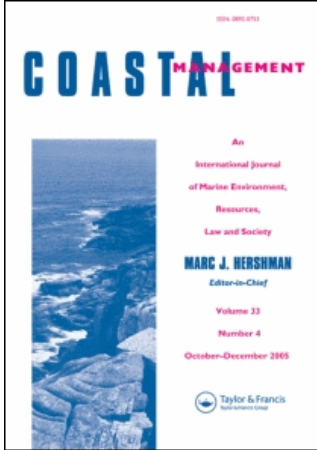


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The Disappearance of Oyster Reefs from Eastern Australian Estuaries—Impact of Colonial Settlement or Mudworm Invasion?

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The Disappearance of Oyster Reefs from Eastern Australian Estuaries—Impact of Colonial Settlement or Mudworm Invasion?

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Oysters have been harvested on the east coast of Australia for many thousands of years. Coastal Aboriginal communities used the extensive estuarine oyster resource and may have farmed oysters by establishing shell cultch beds in shallow areas of estuaries. The British colonization of Australia commenced in 1788 and oysters were initially used for food and production of lime. Concerns about unsustainable exploitation led to introduction of legislation that directed the oyster industry to aquaculture in 1884. Translocation of oyster stock for fattening, from New Zealand to Australian east coast estuaries, was encouraged. Here evidence is presented that this activity resulted in “mudworm disease” appearing in oyster farming estuaries on the Australian east coast between 1880 and 1900. The pandemic permanently destroyed natural sub-tidal oyster reefs and forced the oyster industry to adopt avoidance farming techniques including intertidal farming to cope with mudworm.

Keywords Australia, estuaries, historic sub-tidal oyster reefs, mudworm, New Zealand, translocation

Introduction

Australia has a long history of use of coastal marine resources. Indigenous Australians extensively used them for thousands of years. Europeans have also exploited marine

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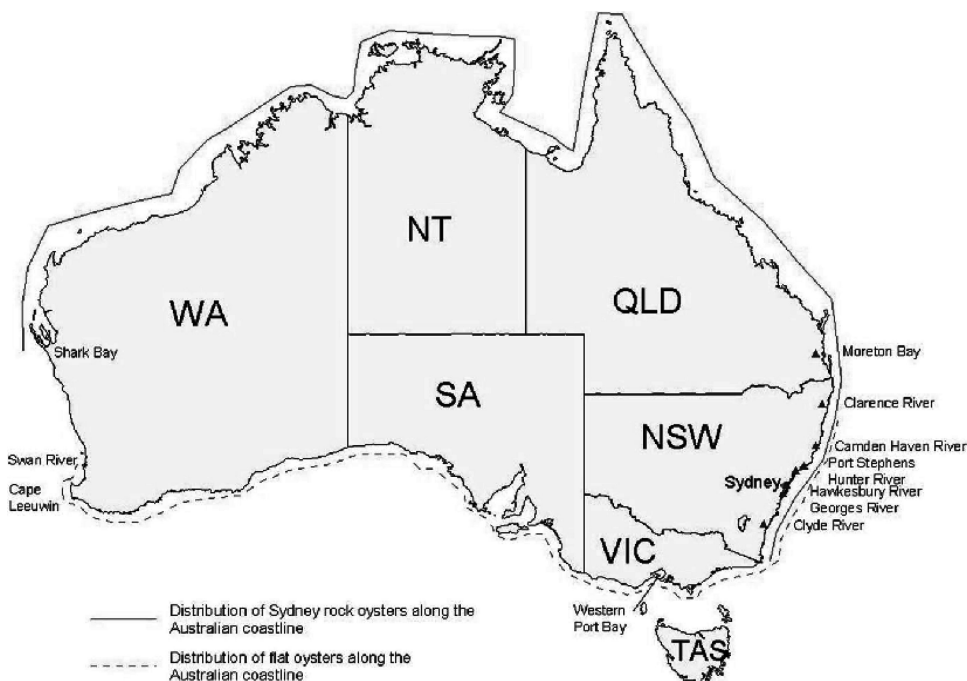


Figure 1. Distribution of *Ostrea angasi* and *Saccostrea glomerata* along mainland Australian coast.

resources after settlement commenced in eastern Australia at Sydney in 1788. Two coastal shellfish with a long and continual history of use are flat oysters (*Ostrea angasi*) and Sydney rock oysters (*Saccostrea glomerata*). Both have been used for centuries as source of food and to make implements such as fishhooks and produce lime. *Saccostrea glomerata* is now the predominant native oyster in south-eastern Australian estuaries, attaching to rock and shell in sub-tidal and inter-tidal areas of coastal and estuarine environments (Roughley, 1925). A continuous distribution of the hardy *Saccostrea glomerata* extends from the Victoria/New South Wales (NSW) border (36°S) up the east coast, across the tropical north of Australia and along the west coast as far south as Shark Bay in Western Australia (25°S) (Figure 1). Recent taxonomy indicates it is the same species as that found in New Zealand (Anderson and Adlard, 1994). It is cultured along the eastern seaboard of Australia from 27°S to 37.5°S (Smith et al., 2000) and is capable of living out of water for three weeks in cool, damp, hessian bags (Oyster Culture Commission, 1877). The range of osmo-conformity for adult *Saccostrea glomerata* is from 15 to 45 ppt salinity (Nell and Dunkley, 1984).

Both the *Saccostrea glomerata* and *Ostrea angasi* are reef-forming organisms, but vary throughout their range in growth form and the habitat in which they live. At European settlement, large sub-tidal oyster reefs of both species were predominant features of estuaries within their species range along the east coast of Australia. However, such reefs are now absent from these areas. To explain the disappearance of sub-tidal oyster reefs in Australia and parts of the United States, Kirby (2004) hypothesised that these reefs were destroyed by destructive fishing practices such as oyster dredging. In this article

we use historical information to re-examine the hypothesis of Kirby (2004) and investigate alternative hypotheses for the permanent loss of sub-tidal oyster reefs in Australian east coast estuaries involving the polydorid complex of spionid polychaete worms, including the genera *Boccardia*, *Pseudopolydora*, *Dipolydora* and *Polydora*, each commonly referred to as mudworm. The first alternative hypothesis is that polydorid spionids were endemic in eastern Australian estuaries and increased in numbers due to siltation following land clearing by colonial settlers. The second hypothesis is that a new and virulent species of mudworm was introduced with translocated shellfish from New Zealand. We suggest that the loss of oyster reefs has led to profound and, most likely, irreversible changes in the ecological structure and function of Australian east coast temperate and sub-tropical estuaries.

Pre-European *Saccostrea glomerata* Harvest and Culture

Aboriginal Australians came to Australia at least 60,000 years ago and possibly as long as 120,000 years ago based on fire frequency records (White, 1994). Throughout this long history, oysters have played a significant role in coastal aboriginal communities (Bailey, 1975; Nicholson and Cane, 1994). Shell middens adjacent to estuaries reveal that oysters were collected in great numbers (Attenbrow, 2002). The relatively recent age of many shell middens (mostly less than 2,000 years old) in eastern estuaries may be due to earlier middens being destroyed by rising sea levels that occurred up until about 2,000 years before present (B.P.) (Attenbrow, 2002). These shell middens were still being used by local Aboriginal communities in the mid-19th century on the Richmond River and many other areas on the east coast (Bailey, 1975; Attenbrow, 2002).

Shell was commonly used for implements in Aboriginal communities. Shell fish-hooks are the most numerous shell implements found, first appearing in the Sydney region about 900 years ago (Attenbrow, 2002). Use of oyster shell cultch (oyster shell) as catching material to restore oyster reefs is widely practiced today in the United States (Wesson et al., 1999). In sandy rivers in NSW, such as the Richmond, a pattern of periodic flooding denuded the main riverbed of natural oyster reef material (Black, 1876a). Cultch material was probably placed by Aboriginal communities in the estuary just prior to the oyster spawning period, to restore oyster beds by providing substrate for catching new oyster stock. This method was also employed on NSW rivers such as the Richmond (Black, 1876a) in the very early years (1878–1884) of European colonial oyster farming. The *Saccostrea glomerata* industry is possibly the oldest extant farming sector in Australia, predating European arrival by at least 2,000 years.

Changes in the relative abundance of principal shellfish species during the late Holocene (2,000 B.P.) have been documented in several excavated shell middens around Sydney (Attenbrow, 2002). *Saccostrea glomerata*, cockle (*Anadara trapezia*) and hairy mussel (*Trichomya hirsuta*) were the predominant aquatic species in middens in the middle and upper estuarine reaches. *Ostrea angasi* were also common. However, the trends in the amounts of these species collected at different places around Port Jackson (Sydney) varied over time. The changes were not the same at all sites, suggesting that small-scale environmental changes occurred (associated with changing sea-levels or other natural processes), which affected the habitat and therefore the abundance of particular shellfish (Attenbrow, 2002).

Oysters were an important component of the diet in the annual cycle of Aboriginal communities. Aboriginal communities in southern Queensland used the flowering of the native hop (*Dodonea viscosa*) as an indicator of the “ripeness” of oysters in the estuaries and hence the time to move to the estuary to commence harvest (Smith, 1985). The widespread abundance of oyster stocks on reefs in east coast Australian estuaries when Europeans settled in 1788 suggests that the impact of Aboriginal groups on oyster populations appears to have been relatively small (Attenbrow, 2002).

The environment in which the *Saccostrea glomerata* industry operates has undergone its most profound changes during the last 200 years since European arrival. Catchment clearance and disturbance has increased runoff rates and sediment loads in streams discharging into estuaries particularly in north eastern Australia (State of Environment Report Australia, 1996).

The Oyster Industry from the 18th Century Onward

The English explorer Captain Cook reported large *Ostrea angasi* in Botany Bay in 1770, the largest he had ever seen. The first European settlers in 1788 reported vast quantities of oysters in Sydney Harbour and oysters of an “amazing” size in the uppermost coves (Attenbrow, 2002). Extensive oyster reefs were present on the beds of most NSW and southern Queensland estuaries at the time of European arrival (Oyster Culture Commission, 1877). *Saccostrea glomerata* was found both as “dredge (or drift) oysters,” which were oysters found at least two feet below low water mark or “bank oysters,” which were oysters in beds occurring in the inter-tidal zone between high and low water marks (Smith 1985). During the early years of the European oyster industry, debate occurred over the species synonymy of the dredge and bank oysters (Tenison-Woods, 1883; Cox, 1893). However, bank oysters transferred from inter-tidal areas to deepwater leases gained the same appearance as dredge oysters and it was concluded that the two oyster types were *Saccostrea glomerata* (Roughley, 1925). Oyster beds in the estuaries were individually identified and named, usually in reference to geographical location (Thompson, 1883).

The huge quantity of oyster shell found in the substrate of NSW estuaries (e.g. Peat and Roy, 1975; Figure 2) at water depths of 2–10 m is evidence of the prolific nature of these oyster beds in the past. In the mid-19th century oyster reefs in NSW were inter-tidal and sub-tidal, fringing or patch reef and varied in area from 10 m² to greater than 100,000 m². They were described as “close set clumps of five or six oysters and two or four clumps thick all over the bed, averaging about eighteen mature oysters beside spat on every 5 square inches over an unbroken bed of shell on a tolerably hard bottom” (Oyster Culture Commission, 1877).

Massive oyster populations were exploited from many of the NSW estuaries during the 1850s–1870s resulting in drastic declines in oyster populations within estuaries in a practice referred to as “skinning.” Schooners supplying lime kilns in Newcastle and Sydney simply berthed on mudflats at low tide, raked together the live oysters, and completed loading the vessel within its length. Numerous smaller boats operated within estuaries targeting dredge oysters (Black, 1876b). In shallow (<2 m) areas, the shell beds underlying the live oyster reefs were even excavated for lime production (Oyster Culture Commission, 1877). Whole rivers were “leased” by individuals, often Sydney merchants, who contracted labor to undertake the harvest. Oysters were usually shipped live in sacks on the decks of steamboats plying Australian coastal waters.

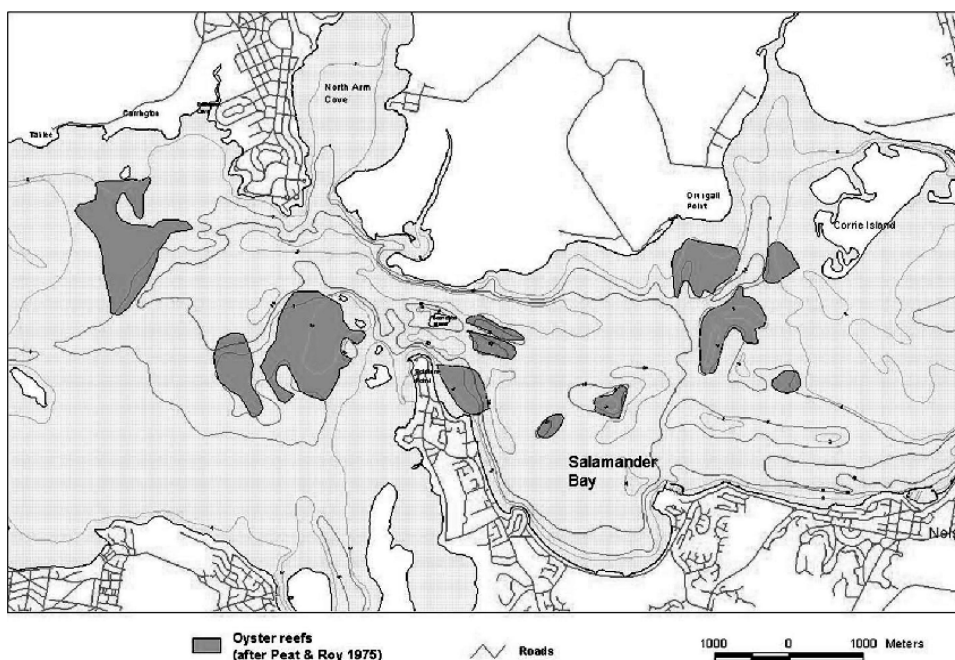


Figure 2. Extent of extinct natural oyster shell beds up to 8 m thick in lower Port Stephens estuary overlaid with bathymetry.

Older techniques for oyster fishing elsewhere in the world have been particularly destructive for oyster reef habitat. With the exception of hand-harvesting on inter-tidal reefs, harvesting practices are analogous to strip mining, breaking off pieces of the reef and removing all size-classes of oysters (Coen & Luckenbach, 2000). Concerns were raised about the sustainability of these fishing practices and the great depletion by dredging in eastern Australia resulting in the establishment of a Royal Commission by the Governor of the Colony of NSW (Oyster Culture Commission, 1877). Its purpose was to inquire into the best mode of cultivating the oyster, of improving and maintaining the natural oyster beds of the colony, and also concerning the legislation necessary to carry out these objectives.

The Commission took testimony from a range of industry experts and government inspectors. One company reported undertaking a large stocking exercise of *Ostrea angasi* (source unknown but possibly New Zealand) in Western Port Bay, Victoria in 1861. Subsequently, all stocked beds and surrounding natural beds throughout the bay died mysteriously in 1862. The company attributed this mass mortality to some form of disease. The same company operated leases in Tasmania at that time and subsequently in southern NSW. Others testified that *Ostrea angasi* had inexplicably died off in many of the southern estuaries during the 1860s and had largely disappeared from NSW by the mid-1870s (Oyster Culture Commission, 1877). Whether this was because of the introduction of a new disease (e.g., the parasite *Bonamia* sp.) remains unclear. Adlard (2000) identified in the haemocytes of *O. angasi* in southern Australia an ultra-structurally identical and genetically similar *Bonamia* sp., to that found in New Zealand.

The Commission undertook an audit of NSW estuaries in relation to the oyster fishery. The audit report on the Camden Haven oyster beds on the New South Wales (NSW)

mid-north coast exemplifies the extent of the oyster reefs at the time of commencement of European exploitation:

In the 1860's a man could work his warp stake into the bed and not leave that spot for sixteen or twenty days, getting fifteen to twenty bags¹ a day all that time. For a long time ten to twelve or even fifteen boats were so employed until only three or four bags could be got . . . some came back in about three years only to get at most six or seven bags per day. (Black, 1876b)

Unfortunately, none of the estuary oyster reef maps referred to in this audit appear to have survived a fire in 1882 at the Garden Palace in Sydney that destroyed many NSW government fisheries records (C. Brand, NSW Fisheries, personal communication) but local knowledge can still identify many of the geographical areas referred to in the detailed Fisheries annual reports of 1884–1902.

The commission also reported on the commencement of oyster farming in 1858 at the Island of Ré in France by a stonemason named Buf and the rapid success that it had subsequently enjoyed. The Commission concluded that:

The same temperature which makes the vines grow makes the oysters spat . . . in view of the fact that this (NSW) climate is so admirably adapted for producing oysters in quantities almost without limit, and at the minimum cost.

The Commission also observed in England that “in many instances the oysters are not ‘natives’ but a grand mixture of all kinds of oysters being brought from many other places to augment the stock.” This promotion of translocation, including non-endemic species from the Old World, was commonly practised during this era, often with dire results to the native fauna and flora. One of the most infamous terrestrial introductions to Australia was the rabbit, one of whose importers included the head of the Oyster Commission, Thomas Holt.

Key recommendations of the Commission (Oyster Culture Commission, 1877) were:

- The cancellation by the Government of all the so-called existing leases of natural oyster-beds as none of them have been granted by law: “The only wise cause of action to adopt to save the oyster beds from ruin.”
- Granting of licenses to dredge for oysters in future.
- No royalty on stock collected from these natural beds for fattening on leases.
- All lands which are covered by tidal waters should be leased for a term of fifty years in areas not exceeding five acres.
- Appoint an efficient staff of Inspectors for supervision and preservation of our oyster fisheries, as their services are urgently required.

Causes of Decline

Overharvesting

Kirby (2004) put forward the hypothesis that the destructive fishing practice of oyster dredging was principally responsible, in conjunction with sedimentation and nutrient loading for the destruction of oyster beds along the Australian east coast. We acknowledge that oyster dredging had a significant impact on sub-tidal oyster beds, however, the

disappearance of these beds and their permanent failure to recover in Australian east coast estuaries does not appear to have been only caused by oyster dredging, overfishing and catchment clearance.

The collapse of oyster fisheries in Australian east coast estuaries did not follow a linear sequence away from urban centres. Firstly we report on the date of disappearance of the oyster fishery in each of the major NSW estuaries, revealing a pattern unrelated to distance from major urban centres. Secondly, the collapse occurred in some estuaries with near pristine catchments that were not dredged. Thirdly, we demonstrate that complete and permanent collapse of the oyster fishery in each estuary was directly correlated with recorded translocation of oysters from New Zealand and the subsequent appearance of mudworm in the respective receiving estuary.

Sedimentation and Nutrient Loading

Sedimentation and nutrient loading, may have contributed to a decline in subtidal oyster reefs, but not their complete disappearance and failure to recover. There are several lines of evidence for this. Firstly, there were extensive oyster reefs widespread in deepwater areas of most estuaries in south-east Australia in 1884 including those that had been heavily cleared for agriculture at least 50 years before the sudden disappearance of the oyster fishery, such as the Hawkesbury River, Port Stephens, Richmond and Clarence River catchments. Secondly, in estuaries surrounded by undisturbed catchments, sub-tidal oyster beds would be expected to still remain. However, this is not the case as evidenced by Clyde River, Wonboyn Lake and Nelson Lagoon (southern NSW), areas with a still largely undeveloped catchment from where sub-tidal oyster beds also disappeared. Thirdly, coral records show that significant sediment discharges occurred at the end of prolonged droughts in eastern Australia prior to European settlement and catchment clearance and grazing (McCulloch et al. 2003). Fourthly, estuary infilling is a natural part of estuary evolution to which oysters have adapted and research has shown that decadal siltation rate within east coast Australian estuaries appears not to have varied significantly in the last 200 years (Roy, 1984, 1994).

We consider that catchment development and subsequent increases in sedimentation and nutrient loading may have played a role in the decline of the oyster beds, but not as the primary causative agent. Disturbed environments are considered to be more easily invaded than undisturbed environments (Elton, 1958; Cohen & Carlton, 1998). We therefore do not consider sedimentation and nutrient loading as the causative agent of the disappearance of sub-tidal oyster beds; rather it is a potential factor that increased the invasiveness or “virulence” of a polydoridae spionid polychaete.

Introduction of *Polydora* spp.

Australia, an island continent, is particularly susceptible to introduced and translocated species and they have been one of the most significant sources of declines and extinctions of native fauna (White, 1994). The number of introduced species and their ecological impacts is generally underestimated (Carlton, 1996). We suggest that the disappearance of the subtidal oyster beds along the Australian east coast is consistent with the impact of an introduced species. Correlative evidence implicates a polydoridae spionid.

Globally, spionid polychaetes including those from the genus *Polydora* are well documented invasive species being introduced through ballast water and with the translocation of oysters and oyster material (Blake, 1999; Bailey-Brock, 2000; Leppäkoski

& Olenin, 2000; Essink & Dekker, 2002). The challenge with polydorid spionids is ascertaining the “natural” distribution of the various species owing to the long-term potential translocation events and the uncertainties regarding the taxonomy of the group. This has led to such species being classified by Carlton (1996) as cryptogenic.

The Appearance of Mudworm in Australia

The Fisheries and Oyster Farms Act (FOFA) was implemented and the granting of leases for purposes of cultivating oysters commenced in NSW in 1884. At this time quantities of live *Saccostrea glomerata* and *Ostrea angasi* were being imported in crates from New Zealand for eastern Australian markets (Oyster Culture Commission, 1877; Edgar, 2001). Transport costs from New Zealand were cheaper than from NSW estuaries and imported oysters were also not subject to royalty payments, making New Zealand oysters significantly cheaper, though allegedly of poorer quality, than NSW oysters (Fisheries of the Colony, 1887). On arrival at east coast ports, the crates were immediately lowered into the sea to refresh the oysters (Edgar, 2001). The first reports of New Zealand *Saccostrea glomerata* being placed on leases in NSW was in Port Jackson and further north in the Hunter River in the 1880s for fattening purposes (Quinan, 1883). Similar translocations at later dates were documented in other estuaries (Table 1).

The spionid polychaete mudworm (*Polydora* sp.) (Whitelegge, 1890) was first reported in *Saccostrea glomerata* stock in Australia at the Hunter River, north of Sydney around 1882 (Quinan, 1884). In November 1886, a major outbreak of “worm disease” of oysters

Table 1

Records of Sydney rock oysters being introduced from New Zealand or subsequent stock movement from mudworm infected estuaries into various New South Wales/Queensland estuaries and occurrence of worm disease outbreak

Estuary and source of information		Year of translocation	First report of worm disease mass mortality
Hunter	(Quinan, 1883, 1884)	1880s? ^a	1882
Hawkesbury	(Benson & Gyler, 1887)	1885	1886
Port Jackson	(Quinan, 1884)	1885	1886–87
Georges	(Grant, 1889)	1886	1887
Tweed/Richmond	(Temperley, 1888)	1885–86	1887
Manning	(Gyler, 1887; Temperley, 1888)	1887	1887
Port Stephens	(Laman, 1890)	1887	1888
Clarence	(Temperley, 1888, 1889)	1885–86	1889
Crookhaven	(Gordon, 1889; Benson 1891)	1888	1891
Coomera, Qld	(Smith, 1985)	1890s?	1895
Wallis	(Massingham, 1901)	1897	1899
Clyde	(Aldrich, 1901)	?	1899
Camden Haven	(Brodie, 1898; Massingham, 1901)	1898	1899

^aF. J. Gibbins, oyster lessee in the Clyde, Georges, Hawkesbury, Hunter, Camden Haven, Bellinger, and Clarence estuaries from the 1860s to early 1900s appears to have been one of the first to have commenced translocation of oysters from New Zealand by steam boat to his leases in these estuaries.

was first documented by Inspector P. Smith on the Hawkesbury River (Benson & Gyler, 1887). This caused mass mortality of oyster stock below the mid tide level. In the following year in the Georges River in NSW, translocated New Zealand stock were reported to be dying of worm disease as were native oysters on adjacent leases (Grant, 1889). In the same year, outbreaks of the worm were reported in the Clarence and Tweed River estuaries (Cox, 1889).

A detailed epidemiological study on the “worm disease” affecting the oysters on the coast of NSW, prepared by Thomas Whitelegge, zoologist at the Australian Museum, was published in 1890. The report provided a detailed description of the worm and its habits, the method of infection in oysters through the gape, reproduction of the worms while in the oyster and how infection caused the eventual death of the oyster. Due to their negative effects on the host, mudworm is considered a parasite (Handley, 1998). Whitelegge made recommendations on possible treatment methods using freshwater dips or air-drying of oysters. The latter practice is still used today for floating cultivation. Whitelegge (1890) noted that he had found the worm in a range of other bivalves and concluded that the distribution of the species appears to be worldwide and that a large amount of mud is necessary for the worm to thrive. Whitelegge collected his mudworm samples from affected estuaries in 1887–88, well after reported translocation of New Zealand oysters into these estuaries (e.g., Quinan, 1884) and after first reports of outbreaks of major worm infection in these estuaries.

Was a New Species of Mudworm Introduced?

The suggestion that an exotic species of mudworm was introduced to Australian waters, probably from New Zealand, has been a matter of debate for decades (Roughley, 1925). It has been recognised that crates of live oysters transported from New Zealand were a significant source of introduced foreign species such as the sea star *Patriella regularis* and the screw shell (*Maoricolpus roseus*) (Edgar, 2001) and it is possible that a similar process occurred with mudworm.

The impact of mudworm, in NSW estuaries such as Port Jackson, was noted to have taken place in all species of bivalves including *Trigonia sp.* and Venus shells (Veneridae), which existed in profusion at the time of settlement but had subsequently disappeared (Cox, 1893). At the time, debate on the cause for the proliferation of mudworm disease centred on the hypothesis of increased siltation due to catchment clearing (Saville-Kent, 1891; Cox, 1893), a hypothesis that is still widely supported (J. Nell, NSW Fisheries, 2005, personal communication).

The arguments in favor of the hypothesis that a foreign species of mudworm was introduced over the hypothesis of increased siltation leading to mudworm proliferation are:

- Mud worm infections also occurred in estuaries where catchments were uncleared.
- Similar catchment development and siltation has not led to rapid and permanent removal of sub-tidal oyster reefs in areas such as east coast of the USA.
- There were no reports of mudworm in NSW estuaries at the time of the Oyster Culture Commission in 1877 despite over 50 years of catchment clearance in some estuaries. A lag period of two to three year between initial introduction and a severe outbreak of mudworm at the introduction site is consistent with the invasion of spionids elsewhere (Essink & Dekker, 2002).
- Field investigations, as part of this study, in the Pambula River, Clyde River Georges River, Hawkesbury River, Port Stephens, and Wallis Lake confirmed significant

deposits of oyster shell (both *Saccostrea glomerata* and/or *Ostrea angasi*) in extinct sub-tidal shell beds and the absence of live oysters.

- The sudden reported appearance and rapid and dramatic impact of mudworm between 1880 and 1900 in various estuaries coincided closely with the New Zealand oyster translocations (Table 1).
- The records found in this study, of New Zealand oysters translocated to estuaries in NSW during this period, correlate with subsequent outbreaks of mudworm.
- The spread of mudworm through estuaries across an extended range in NSW and subsequently Queensland during this twenty-year period and was well documented as surveillance increased.
- Mudworm was first detected in oysters in 1895 on banks at the mouth of the Coomera River in southern Moreton Bay in Queensland from where it spread throughout the Queensland oyster fishery (Smith, 1985).
- Permanent extinction of natural oyster populations below the neap tide level in estuaries occurred rapidly once mudworm appeared
- Sub-tidal cultivation methods became impossible (Roughley, 1925) and remain so until the present without frequent air drying of the crop.
- Inspectors speculated that in the few remaining rivers where there was no worm disease, it was because it had not been carried there (Smithers, 1904).

By the end of the 1880s, a catastrophic reduction in oyster production in NSW was recorded (Figure 3). Sub-tidal oyster reefs in major estuaries were permanently decimated. For example, it was reported that the worm first manifested itself in the Clarence river (Figure 4), after some cultch shell (from an unspecified source) had been laid down in a lower part of a channel lease; from this the disease spread over the whole of the beds (Thompson, 1894). Movement of cultch shell between estuaries had been common practice up to this point; however fisheries managers subsequently targeted cultch from worm-infected estuaries as a source of introduction of worm disease to previously uninfected estuaries (Massingham, 1899).

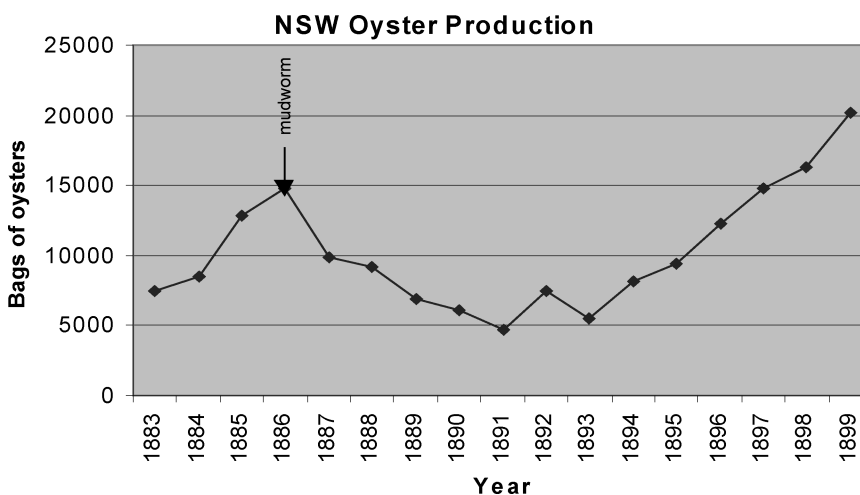


Figure 3. Decline in the production of *Saccostrea glomerata* following appearance of mudworm and subsequent recovery as inter-tidal cultivation practices were developed (Source: Commissioners of Fisheries Annual Reports 1883–1899).

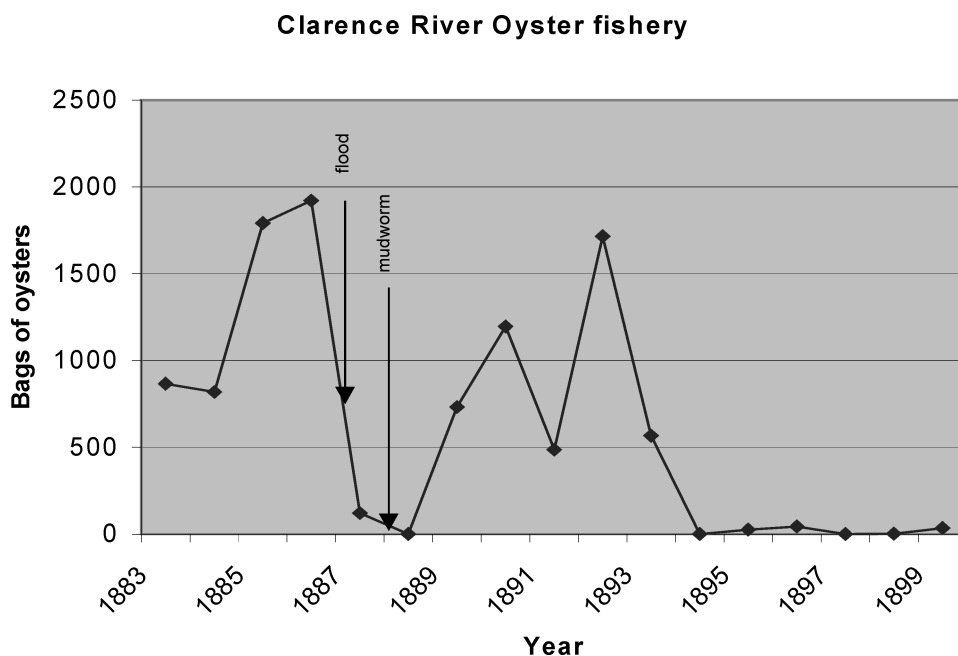


Figure 4. The impact of mudworm appearance and spread on the Clarence River oyster fishery (source: Commissioners of Fisheries Annual Reports 1883–1899).

The *Saccostrea glomerata* Industry Response to Mudworm

Documented translocation of *Saccostrea glomerata* to South Australia, Tasmania, Fiji, and other locations also occurred through this period. Legislation was introduced in 1889 in an effort to prevent the spread of the worm (Cox, 1889). This included the requirements for the thorough drying of shell cultch material from infected estuaries before transfer to other estuaries and for the clean up of infected leases. It does not, however, appear to have precluded live transfer of live oysters, including stock from New Zealand.

The evidence suggests that within the first two years of the proclamation of the Fisheries and Oyster Farms Act (FOFA, 1884), an irreversible introduction of a new and major pest species for the *Saccostrea glomerata* and other shellfish species into Australia was complete. The advent of mudworm disease has permanently precluded methods of subtidal dredge bed cultivation (a most effective form of cultivation) of oysters in NSW and southern Queensland estuaries because oysters placed below the mid-low tide mark rapidly become infected with mudworm (Roughley, 1922; Smith, 1985). At Berowra Creek in the Hawkesbury River Inspector Smith first observed the outbreak of mudworm in November 1886. He later observed that “when first known to me when I arrived thirty five years ago, the daily catch of oysters from this creek would be over 100 bags and now everything is exterminated” (Smith, 1904). Ironically, the major objective of the FOFA, to protect natural beds of oysters from ruin had failed. Natural beds of sub-tidal oysters have never recovered in NSW or Queensland estuaries since this time.²

Largely as a consequence of mudworm impacts, the FOFA was repealed and a new Fisheries Act (1902) was proclaimed. This contained enforceable provisions requiring lessees to make improvements to leases to deal with mudworm. Inter-tidal foreshore leases

were used and lessees took precaution not to place any oysters below the medium low-water mark as mudworm could not proliferate if oysters were exposed to air for a minimum period in each tide cycle (Newton, 1904).

Growing height was critical to optimise oyster growth and avoid mudworm, a practice that continues today (Medcof & Malcolm, 1974). This effectively has restricted operations to a thin layer of water in the intertidal zone where mudworm cannot proliferate but oysters can continue to grow satisfactorily. It became necessary to develop off-bottom cultivation methods, farming above the mid-tide level using raised beds of gravel or oyster shells, cut stone placed on cabbage tree palm logs, mangrove sticks and cement- and tar-treated sticks (Roughley, 1922) and, most recently, techniques using plastic infrastructure.

The method of placing oysters on racks situated on the inter-tidal plane at approximately mean low water neap (equivalent to -0.5 m Australian Height Datum) is still the major form of cultivation today. This ensures that oysters are out of water for approximately 30% of the time in a daily tide cycle (Smith, 1989), which is sufficient to limit mudworm infestation. Mudworm in NSW oyster cultivation "is the greatest obstacle to intensive oyster culture . . . except for these worms the growers could use all depths within their leased areas" (Medcof & Malcolm, 1974). Adoption of English methods for controlling mudworm using crop drying procedures (Whitelegge, 1890) is also widely practiced in floating oyster cultivation methods today.

Discussion and Conclusions

Prior to the 1880s oysters grew sub-tidally in reefs in eastern Australia. After the 1880s these reefs progressively disappeared and have never returned. Several hypotheses have been advanced for the demise of oyster reefs. One is overharvesting of reefs, another is increase in estuarine siltation due to catchment clearance following European settlement, or perhaps a combination of both. We have here suggested an alternate cause, the introduction of mudworm in oysters translocated from New Zealand. Our arguments here are based on the fact that oyster reefs also disappeared from estuaries in which there was no dredging and where the catchments remained essentially pristine and on the coincidence of the appearance of mudworm in estuaries with the translocation of oysters.

Much of the ecology of eastern Australian estuaries over the past millennia was arguably dependent on the reef-forming habit of oysters. The ecological impact of the permanent and complete demise of subtidal oyster reefs in these estuaries is unknown. However, overseas studies examining the impacts of oyster dredging on oyster reefs indicate significant changes to other benthic fauna as well as changes in the structure of fish assemblages due to the depletion of oyster reefs (Lenihan & Peterson, 1998; Breitburg, 1999; Dayton *et al.*, 1995; Coen & Luckenbach, 2000).

Active sub-tidal oyster reef restoration programs, such as those currently underway in Chesapeake Bay (Mann, 2000), are not an option in south-east Australian estuaries because of mudworm, however, it can be argued that it is important to restore/maintain oyster populations through aquaculture. Restoration objectives have typically included reduction of public health risks through improved water quality and increased harvest. However, direct and indirect ecosystem services (e.g., filtering capacity, benthic-pelagic coupling, nutrient dynamics, sediment stabilisation, provision of habitat) derived from oyster habitats have been largely ignored or underestimated in eastern Australia (Coen & Luckenbach, 2000).

Oyster reefs are a vital component of estuarine ecosystems through their consumption of phytoplankton and suppression of organic matter accumulation in the water column (Kirby & Miller, 2004). Large reductions in filtration rates of estuaries have been suggested as a significant consequence of declining oyster populations (Newell, 1988). An understanding of the dynamic processes by which both mobile and resident species use oyster reef habitat and consequent importance in the maintenance of biodiversity is just beginning to emerge (Breitburg, 1999). There is limited understanding of contribution of oyster populations to the broader ecological functioning of tidal creek systems (Coen & Luckenbach, 2000). There is also evidence that dense populations of suspension feeding shellfish can have a significant impact on basin-wide water quality and phytoplankton dynamics (Dame, 1996; Gifford et al., 2003). The ecological functions that oyster populations must have provided in south-east Australian estuaries need to be considered in current estuary management strategies.

Planning to maintain oyster farming in NSW estuaries is underway (White, 2001; Ogburn, 2003) but mudworm continues to have a significant impact on oyster cultivation in NSW (an estimated direct loss of 5% of industry gross sales in 2002). Meanwhile, treatment methods and knowledge of the biology and taxonomy of mudworm species on the Australian coast have not increased significantly in the last century. Characterization of each species—in terms of its biology, life cycle stages and reproductive strategy would be a primary step to enable the development of improved management strategies and treatment methods for mudworm infestation of cultured oysters.

Notes

1. A bag of oysters is 100 dozen.
2. Some limited natural beds do occur in areas of high estuarine flow on hard bottoms such as the southern arm of the Manning River when open and Berry's canal, constructed in the 1820's in the Crookhaven River.

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