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Introductions of marine bivalve molluscs into the United Kingdom for commercial culture – case histories

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Most introductions of non-indigenous bivalves into UK coastal waters have been deliberate and all have involved species of commercial value. The introduction of *Mercenaria mercenaria*, whether deliberate or accidental, remains subject to speculation. Imports of live oysters from Europe and the USA, which probably began in the 1870s, continued until 1962 when trade in live oysters had declined. *Ostrea edulis* seed for relaying was imported from France and Holland in quantities that ranged from less than 100 t year^{-1} to 1100 t year^{-1}. *Crassostrea virginica* seed was imported from America and Canada until 1939, to be replaced by *Crassostrea angulata* from Portugal which had been imported since 1926. Imports of seed *Crassostrea* spp. never exceeded 300 t year^{-1}. Before the 1960s the deposit of imported species was not controlled to prevent the introduction of pests, parasites, and diseases. Legislation, codes of practice, and guidelines have since controlled the introduction, deposit, and release into the wild of non-indigenous bivalves in UK territorial waters. As a result of this, and the availability of seed from UK hatcheries since the 1960s, no new pests, etc., have been introduced with seed of non-indigenous species. The Ministry of Agriculture, Fisheries and Food, Conwy, UK, has introduced seven species of non-indigenous bivalves under strict quarantine to assess their commercial viability. *Crassostrea gigas* and *Tapes philippinarum* have considerable potential since they grow faster and survive better than the native equivalents. *Tiostrea lutaria* may be of some value, and *C. virginica*, reintroduced in 1984, is currently being assessed. The three other species were unsuitable for commercial culture or no better than indigenous species and were destroyed. Further introductions are not planned at present. The UK bivalve industry has a range of temperate water species with which to trade in home and overseas markets.

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Introduction

Probably more species of bivalve molluscs have been introduced into the coastal waters of the United Kingdom (UK) than of any other group of marine animals. Most of these introductions were made deliberately and all of the latter involved species of commercial value. This paper catalogues the bivalves which have been introduced, explains the rationale for the introductions, describes the fate of the various species, and summarizes the legislation which was enacted to control the movement and spread of molluscan shellfish pests which were co-introduced with the earlier imports of bivalves.

Case histories of introductions

1. Introductions of non-native species before 1960

Before 1960 the ecological implications of importing and depositing non-native bivalves were disregarded. Imported species received no quarantine treatments and as a result a number of other unwanted marine invertebrates were introduced and successfully colonized some areas of the UK.

1.1. Oysters

The expansion of the railway network in the mid-19th century, with the potential for the rapid transit of perishable products to the main centres of population, led to a great increase in the rate of exploitation of what were considered to be the richest natural oyster beds in Europe. These were located in the Thames estuary and in the rivers of Essex. In 1864 almost 500 million oysters, equivalent to 30 000 t, were sold on Billingsgate Market, London (Yonge, 1960).

By 1876 the native flat oyster (*Ostrea edulis*) had dramatically decreased in abundance owing to the continuous over-dredging for it in open waters without allowing sufficient closed time. In response to the scarcity of the flat oyster a trade in live American oysters (*Crassostrea virginica*) from the United States and Canada had already started. These were being shipped across the Atlantic, as deck cargo, during winter and early spring to be relaid for fattening in coastal waters or to be sold direct for consumption. The American oysters fattened in the summer months but failed to breed.

This trade probably started in the early 1870s with the formation of two companies, the Conway Oyster Company Ltd. and the Anglo-American Oyster Company. The latter, which had relaying sites at Shoreham, in the Salcombe estuary, and in the Menai Strait was short lived and went into liquidation in 1876 following disastrous losses of oysters in transit from America. The Conway Oyster Company experienced poor fattening of the imported oysters in the Conwy estuary and subsequently gained the lease to ongrowing ground off Cleethorpes and at Brightlingsea, Essex.

From 1876 to 1902 records of the numbers of oysters (not differentiated by species) landed in the UK were kept by the Sea Fisheries Inspectorate of the Board of Trade. Quantities of oysters imported for consumption or for relaying in coastal waters appeared as a statistical record in 1901. Data were collated by the Board of Agriculture and Fisheries from 1902 and from 1919 by the Ministry of Agriculture, Fisheries and Food (MAFF). Figure 1, drawn from the published statistics, shows the decline of the industry from its peak in the mid-19th century. It also shows that demand from 1900 until 1940 was met largely by importations.

The practice of importing half-grown oysters of about 35 g mean weight for relaying was well established in the latter part of the 19th century and undoubtedly contributed significantly to British landings during that period. For example, the Conway Oyster Company was importing 1 million seed American oysters per week in the early 1870s, of which an unknown proportion were for relaying (Report of the Commons Select Committee, 1876). In 1879, 90 663 barrels at a little over 1000 oysters per barrel were imported from New York (Philpots, 1890).

Quantities imported for relaying from 1901 to 1962, when the practice had diminished, are shown in Fig. 2. Importations, which were mainly of *O. edulis* from Holland and France, reached a peak, at 40 million individuals, in 1937. This was towards the end of a period of restocking beds that were severely depleted by

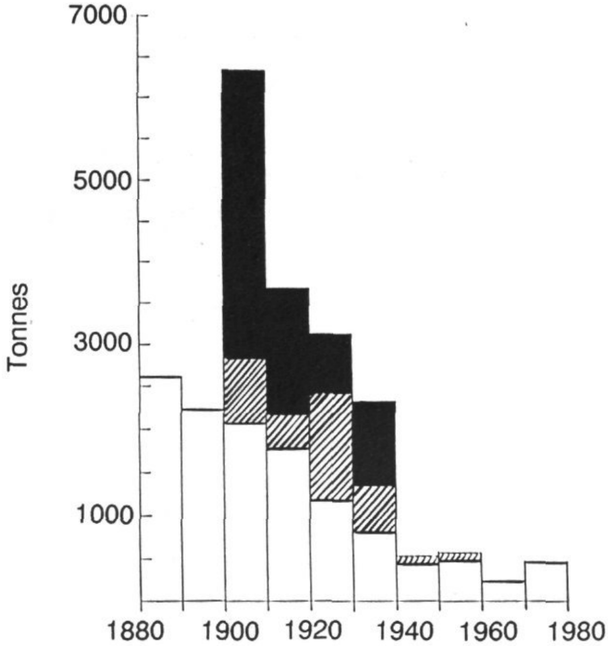

Figure 1. Landings of oysters of mixed species in the UK (open histograms) and imports, for direct consumption, of European flat oysters (hatched histograms) and American oysters (closed histograms). Values are 10-year means extracted from official statistics for 1880 to 1980. Before 1901 no data were collected of quantities of oysters imported for consumption. Tonnages are calculated using the official convention of 800 oysters per cwt., equivalent to 15 748 oysters tonne^{-1}.

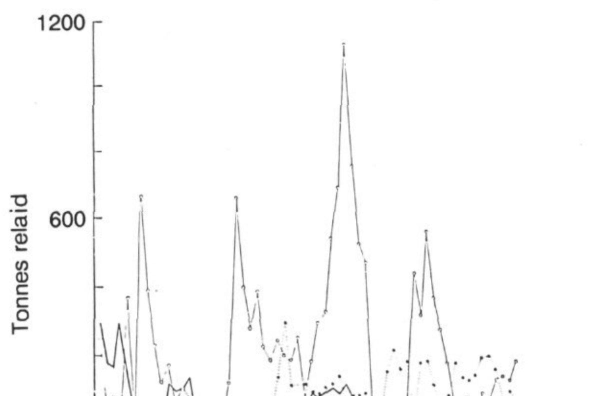

Figure 2. Tonnages, for relaying, of imported *Ostrea edulis* from Holland and France (○—○), *Crassostrea virginica* from the USA (——) and *Crassostrea angulata* from Portugal (●--●) from 1901 (when records began) to 1962 (when imports ceased).

an unknown disease in the 1920s. American oysters were imported for relaying until 1939. After World War II trade in this species was not re-established and it was replaced by the Portuguese oyster (*Crassostrea angulata*), which had been imported since 1926. Importations of the latter species ceased in the 1960s as a consequence of a disease in its native habitat.

Importations for relaying were successful in maintaining a reasonable level of supply of consumable oysters, although the scale was never sufficient to restore production to levels achieved in the late 19th century.

Importations were not controlled in such a way as to avoid the introduction of pests. As a result, the slipper limpet (*Crepidula fornicata*) and the American tingle (*Urosalpinx cinerea*), which are both native to the USA, became established in Britain. *Urosalpinx*, a shell-boring gastropod preying especially on flat oyster spat, became a serious pest to oyster fisheries in some parts of England (in Essex and Kent). Its distribution never extended beyond these areas and it has declined in abundance since the 1960s due to the collapse of oyster fisheries in these areas and, more recently, by the effect of tri-butyl tin (TBT) on its reproductive capability. *Crepidula* is more widely distributed, especially around the south coast of England and Wales. It competes with other filter-feeding invertebrates for food and space, and in waters with high concentrations of suspended particulate material it encourages the deposition of mud.

During the earlier part of this century another pest had been introduced, the crustacean gut parasite of mussels (*Mytilicola intestinalis*). It is generally considered to have been introduced from the Mediterranean (where it is endemic in *Mytilus galloprovincialis*), probably with mussels fouling the hulls of ships. It was first found in 1937 in Southampton Water. Although heavy mortalities of mussels in Europe in 1949–1950 were attributed to heavy infestations with *Mytilicola* it is now considered not to be a serious pest. It can live in a number of bivalve hosts including *Mytilus edulis*, *O. edulis*, *C. gigas*, and some clam species.

1.2. Clams

The American hard shell clam (*Mercenaria mercenaria*) was introduced at the same time as the American oyster but, unlike the American oyster, became established as a self-sustaining population on the south coast of England, in Southampton Water. Its introduction, whether deliberate or accidental, is subject to speculation. It may have been brought by American servicemen during World War I, or as ballast in sailing ships from New York, or it may have been discarded from transatlantic liners returning from New York.

The first major survey in 1979 of the extent of the fishery revealed a total population of around 15 000 t. Clams were harvested by hand before 1970 for marketing on the Continent but by the mid-1970s a dredge fishery had started and this increased landings until the mid to late 1980s, when the stock declined. Irregular recruitment and the lack of any significant spatfall after the closure in the early 1970s of the Marchwood Power Station at the head of Southampton Water probably accounted for this decline.

2. Introductions of non-native species after 1960

The era of massive commercial importations of oyster seed for relaying ended in the 1960s with a growing awareness of the risks involved in introducing alien pests, parasites, and diseases and of the possible ecological consequences for native communities.

The 1960s were notable for two reasons, the implementation of the Molluscan Shellfish (Control of Deposit) Order 1965 and the development of hatchery culture techniques.

2.1. Legislation

The Molluscan Shellfish (Control of Deposit) Order 1965, revoked and strengthened as the Molluscan Shellfish (Control of Deposit) Order 1974 and further amended in 1983 under the Sea Fisheries (Shellfish) Act 1967, prohibits the deposit in tidal waters, within the seaward limits of the territorial waters adjacent to England and Wales, of any part of any kind of molluscan shellfish, whether live or dead, taken from outside these waters, unless a licence to deposit has been granted by the Minister of Agriculture, Fisheries and Food (in England) or the Secretary of State (in Wales), and the conditions of that licence have been complied with. A similar order, The Molluscan Shellfish (Control of Deposit) (Scotland) Order 1978, applies to Scotland.

These Orders enable the control of movements for deposit of molluscan shellfish around the coastline and the control of the deposit of molluscan shellfish from outside territorial waters. Deposit refers to the immersion of the animals in coastal waters, in other tidal areas, or on adjacent land where there is the risk that effluent from tanks, pits, ponds, or hatcheries may be discharged into designated waters. As far as the Order relating to deposits in England and Wales is concerned the transfer and deposit of molluscan shellfish between areas around the coast needs to be administered flexibly to avoid undue constraint to trade, but with care to avoid the spread of pests and disease. To this end the coastline of England and Wales is divided into 27 designated areas which are related to the prevalence and intensity of major pests and disease (Fig. 3). This map shows the distribution of the principal pests, *Mytilicola*, *Crepidula*, and *Urosalpinx*, and of the microcell sporozoan parasite (*Bonamia ostreae*), which has been responsible for severe mortalities of the European flat oyster throughout the Atlantic coast of Europe. This parasite became

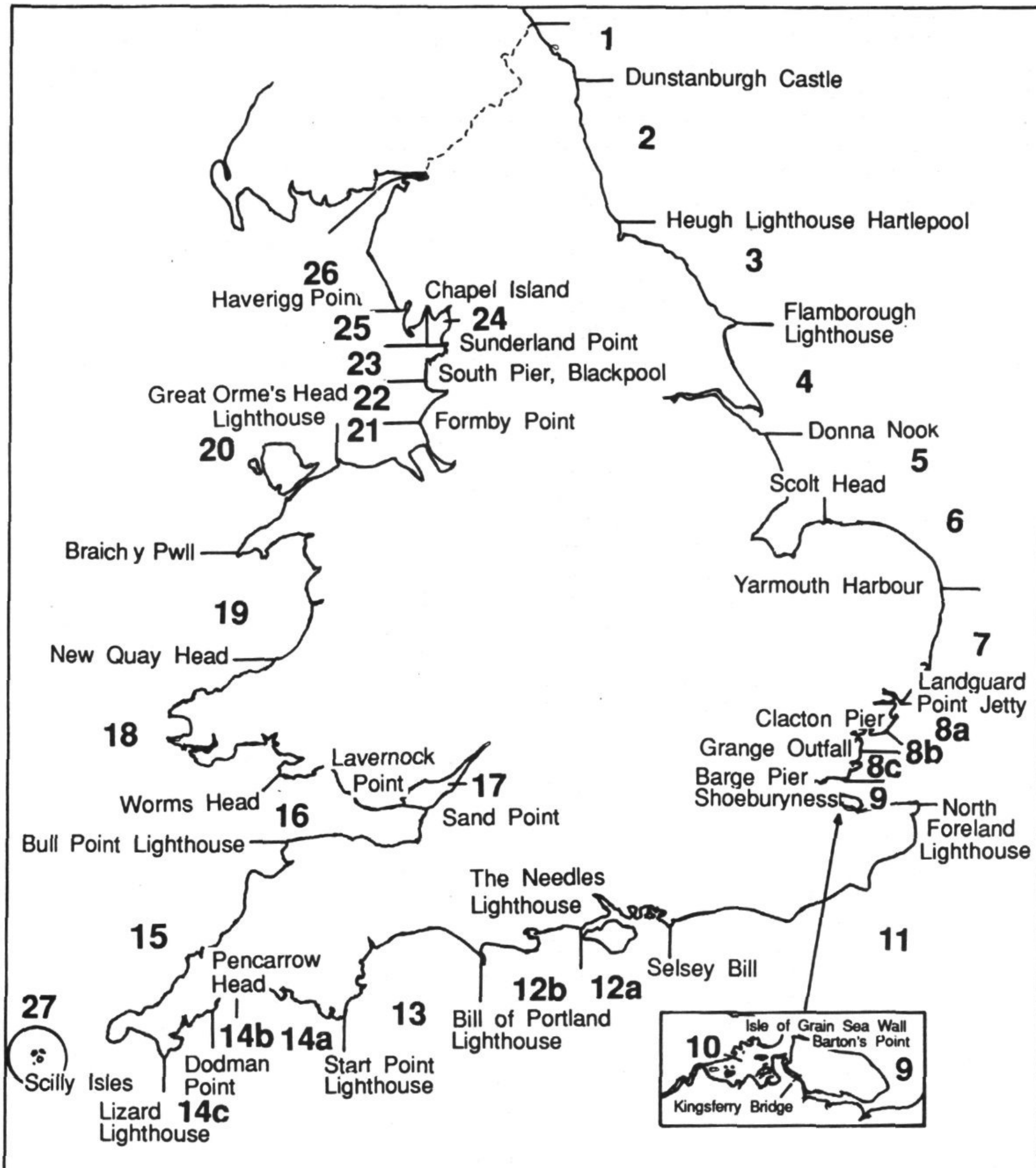

Figure 3. A map of England and Wales showing coastal areas designated in the Molluscan Shellfish (Control of Deposit) Order 1974, as varied in 1983, and the incidence of shellfish pests and diseases. Key: Areas 1, 3, 5, 6, 19, 20, 21, 22, 23, 26, and 27 = no pests or diseases recorded; Areas 24 and 25 = *Mytilicola* only; Area 4 = *Crepidula* only; Areas 2, 7, 10, 11, 13, 14(a) (b), 15, 16, 17, and 18 = *Mytilicola* and *Crepidula*; Area 9 = *Mytilicola*, *Crepidula*, and American tingle; Areas 12(a) (b) and 14(c) = *Bonamia*, *Mytilicola*, and *Crepidula*; Areas 8(a) (b) (c) = *Bonamia*, *Mytilicola*, *Crepidula*, and American tingle.

evident in the River Fal in 1982 and before effective control measures could be introduced had been transferred with licensed and unlicensed oyster deposits to the Helford River, to north and mid-Essex, and to some parts of the south coast. Since that time, with variation of the Control of Deposit Order in 1983, the further spread of this parasite has largely been prevented.

Movements of bivalves for deposit between coastal

Table 1. Species of bivalves introduced to the UK since 1960 by the MAFF Fisheries Laboratory, Conwy.

Species	Year	Fate
1. Chilean oyster, *Tiostrea chilensis*	1962	Stock intentionally destroyed
2. Chilean mussel, *Choromytilus* (syn. *Mytilus*) *choros* (syn. *chilensis*)	1965	Stock intentionally destroyed
3. New Zealand oyster, *Tiostrea lutaria*	1963, 1966	Self-sustaining population in Menai Strait
4. Pacific oyster, *Crassostrea gigas*, Canada	1965, 1972	Commercially grown
5. Pacific oyster, *Crassostrea gigas*, USA	1978	Commercially grown
6. Manila clam, *Tapes* (syn. *Venerupis*) *philippinarum* (syn. *semidecussata*), USA	1980	Commercially grown
7. Mangrove oyster, *Crassostrea rhizophorae*, Brazil	1980	Research. Stock intentionally destroyed
8. American oyster, *Crassostrea virginica*, USA	1984	Evaluation of culture potential

areas of England and Wales are controlled by a system of licensing. There are two forms of licence (a) a General licence which permits deposits anywhere within the designated area from which they were taken and between areas with similar types and/or levels of infestation, and (b) a Special licence which permits the deposit of molluscs from an infested area to areas which are free from infestation or have a lower level of infestation than the area of origin.

Importations from overseas of molluscs for deposit require special licences and these may only be granted subject to certification, by the authorities in the country of origin, that the shellfish are pest and disease free. At present, few countries can provide adequate information on the health status of their stocks or have the ability to establish a satisfactory certification scheme. Consequently the importation of molluscan shellfish species for deposit in the form of direct relaying in the sea from outside of the UK, except for the Channel Island of Guernsey and some parts of Eire, is prohibited. If sufficient justification can be shown and if suitable and well-managed quarantine facilities are available, it may be permissible to introduce and deposit non-indigenous species for research purposes or with the intention to breed them and subsequently release their progeny in tidal waters. The issue of a special licence in these cases is assessed on individual merit. Also, conditions are attached to the licence which define water sterilization and handling treatments and the method of disposal of the stock when experiments are completed, to ensure that the risk of escape of non-indigenous organisms is reduced to an acceptable level.

Introduction of non-indigenous species to evaluate their culture potential is only permitted through the quarantine facilities of the MAFF Fisheries Laboratory, Conwy. The decision to import a new species is reached after careful evaluation of the need for the introduction and of the status of the species in its native habitat. This is dealt with in more detail later.

Since 1981 the introduction of non-indigenous species for deposit and cultivation in the sea has been more strictly controlled under the Wildlife and Countryside Act (1981). Under Section 14 of the Act it is an offence to permit, except under licence, the release of non-indigenous species into the wild. Cultivation of non-native bivalve species, for example the Manila clam (*Tapes philippinarum*), in well-secured trays or beneath secure and well-maintained mesh covers on the ground of the foreshore may be allowed under special licence of the Control of Deposit Order. Fisheries Departments are responsible for issuing licences and may consult with the Nature Conservancy Council to obtain an opinion of the consequences of the deposit on the local ecology.

2.2. *The role of bivalve hatcheries with introductions*

Techniques for the hatchery production of marine bivalves were sufficiently reliable in the 1960s to be applied on a commercial scale (Walne, 1974). Since then, seven species of non-indigenous commercially valuable bivalves have been introduced into the UK (Table 1). Imported broodstock, after thorough cleansing to free them of epifauna and flora, were deposited in quarantine tanks within the laboratory at Conwy. Effluent sea water discharged from these tanks was collected in large-volume, outdoor, concrete tanks, where it was sterilized by adding powdered, or a solution of, sodium hypochlorite at a rate to give 100 ppm free-chlorine. The treated water was held for a minimum of 24 h before discharge into the sea (Dare *et al.*, 1977).

Once induced to spawn, the parent stock was destroyed by boiling and buried on land. Up until 1979 the progeny were reared without quarantine to a size suitable for planting in trays in the sea to assess their culture characteristics in home waters. This was done by MAFF in controlled experiments to establish that the new species had advantageous characteristics and presented little or no risk to the environment. Then small quantities of animals were given to commercial hatcheries as broodstock.

Over the years the way in which introductions have been made has gradually been improved to further minimize any risk. Quarantine has been strengthened to include the rearing of the larval and juvenile stages in

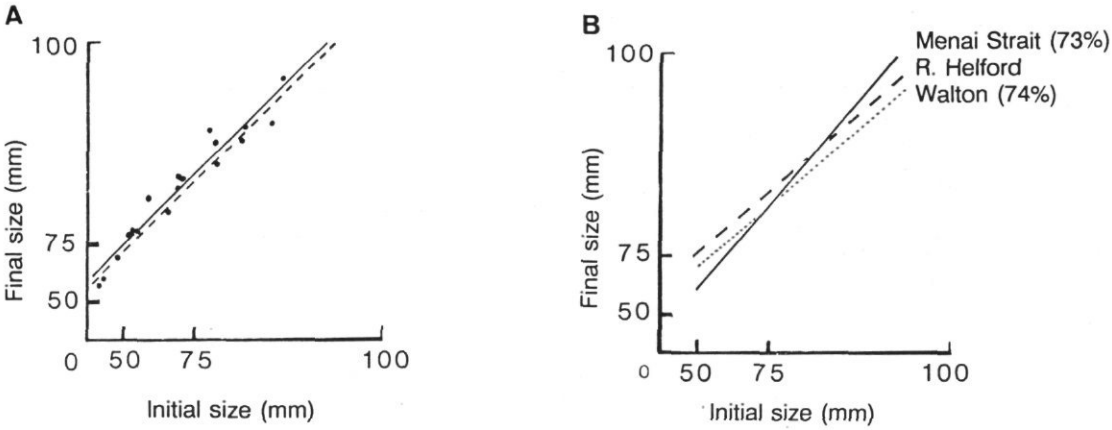

Figure 4. A. The growth in one year in North Wales of the flat oyster (*Ostrea edulis*) and the New Zealand oyster (*Tiostrea lutaria*). —— New Zealand oyster; - - - European oyster (Walne and Mann, 1975). B. The growth and survival of the New Zealand oyster at three sites in the UK. Percentage survival in parentheses for two sites.

line with the code of practice and guidelines produced by the ICES "Working Group on Introductions and Transfer of Marine Organisms" and the EIFAC "Working Party on Introductions" (1988).

For introductions made in the 1980s (Table 1) MAFF has held F1 juveniles in quarantine at Conwy for eight months, during which time 200 individuals were removed at two-monthly intervals for histopathological examination by the MAFF Fish Diseases Laboratory, Weymouth. Once it was established that the animals were free of disease, progeny were permitted to be transferred to the sea in suitable containment, so as to comply with the Wildlife and Countryside Act, for performance assessment. A further sample was taken for examination four months later as a final check on the health of the progeny.

Since the adoption of quarantine procedures no new pests or disease organisms have been introduced into coastal waters in association with hatchery produced seed of exotic species.

Six of the seven species introduced through Conwy (Table 1) were assessed for their suitability for aquaculture. The seventh, the mangrove oyster (*Crassostrea rhizophorae*) from Brazil was required for physiology experiments undertaken in a quarantine facility at the University of Southampton. In all cases broodstock were brought in under MAFF control and deposited at the Conwy Laboratory. F1 progeny from the mangrove oyster were subsequently released to the University of Southampton for research.

Three species unsuitable for commercial culture, either because of poor survival in our climatic conditions (Chilean oyster and mangrove oyster) or because they offered no cultural advantages over related native species (Chilean mussel), were destroyed. One species, the New Zealand flat oyster (*Tiostrea lutaria*), kept at MAFF's experimental site in the Menai Strait is now resident there as a self-sustaining population. This oyster broods its larvae to the stage of metamorphosis, so that upon liberation from the parent the larvae settle within a few hours in the vicinity of the parent. Consequently the stock is contained within a small area. *T. lutaria* is superficially similar to *O. edulis* and grows at a similar rate (Fig. 4A). It is not cold tolerant and survives poorly in the intertidal zone in cold winters. It is also susceptible to the pathogen *Bonamia ostreae*. At present there are no plans to transfer the species to other parts of the UK, although MAFF trials have shown that it grows well in other areas (Fig. 4B).

Two species have considerable potential for commercial culture, the Pacific oyster (*C. gigas*) and the Manila clam (*T. philippinarum*). The Pacific oyster was first introduced in 1965 (Table 1). Summaries of its introduction and the results of culture assessments are given by Walne and Spencer (1971) and Walne and Helm (1979). UK production is currently around 600 t year^{-1} but production in some areas of the UK has been severely constrained by TBT, from anti-foulant paints, which has been present in the sea water. Since 1987 the use of TBT-based anti-foulant paints has been restricted and growth of Pacific oysters in areas which were previously affected by TBT has improved significantly; production is expected to increase by 30% per year.

The Pacific oyster is an extremely robust, fast-growing animal which requires temperatures well in excess of those prevailing in British waters for successful recruitment. There have been reports of small numbers of naturally recruited spat in exceptionally warm summers in shallow, enclosed bodies of water, for example, Emsworth Harbour, but widespread and substantial recruitment such as occurs along the southern Atlantic coast of France is considered most unlikely. Commercial production is sustained by supplies of hatchery produced seed.

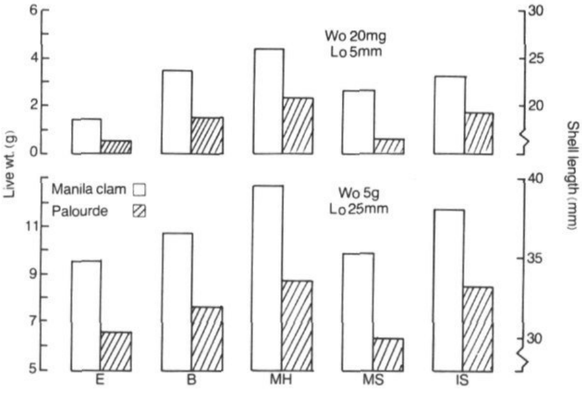

Figure 5. The growth, measured as live weight (g) and shell length (mm) of the Manila clam (*Tapes philippinarum*) and the native palourde (*Tapes decussatus*) at five sites in the UK. The initial sizes of clams were 20 mg (5 mm) and 5 g (25 mm). Sites: E = Essex – dammed creek; B = R. Beaulieu – raft; MH = Milford Haven – nursery; MS = Menai Strait – intertidal; IS = Inland Sea – intertidal.

The Manila clam is a more recent introduction. Broodstock were imported from the State of Washington, USA, in 1980 and, like the New Zealand and Pacific oysters, pre-dates the Wildlife and Countryside Act of 1981. It has proved to be another hardy, fast-growing species with substantial potential for commercial production (Utting, 1987a, b; Spencer, 1990). The rationale for its introduction was to prevent the UK industry from being severely disadvantaged in the lucrative European market for clams, where first sale value exceeds £5000 per tonne. The species was introduced into France in 1973 and is now being cultured from hatchery seed in many European countries.

Manila clams are well suited to the UK environment and grow faster than the native palourde, *Tapes decussatus* (Fig. 5). Production in the UK, which currently stands at less than 5 t $year^{-1}$, is sustained from a supply of hatchery produced seed because, like the Pacific oyster, it is most unlikely to recruit in UK waters.

To further reduce the remote chance of recruitment, methods of producing triploid seed of Manila clams are being investigated at Conwy. To date 67–77% of fertilized embryos treated with the chemical cytochalasin-B (Allen *et al.*, 1989) have been found to be triploid. Survival of treated embryos ranged from 60 to 80% of control diploid batches and was probably related to seasonal changes in water quality which occur at the laboratory (Utting and Helm, 1985).

The recent reintroduction of the American oyster was made in 1984 (Utting, 1987a) from a stock in the James River, Chesapeake Bay. This particular stock has been under the close health scrutiny of the American National Marine Fisheries Service and was free of known oyster pathogens, coming from an area with a mean salinity of 8 ppt. Culture evaluation with F1 progeny reared in the Conwy hatchery has shown that this species grows more slowly than the Pacific oyster in most areas tested (Fig. 6). The American oyster appeared more suited to conditions in the Essex river systems and Poole Harbour than elsewhere.

It is too early to assess the commercial potential of the species in UK waters, but since it has previously had an impact in UK oyster production without any sign of successful natural recruitment over a long period, the outlook is hopeful. Its future will probably depend on how the Pacific oyster industry develops now that the problem over TBT has been alleviated.

Conclusion

With the more recent introductions the UK shellfish industry now has a wide range of the world's more valuable temperate water bivalve species with which to compete in European and worldwide trade. There are no plans, nor does there appear to be the need, for further introductions in the foreseeable future.

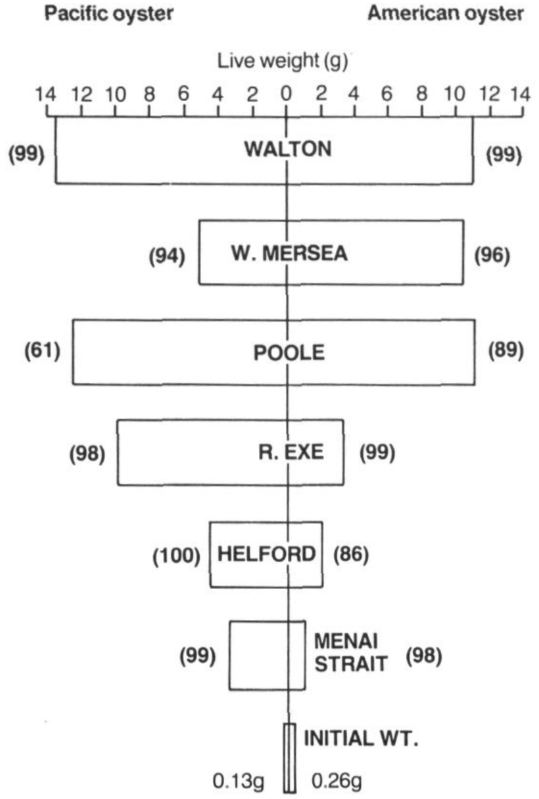

Figure 6. The growth, measured as live weight (g), and survival (%) of American oysters (*Crassostrea virginica*) and Pacific oysters (*Crassostrea gigas*) in trays at six sites in the UK during 1986. Percentage survival in parentheses. Note TBT affected growth of Pacific oyster at West Mersea.

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