Sexless oysters and self-tipping hats. Sasquatch Books, Seattle, WA. pp. 137–141.

Zabaleta, A. I. & B. J. Barber. 1996. Prevalence, intensity, and detection of Bonamia ostreae in *Ostrea edulis* L. in the Damariscotta River Area, Maine. *J. Shellfish Res.* 15: in press.

PERSONAL COMMUNICATIONS CITED

Allen, S. Associate Professor, Marine and Coastal Science, Haskin Shellfish Research Laboratory, Port Norris, NJ.

Bassano, L. Extension Agent, Washington County, Machias, NE.

Beal, B. Assistant Professor, Marine Ecology, University of Maine, Machias, ME.

Beyea, W. Research Assistant, Maine Rural Development Council, Orono, ME.

Bol, J. Emeritus Senior Technician, Aquaculture, Netherlands Institute for Fishery Investigations, Yerseke, Netherlands.

Bonacker, G. President, L.A. Bonacker and Assoc., Swans Island, ME.

Castagna, M. Emeritus Professor, Virginia Institute of Marine Science, Wachapreague, VA.

Chapman, S. Aquaculture Specialist, Darling Marine Center, University of Maine, Walpole, ME.

Chew, K. Director, Administrative Office, The Western Regional Aquaculture Center and Professor of Shellfisheries, School of Fisheries, University of Washington, Seattle, WA.

Clime, R. President, Dodge Cove Marine Farm, Newcastle, ME.

Dijkema, R. Research Scientist, Netherlands Institute for Fishery Investigation, Yerseke, Netherlands.

Donaldson, J. Quilcene Area Manager, Coast Seafoods, Quilcene, WA.

Edwards, E. Director, The Shellfish Association of Great Britain, London, England.

Ford, S. Associate Professor, Marine and Coastal Science, Haskin Shellfish Research Laboratory, Port Norris, NJ.

Guo, X. Post-Doc, Haskin Shellfish Research Laboratory, Port Norris, NJ.

Helm, M. President, Michael M. Helm and Assoc., Halifax, Nova Scotia, Canada.

Hidu, H. Emeritus Professor, Department of Animal, Veterinary and Aquatic Sciences, University of Maine, Orono, ME.

Hurst, J. Director, Fisheries Health, Maine Department of Marine Resources, West Boothbay Harbor, ME.

Kirkley, J. Marine Economist, Virginia Institute of Marine Science, Gloucester Point, VA.

Lewis, R. Statistician, Maine Department of Marine Resources, Augusta, ME.

Lipton, D. Professor, Agricultural Economics, University of Maryland, College Park, MD.

Mant, R. Shellfish Warden and Water Resource Coordinator, Brewster, MA.

Minchin, D. State Biologist on Marine Introductions, Fisheries Research Center, Dublin, Ireland.

Mook, W. President, Mook Sea Farms, Walpole, ME.

Morril, R. Maine State Supervisor, National Marine Fisheries Service Statistics, Portland, ME.

Richmond, M. Former President, Maine Coast Oyster Company, Blue Hill, ME.

Scully, K. Aquaculture Technician, Darling Marine Center, University of Maine, Walpole, ME.

Shalfont, J. Vice President, Sales, Great Eastern Mussel Farms, Inc., Tenants Harbor, ME.

Shalpack, J. General Manager, Legal Seafoods, Boston, MA.

Shapman, L. Professor, Environmental Economics, Virginia Technical Institute, Blacksburg, VA.

Shatkin, A. Director, Center for Advanced Biotechnology and Medicine, Piscataway, NJ.

Sherburne, S. Water Quality Coordinator, Maine Department of Marine Resources, West Boothbay Harbor, ME.

Smith, T. Director, Pacific Oyster Growers Association, Seattle, WA.

Walker, I. President, Aquaculture Resource Development, Madbury, NH.