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BK Diggles^a

^a DigsFish Services Pty Ltd , Banksia Beach, Queensland , Australia

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Historical epidemiology indicates water quality decline drives loss of oyster (*Saccostrea glomerata*) reefs in Moreton Bay, Australia

BK Diggles*

DigsFish Services Pty Ltd, Banksia Beach, Queensland, Australia

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Sydney rock oysters (*Saccostrea glomerata*) were historically abundant throughout the intertidal and subtidal zones of the Pumicestone Passage. However, today subtidal oyster reefs are extinct, and loss of around 96% of the vertical zonation suitable for oyster habitation has occurred. European land use practices caused large increases in sediment flux into inshore regions by 1870. This may explain why subtidal oyster reefs declined after major flood events in the late nineteenth century, associated with infestations by spionid polychaete mudworms. Today, mortalities of *S. glomerata* in the region are associated with QX disease caused by *Martellia sydneyi*. Increased virulence of *M. sydneyi* is likely due to a combination of increased abundance of intermediate hosts in habitat utilised by oysters, together with immunosuppression of the oysters. These processes are all driven by declining water quality derived from anthropogenic catchment development. Recently expanded marine park sanctuary zones fail to protect the ecosystem against continuing water quality decline. Rehabilitation of the ecosystem will require effective catchment management targeting reductions in nutrient and sediment loading, as well as restoration of oyster reefs using QX-resistant oysters.

Keywords: MPA; diseases; water quality; recruitment failure; ecosystem management; shifting baselines

Introduction

Oysters are important ecosystem engineers in estuaries worldwide (Grabowski & Peterson 2007; Beck et al. 2011). Like corals, oysters can completely structure entire ecosystems, providing hard subtidal and intertidal reef structure, food and habitat for invertebrates and fishes, as well as services such as filtration of phytoplankton, nutrient uptake and fixation, benthopelagic coupling and shoreline stabilisation (Newell 2004; Kemp et al. 2005; Grabowski & Peterson 2007; Beck et al. 2011). Historically, wild oysters supported important fisheries and aquaculture industries worldwide. But today, natural oyster reefs are declining due to anthropogenic impacts that are adversely affecting

estuaries and inshore marine ecosystems (Kirby & Miller 2005; Claudet & Fraschetti 2010; Beck et al. 2011).

Moreton Bay (Latitude 27.13 S, Longitude 153.20 E) in south-east Queensland, Australia, is a wedge-shaped embayment approximately 80 km long and 5–30 km wide (Fig. 1). Pumicestone Passage is the largest estuary in the northern part of the bay. It was formed during Pleistocene and Holocene transgressions when beach ridge accretion formed a low sand island now called Bribie Island (Maxwell 1970; Jones et al. 1978). The bottom of Pumicestone Passage was composed mainly of sandy lithofacies due to a lack of large river systems emptying into the passage, together with its

*Email: ben@digsfish.com

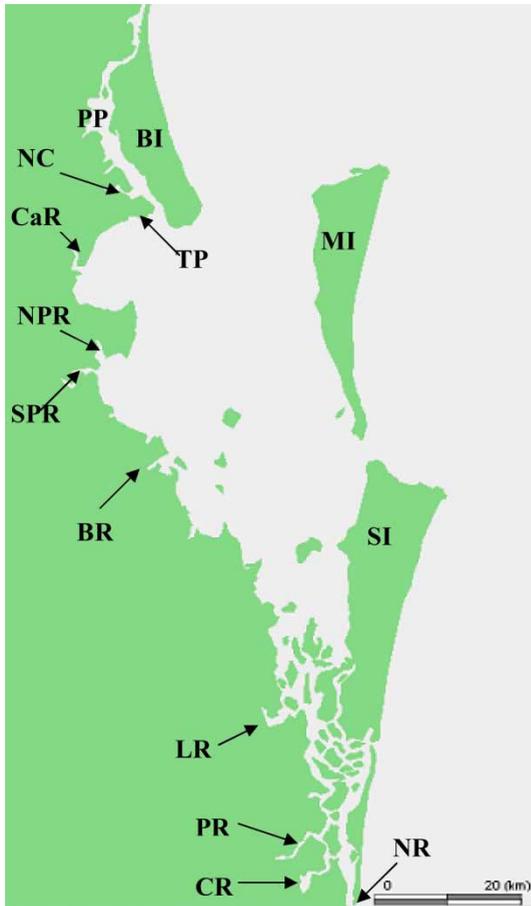


Figure 1 Map of Moreton Bay, southeast Queensland, showing the locations of the various places mentioned in the text. BI, Bribie Island; BR, Brisbane River; CaR, Caboolture River; CR, Coomera River; LR, Logan River; MI, Moreton Island; NC, Ningi Creek; NR, Nerang River; NPR, North Pine River; PP, Pumicestone Passage; PR, Pimpama River; SI, Stradbroke Island; SPR, South Pine River; TP, Toorbul Point.

close proximity to the sandy inner tidal delta system of the northern entrance to Moreton Bay (Harris et al. 1992). Several rivers flow into the southern and western bay (Fig. 1), introducing fluvial sediments, nutrients and generating turbidity and salinity gradients, with turbidity increasing and salinity decreasing from east to west (Blaber & Blaber 1980).

When European settlement in the region began in 1824 (Oxley 1825), deforestation for agricultural and urban development rapidly followed (Petrie 1904; Neil 1998; Morelli et al. 2012). Today, because of widespread catchment clearing, baseline sediment loads carried by the rivers entering Moreton Bay has increased by a factor of 4–5 compared with those pre-European settlement (Morelli et al. 2012). This is despite disruption of environmental flows by dams and weirs erected for municipal water supply and flood mitigation for the region's rapidly growing human population, which has increased from 20,000 in 1876 to 2 million by 2011 (Queensland Government 2011), with authorities projecting this to double to 4 million by 2050. Because of the many unique aspects of the region, Moreton Bay Marine Park was established in 1993 (see <http://www.derm.qld.gov.au/parks/moreton-bay/about.html>). 'No take' sanctuary zones in the marine park were subsequently expanded in 2009, after being advocated by some authors (e.g. Pillars et al. 2007), as a method to protect biodiversity and fisheries productivity in the area.

Loading of nitrate, phosphate, metals and other pollutants in the bay have increased significantly compared with historical baselines (Costanzo et al. 2005; Wiegand et al. 2011; Wulff et al. 2011; Morelli et al. 2012). This has resulted in a minimum 10-fold increase in algal production since European settlement (McEwan et al. 1998), including emergence of toxic cyanobacterial blooms (*Lyngbya majuscula*) since the early 1990s (Watkinson et al. 2005; Wulff et al. 2011). Despite this, Moreton Bay remains an important nursery area and today still supports commercial and recreational fisheries for a variety of species of finfish and crustaceans (Thompson 1951; Young 1978; Weng 1990). In contrast, the peak of production for the oyster culture industry in Moreton Bay was in 1891, after which time it collapsed to less than 10% of its former peak (Smith 1981), a level from which it has not recovered since.

This paper reviews the history of the decline of Sydney rock oysters (*Saccostrea glomerata*,

formerly classified as *Saccostrea commercialis*; Anderson & Adlard 1994) in Moreton Bay, and particularly the Pumicestone Passage. It utilises epidemiological assessment of disease agents of *S. glomerata* to reveal not only important historical baselines (Dayton and Dayton 2011), but the likely mechanisms responsible for the decline of the oyster populations to their current state. This information adds to debate regarding causes for oyster declines in Australia (Kirby 2004; Ogburn et al. 2007) and will be useful for managers to inform and focus management decisions designed to address these changes and begin to initiate restoration of the Moreton Bay ecosystem.

Methods

Historical data on the occurrence, exploitation, culture and diseases of Sydney rock oysters in Moreton Bay were obtained from original descriptions (Oxley 1825), reviews (Smith 1981; Ogburn et al. 2007; Lergessner 2008, 2011) and the references cited therein. The scientific literature was reviewed to obtain data on farming and diseases of *S. glomerata* in Australia. Updated information on the present situation regarding oyster production and disease status in Moreton Bay was obtained by contacting Government authorities, interviewing scientists and local oyster farmers, and by examination of wild and cultured *S. glomerata* in Pumicestone Passage for QX disease and other oyster pathogens. This was done by examining air-dried imprints of digestive gland and palps on microscope slides stained with Diff Quik (Lab Aids Pty Ltd) and examined under a compound microscope using the methods described by Adlard & Ernst (1995). Details of the timing and number of oysters sampled in this manner are contained in the relevant sections. Tide data for the lower Pumicestone Passage and percentage tidal exceedences above Port of Brisbane gauge datum for Bongaree Jetty, Pumicestone Passage, between 1992 and 2010 were obtained from the QLD Department of Transport and Main Roads. Correlation of vertical oyster heights in the intertidal zone to

Port of Brisbane tidal gauge datum was done by embedding graduated 20-mm diameter polyvinyl chloride marker poles into oyster bank sediments and monitoring tidal heights against the graduations at high tide over several tidal cycles. Flood data recorded in the Brisbane River at the city gauge was obtained from the Australian Bureau of Meteorology.

Results and discussion

History of the decline of oysters in Pumicestone Passage

Historically, Sydney rock oysters were extremely abundant in Moreton Bay and Pumicestone Passage, with reports from European explorers in the early nineteenth century recording that *S. glomerata* formed oyster reefs throughout the intertidal and subtidal zones (Ogburn et al. 2007). Explorer William Edwardson described the bay in June 1822 as follows:

From this point (Skirmish Point) to the south part of the bay, a distance of about 30 miles by 22 miles, the whole is composed of sand ridges and deep holes, interdispersed with mangrove islands, and these again surrounded for miles by mud flats and oysters or muscle (*sic*) beds. (Smith 1981)

First settlement of the area by Europeans occurred when a penal colony was established at Redcliffe in 1824 (Oxley 1825), which was later moved to a new location (now Brisbane) on the Brisbane River in 1825. Free settlement was not permitted until 1841 (Lergessner 2008, 2011), after which the oyster industry became one of the first industries established. Initially it focused on shovelling bank oysters and dredging oysters from subtidal reefs. 'Bank oysters' were defined as those oysters occurring in the intertidal zone and to a depth of 60 cm below the low water mark, while 'dredge oysters' occurred in deeper water below bank oysters (Oyster Act 1874) to a depth of around 3.6 m below the low tide mark (Lergessner 2008). Both types were *S. glomerata*; however, the dredge oysters were preferred over bank oysters

as they were ‘collected faster, taste better and attract higher prices than bank oysters’ (Lergessner 2008). The majority of oysters collected were eaten and the shells were burnt to produce lime for building cement (Smith 1981). Oyster populations were extremely abundant. Mr Alexander Archer described a trip to Pumicestone Passage in 1862 as follows:

... the water teems with fish, great and small and as for the oysters, I never saw anything like it. This day we saw something like a reef of rock about 3 feet out of the water and 300 yards long. On pulling up to see what it was, we found it to be a huge and apparently solid bed of oysters, large enough to load several large ships. (Lergessner 2008, 2011)

Opposite Donnybrook (8 km north of Ningi Creek) in number 33 dredging section, thousands of oysters in piles 1.2–1.5 m deep were taken, with a Mr Bill Freeman in 1865 ‘tying his boat to a stake, then commenced to dredge for 6 months’ (Lergessner 2008).

During the early years of European settlement, prolific oyster spatfalls were observed to occur in intertidal and subtidal areas of Moreton Bay and areas further north. In Tin Can Bay and the Great Sandy Straits (around 160 km north of Moreton Bay), *S. glomerata* spat grew abundantly on rocks within the intertidal zone and also on the bottom of the channels (Brown 2000). In the late nineteenth century, while inspecting the Great Sandy Straits, forester Jules Tardent described ‘the astronomical quantity of seed-oysters, stretching for miles, which has to be seen to be believed’ (Brown 2000). Indeed, the intertidal and subtidal sand flats of Tin Can Bay, Great Sandy Straits and Hervey Bay became well known as a prolific source of seed oysters (also known as culture) that were used after 1870 to restock Moreton Bay oyster beds after commercial harvest (Smith 1981; Lergessner 2008).

The burgeoning oyster industry underpinned the early economy of the growing colony from the 1840s until the early twentieth century, with oyster production from Moreton

Bay escalating gradually to its peak in 1891 of nearly 21,000 sacks (at 90 kg per sack, = 1890 tonnes) (Smith 1981; Lergessner 2008). However, following a series of major floods that began in 1887 and culminated in the multiple ≥ 8 -m flood events of 1893 (Fig. 2), production of oysters declined. Initially this was due to a significant loss of production from subtidal dredge leases, which began when large numbers of oysters were smothered by sediment brought down by the 1887 and 1893 floods (Brisbane Courier 1898, *The Queenslander* 1906). Subsequently, further loss of production occurred following the first outbreaks of a new disease due to spionid polychaete mudworm (*Polydora*, *Pseudopolydora*, *Dipolydora* and *Boccardia* spp.) infestations of the shell in 1894 and 1895, then again in 1898–1900 following another major flood in 1898 (Brisbane Courier 1898; Smith 1981; Lergessner 2008, 2011; Fig. 2). A description of these events was published in *The Queenslander* (1906) on 8 September 1906, as follows:

In 1887, a flood killed all the oysters in the southern part of the Bay, the rivers bringing down immense deposits of mud which simply smothered the bivalves. Then in 1892 and 1893, floods in the northern end of the Bay smothered the Bribie beds. About the same time, the dreaded mudworm disease made its appearance at the mouth of the Coomera River.

By 1910, the dredge sections that exploited the formerly abundant subtidal oyster reefs were all but abandoned due to recurring mudworm problems (Welsby 1937; Smith 1981; Lergessner 2008). Mudworm prompted oysterers to move exclusively to culture on intertidal banks by around 1920, where they captured spat on a variety of collection gear such as wooden sticks, tiles, oyster shell cultch or rocks (Smith 1981). At Toorbul Point around 4 km south of the mouth of Ningi Creek, photos from the early twentieth century show prolific recruitment of oysters onto rocks placed in the intertidal zone (Fig. 3). However, by the 1940s oyster farmers had moved their oysters even higher into

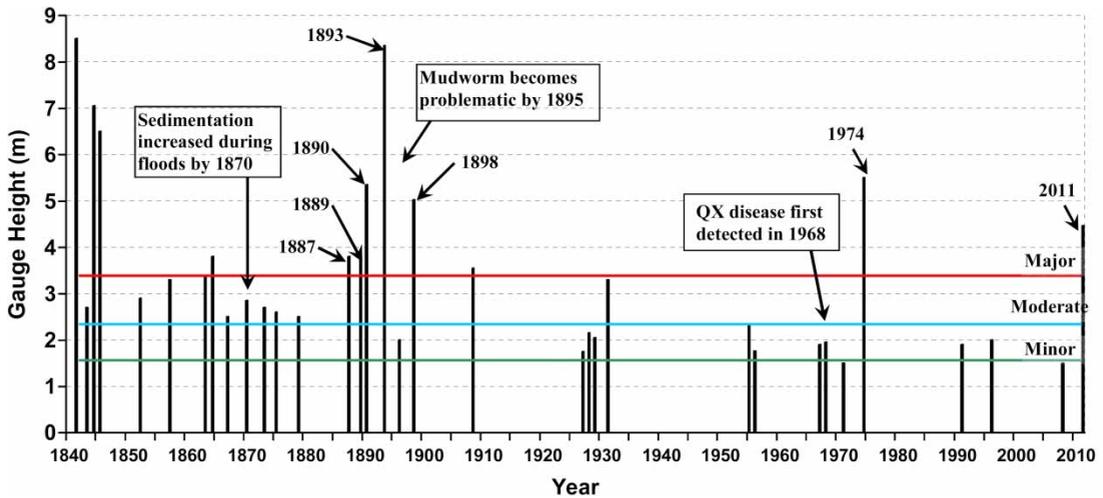


Figure 2 History of the highest annual flood peaks recorded in the Brisbane River at the city gauge between 1840 and 2011. Data from Australian Bureau of Meteorology. Highest flood peak occurred in 1841 (8.43 m), with three flood peaks occurring in February 1893 [6 February (8.35 m), 13 February (3.29 m) and 19 February (8.1 m)].

intertidal rack and tray furniture as they continued to try to avoid problems with mudworm infestation (Lergessner 2008). Indeed, ‘mud worm disease’ was acknowledged as the greatest single contributor to the decline of the

oyster industry in Southern Queensland until the 1980s (Smith 1981).

In the late 1960s, a new oyster disease emerged, called ‘QX disease’ (Queensland unknown disease; Wolf 1972) caused by the newly



Figure 3 Intertidal oyster bank, Toorbul Point, c. 1906. Photo from John Oxley Library.

described paramyxean oyster pathogen *Marteilia sydneyi* Perkins & Wolf (1976). The disease was first discovered in oysters from Pumicestone Passage and Toorbul Point after mortality events in 1968 (Wolf 1972), and subsequently emerged (Wolf 1979) or was translocated into more southern estuaries via movements of infected oysters (Adlard & Ernst 1995; Kleeman et al. 2004). Oyster production in most areas affected by QX disease outbreaks has not recovered, and many oyster farmers have subsequently left the industry (Nell 2001; O'Connor & Dove 2009). By 1980, the production of the oyster industry in southeast Queensland was less than a tenth of its peak (Smith 1981). Oyster farmers working in Ningi Creek reported that QX epizootics continued to increase in severity throughout the 1980s and 1990s (Carlo Sain, oyster farmer, pers. comm. August 2011). A notable change to fisheries management occurred in October 1995 when commercial fishing was removed and Pumicestone Passage was declared Queensland's

first recreational only fishing area (Pillans et al. 2007).

In the first decade of the twenty-first century, wild and cultured oysters in intertidal areas of Pumicestone Passage continued to decline (Carlo Sain pers. comm. August 2011; B.K. Diggles, pers. obs.; Fig. 4), due to recurring QX epizootics. Meanwhile, the 'mushroom shape' of historic wild oyster clumps at the mouth of Ningi Creek (Fig. 5) demonstrates that significant upwards compression of the intertidal zone suitable for oyster habitation has continued to occur in recent decades (Fig. 6). In 2011, the zone suitable for growth of live *S. glomerata* in these clumps was measured at around 20 cm high, spanning between approximately 1.1 and 1.3 m above low tide datum (Fig. 5). Given that historically *S. glomerata* in Pumicestone Passage occurred subtidally down to 3.6 m below the low water mark (Lergessner 2008), this represents a loss of around 4.7 m of the original



Figure 4 Same location as Figure 3 as seen over 100 years later in July 2011. There is a very high number of dead oysters, and a lack of oyster recruitment. Abundant algal growth has trapped a significant amount of sediment, giving the rocks a dirty appearance.



Figure 5 Mushroom shaped oyster clump at the mouth of Ningi Creek, Pumicestone Passage, January 2011. Note large numbers of shell fragments on the sand bank from decaying clumps that were formerly monolithic in shape. The arrow points to the delineation between the mud/silt layer (far field) and the sand from the original oyster bank. Scale shows height above gauge datum (meters).

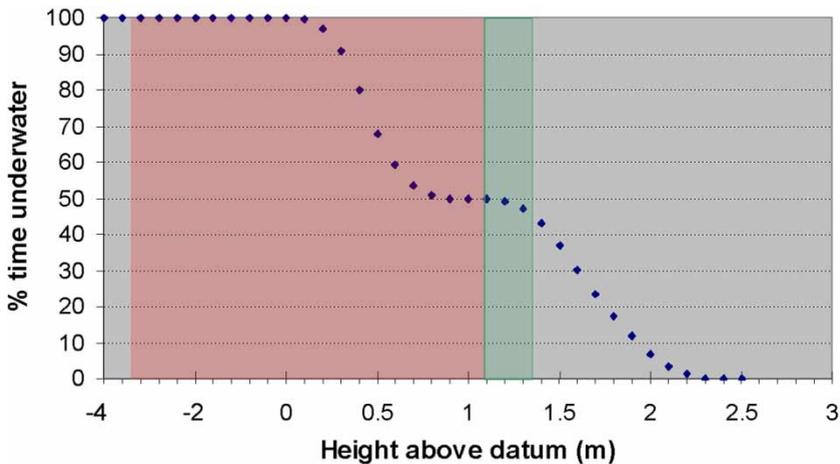


Figure 6 Percentage tidal exceedences above gauge datum for Bongaree Jetty, Pumicestone Passage between 01 January 1992 and 31 December 2010. Gauge datum 0 = lowest astronomical tide, Port of Brisbane. Green shading denotes the c. 20-cm level where live oysters remain today (see also Figure 5). The red area shows the 4.7 m of subtidal and intertidal zonation of oysters lost since c. 1850.

4.9 m (c. 96%) of vertical zonation suitable for oyster growth over a period of around 120 years (Fig. 6). Following the January 2011 flood event, the only remaining oyster leases in Pumicestone Passage (in Ningi Creek) experienced a total (100%) mortality due to QX (B.K. Diggles unpubl. data), resulting in record low (zero) production from the formerly prolific Pumicestone Passage oyster industry (Carlo Sain pers. comm. August 2011).

In summary, in as little as 120 years, substantial changes to the ecology of Pumicestone Passage have been observed compared with historical baselines. Subtidal oyster reefs are extinct and oysters have vanished from many other areas where they were once abundant. At the mouth of Ningi Creek, clumps of wild oysters that were once monolithic in shape are degrading from the bottom up (Fig. 5). All of these data demonstrate that the zone suitable for oyster growth and survival in Pumicestone Passage has been gradually compressed upwards over the past 120 years.

Potential mechanisms driving decline of oysters in Pumicestone Passage

There are several processes described in the scientific literature that are regularly cited as contributing to the decline in populations of oysters from estuarine ecosystems around the world (Grabowski & Peterson 2007; Beck et al. 2011). The processes that may explain the loss of formerly prolific populations of Sydney rock oysters in many of Australia's east coast estuaries encompass historical overfishing (Jackson et al. 2001; Kirby 2004), introduction of disease (Burreson et al. 2000; Ogburn et al. 2007) and declining water quality (Kemp et al. 2005; Kirby & Miller 2005).

Historical overfishing

In other parts of the world, the decline of wild oyster populations in estuaries has followed a sequence of events that usually begins with intensive harvest of oyster populations resulting

in loss of oyster reef structure, particularly vertical relief and complexity (Kirby 2004; Beck et al. 2011). Dredging and trawling of oyster reefs is considered the main impact that destroys natural reef structures, a process that exacerbates the impact of other stressors such as disease and reduced water quality (Cranfield et al. 2005; Grabowski & Peterson 2007; Beck et al. 2011). For example, in Chesapeake Bay (east coast USA), excessive removal of adult oysters and their shell substrate resulted in loss of vertical relief in oyster reefs, making the remaining oysters more susceptible to siltation and later, anoxia of bottom waters (Kirby & Miller 2005). However, in Moreton Bay and Pumicestone Passage, while historic fishing of oysters (including dredging) was certainly intensive, it was managed from 1874 onwards (Oyster Act 1874, 1886; Smith 1981), and there is evidence that prolific recruitment of new oyster spat occurred in subtidal dredge sections up until at least 1887, replenishing oyster dredge sections within 1–3 years (Fison 1889). Indeed, Fison (1889) noted a 'wonderful fall of spat' occurred after the 1887 flood, despite silt from the flood smothering oyster banks in the southern sections of Moreton Bay earlier that year (*The Queenslander* 1906).

Some oyster farming companies had been reseeded dredge sections with spat from Tin Can Bay and the Sandy Straits since the mid-1870s (Lergessner 2008), and this had apparently been effective until the series of major floods that began in 1887. However, by 1889, laying down cultivation in deep water dredge sections has been almost entirely discontinued due to it being 'a waste of time and money' (Fison 1889). These observations suggest that subtidal oyster populations in Moreton Bay were being supported by good recruitment until the 1887 flood. As oysters were being harvested at an average of 3–4 years old, this last example of prolific recruitment in 1887 correlates more or less with the peak of the industry's production in 1891 (Smith 1981; Lergessner 2008). In contrast, the fact that reseeded dredge sections had become a 'waste of time and

money' by 1889 suggests that smothering of subtidal oyster beds after the 1887 flood signalled the beginning of recruitment failure for oyster reefs in subtidal areas. The floods of 1889 and 1890 and the extreme multiple ≥ 8 -m flood events of 1893 (Fig. 2) would have introduced large amounts of sediments and nutrients into Moreton Bay. It is notable that following the floods of 1893, a significant loss of production from subtidal dredge leases occurred (Smith 1981; Lergessner 2008) as the oysters were killed by the silt (*The Queenslander* 1906), which is a major cause of mortality of oysters in subtidal oyster reefs (Lenihan 1999). Then, following subsequent recruitment and just as the next cohort of subtidal oysters were maturing, the first outbreaks of disease associated with mudworm infestation of the shell were recorded near the mouth of the Coomera River in 1895 (*The Queenslander* 1906; Smith 1981) and then again in 1898–1900 following the next major flood in 1898 (Brisbane Courier 1898; Smith 1981; Lergessner 2008, 2011; Fig. 2). These observations documented at the time present a different view from that proposed by Kirby (2004), who suggested that collapses on subtidal oyster reefs along Australia's east coast were caused mainly by fishing pressure.

The oyster industry in Moreton Bay recovered somewhat from the first outbreaks of 'mud worm disease' by concentrating its efforts above the low tide mark, but it was never the same after 1893 as the subtidal leases no longer approached anywhere near their former productivity (Lergessner 2008). Detailed study of the chronology of events in Moreton Bay and Pumicestone Passage leading up to peak oyster production in 1891, and the circumstances surrounding subsequent declines in production after that, therefore suggest that it is unlikely that overfishing was the primary factor responsible for decline of the oyster industry in this region.

Introduction of parasites or other disease agents

Introduced disease agents can cause much damage to oyster populations (Burrenson et al.

2000). In Australia, introduction of exotic species of spionid polychaetes (genera *Boccardia*, *Dipolydora* *Pseudopolydora* and *Polydora*) has been hypothesised as a potential cause for the loss of subtidal oyster reefs along Australia's east coast, including Moreton Bay (Ogburn et al. 2007). This hypothesis was based on one theory that originated in the late nineteenth century when temporal correlations were observed between outbreaks of mudworm infestations in New South Wales (NSW) estuaries and arrival of oysters translocated from New Zealand (Ogburn et al. 2007).

Spionid polychaetes are predominantly free-living organisms that are found in muddy estuarine sediments worldwide, although several species are commonly associated with molluscs, using their shells as settlement substrates (Read 2010; Walker 2011) as they feed on plankton (Dauer et al. 1981). Thus, most spionids infesting molluscs are ectocommensal with their planktonic larvae settling mainly on the outer shell. However, some larvae settle inside the mantle cavity, burrowing into the inner surface of the shell valve under the mantle margin. These worms accumulate sediment inside their burrow as the mollusc covers it with nacre, resulting in shell blisters that fill with mud, thus the name 'mudworm' (Read 2010). While the vast majority of mudworm infestations are non-fatal to their host, they can reduce growth (Royer et al. 2006), marketability and commercial value of oysters served in the half-shell (Nell 2001). In exceptional circumstances where heavy mudworm infestations occur, they can be associated with disease (Leonart et al. 2003a, b). These data suggest that it is possible that the heavy mudworm infestations first reported in Australia after 1870 could have predisposed at least some affected subtidal oysters to disease, as suggested by Whitelegge (1890).

At least 37 species of spionids have been recorded in Australia to date, with at least 12 species of *Polydora* and 10 species of *Dipolydora* occurring on the east coast alone (Walker 2009, 2011). Recent taxonomic work

suggests the mudworm species associated with the first oyster mortality events in Australia were misidentified (Walker 2011). The main species that are usually reported to be problematic in mollusc aquaculture include *Polydora websteri*, *Polydora haswelli* and *Polydora hoplura*, *Boccardia knoxi* and *Boccardia chilensis* (Nell 2001; Leonart et al. 2003a, b). It is notable that many of the early museum specimens originally identified as *P. websteri* from Australian oysters were, upon re-examination, other species such as various *Dipolydora* spp., while some specimens identified as *Polydora polybranchia* by Haswell (1885) and Whitelegge (1890) from *S. glomerata* were re-identified as *Boccardia polybranchia* and *Polydora wellingtonensis* (Walker 2009, 2011). This suggests that at least some and possibly all of the mudworms that were associated with disease in *S. glomerata* in the late nineteenth century were endemic species.

Further evidence that refutes the theory that mudworm infestations of subtidal oysters in Australian estuaries were due to introduction of 'more virulent' exotic species comes from the work of Read (2010). While trans-Tasman exports of live oysters from New Zealand were commonplace during the late nineteenth century (including *S. glomerata* that also occur in New Zealand; Anderson & Adlard 1994), there is no evidence that mudworms were problematic in New Zealand at that time (Read 2010). The earliest reports of mudworm in New Zealand oysters date from the early 1970s and only from northern New Zealand, whereas a century earlier mudworms had become widespread and associated with disease in oysters along Australia's eastern coast (Roughley 1939; Nell 2001; Ogburn et al. 2007; Read 2010). These data prompted Read (2010) to conclude that mudworm disease of subtidal oysters on Australia's east coast beginning from around 1870 onwards was highly unlikely to have been due to introduction of 'exotic mudworms' from New Zealand.

Prevalence and intensity of mudworm infestation in Sydney rock oysters increases in the vicinity of muddy substrates (Whitelegge,

1890), and mudworm infestations can be reduced by off bottom bivalve culture techniques, preferably at heights that dry out the mollusc for at minimum 2 h in each tidal cycle to kill mudworm larvae (Whitelegge 1890; Nell 2001; Ogburn et al. 2007). Mudworms are abundant in muddy tidal flats and less abundant on clean sandy flats because the seasonal (Handley 2000; Leonart et al. 2003a, b) settlement of mudworm larvae from the plankton is stimulated by high microbial counts associated with nutrient enriched sediments (Sebesvari et al. 2006). This suggests that organic enrichment, eutrophication and sedimentation (the first anthropogenic changes that tend to occur in estuaries after extensive development in the catchment; Airoldi 2003) will promote increased abundance of mudworms (Nell 2001). In effect, Haswell (1885) noted this by stating 'some local circumstances, such as muddiness of the water produced by increasing traffic, tend to decrease the vital powers of the oysters and thus favour the inroads of the parasites'.

Ogburn et al. (2007) stated that 'an 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'. Historical epidemiological evidence, modern scientific understanding of settlement cues of spionid polychaete larvae and recent taxonomic work on Australian spionids all suggest that this alternative hypothesis provides a more parsimonious explanation for the rise of mudworm and the demise of subtidal oyster reefs in Pumicestone Passage and Moreton Bay.

Since the late 1960s, mortalities of wild and cultured *S. glomerata* in the Pumicestone Passage region have been associated with *M. sydneyi* (Phylum Paramyxea), aetiological agent of QX disease (Wolf 1972; Perkins & Wolf 1976). However, it appears that *M. sydneyi* is an endemic disease agent (Kleeman et al. 2004). Indeed, today *M. sydneyi* occurs in apparently healthy oyster populations at low prevalences in all but one of the major oyster-growing estuaries along Australia's east coast (Adlard &

Wesche 2005), even though QX disease outbreaks do not occur in most of these locations (Butt et al. 2006; Green et al. 2011). This demonstrates that *S. glomerata* is well accommodated to the parasite, suggesting a long standing host–parasite relationship, and indeed oysters carrying low intensity *M. sydneyi* infections can shed the parasite under favourable environmental conditions (Roubal et al. 1989).

The role of QX disease in the decline of rock oysters in Pumicestone Passage and Moreton Bay will be discussed in more detail in the next section on water quality. However, given that large numbers of oysters died after flooding in Moreton Bay and Pumicestone Passage in 1887 and 1893 (Brisbane Courier 1898; Lergessner 2008), and assuming *M. sydneyi* is an endemic pathogen, this means that some of the mortalities recorded after these flood events could have been the first epizootics due to QX disease. Oyster farmers and scientists in the late 1800s had a rudimentary ability to diagnose oyster pathogens and they would have been more likely to blame the visible mudworm for any oyster deaths, rather than a microscopic protozoan unknown to science at the time (Read 2010). Further study of suitably fixed archived oyster tissues held in museum collections with molecular diagnostic techniques (Kleeman & Adlard 2000; Kleeman et al. 2002, 2004; Adlard & Nolan 2008) may be able to confirm whether *M. sydneyi* was associated with disease in Sydney rock oyster populations in the late nineteenth and early twentieth centuries.

Declining water quality

The long-term impacts of declining water quality on inshore ecosystems can be significant, but are rarely quantified due to a lack of baseline studies (Shepherd et al. 2009). Baselines are very important, however, due to the problem of sliding baselines, which erode our understanding of natural ecosystem processes and blur our ability to understand what a healthy ecosystem looks like (Pauly 1995; Dayton et al. 1998;

Jackson et al. 2001; Papworth et al. 2008). The Pumicestone Passage is a valuable case study in the context of baselines for Australia's east coast estuaries, as European colonisation of the region was comparatively recent, and detailed historical records are available. Furthermore, if water quality baselines are of interest, oysters are appropriate research subjects as they are excellent water quality indicators. Being filter feeders, they are particularly vulnerable to water quality declines (Auffret 2005; Giron-Perez 2010).

The modern understanding of natural baselines for 'new world' civilisations is usually the state of ecosystems prior to European settlement. In Australia, however, indigenous Australian aboriginals occupied the continent for at least 40,000 years, and in that time both climate change and human influences combined to alter the pre-European landscape (Mooney et al. 2011). Indeed, 'firestick farming' through use of deliberately lit fires to clear undergrowth was an important form of landscape management in the Moreton Bay catchment prior to European settlement (Lilley 1984; Walters 1992). Temporary loss of vegetation from anthropogenic and/or natural fires within the catchment may have increased sedimentation in Moreton Bay, as suggested by the replacement between 1000 and 2000 years ago of clear water *Acropora* corals with sediment resistant species of *Favia* in historical coral facies within the bay (Walters 1992). A slight increase in sedimentation probably would have also increased nutrient flow and the extent of intertidal mud flats in the western bay, a process that may have increased fisheries production compared with pre-human baselines (Walters 1992). Certainly, if slight increases in nutrient loading over pre-human baselines had occurred, these would have probably increased the productivity of oyster populations, as was noted for oysters in Chesapeake Bay during the initial stages of European colonisation (Kirby & Miller 2005; Harding et al. 2008).

In contrast, since 1840, European land use practices resulted in large-scale clearing of the Moreton Bay catchment for agriculture and urban development, a process that has continued to accelerate with the region's rapidly increasing population. Coral cores from the Great Barrier Reef show that it took less than 30 years of European land use in the Burdekin River catchment (1840–1870) to clear enough land to generate a 5–10-fold increase in sediment loading in river run-off during drought-breaking floods (McCulloch et al. 2003). This decline in water quality during flood events has resulted in significant changes to community structure in inshore coral reefs (Roff et al. 2013). As the Brisbane River did not have a major flood between 1870 and 1887 (Fig. 2), this suggests that the 1887 flood would have introduced an unprecedented amount of sediment and nutrients into the Moreton Bay ecosystem, an assumption that fits well with historical records and observations of people living and working in Moreton Bay at the time.

The 1887 flood event, combined with floods in 1889/1890 and the multiple > 8 meter flood events in 1893, may have introduced enough sediment and nutrients into the previously sand-dominated Pumicestone Passage system to begin to alter its structure. These events may have triggered a regime shift (Spencer et al. 2011), which manifested firstly through loss of subtidal oyster beds by smothering, followed by outbreaks of mudworm disease in the recovering subtidal beds due to increased organic enrichment and sedimentation, as was suggested and observed by researchers at the time (Haswell 1885; Whitelegge 1890; Saville-Kent 1891a,b). Sustained catchment development in the 120 years since 1893 has further increased both baseload (Morelli et al. 2011) and flood-generated (McCulloch et al. 2003) sedimentation rates, so that today, sediment plumes from drought breaking floods not only affect inshore areas, they can adversely affect coral reef biota many kilometres offshore (McCulloch et al. 2003; Roff et al. 2013).

In Chesapeake Bay, the productivity of oyster populations increased during the initial stages of European colonisation, but then collapsed due to continued heavy fishing in the face of reduced water quality due to eutrophication and sedimentation, as well as significant losses due to introduced disease agents (Burreson et al. 2000; Boesch et al. 2001; Kemp et al. 2005; Kirby & Miller 2005; Harding et al. 2008). A similar process of decline has occurred in Moreton Bay; however, in the absence of introduced pathogens or sustained overfishing, it appears that reduced water quality has been the primary driver responsible for ongoing declines of oysters in this ecosystem. This may be predictable to some extent, given that the El-Nino Southern Oscillation (ENSO) climate variability (Quinn 1993), geomorphology and pre-European land use which shaped the ecosystem would have resulted in evolution of estuarine ecosystems adapted to relatively low sediment and nutrient levels (Wulff et al. 2011).

Examination of several hundred contemporary Sydney rock oysters collected in 2011 from Pumicestone Passage (Fig. 7) found their shells were much thinner than historical oyster shells ($n=2$) obtained from the same location by digging under 30–40 cm of silt deposited near the oyster clumps depicted in Fig. 5. Deposition of over 30 cm of sediment is likely to have taken at least 100 years at today's accelerated sedimentation rates of 0.27 cm/year for sites in northern Moreton Bay (Morelli et al. 2012), suggesting that these oyster shells are likely to be over 100 years old, and may have even been covered over during the floods from the 1887–1893 period (though dating methods will be required to confirm this). Even casual observers note that the contemporary oyster shells appear very different from the historic ones (Fig. 7). The relatively thick shells of historical oysters suggest slow growth, which indicates the historic Moreton Bay ecosystem was probably nutrient limited. Paterson et al. (2003) found that Sydney rock oysters grown at sites adjacent to urban development grew



Figure 7 Comparison of two historical *Saccostrea glomerata* shells (left and middle) collected from underneath 33 cm of silt at the edge of a sand oyster bank at the mouth of Ningi Creek, against a contemporary (2011) oyster shell (right). Both large oysters are 72 mm shell length, but the shell weight for the historical shell on the far left is 31 g, vs 20 g for the contemporary oyster shell on the far right.

faster, but had higher mortality rates, than those grown at undeveloped sites. So while food availability may no longer be limiting for oysters in Australia's east coast estuaries today, reduced food quality in estuaries adjacent to human development may be compromising oyster health. This was also noted by Kirby & Miller (2005), who suggest that algae found in eutrophic environments, such as cyanobacteria and dinoflagellates, are likely to be less nutritional and/or more toxic than the diatoms that usually dominate oyster diets and which historically formed a greater proportion of estuarine primary production (Cooper 1995). These cursory observations suggest that detailed scientific comparison between historical and contemporary Sydney rock oyster shells is needed, and is likely to uncover new information regarding historical changes to the ecology of Moreton Bay, as it has done in other parts of the world (Kirby & Miller 2005; Harding et al. 2008).

In Moreton Bay, QX disease caused by *M. sydneyi* emerged in the late 1960s (Wolf 1972; Perkins & Wolf 1976), but as discussed previously, all available evidence suggests that *M. sydneyi* is an endemic disease agent which is well adapted to its host and does not cause disease under normal environmental conditions. Sydney rock oysters become infected with *M. sydneyi* during their filter-feeding process when the gills and palps contact a planktonic infective stage that is emitted from intermediate hosts (Kleeman et al. 2002). Early studies found that *M. sydneyi* has an indirect life cycle that requires an intermediate host (Lester 1986), which was likely to be a filter-feeding or detritivorous invertebrate (Roubal et al. 1989). Oysters with clinical QX disease harbour large numbers of *M. sydneyi* developmental stages that are shed into the water column via the digestive tubules or upon death of the host (Lester 1986; Roubal et al. 1989; Kleeman et al. 2002). Sydney rock oysters

appear to be exposed to the infective stage of QX disease for only a short period, usually after heavy rainfall in the summer months (Anderson et al. 1994; Wesche 1995; Wesche et al. 1999), and under suitable conditions for disease development oyster deaths increase in late summer and autumn (Lester 1986; Roubal et al. 1989; Wesche 1995). Alternate life history stages of *M. sydneyi* have been identified using *M. sydneyi*-specific molecular probes in benthic polychaetes in the family Nephtyidae sampled from the Hawkesbury River following an unprecedented and severe outbreak of QX disease in that estuary (Adlard & Nolan 2008; Cribb 2010). The polychaete *Nephtys australiensis*, which Adlard & Nolan (2008) identified as harbouring alternate developmental stages of *M. sydneyi*, is described as being more common in muddy rather than sandy sediments (Rainer & Hutchings 1977). Even so, until such time as the life cycle of *M. sydneyi* is completed and naïve oysters can be reinfected experimentally, it is possible that other organisms or additional alternate life cycle stages in other hosts (besides oysters and polychaetes) could also play a role in the life cycle of *M. sydneyi*.

Nevertheless, given that at least one alternate stage of the life cycle of *M. sydneyi* is associated with benthic mud-dwelling polychaetes, this may explain the emergence and apparent increased virulence of QX disease in oysters from Pumicestone Passage. Extensive catchment development in Moreton Bay has resulted in increased sedimentation throughout the lower estuaries and inner bay. This will have provided a vast increase in the area available for mud-dwelling polychaetes such as *N. australiensis*, populations of which may have been restricted to much smaller areas of mud in the upper reaches of estuaries prior to European settlement. Furthermore, some polychaetes are known to be sensitive biomarkers of organically enriched sediments (Cardoso et al. 2007), as evidenced by their domination of the benthic footprint under marine fish farms (Tomassetti & Porrello 2005; Hall-Spencer et al. 2006; Sutherland et al. 2007). Because of this,

it is very possible that *M. sydneyi* infection pressure has increased substantially in modern times compared with historic baselines, due to environmental changes that have favoured range expansion and proliferation of its alternate host(s).

Expression of QX disease is associated with a decline in the immunocompetence of the host oyster (Peters & Raftos 2003; Newton et al. 2004; Butt et al. 2006, 2007; Butt & Raftos 2007, 2008; Green & Barnes 2010; Green et al. 2011). Reduced salinity is an important risk factor in QX disease expression (Lester 1986), due to its ability to immunocompromise oysters (Butt et al. 2006; Green & Barnes 2010). However, low-salinity flood waters from anthropogenically disturbed catchments not only stop oysters feeding for some time (increasing nutritional stress; Butt et al. 2007), today they also transport sediments and a wide array of other pollutants. Many types of pollutants are modulators of the immune system of molluscs at normal environmental concentrations (Fisher et al. 1999; Auffret 2005; Giron-Perez 2010). Furthermore, flood events are known to result in large die-offs of marine polychaetes in subtropical Australian estuaries, including members of the Family Nephtyidae (Moverley et al. 1986). If polychaetes such as *N. australiensis* die off in large numbers during floods, this could result in mass releases of QX-infective stages from dying alternate hosts infected with *M. sydneyi*, thus driving the life cycle to completion once immunocompromised oysters recommence feeding after flood events. When all these factors are considered, it is perhaps not surprising that QX epizootics in Sydney rock oysters are particularly severe following flood events in estuaries with high anthropogenic disturbance in their catchment.

The oyster clumps at the mouth of Ningi Creek in Pumicestone Passage are at least seven decades old (T. Clayton, fisherman, pers. comm. August 2011) and are remnants of the original oyster culture industry from the early twentieth century. The degradation of these formerly monolithic clumps into their

current mushroom shape (Fig. 5) requires scientific investigation. Using surveys conducted with digestive gland impressions in November 2010, I found that the prevalence of *M. sydneyi* infections in *S. glomerata* ($n=20$, mean shell length 50 mm, range 25–72 mm) sampled from the top of wild oyster clumps from two different banks ($n=10$ oysters randomly selected per bank) was 30% with a low intensity of infection and only one oyster (prevalence 5%) infected by other pathogens (ciliates). In contrast, oysters ($n=20$, mean shell length 51 mm, range 40–62 mm) moved 60 days previously from the top of these same clumps (c. 1.2 m above tidal datum), into oyster trays 500 m away in Ningi Creek at a lower growing height (c. 0.7 m above tidal datum), had 100% prevalence of mainly high-intensity QX infections, as well as infection by digenean sporocysts in one oyster (prevalence = 5%). No mudworms were evident in any of the oysters examined. These data confirmed that QX, not mudworm, was the disease agent responsible for the increased mortality rate of oysters in Ningi Creek over the summer months of 2010/11, including 100% mortality of oysters held in trays at the 0.7-m growing height by May 2011 (Carlo Sain pers. comm. August 2011). These data also show that oysters lower in the water column had heavier *M. sydneyi* infections and therefore were more likely to die from QX disease than oysters growing at or above 1.1 m above tidal datum.

The fact that *S. glomerata* held at lower levels in the intertidal zone are more susceptible to disease has been previously observed for not only QX disease (Wolf 1979), but also winter mortality (caused by *Bonamia roughleyi*; Smith et al. 2000), and other oyster diseases where infective stages are waterborne (Gagnaire et al. 2006). It is probable that *S. glomerata* that occur lower in the water column are being exposed to higher quantities of *M. sydneyi* infective stages, which could help explain why mortalities of 100% occurred over the summer of 2010/11 in oysters grown below a level of around 1.1 m above tidal

datum in Ningi Creek. Oysters lower in the water column are exposed to poor water quality for longer periods, and therefore may be more likely to be immunosuppressed. Certainly these observations demonstrate that further research on the immunocompetence and disease tolerance of *S. glomerata* in relation to both water quality and their growing height in the water column is urgently required.

Ogburn et al. (2007) stated that ‘Sedimentation and nutrient loading, may have contributed to a decline in subtidal oyster reefs, but not their complete disappearance and failure to recover.’ However, there is a large amount of observational, empirical experimental and epidemiological evidence to challenge this statement. Larval settlement is a critical bottleneck in the life history of bivalve molluscs. Survival of oyster larvae is highest on sediment free, hard substrates, particularly the shells of conspecifics, and oyster larvae have evolved over time to respond to a variety of physical and chemical settlement cues that are emitted by adult conspecifics, and/or particular bacterial biofilms (Tamburri et al. 2008). In organically enriched environments with high quantities of resuspended sediment, algal turfs form on all available hard subtidal surfaces (McEwan et al. 1998). This biofilm traps sediment and detritus, making the surface unsuitable for settlement or post-settlement survival of oyster spat (Tamburri et al. 2008; B.K. Diggles pers. obs.). Because of these reasons, a combination of sedimentation, sediment resuspension and nutrient loading that generates sediment laden algal turfs over hard surfaces appears sufficient to cause multigenerational recruitment failure for oyster spat that settle in subtidal areas. Indeed, such a process would explain the existence of mushroom shaped oyster clumps in the Pumicestone Passage (Fig. 5), which form these shapes when the lowest oysters that die first during QX epizootics are not replaced by new recruits.

Conclusion

While there is no doubt that overfishing can adversely affect populations of oysters, there is little evidence to suggest that overfishing alone was primarily responsible for the decline of oyster populations in Moreton Bay and Pumicestone Passage. Organic enrichment and sedimentation in Pumicestone Passage originating from episodic flood events as far back as 1887 has resulted in deposition of mud and silt over what were once clean sandy areas. This process is likely to have smothered subtidal oyster reefs and favoured increases in populations of polychaetes and other invertebrates, which may directly or indirectly play key roles in disease processes that adversely affect oyster populations. Initially the change to the ecosystem was signalled by emergence of 'mud worm disease', as populations of spionid polychaetes responded to favourable environmental conditions of increased availability of silt and organic loading in subtidal and lower intertidal areas. Other mud-dwelling polychaetes, which have been identified as intermediate hosts for the agent responsible for QX disease, may have originally been restricted to the middle and upper reaches of rivers, but following increased sedimentation they would have been released to colonise a much wider area in the lower estuaries and into Moreton Bay proper, where the majority of oysters occurred. In contrast to the rapid onset of mudworm infestations, the onset of epizootics caused by QX disease was delayed as water quality between flood events remained relatively high and the immune response of oysters to this endemic parasite were not unduly compromised. Only since the late 1960s, as water quality continued to deteriorate due to accelerating catchment development, does it appear that the immune responses of oysters were compromised to a level that permitted QX disease epizootics to become noticeable. Today, oyster populations in Pumicestone Passage experience recurring severe QX epizootics resulting in increased 'natural' mortality rates, with oysters exposed to the water

for longest dying first, probably due to exposure to larger numbers of infective stages of *M. sydneyi*, increased immunosuppression due to longer periods of exposure to poor water quality, or both.

Historical epidemiology therefore suggests the overriding mechanism responsible for the decline of oyster populations in Pumicestone Passage and Moreton Bay is one of declining water quality over the last 120 years, forcing disease processes by modulating the host/pathogen relationship and allowing what were once innocuous endemic agents to proliferate and overwhelm their hosts. Furthermore, in stark contrast to the once prolific recruitment of 120 years ago, dying oysters are no longer being regularly replaced by new spat at levels below around 1.1 m above low water datum. This is a form of recruitment failure, which is likely due to the lack of availability of suitable surfaces for oyster larvae to settle on as constantly resuspended sediments lodge in algal biofilms stimulated by eutrophication, resulting in spatfall failure.

Some authors (e.g. Pillans et al. 2007), as well as Queensland Government agencies, have suggested that increased implementation of 'no take' sanctuary zones will protect biodiversity and fisheries productivity in Pumicestone Passage and other areas of the Moreton Bay Marine Park. However, when the mechanisms affecting this ecosystem are considered, it is clear that the ecosystem will not recover spontaneously from its current degraded state if the remaining recreational fishing effort in Pumicestone Passage is removed. This is because 'no take' sanctuary zones do not protect biodiversity whenever habitat and water quality are being degraded (Jones et al. 2004). The processes driving changes to the Pumicestone Passage and wider Moreton Bay ecosystems, like those affecting the coral reefs further north (Roff et al. 2013), appear primarily driven by declining water quality due to sedimentation, eutrophication and other anthropogenic changes derived from catchment development.

Because of this, management and restoration efforts should instead focus on improving inshore water quality by reducing sediment and nutrient loading and other pollutants from both point and non point sources. Efforts to restore water quality and replenish lost oyster reefs with QX-resistant oysters to attempt to regain the ecosystem services they provide (Boesch 2006; Grabowski & Peterson 2007; Schulte et al. 2009; Ruhl & Rybicki 2010; Beck et al. 2011) are likely to result in improvements in water clarity, improved benthic-to-planktonic production ratios (Kemp et al. 2005), increase fisheries productivity (Peterson et al. 2003) and increased biodiversity (Hosack et al. 2006; Airoidi et al. 2008). While reversing the changes of the last 120 years will not be an easy task, there are examples of community-based restoration programmes from Chesapeake Bay (Ruhl & Rybicki 2010) that can be used as models for integration with existing local water quality programmes so that the process of restoration can begin.

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