Research Article

Quantifying abundance and distribution of native and invasive oysters in an urbanised estuary

Elliot Scanes[1,2,*], Emma L. Johnston[3,4], Victoria J. Cole[1,2], Wayne A. O'Connor[5], Laura M. Parker[1] and Pauline M. Ross[1,2]

[1]*School of Life and Environmental Sciences, Coastal and Marine Ecosystems Group, The University of Sydney, Sydney, NSW 2006, Australia*
[2] *School of Science and Health, Western Sydney University, Penrith, Sydney NSW 2750, Australia*
[3]*School of Biological, Earth and Environmental Sciences, Evolution and Ecology Research Centre, The University of New South Wales, Sydney, NSW 2052, Australia*
[4]*Sydney Institute of Marine Science, Mosman, NSW 2088, Australia*
[5]*New South Wales Department of Primary Industries, Port Stephens Fisheries Institute, Taylors Beach, NSW 2316, Australia*

**Corresponding author*

E-mail: Elliot.scanes@sydney.edu.au

Abstract

Human activities have modified the chemical, physical and biological attributes of many of the world's estuaries. Natural foreshores have been replaced by artificial habitats and non-indigenous species have been introduced by shipping, aquaculture, and as ornamental pets. In south east Australia, the native Sydney rock oyster *Saccostrea glomerata* is threatened by pollution, disease and competition from the invasive Pacific oyster *Crassostrea gigas*. This study assessed the abundance (as number m^{-2}), size, and distribution of both invasive and native oyster species at 32 sites in the heavily urbanised Port Jackson Estuary, Australia. We tested the hypotheses that there would be: (1) a difference in the proportion of *C. gigas* and *S. glomerata* among locations; (2) a greater proportion of *C. gigas* on artificial compared to natural substrates; (3) a greater numbers of all oysters, with differing size characteristics, on artificial compared to natural substrates; and (4) that the abundance and size of all oysters would vary among locations along an environmental gradient. Environmental variables included distance from the estuary mouth and salinity. We found the abundance and size of all oysters differed among locations; smaller oysters occurred at greater abundances near the mouth of the estuary. Abundance was also higher on artificial, than on natural substrate. Habitat type, however, had no effect on which species of oyster was present. In contrast, distance from the estuary mouth strongly influenced the relative proportion of the two species. The invasive *C. gigas* comprised 16 % of the oysters sampled, and up to 85 % at some of the upper estuary sites. As predicted, *C. gigas* was more abundant at locations in the bay ends and upper channel of the estuary; it was also larger in size than the native *S. glomerata.* This is the first assessment of oyster distribution in Port Jackson and provides a solid base for monitoring changes in the estuarine distribution of a globally invasive pest.

Key words: invasive species, oysters, Port Jackson, Sydney Harbour, pollution, urbanisation

Introduction

Many of the world's major cities are located on the coast and surround large estuaries (Timmerman and White 1997; Dafforn et al. 2015). As centres of trade and recreational activity, these areas are subject to substantial shipping traffic, changing shorelines, and have become hot spots for the spread of non-indigenous species or NIS (Glasby et al. 2007; Johnston and Roberts 2009). The establishment of NIS in previously undisturbed environments can result in a host of changes to that ecosystem including a loss of biodiversity and changes in ecosystem structure and function (e.g., Burlakova et al. 2000; Karatayev et al. 2002; Ruesink et al. 2005; Troost 2010). Although many NIS never establish themselves in a new environment (Lodge 1993), some flourish and can drastically alter that ecosystem (Burlakova et al. 2000; Karatayev et al. 2002). These highly successful NIS are often referred to as invasive (e.g., Burlakova et al. 2000; Karatayev et al. 2002).

Urban sprawl of coastal cities has increased to such an extent that in some, greater than 50 % of their foreshores have been altered (Chapman and Bulleri

2003; Bulleri et al. 2005; Dafforn et al. 2015). Modification of shorelines is done to support maritime craft (Johnston et al. 2011), reclaim land, and armour shorelines (Airoldi et al. 2005). Such extensive modification creates an artificial habitat, which is often different in structure to the prior natural habitat (Chapman and Bulleri 2003; Bulleri et al. 2005). Assemblages of marine organisms in these highly disturbed areas are often different to those areas that have remained undisturbed (Chapman and Bulleri 2003; Bulleri et al. 2005). The anthropogenic removal of natural shoreline in estuaries, and its replacement with artificial surfaces such as seawalls and pilings and the modification of indigenous assemblages has been shown to create windows of opportunity for NIS to colonise habitat that might have been otherwise been inaccessible (Dafforn et al. 2012). The removal of indigenous species does not occur only through anthropogenic alterations in habitat. Contamination (Johnston and Roberts 2009) can impact indigenous marine assemblages by reducing species richness and evenness (Johnston and Roberts 2009). These reductions in the biodiversity of indigenous assemblages can make them vulnerable to colonisation by NIS (Stachowicz et al. 1999).

Globally, oysters are one of the dominant organisms in intertidal temperate systems (Ruesink et al. 2005). Oysters are well known as ecological engineers (Gutiérrez et al. 2003) and providers of ecosystem services (Coen et al. 2007). Oysters are capable of quickly colonising novel habitats (Anderson and Underwood 1994; Glasby et al. 2007) and are among the most translocated marine species on the globe (Ruesink et al. 2005). Up to 18 oyster species have been translocated to 73 different countries, allowing some to become established NIS in northern Europe, North America, Argentina, South Africa, New Zealand, and Australia (Ruesink et al. 2005). The Pacific oyster, *Crassostrea gigas* (Thunberg, 1793) has been introduced to 66 countries around the globe, with 17 of these introductions recorded as successful (Ruesink et al. 2005). The high aquaculture value of *C. gigas*, and its ability to bioengineer habitat to its advantage (Troost 2010), has allowed the oyster to rapidly establish breeding populations in many estuaries. It has been responsible for displacing native bivalves in north-western Europe (Reise 1998; Orensanz et al. 2002), North America (Carlton 1992), and New Zealand (Dinamani 1991). In 1952, *C. gigas* was introduced to southern Australia from Japan for the purpose of aquaculture (Polland 1990). Reports from 1967 describe *C. gigas* present amongst the wild oyster populations, albeit in low abundance, in New South Wales (NSW) (Medcof and Wolf 1975). It is now found alongside the native

Sydney rock oyster, *Saccostrea glomerata* (Gould, 1850), in all major estuaries south of the Hastings River (31.424657º, 152.92227º), along the east coast of Australia (Nell 2001). It is classed as a noxious pest in NSW (NSW Department of Primary Industries 2012), and is regarded as one of Australia's top 10 most damaging invasive species (Commonwealth Science and Industrial Research Organisation 2005).

The native Sydney rock oyster is cultured in many NSW estuaries and is of significant economic value to Australia (Nell 2001). Natural oyster aggregations are also a major source of biogenic habitat in south eastern Australia (Cole et al. 2007; McAfee et al. 2016). Historically, populations of *S. glomerata* were harvested for food and lime production by indigenous and European Australians until natural populations were exhausted (Nell 2001).

Natural and aquacultured populations of *S. glomerata* in eastern Australia have been afflicted by two diseases: QX disease, and winter mortality (Nell 2001). In south eastern Australia, *C. gigas* is also affected by disease, recently the ostreid herpesvirus-1 microvariant (OHsV-1 µvar) has caused mass mortality of *C. gigas* in Europe (Soletchnik et al. 2007), New Zealand, and Australia (Jenkins et al. 2013), but has not affected *S. glomerata*.

Despite the greater growth, feeding rates (Bayne 2002), and wider salinity tolerance of *C. gigas* (Nell and Holiday 1988), research has shown that *C. gigas* and *S. glomerata* potentially co-exist in NSW (Krassoi et al. 2008; Bishop et al. 2010). Krassoi et al. (2008) suggested that the greater growth rate and subsequent metabolic demand has compromised the ability of *C. gigas* to withstand extended periods of emersion, allowing *S. glomerata* to dominate higher tidal elevations. When present in low abundance, *C. gigas* can positively influence the recruitment of larvae of *S. glomerata* (Wilkie et al. 2012), but at high abundance the rapid rate of filtering by *C. gigas* can negatively affect recruitment of *S. glomerata* (Wilkie et al. 2012).

There is very little knowledge of the abundance, distribution, and species composition of wild oyster populations in NSW estuaries, especially in urbanised estuaries where the risk of establishment of an invasive species is high (Johnston et al. 2008). Port Jackson is a large natural harbour with very high biological diversity (Johnston et al. 2015). It is a heavily urbanised estuary (up to 86 % of the catchment has been covered in concrete; Pinto et al. 2015), and is the focus of the city of Sydney, with approximately 4.5 million residents (Australian Bureau of Statistics 2014). The harbour itself is highly disturbed (Pinto et al. 2015) and over 50 % of the foreshore is
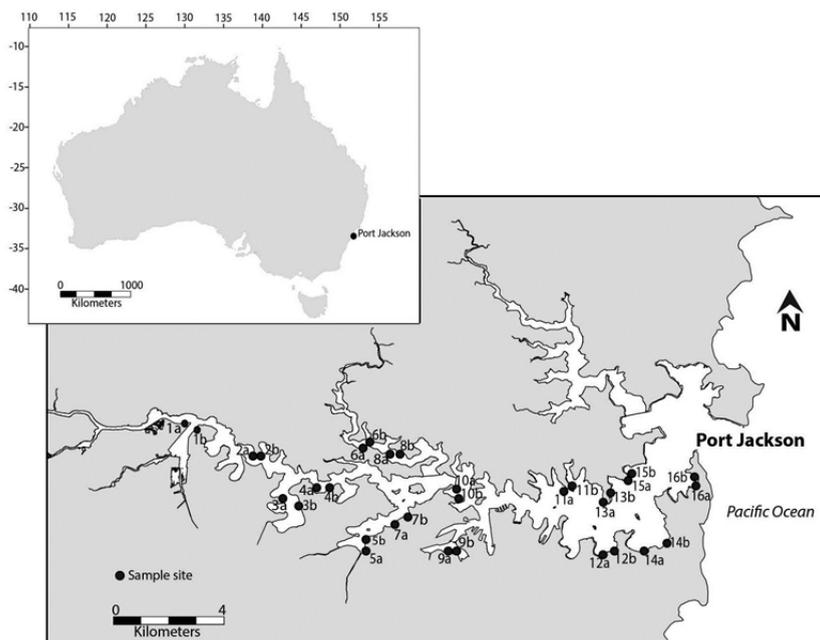
Figure 1. Sampling sites in Port Jackson. Each dot represents a sampling site, corresponding numbers are sites within the same location. Upper left is Port Jackson in relation to Australia, Latitude and longitude are shown on the axes (for details see supplementary material Table S1).

armoured by seawalls (Chapman and Bulleri 2003). Recent non-quantitative surveys of oysters in Port Jackson suggested that oyster populations have increased, especially in the upper reaches of the estuary (Birch et al. 2013, 2014). Despite the apparent increase, environmental conditions for oysters continue to be highly stressful due to contamination (Edge et al. 2014). Both *S. glomerata* and *C. gigas* are known to be present in Port Jackson (Hutchings et al. 2013), but accurate identification to species level based on external morphology in the field is practically impossible (Thomson 1954). Potentially *C. gigas* could be expanding in range within Port Jackson undetected because of the similarities in external morphology. As novel habitat and anthropogenic pressures become more of a feature of the harbour, the risk of invasive species colonising and native species declining becomes greater (Glasby et al. 2007; Piola and Johnston 2008; Dafforn et al. 2015). To determine the extent of *C. gigas* invasion requires a comprehensive survey of oyster populations in Port Jackson, which will also provide a baseline for detecting changes to distributions in the future.

The aim of this study was to measure the distribution, abundance, and size characteristics of the invasive *C. gigas* and the native *S. glomerata* population in Port Jackson. We tested the hypotheses that there would be: (1) a difference in the proportion of *C. gigas* and *S. glomerata* among locations within Port Jackson; (2) a greater proportion of *C. gigas* on

artificial compared to natural substrate; (3) a greater abundance of all oysters, with different size characteristics on artificial compared to natural substrates; and (4) that the abundance and size distribution of all oysters would vary among locations within Port Jackson. Potential environmental factors (i.e. salinity and distance from estuary mouth) which may contribute to observed patterns of abundance, distribution, and size of oysters within the estuary were also investigated. This study is the first to quantify the distribution of *C. gigas* in Port Jackson, and provides a solid base for gauging changes in the distributions of native and invasive oysters in the estuary as a result of further environmental change.

Material and methods

Study location

Port Jackson, also known as Sydney Harbour (33.8600ºS, 151.2094ºE), is a drowned river valley approximately 30 km long and 3 km across at its widest point (Figure 1) (Roy et al. 2001). The large bays and upper channel of the estuary receive considerably less flushing than the more oceanic down-stream regions (oceanic regions include sites 11–16; Figure 1 [Birch et al. 2010]). Port Jackson is surrounded by the greater metropolitan Sydney region, with over 4.5 million people (Australian Bureau of Statistics 2014). This high degree of

urbanisation and industrialisation has resulted in Port Jackson becoming one of the world's most polluted waterways by heavy metals and organic compounds (Pinto et al. 2015). Approximately 50 % of Port Jackson's shoreline has been replaced by artificial seawalls (Chapman and Bulleri 2003), and 22 % of the total area of the estuary has been reclaimed (Birch et al. 2007; Birch et al. 2010). As a result of the historical pollution in the estuary, culture of oysters is not permitted, commercial fishing has been banned, and the consumption of fish is restricted by government guidelines (Pinto et al. 2015).

Distribution, abundance, and size of oysters

To determine the abundance and distribution of oysters within Port Jackson, 16 locations were sampled during the austral summer/autumn of 2014 (Figure 1; Table 1; Supplementary material Table S1). Locations were selected along the full length of the lower estuary. Locations were dependent on suitable habitat being available. Two sampling sites were arbitrarily selected at each location and were at least 50 m apart. Sites were either on natural or artificial hard substrate. Artificial substrate sites were only sampled if they had been in existence for more than 3 years and showed no obvious signs of recent disturbance or construction. Artificial substrate sites were all vertical surfaces and predominantly made of sandstone. Natural substrate sites were predominantly sloping, sandstone, rocky shores of varying angles. Sandstone walls are the dominant artificial habitat in Port Jackson that is available to oysters. There were 18 sites with artificial surfaces, and 14 sites with natural rocky intertidal surfaces (Figure 1; Table 1).

Because of the external morphological similarities between *S. glomerata*, and *C. gigas*, abundance was determined by counting all live oysters present within a quadrat. At each site, the number of all live oysters was recorded in ten randomly placed, 50 × 50 cm quadrats on the shore, 0.4–1.1 m above Indian Spring Low Water (ISLW). The substrate type on which abundance of oysters was measured at each site was kept consistent among all 10 quadrats. Oyster abundance was standardised to the number m^{-2}. Oyster species (proportion), size and weight were determined from measurements of oysters removed from the site. At each site, all live oysters within at least five 20 × 20 cm randomly placed quadrats were chiselled from the substrate and collected. Enough quadrats were sampled to ensure that at least 20 individual oysters were collected (number determined by pilot studies).

Oyster species identity and morphology was determined by dissection in the laboratory. Shell length

Table 1. List of location names, their corresponding number and the habitat type present. Locations are ordered from west (upstream) to east (downstream) in the estuary.

Location name	Number	Site	Habitat
Olympic Park	1	A	Natural
		B	Natural
Kissing Point Park	2	A	Natural
		B	Natural
Bayview Park	3	A	Natural
		B	Natural
Abbotsford	4	A	Artificial
		B	Artificial
Hawthorne Canal	5	A	Artificial
		B	Artificial
Burns Bay rd Bridge	6	A	Artificial
		B	Artificial
King Georges Park	7	A	Artificial
		B	Artificial
Tambourine Bay	8	A	Artificial
		B	Artificial
Glebe Point	9	A	Artificial
		B	Artificial
Birchgrove Park	10	A	Artificial
		B	Artificial
Cremorne Point	11	A	Natural
		B	Natural
Double Bay	12	A	Artificial
		B	Natural
Bradleys Head	13	A	Natural
		B	Artificial
Rose Bay	14	A	Artificial
		B	Natural
Chowder Head	15	A	Natural
		B	Artificial
Watsons Bay	16	A	Artificial
		B	Natural

(anterio-posterior measurement), and shell height (perpendicular to shell length) was measured using digital Vernier callipers (± 0.02 mm). Following this, wet flesh mass was determined by opening the oysters, draining the excess water, removing the viscera and mantle, blotting on paper towels, and using an electronic balance to determine the weight of oyster flesh (± 0.01 g). Species identification was made based on internal morphology. Oysters with small denticles adjacent to the hinge along the ventral edges of the valves were identified as *S. glomerata*. Oysters lacking these denticles were identified as *C. gigas* (Thomson 1954).

To give an indication of the area of oyster shells, the area of the upper valve of oysters was calculated.

This was done by considering the upper valve to be an ellipse (McAfee et al. 2016), and the formula for the area of an ellipse was used:

$$A = \pi ab$$

Where: A = area of oyster's upper valve; a = shell length × 0.5; and b = shell height × 0.5.

Environmental variables

Selected environmental variables were recorded at each site to examine possible relationships between oyster abundance, size, and species composition as a function of salinity and distance from the estuary mouth. Salinity was monitored using a calibrated water quality sonde (model 612, Yeo-kal, Brookvale, Australia) for one month (April 2014) at four locations concurrently, one in each arm of the estuary (Locations 1, 5, 8, 15; Figure 1). The mean salinity at each location for the monitoring time was taken and used for each location within that arm of the estuary. Distance of each site from the estuary mouth (33.828092ºS, 151.284139ºE) was measured using GIS software (Google Inc. 2016) from the mid-point between the heads, along the shortest path remaining within the estuary.

Data analysis

Permutational multivariate analysis of variance (PERMANOVA) was used to compare means among the experimental factors for the variables: total number m^{-2} of oysters, species proportions, and oyster size (shell length, flesh weight and upper valve area) with 9999 permutations, based on Euclidean distance measures, using PRIMER 6+ software (PRIMER-E Ltd). The data were untransformed. PERMANOVA was used because it is robust to unbalanced data sets, and large nested deigns (Anderson 2001; Anderson et al. 2008). To test our first and second hypotheses relating to species proportions, the proportion of the assemblage comprised of the native *S. glomerata* at each site was analysed using a two factor PERMANOVA between "Habitats" (Artificial or Natural, fixed; orthogonal), and among randomly selected "Locations" (nested in Habitat). To test our third and fourth hypotheses relating to oyster abundance and size, the total abundance of oysters (both, *S. glomerata* and *C. gigas* n = 10), shell length, flesh weight and upper valve area of *S. glomerata* (n = 5–20; *C. gigas* were too scarce for a valid comparison) were analysed using a three factor PERMANOVA, where "Habitat" was fixed and orthogonal (with two levels, Natural or Artificial), "Location" was random and nested in "Habitat", and

"Site" was random and nested in both "Habitat" and "Location".

Differences in shell length, flesh weight, and upper valve area of oysters between species (*S. glomerata* or *C. gigas*) and among sites, were determined at those sites where both oyster species occurred and where there were at least 5 individuals of each species sampled (n = 5-10). For this analysis, we used a two-factor PERMANOVA: "Species" (*S. glomerata* or *C. gigas*) was a fixed factor and "Site" was random.

To determine any relationship between shell length of *S. glomerata* and oyster abundance, linear regression analysis was used. Abundance of *S. glomerata* was the independent variable, and shell length of *S. glomerata* the dependent. Invasive *C. gigas* was not present at enough sites to warrant regression analysis. Linear regression was also used to determine which environmental variables were potentially influencing patterns of oyster abundance, species proportions, and morphology. Environmental variables including distance from estuary mouth and mean salinity were analysed using regression against the biotic measures of oysters, abundance (both *S. glomerata* and *C. gigas*), mean shell length of *S. glomerata*, and proportion of *S. glomerata* (of total oysters) per site. *Crassostrea gigas* was not present at enough sites to analyse its shell length, or its species proportion. In all regressions, the environmental measurement was the independent variable and the biotic measure was the dependent variable.

Results

Proportion and abundance of oysters

There was no significant effect (P = 0.34) of location on the proportion of *S. glomerata* that comprised the total oyster assemblage. We found that in Port Jackson, *S. glomerata* was present at all sites and locations, but *C. gigas* was not (Figure 2). *Crassostrea gigas* was found in greater proportions than *S. glomerata* at two locations; Bayview Park (Location 3) where 85 % of the assemblage was comprised of *C. gigas*, and Olympic Park (Location 2; 90 % *C. gigas*). Some sites within locations had a high proportion of *C. gigas*, such as location 9 (Glebe Point; 35 % *C. gigas*) and 5 (Hawthorne canal; 25 % *C. gigas*). All these sites were bay ends or on the upper channel. Even at locations where *C. gigas* was present, the distribution was inconsistent, present at one site but not the other within the same location (e.g., Locations 14 and 15). Overall, the mean percentage of *C. gigas* among sites in Sydney Harbour was 16 %.

Abundances of both species of oysters were greatest in the oceanic regions of the Estuary; this is also
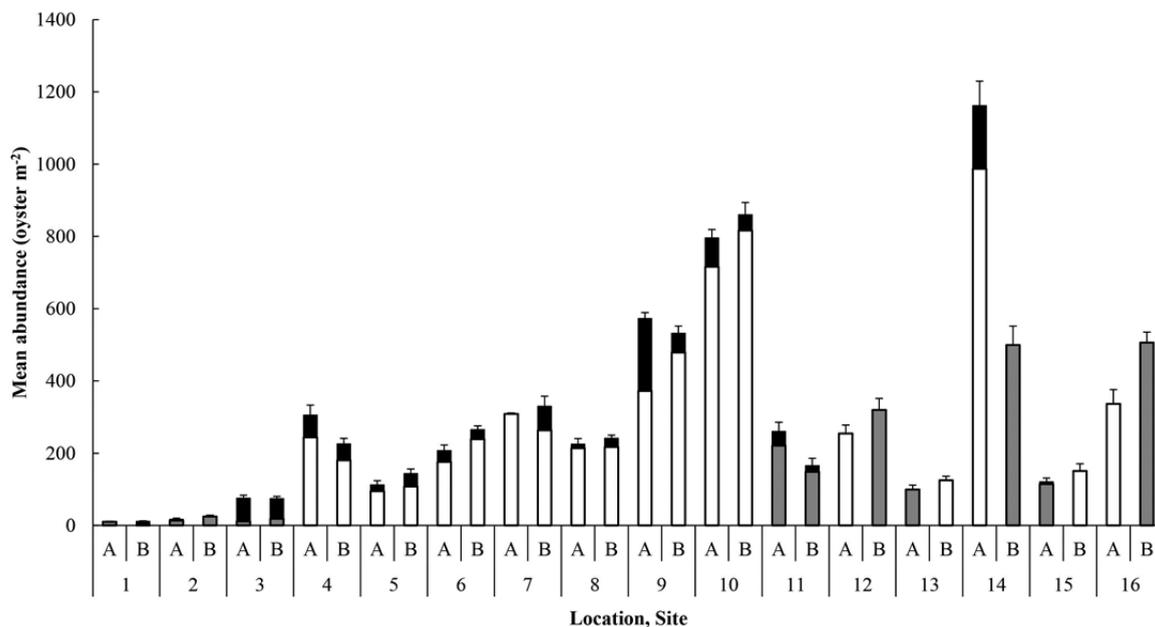
Figure 2. Mean abundance (+SE; n = 10) of all oysters (m^{-2}) on either natural or artificial habitat at each site. Open bars represent artificial habitat and shaded bars, natural habitat. The black portion of the bars of either habitat represents the relative proportion of the total oyster assemblage comprised of *C. gigas*. Locations are ordered from upstream to downstream along the estuary.

where there was a tendency for *S. glomerata* to comprise a greater proportion of the oyster assemblage (Figure 2). In contrast, there was a tendency for *C. gigas* to be more common in the bay ends, and upper channel of the estuary. There was no effect of habitat type on the species of oysters present. There was a significantly greater mean abundance of oysters (both species) on artificial (376 m^{-2} ± 21) compared to natural habitat (169 m^{-2} ± 16) (PERMANOVA; $F_{1,15}$ = 6.742; P = 0.014). Further-more, there were significant differences in the abundance of oysters among locations (PERMANOVA; $F_{15,15}$ = 16.139; P = 0.001) and between sites (PERMANOVA; $F_{15,288}$ = 5.528; P = 0.001) within Port Jackson. Abundances of oysters among sites were highly variable, the lowest recorded abundance was 10 ± 1.4 m^{-2}, and the greatest abundance was 1,161 ± 68.1 m^{-2}.

Shell length, flesh weight and upper valve area

The shell length (PERMANOVA; $F_{15.02,15}$ = 18.761; P = 0.0001), flesh weight (PERMANOVA; $F_{15.02,15}$ = 12.694; P = 0.0001) and upper valve area (PERM-ANOVA; $F_{15.02,15}$ = 17.99; P = 0.0001) of *S. glomerata* all differed significantly among locations but not between sites. There was, also, a significant relationship between shell length of *S. glomerata* and abundance of oysters (Figure 3). There was no

effect (P > 0.11) of habitat type on the shell length, flesh weight, or upper valve area of *S. glomerata*. Because of the inconsistent distribution of *C. gigas*, sites, not locations, were chosen where both species co-existed to compare oyster sizes. At locations where individuals of both oyster species co-occurred, there were no significant differences (P > 0.15) between the shell length, flesh weight, or upper valve area of *S. glomerata* compared to *C. gigas*. Among all locations, the overall mean flesh weight of *S. glomerata* was roughly half that of *C. gigas* (Table 2).

Relationship of oysters to environmental variables

There was a significant correlation between salinity and the proportion of the assemblage comprised of *S. glomerata* (Figure 4). As salinity decreased, so did the proportion of *S. glomerata*. Salinity was not significantly correlated with abundance of all oysters or shell length of *S. glomerata*. There was a significant relationship between distance from the estuary mouth and all biotic measurements of oysters. As distance from the estuary mouth increased, the proportion of the assemblage comprised of *S. glomerata* decreased as did the total abundance of all oysters. As the distance from the estuary mouth increased, the mean shell length of *S. glomerata* also increased.
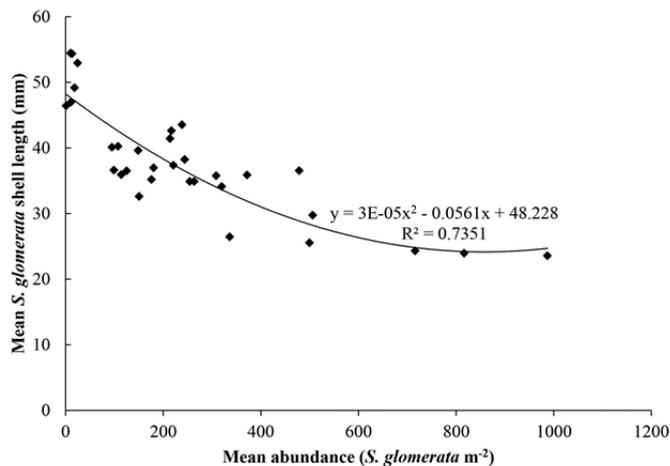
Figure 3. Regression relationship between mean *S. glomerata* shell length (mm) and *S. glomerata* abundance (mean number m^{-2}) for 32 sites within the Port Jackson Estuary.

Table 2. Mean (±SE) shell length (mm), upper valve area (mm), and flesh weight (g) of *Saccostrea glomerata*, and *Crassotrea gigas* among all Locations and Sites.

Species/variable	S. glomerata	C. gigas
Mean shell length (mm) ± SE	37.6 ± 0.49	42.2 ± 1.2
Mean upper valve area (mm^2) ± SE	1,527.3 ± 120.5	1,474.6 ± 178
Mean flesh weight (g) ± SE	3.7 ± 0.1	6.4 ± 0.4

Discussion

Native oysters *S. glomerata* and the invasive oysters *C. gigas* were both present in Port Jackson, and their abundance, size, and distributions were spatially variable. Overall, the native oyster, *S. glomerata* remains the dominant oyster species in Port Jackson, the mean relative percentage of *C. gigas* among all locations in the Port Jackson estuary was 16 %. The invasive *C. gigas* is, however, in greater abundances than previously estimated in Port Jackson, and greater than that recorded in other NSW estuaries (Summerhayes et al. 2009), including those where culture of non-triploid *C. gigas* is permitted (Bishop et al. 2010). Both species of oyster were less abundant with increasing distance upstream, but there was a greater relative abundance of *C. gigas* with distance upstream. The invasive *C. gigas* was also more prevalent, and in some instances, proportionally more abundant than *S. glomerata* in the bay ends and upper main channel of the estuary.

Several factors affect the distribution of intertidal bivalves, including wave-action (e.g., Rius and McQuaid 2006; McQuaid and Lindsey 2000), food availability (e.g., Minchinton and McKenzie 2008; Rico-Villa et al. 2009), predation (e.g., Fairweather et al. 1984; Connell and Anderson 1999; O'Connor et al. 2008), and salinity (Whitfield et al. 2012). In this study, distance from the estuary mouth was the environmental variable most correlated with the abundance of oysters (*S. glomerata* and *C. gigas*); total oyster abundance decreased with distance upstream in the estuary. Salinity measured in this investigation did not include any high precipitation events. Mean salinity was measured over a month to provide the average dry-weather salinity conditions experienced by oysters. Port Jackson is a relatively short drowned river valley with minimal freshwater input in dry weather (Roy et al. 2001), meaning that dry weather salinities are similar along its entire length (Birch and O'Hea 2007). As the monitoring period in this study didn't capture any major low salinity events (Birch et al. 2010), this may explain why biotic measures were more strongly correlated with distance from the estuary mouth than with salinity, even though rainfall is known to affect salinity in the upper reaches of the river (Birch and O'Hea 2007).

Salinity is a powerful environmental factor driving estuarine ecological patterns (Whitfield et al. 2012). Pollack et al. (2011) showed that short term, low salinity events rather than long term trends affect oyster populations. These acute but short lived events are more likely to affect the survival of juveniles than of adults. The spat of *S. glomerata* have greatest survival at salinities around 30 and cannot survive for prolonged periods <19 (Dove and O'Connor 2007). During events of high precipitation, surface waters of
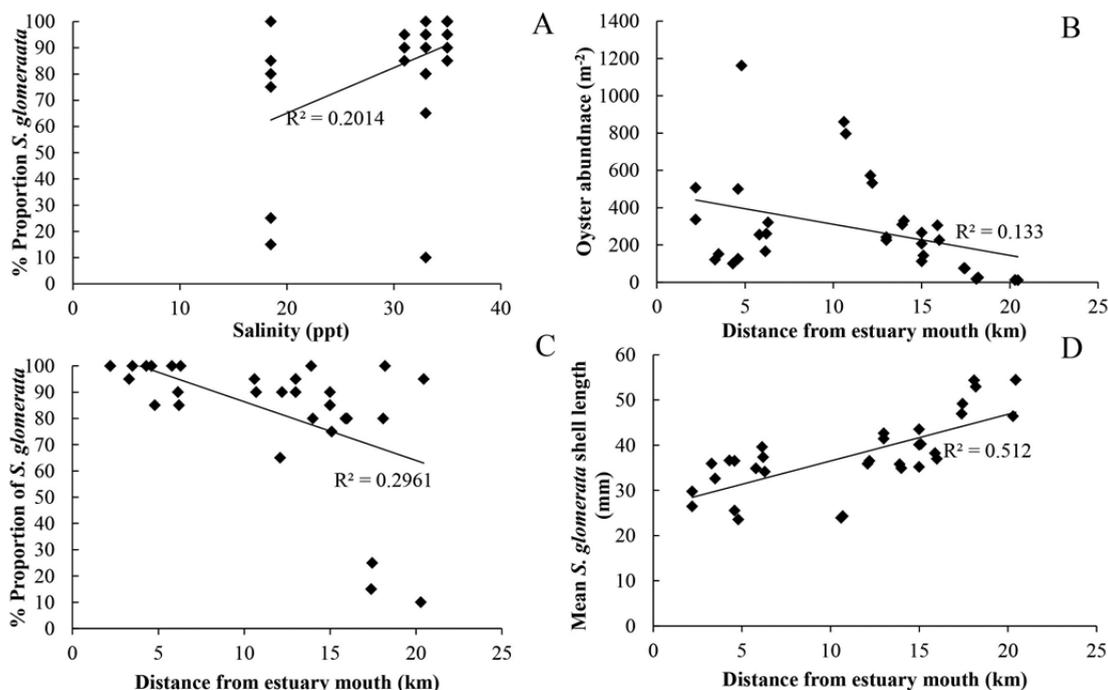
Figure 4. Scatter diagram and line of best fit from linear regression analysis of environmental (*x* – axis) and biotic measurements (*y* – axis) measured at sites. Only significant regression analyses are shown. A; percentage proportion of the entire assemblage comprised by *S. glomerata* at mean salinities (ppm) B; mean oyster abundance m^{-2} at distance from the estuary mouth (km) C; percentage proportion of the entire assemblage comprised by *S. glomerata* at distances from the estuary mouth (km) D; mean shell length of *S. glomerata* (mm) at distances from the estuary mouth (km). The statistical relationships between total abundance of oysters and shell length of *S. glomerata* and mean salinity were not significant (P > 0.1) in both cases.

Port Jackson's bay ends, and upper main channel can reach a mean salinity of 11 (Birch and O'Hea 2007), low enough to kill spat of *S. glomerata* (Dove and O'Connor 2007). Stress associated with low salinity is, also known to negatively affect survival of adult *S. glomerata* oysters when they are infected with QX disease (Butt et al. 2006). *Crassostrea gigas* was more prevalent at locations in the bay ends where *S. glomerata* abundance was low, perhaps due to greater tolerance of low salinity (Nell and Holiday 1988).

The distance from the estuary mouth was also correlated with shell length of *S. glomerata* and abundance of all oysters. There was a strong inverse correlation between the size and the abundance of *S. glomerata* in Port Jackson, which could be indicative of intraspecific competition for food or space. Greater oyster abundance in the lower estuary may be due to greater survivorship of larval and juvenile *S. glomerata*. Favourable conditions, such as increased salinity and pH facilitated by more oceanic input in the lower reaches may promote greater survivorship. The gregarious nature of oyster settle-

ment (Hidu et al. 1969; Coon et al. 1985; Anderson 1996) and settlement of oyster spat on top of adults can increase oyster abundance. In areas of high spat supply, this may lead to intraspecific competition (Hutchinson and MacArthur 1959; Underwood et al. 1983) and reduce oyster size.

Overall, the mean flesh weight and size of individual *C. gigas* was greater than *S. glomerata*. There were, however, no significant differences in the weight or size of oysters between species at locations where they co-occurred. The at times disjunct distributions of the two species between sites and among locations could potentially be attributed to interspecific competition within sites; however, the low abundances of both species where they co-occurred may mean that competition between *C. gigas* and *S. glomerata* within sites was unlikely even though *C. gigas* grows faster than *S. glomerata* and reaches a larger size (Bayne 2002). The inability of *C. gigas* to withstand tidal emersion may further restrict competitive ability at upper shore heights (Krassoi et al. 2008). Future manipulative experiments are required to test the extent, if

any, of interspecific competition between *C. gigas* and *S. glomerata* in Port Jackson.

Artificial habitat had no effect on the relative abundances of the two species of oyster, but total oyster abundance on artificial surfaces was approximately twice that on natural surfaces. Habitat type did not influence size of *S. glomerata*. The topographically homogenous, vertical nature of artificial seawalls, unlike a natural rocky shore, favours oysters (Anderson and Underwood 1994) and other filter feeding invertebrates (Dafforn et al. 2012) that are capable of quickly colonising and dominating an environment. As a result, artificial sea walls often support different assemblages of organisms compared to the natural shore (Bulleri et al. 2005; Bulleri 2005). It is not only the vertical nature of artificial surfaces that drives these patterns, natural or artificial surfaces both of vertical orientation can still support different abundances of organisms (Bulleri et al. 2005). The compressed nature of vertical habitats creates less available surface area in the intertidal zone (Whorff et al. 1995), but the within habitat abundance of organisms may still be high. Invasive species are often associated with artificial habitat; however, unlike other studies (e.g., Glasby et al. 2007; Dafforn et al. 2012), this study found no tendency for the invasive oyster, *C. gigas* to be in greater abundance than the native *S. glomerata* on artificial habitat. Previous studies (Glasby et al. 2007; Dafforn et al. 2012), which have found trends for invasive species to be associated with artificial habitats, investigated invasibility of a range of functional groups and phyla on artificial structures whereas we compared species with similar ecological requirements and recruitment capacity.

Globally, *C. gigas* is an extremely successful coloniser and can become invasive (Ruesink et al. 2005). In South African estuaries, *C. gigas* has spread from aquaculture and become naturalised among native oysters. There, *C. gigas* co-exists with wild native oysters albeit restricted to the low intertidal, at low abundances (>8 m^{-2}; Robinson et al. 2005), a situation similar to Australia. In contrast, in the Wadden Sea, *C. gigas* is an invasive species. There it settles upon native mussels at abundances that can exceed 300 m^{-2} (Diederich et al. 2005). Like the populations reported in this study, the South African and European populations of *C. gigas* have also shown to be spatially inconsistent (Robinson et al. 2005; Diederich et al. 2005).

It is likely that the large scale patterns of distribution and abundance of the two oyster species are driven by factors such as salinity and substrate type (as discussed above), but the complex small-scale variation observed in Port Jackson is due to a wide range of other biotic and abiotic factors, including the presence of fatal diseases and varying susceptibility to those diseases. The ostreid herpesvirus-1 microvariant (OHsV-1 μvar) has been responsible for considerable declines in natural and cultured populations of *C. gigas* globally (Soletchnik et al. 2007; Jenkins et al. 2013). As of 2011, OHsV-1 μvar has been confirmed in Port Jackson and surrounding estuaries (Jenkins et al. 2013). Dead shells were not counted in this investigation, however, doing so might have provided insight into the extent that OHsV-1 μvar may have on naturalised populations of *C. gigas*. The discontinuous distribution of *C. gigas* observed in this study may be a consequence of the effects of OHsV-1 μvar. Further investigation into the extent of the effects and prevalence of OHsV-1 μvar among naturalised populations of *C. gigas* in Australia may be of value to understanding the potential of *C. gigas* colonisation in Australian estuaries.

Port Jackson is not an oyster culturing estuary and there is limited historical data on the distribution and health of *S. glomerata* within the estuary. There is, however, QX disease in the estuaries immediately to the north (Hawkesbury River) and to the south (Georges River) of Port Jackson, as well as many other oyster culturing estuaries on the NSW coast (Adlard and Ernst 1995; Nell and Hand 2003; Butt and Raftos 2006). It is highly likely that the causative agent of QX disease (*Marteilia sydneyi;* Perkins and Wolf, 1976) is present in Port Jackson, having been found in almost all estuaries in NSW where testing has occurred. Therefore it is possible, although never detected, that epizootics of QX disease occur in Port Jackson too. In the estuaries immediately to the north and south of Port Jackson, the Hawkesbury River and Georges River, outbreaks of QX have occurred annually for over a decade, and it has been suggested that QX facilitates *C. gigas* prevalence (Summerhayes et al. 2009). QX disease is especially fatal to *S. glomerata* when under salinity stress (Butt et al. 2006). Since the 1970s, environmental pollution from anti-fouling paints and from surrounding industry have also been suggested as causing historical declines in oyster (un-specified species) abundance in Port Jackson (Birch et al. 2014). Human activities in the upper reaches of the estuary are known to have compromised the health and biotic resistance of *S. glomerata* (Birch et al. 2014; Edge et al. 2014). In the last two decades there has been a marked expansion of oysters back into the upper reaches (compared with Scanes et al. 1999). The low abundance in the upper reaches in 1970s and 1980s and subsequent recolonisation in the past two decades may be allowing a partially vacant

ecological niche to be filled by *C. gigas* as an opportunistic invasive species. Although it has been reported that populations of *S. glomerata* in Port Jackson are recovering (Birch et al. 2014), the lack of accurate identification in previous studies may have overestimated this recovery.

In conclusion, we rejected the hypotheses: that there were differences in relative abundance of the two species among locations; that artificial surfaces had a greater relative abundance of the invasive *C. gigas*; and that artificial substrates had different sized oysters. We supported the hypothesis that artificial substrates supported greater abundances of both species of oyster. We also supported the hypothesis that abundance and size of oyster populations in Port Jackson varied considerably among sites and locations. We found that there was an over-riding trend for abundance, size, and species composition that was dependent on distance to the estuary mouth. There was a greater abundance and smaller size of oysters in the oceanic reaches of the estuary, most likely a reflection of greater salinity, higher pH, and less contamination. Despite the absence of significant differences among locations, invasive *C. gigas* were found to be larger than native *S. glomerata*, and more prevalent at sites in bay ends and the upper main channel of the estuary. Taken together, these results show that *C. gigas*, despite their high fecundity and faster rate of growth, have not displaced native *S. glomerata* throughout Port Jackson. New South Wales estuaries including Port Jackson still have robust populations of *S. glomerata*, which may assist to slow the spread of *C. gigas*. We found Port Jackson had the highest mean proportion of *C. gigas* compared to any other NSW estuary (e.g., Summerhayes et al. 2009; Bishop et al. 2010). In the future, if pollution or disease further depletes the populations of *S. glomerata*, this may provide *C. gigas* with a competitive advantage. This study provides a solid base for gauging any future changes in Port Jackson oyster populations. Ongoing monitoring of these populations is essential in understanding the effects that urbanisation has on an ecologically important species such as oysters, and retaining native species in highly urbanised estuaries.

Acknowledgements

References

Adlard RD, Ernst I (1995) Extended range of the oyster pathogen, *Marteilia sydneyi*. *Bulletin of the European Association of Fish Pathologists* 15: 119–121

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelöf A, Thompson RC, Åberg P (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. *Coastal Engineering* 52: 1073–1087, http://dx.doi.org/10.1016/j.coastaleng.2005.09.007

Anderson M (1996) A chemical cue induces settlement of Sydney rock oysters, *Saccostrea commercialis*, in the laboratory and in the field. *The Biological Bulletin* 190: 350–358, http://dx.doi.org/10.2307/1543027

Anderson M (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26(1): 32–46

Anderson M, Gorley RN, Clarke RK (2008) Permanova+ for Primer: Guide to Software and Statistical Methods. PRIMER-E, Plymoth, UK

Anderson M, Underwood A (1994) Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. *Journal of Experimental Marine Biology and Ecology* 184: 217–236, http://dx.doi.org/10.1016/0022-0981(94)90006-X

Australian Bureau of Statistics (2014) Australian Demographic Statistics. Cat. No. 3101.0 ADS, ABS Canberra, Australia

Bayne B (2002) A physiological comparison between Pacific oysters *Crassostrea gigas* and Sydney Rock oysters *Saccostrea glomerata*: food, feeding and growth in a shared estuarine habitat. *Marine Ecology Progress Series* 232: 163–178, http://dx.doi.org/10.3354/meps232163

Birch G, Apostolatos C, Taylor S (2013) A Remarkable Recovery in the Sydney Rock Oyster (*Saccostrea glomerata*) Population in a Highly Urbanised Estuary (Sydney Estuary, Australia). *Journal of Coastal Research* 25: 1009–1015, http://dx.doi.org/10.2112/JCOASTRES-D-12-00197.1

Birch GF, Cruickshank B, Davis B (2010) Modelling nutrient loads to Sydney estuary (Australia). *Environmental Monitoring and Assessment* 167: 333–348, http://dx.doi.org/10.1007/s10661-009-1053-z

Birch G, Harrington C, Symons R, Hunt J (2007) The source and distribution of polychlorinated dibenzo-p-dioxin and polychlorinated dibenzofurans in sediments of Port Jackson, Australia. *Marine Pollution Bulletin* 54: 295–308, http://dx.doi.org/10.1016/j.marpolbul.2006.10.009

Birch G, O'Hea L (2007) The chemistry of suspended particulate material in a highly contaminated embayment of Port Jackson (Australia) under quiescent, high-wind and heavy-rainfall conditions. *Environmental Geology* 53: 501–516, http://dx.doi.org/10.1007/s00254-007-0662-5

Birch G, Scamell MS, Besley CH (2014) The recovery of oyster (*Saccostrea glomerata*) populations in Sydney esturay (Australia). *Environmental Science and Pollution Research* 21: 766–773, http://dx.doi.org/10.1007/s11356-013-2168-x

Bishop MJ, Krassoi FR, McPherson RG, Brown KR, Summerhayes SA, Wilkie EM, O'Connor WA (2010) Change in wild-oyster assemblages of Port Stephens, NSW, Australia, since commencement of non-native Pacific oyster (*Crassostrea gigas*) aquaculture. *Marine and Freshwater Research* 61: 714–723, http://dx.doi.org/10.1071/MF09177

Bulleri F (2005) Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. *Marine Ecology Progress Series* 287: 53–65, http://dx.doi.org/10.3354/meps287053

Bulleri F, Chapman M, Underwood A (2005) Intertidal assemblages on seawalls and vertical rocky shores in Sydney Harbour, Australia. *Austral Ecology* 30: 655–667, http://dx.doi.org/10.1111/j.1442-9993.2005.01507.x

Burlakova LE, Karatayev AY, Padilla DK (2000) The Impact of *Dreissena polymorpha* (Pallas) Invasion on Unionid Bivalves. *International Review of Hydrobiology* 85: 529–541, http://dx.doi.org/10.1002/1522-2632(200011)85:5/6<529::AID-IROH529>3.0.CO;2-O

Butt D, Raftos D (2006) Immunosuppression in Sydney rock oysters (*Saccostrea glomerata*) and QX disease in the Hawkesbury River, Sydney. *Marine and Freshwater Research* 58(3707): 213–221

Butt D, Shaddick K, Raftos D (2006) The effect of low salinity on phenoloxidase activity in the Sydney rock oyster, *Saccostrea glomerata*. *Aquaculture* 251: 159–166, http://dx.doi.org/10.1016/j.aquaculture.2005.05.045

Carlton JT (1992) Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. *Journal of Shellfish Research* 11(2): 489–505

Chapman M, Bulleri F (2003) Intertidal seawalls—new features of landscape in intertidal environments. *Landscape and Urban Planning* 62: 159–172, http://dx.doi.org/10.1016/S0169-2046(02)00148-2

Coen LD, Brumbaugh RD, Bushek D, Grizzle R, Luckenbach MW, Posey MH, Powers SP, Tolley S (2007) Ecosystem services related to oyster restoration. *Marine Ecology Progress Series* 341: 303–307, http://dx.doi.org/10.3354/meps341303

Cole V, Chapman M, Underwood A (2007) Landscapes and life-histories influence colonisation of polychaetes to intertidal biogenic habitats. *Journal of Experimental Marine Biology and Ecology* 348: 191–199, http://dx.doi.org/10.1016/j.jembe.2007.05.001

Commonwealth Science and Industrial Research Organisation (CSIRO) (2005) National priority pests. Part II: Ranking of Australian Marine Pests. Australian Government Department of the Environment and Heritage, pp 150.

Connell S, Anderson M (1999) Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. *Journal of Experimental Marine Biology and Ecology* 241: 15–29, http://dx.doi.org/10.1016/S0022-0981(99)00067-2

Coon SL, Bonar DB, Weiner RM (1985) Induction of settlement and metamorphosis of the Pacific oyster, *Crassostrea gigas* (Thunberg), by L-DOPA and catecholamines. *Journal of Experimental Marine Biology and Ecology* 94: 211–221, http://dx.doi.org/10.1016/0022-0981(85)90059-0

Dafforn KA, Glasby TM, Airoldi L, Rivero NK, Mayer-Pinto M, Johnston EL (2015) Marine urbanization: an ecological framework for designing multifunctional artificial structures. *Frontiers in Ecology and the Environment* 13: 82–90, http://dx.doi.org/10.1890/140050

Dafforn KA, Glasby TM, Johnston EL (2012) Comparing the invasibility of experimental "reef" with field observations of natural reef and artificial structures. *PLoS ONE* 7: e38124, http://dx.doi.org/10.1371/journal.pone.0038124

Diederich S, Nehls G, Van Beusekom J, Reise K (2005) Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? *Helgoland Marine Research* 59: 97–106, http://dx.doi.org/10.1007/s10152-004-0195-1

Dinamani P (1991) Introduced Pacific oysters in New Zealand. In: Greer MC, Leffler JC (eds), The ecology of *Crassostrea gigas* in Australia, New Zealand, France and Washington State, Maryland Sea Grant College Program, College Park, Maryland pp 9–12

Dove MC, O'Connor WA (2007) Salinity and temperature tolerance of Sydney rock oysters *Saccostrea glomerata* during early ontogeny. *Journal of Shellfish Research* 26: 939–947, http://dx.doi.org/10.2983/0730-8000(2007)26[939:SATTOS]2.0.CO;2

Edge KJ, Dafforn KD, Simpson SL, Roach AC, Johnston EL (2014) A biomarker of contaminant exposure is effective in large scale assessment of ten estuaries. *Chemosphere* 100: 16–26, http://dx.doi.org/10.1016/j.chemosphere.2014.01.001

Fairweather P, Underwood A, Moran M (1984) Preliminary investigations of predation by the whelk *Morula marginalba*. *Marine Ecology Progress Series*. 17: 143–156, http://dx.doi.org/10.3354/meps017143

Glasby TM, Connell SD, Holloway MG, Hewitt CL (2007) Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? *Marine Biology* 151: 887–895, http://dx.doi.org/10.1007/s00227-006-0552-5

Google Inc. (2016) Google Earth (version 7.1). Mountain View, California, U.S.A.

Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101: 79–90, http://dx.doi.org/10.1034/j.1600-0706.2003.12322.x

Hidu H (1969) Gregarious setting in the American oyster *Crassostrea virginica* Gmelin. *Chesapeake Science* 10: 85–92, http://dx.doi.org/10.2307/1350836

Hutchings PA, Ahyong ST, Ashcroft MB, McGrouther MA, Reid AL (2013) Sydney Harbour: its diverse biodiversity. *Australian Zoologist* 36: 255–320, http://dx.doi.org/10.7882/AZ.2012.031

Hutchinson G, MacArthur RH (1959) A theoretical ecological model of size distributions among species of animals. *American Naturalist* 93: 117–125, http://dx.doi.org/10.1086/282063

Jenkins C, Hick P, Gabor M, Spiers Z, Fell SA, Gu X, Read A, Go J, Dove M, O'Connor W (2013) Identification and characterisation of an ostreid herpesvirus-1 microvariant (OsHV-1 μ-var) in *Crassostrea gigas* (Pacific oysters) in Australia. *Diseases of Aquatic Organisms* 105: 109–126, http://dx.doi.org/10.3354/dao02623

Johnston EL, Marzinelli E, Wood C, Speranze D, Bishop JDD (2011) Bearing the burden of boat harbours: heavy contaminant and fouling loads in a native habitat-forming alga. *Marine Pollution Bulletin* 62: 2137–2144, http://dx.doi.org/10.1016/j.marpolbul.2011.07.009

Johnston EL, Pinto MM, Hutchings P, Marzinelli E, Ahyong S, Birch G, Booth D, Creese R, Doblin M, Figuera W, Gribben P, Pritchard T, Roughan M, Steinberg P, Hedge L (2015) Sydney Harbour: What we do and don't know about a highly diverse estuary. *Marine and Freshwater Research* 66: 1073–1087, http://dx.doi.org/10.1071/MF15159

Johnston EL, Piola R, Clark G (2008) The role of propagule pressure in marine invasions. In: Rilov G, Crooks J (eds), Marine Bioinvasions: Ecology, Conservation, and Management Perspectives. Springer, Berlin, Heidelberg, pp 133–151

Johnston EL, Roberts DA (2009) Contaminants reduce the richness and evenness of marine communities: a review and meta-analysis. *Environmental Pollution* 157: 1745–1752, http://dx.doi.org/10.1016/j.envpol.2009.02.017

Karatayev AY, Burlakova LE, Padilla DK (2002) Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. In: Invasive aquatic species of Europe. Springer, pp 433–446, http://dx.doi.org/10.1007/978-94-015-9956-6_43

Krassoi FR, Brown KR, Bishop MJ, Kelaher BP, Summerhayes S (2008) Condition-specific competition allows coexistence of competitively superior exotic oysters with native oysters. *Journal of Animal Ecology* 77: 5–15, http://dx.doi.org/10.1111/j.1365-2656.2007.01316.x

Lodge DM (1993) Biological invasions: lessons for ecology. *Trends in Ecology & Evolution* 8: 133–137, http://dx.doi.org/10.1016/0169-5347(93)90025-K

McAfee D, Cole VJ, Bishop MJ (2016) Latitudinal gradients in ecosystem engineering by oysters vary across habitats. *Ecology* 97(4): 929–939

McQuaid C, Lindsay TL (2000) Effect of wave exposure on growth and mortality rates of the mussel *Perna perna*: bottom-up regulation of intertidal populations. *Marine Ecology Progress Series* 206: 147–154, http://dx.doi.org/10.3354/meps206147

Medcof JC, Wolf PH (1975) Spread of Pacific oysters worries NSW culturists. *Australian Fisheries* 1: 32–38

Minchinton TE, McKenzie LA (2008) Nutrient enrichment affects recruitment of oysters and barnacles in a mangrove forest. *Marine Ecology Progress Series* 354: 181–189, http://dx.doi.org/10.3354/meps07178

Nell JA (2001) The history of oyster farming in Australia. *Marine Fisheries Review* 63(3): 14–25

Nell JA, Hand RE (2003) Evaluation of the progeny of second-generation Sydney rock oyster *Saccostrea glomerata* (Gould, 1850) breeding lines for resistance to QX disease *Marteilia sydneyi*. *Aquaculture* 228: 27–35, http://dx.doi.org/10.1016/S0044-8486(03)00133-9

Nell JA, Holliday JE (1988) Effects of salinity on the growth and survival of Sydney rock oyster (*Saccostrea commercialis*) and Pacific oyster (*Crassostrea gigas*) larvae and spat. *Aquaculture* 68: 39–44, http://dx.doi.org/10.1016/0044-8486(88)90289-X

NSW Depatment of Primary Industries (2012) New South Wales Pacific Oyster Survey 2010. NSW Department of Primary Industries, Port Stephens, 49 pp

O'Connor NE, Grabowski JH, Ladwig L M, Bruno JF (2008) Simulated predator extinctions: predator identity affects survival and recruitment of oysters. *Ecology* 89: 428–438, http://dx.doi.org/10.1890/06-2029.1

Orensanz JML, Schwindt E, Pastorino G, Bortolus A, Casas G, Darrigran G, Elías R, Gappa JJL, Obenat S, Pascual M (2002) No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic. *Biological Invasions* 4: 115–143, http://dx.doi.org/10.1023/A:1020596916153

Pinto MM, Johnston EL, Hutchings P, Marzinelli E, Ahyong S, Birch G, Booth D, Creese R, Doblin M, Figuera W, Gribben P, Pritchard T, Roughan M, Steinberg P, Hedge L (2015) Sydney Harbour: A review of anthropogenic impacts on the biodiversity and ecosystem function of one of the world's largest natural harbours. *Marine and Freshwater Research* 66: 1088–1105, http://dx.doi.org/10.1071/MF15157

Piola RF, Johnston EL (2008) Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities. *Diversity and Distributions* 14: 329–342, http://dx.doi.org/10.1111/j.1472-4642.2007.00430.x

Pollack JB, Kim HC, Morgan EK, Montagna PA (2011) Role of flood disturbance in natural oyster (*Crassostrea virginica*) population maintenance in an estuary in South Texas, USA. *Estuaries and Coasts* 34: 187–197, http://dx.doi.org/10.1007/s12237-010-9338-6

Polland D (1990) A review of exotic marine organisms introduced to the Australian region. II. Invertebrates and algae. *Asian Fisheries Science* 3: 223–250

PRIMER-E Ltd (2005) PRIMER 6+. Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, United Kingdom

Reise K (1998) Pacific oysters invade mussel beds in the European Wadden Sea. *Senckenbergiana Maritima* 28: 167–175, http://dx.doi.org/10.1007/BF03043147

Rico-Villa B, Pouvreau S, Robert R (2009) Influence of food density and temperature on ingestion, growth and settlement of Pacific oyster larvae, *Crassostrea gigas*. *Aquaculture* 287: 395–401, http://dx.doi.org/10.1016/j.aquaculture.2008.10.054

Rius M, McQuaid CD (2006) Wave action and competitive interaction between the invasive mussel *Mytilus galloprovincialis* and the indigenous *Perna perna* in South Africa. *Marine Biology* 150: 69–78, http://dx.doi.org/10.1007/s00227-006-0322-4

Robinson T, Griffiths C, Tonin A, Bloomer P, Hare M (2005) Naturalized populations of oysters, *Crassostrea gigas* along the South African coast: distribution, abundance and population structure. *Journal of Shellfish Research* 24: 443–450, http://dx.doi.org/10.2983/0730-8000(2005)24[443:NPOOCG]2.0.CO;2

Roy P, Williams R, Jones A, Yassini I, Gibbs P, Coates B, West R, Scanes P, Hudson J, Nichol S (2001) Structure and function of south-east Australian estuaries. *Estuarine, Coastal and Shelf Science* 53: 351–384, http://dx.doi.org/10.1006/ecss.2001.0796

Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual Review of Ecology, Evolution, and Systematics* 36: 643–689, http://dx.doi.org/10.1146/annurev.ecolsys.36.102003.152638

Scanes PR, Gibson PT, Dasey M (1999) Organochlorine and trace metal contamination of wild oysters (*Saccostrea commercialis*) in estuaries of the NSW coast. NSW Environment Protection Authority, Sydney, pp 60

Soletchnik P, Ropert M, Mazurié J, Fleury PG, Le Coz F (2007) Relationships between oyster mortality patterns and environmental data from monitoring databases along the coasts of France. *Aquaculture* 271: 384–400, http://dx.doi.org/10.1016/j.aquaculture.2007.02.049

Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. *Science* 286: 1577–1579, http://dx.doi.org/10.1126/science.286.5444.1577

Summerhayes SA, Kelaher BP, Bishop MJ (2009) Spatial patterns of wild oysters in the Hawkesbury River, NSW, Australia. *Journal of Shellfish Research* 28: 447–451, http://dx.doi.org/10.2983/035.028.0304

Thomson J (1954) The genera of oysters and the Australian species. *Marine and Freshwater Research* 5: 132–168, http://dx.doi.org/10.1071/MF9540132

Timmerman P, White R (1997) Megahydropolis: coastal cities in the context of global environmental change. *Global Environmental Change* 7: 205–234, http://dx.doi.org/10.1016/S0959-3780(97)00009-5

Troost K (2010) Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *Journal of Sea Research* 64: 145–165, http://dx.doi.org/10.1016/j.seares.2010.02.004

Underwood A, Denley E, Moran M (1983) Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia* 56: 202–219, http://dx.doi.org/10.1007/BF00379692

Whitfield A, Elliott M, Basset A, Blaber S, West R (2012) Paradigms in estuarine ecology—a review of the Remane diagram with a suggested revised model for estuaries. *Estuarine, Coastal and Shelf Science* 97: 78–90, http://dx.doi.org/10.1016/j.ecss.2011.11.026

Whorff J, Whorff L, Sweet M (1995) Spatial variation in an algal turf community with respect to substratum slope and wave height. *Journal of the Marine Biological Association of the United Kingdom* 75: 429–444, http://dx.doi.org/10.1017/S0025315400018282

Wilkie EM, Bishop MJ, O'Connor WA (2012) Are native *Saccostrea glomerata* and invasive *Crassostrea gigas* oysters' habitat equivalents for epibenthic communities in south-eastern Australia? *Journal of Experimental Marine Biology and Ecology* 420: 16–25, http://dx.doi.org/10.1016/j.jembe.2012.03.018

Supplementary material

The following supplementary material is available for this article:

Table S1. Oyster sampling data from 16 locations and 32 sites with Port Jackson, NSW, Australia sampled in summer/Autumn 2013–2014, with site details.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2016/Supplements/AI_2016_Scanes_etal_Supplement.xls