

Habitat value of Sydney rock oyster (*Saccostrea glomerata*) reefs on soft sediments

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Abstract. Estimates of the ecological and economic value of ecosystems can provide important information for the prioritisation of conservation and restoration actions. Oyster reefs that were once common in temperate coastal waters have now been largely degraded or lost. Oyster reefs provide a suite of ecological services, including habitat and a food supply for a range of other species. In Australia, there is growing interest in oyster reef restoration, but there are knowledge gaps with regard to their structure and habitat value. Here, we describe the structure of eight remnant Sydney rock oyster (*Saccostrea glomerata*) reefs and estimate the density, biomass, productivity and composition of mobile macroinvertebrate and infaunal communities associated with them. The oyster reefs had a distinct assemblage of macroinvertebrates, with fivefold higher density of larger (≥ 2 mm) macroinvertebrates, fivefold higher biomass and almost fivefold higher productivity, than that of adjacent bare sediments. The productivity of infaunal communities was twice as high under oyster reefs than in adjacent bare sediments. Therefore, *S. glomerata* reef restoration is likely to provide important habitat for macroinvertebrate communities and boost local secondary production.

Additional keywords: ecosystem services, productivity.

Received 20 May 2018, accepted 30 July 2019, published online 28 October 2019

Introduction

Many oyster species are ecosystem engineers that create, modify and maintain habitat at a system-wide scale (Beck *et al.* 2011). At high densities, oysters form the structural elements of oyster reef ecosystems, as living oysters and dead shell accumulations, provide a complex hard surface matrix that support diverse faunal communities (Jones *et al.* 1997; McLeod *et al.* 2019). Formerly covering vast areas in temperate coastal waters, over 85% of oyster reef ecosystems (hereafter oyster reefs) have been lost or severely degraded by destructive fishing practices

(e.g. dredging), water pollution, catchment modification and disease (Beck *et al.* 2011; Gillies *et al.* 2018).

Oyster reefs provide a range of ecosystem services, such as habitat provision and refuge from predation and environmental stressors, supporting the production of commercially important fish and invertebrate species, water filtration and shoreline protection (Coen *et al.* 2007; Grabowski and Peterson 2007; Commito *et al.* 2008; Grabowski *et al.* 2012; McAfee *et al.* 2016). For the American oyster *Crassostrea virginica*, these services have been valued between US\$5500 and \$99 000 ha⁻¹

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year⁻¹ (Grabowski *et al.* 2012). Oyster reefs provide food for other species through direct predation of oysters as well as other organisms inhabiting the reef, and through biodeposits (pseudofaeces) produced by the oyster's filter feeding, which supports both primary and secondary production (Norling and Kautsky 2007; Engel *et al.* 2017). Oyster reefs, particularly those occurring on soft sediments, provide a structurally complex network of hard surface 'islands' amid a sea of sand and mud, increasing habitat diversity on a landscape scale (Jones *et al.* 1997).

Oyster reef restoration is an increasingly common practice in many locations around the world, with objectives often focused on returning ecosystem services (Brumbaugh and Coen 2009; La Peyre *et al.* 2014; Powers and Boyer 2014). However, restoration can be costly and decision makers need information about the effects of restoration activities on ecosystem services to inform their decisions in the context of competing priorities for investment (Grabowski *et al.* 2012; Gillies *et al.* 2015). Qualitative predictions of benefits, such as 'improving biodiversity', may fail to convince managers to support restoration projects (Powers and Boyer 2014). Therefore, a quantitative approach should be taken when possible (zu Ermgassen *et al.* 2016).

One way researchers and managers describe and compare the value of coastal habitats is through their biological production (Fonseca *et al.* 2000; Peterson *et al.* 2003). Biological production (productivity) can provide a proxy for overall ecosystem services because many ecosystem services scale to increased biological production (Fonseca *et al.* 2000; Peterson *et al.* 2008). Oyster reefs have fairly low primary productivity compared with photosynthesising habitats such as seagrass, saltmarsh meadows or macroalgae beds (Lenihan and Peterson 1998; Coen *et al.* 2007). However, oyster reefs often provide habitat and food for a diverse and productive macroinvertebrate community, which provides a pathway for energy and materials to flow from primary producers to predators such as fish (Edgar and Moore 1986; Taylor 1998; Cowles *et al.* 2009). Production at the secondary trophic level may better represent habitat value because it synthesises contributions of local food production, food subsidies from other habitats and the protective benefits of habitat structure (Wong *et al.* 2011). Secondary productivity has been used to quantify benefits of habitat restoration in other systems, such as seagrass beds and salt marshes (French McCay and Rowe 2003) and tidal marshes (Peterson *et al.* 2003). Oyster reefs commonly have high secondary productivity because of the fast growth rates of the oysters and the large communities of associated organisms they support (Wong *et al.* 2011). Knowledge of the relative productivity of macroinvertebrate communities could assist restoration practitioners communicate the value of oyster reefs by identifying these as areas of high productivity, and thus as a potential source of food for fished species.

In Australia, *Saccostrea glomerata* (Sydney rock oyster) formerly developed reefs across its distribution from southern New South Wales (NSW) to south-east Queensland (Gillies *et al.* 2018). These reef ecosystems historically occurred in the intertidal zone to a depth of 8 m, with reefs forming on hard substrates, sand and mud banks, or associated with mangroves (Gillies *et al.* 2018). In the mid-19th century, reefs in NSW

varied in area from 10 m² to greater than 100 000 m² (Ogburn *et al.* 2007). Historically, *S. glomerata* reefs supported one of Australia's largest maritime industries (1790–1900), a fishery that targeted oysters for their food value and their shells, which were burned to produce lime for construction (Gillies *et al.* 2015, 2018). There was very little systematic recording of the extent of early harvests, but the rock oyster harvest (presumed to be dominated by *S. glomerata*) in south-east Queensland peaked in 1891 at 1890 tonnes, with over 200 people employed in the industry (Gillies *et al.* 2015). The fishery generally used destructive harvest techniques, such as dredging and 'skinning', a process where schooners were berthed on intertidal oyster banks as oysters and shells were shovelled onto the schooner until it was full (Ogburn *et al.* 2007; Gillies *et al.* 2015).

Despite the decline in the wild harvest of *S. glomerata* by the mid-1900s, no natural recovery has occurred in the vast areas of former reef. Today, *S. glomerata* are largely only present as fairly small patches within the intertidal zone (Gillies *et al.* 2018). The lack of natural recovery has been attributed to the effects of disease, invasive mud worms, pollution and smothering of adult oysters and larval oyster settlement habitat with large amounts of terrestrially derived sediment (Kirby 2004; Ogburn *et al.* 2007; Beck *et al.* 2009; Diggles 2013). Not only is the spatial extent of these reefs greatly reduced, but the reefs also appear to be absent from up to 96% of their historical vertical distribution, persisting only in the mid-intertidal zone (Diggles 2013). Even in the intertidal zone, larger reefs (tens to hundreds of square metres) are now rare (Gillies *et al.* 2015, 2018). Consequently, *S. glomerata* reefs are recognised as one of Australia's most imperilled marine habitats (Gillies *et al.* 2018).

Interest in oyster reef restoration is gaining momentum in Australia, with restoration projects starting or planned in every state (Gillies *et al.* 2015, 2018). Motivations for oyster reef restoration in Australia include: (1) assisting the recovery of a near extirpated ecosystem; (2) improving local biodiversity; and (3) recovering ecosystem services, particularly fishery production. Quantifying the ecosystem service benefits and ecology of local shellfish reefs was identified as one of 12 key actions to ensure the long-term success of shellfish reef restoration efforts in Australia (Gillies *et al.* 2015). The present study was designed to help fill this critical knowledge gap by describing the structure of remnant *S. glomerata* reefs on soft sediments (sand and mud banks) and their associated macroinvertebrate and infaunal communities. Given that macroinvertebrates are important food sources for fish, estimating their productivity provides information about how oyster reefs may support commercially and recreationally targeted fish species. This study was designed to provide an initial assessment of oyster reef structure and habitat value on soft sediments to inform future detailed studies. Further, this information is important for helping establish reference ecosystems and models to support future restoration efforts.

The aims of this study were to: (1) describe the structure of remnant *S. glomerata* reefs; (2) estimate the composition, density, biomass and productivity of mobile macroinvertebrate communities associated with *S. glomerata* reefs and compare these with those supported by the 'bare' soft sediments that often replace them; and (3) estimate the inhibition or facilitation of infauna under *S. glomerata* reefs.

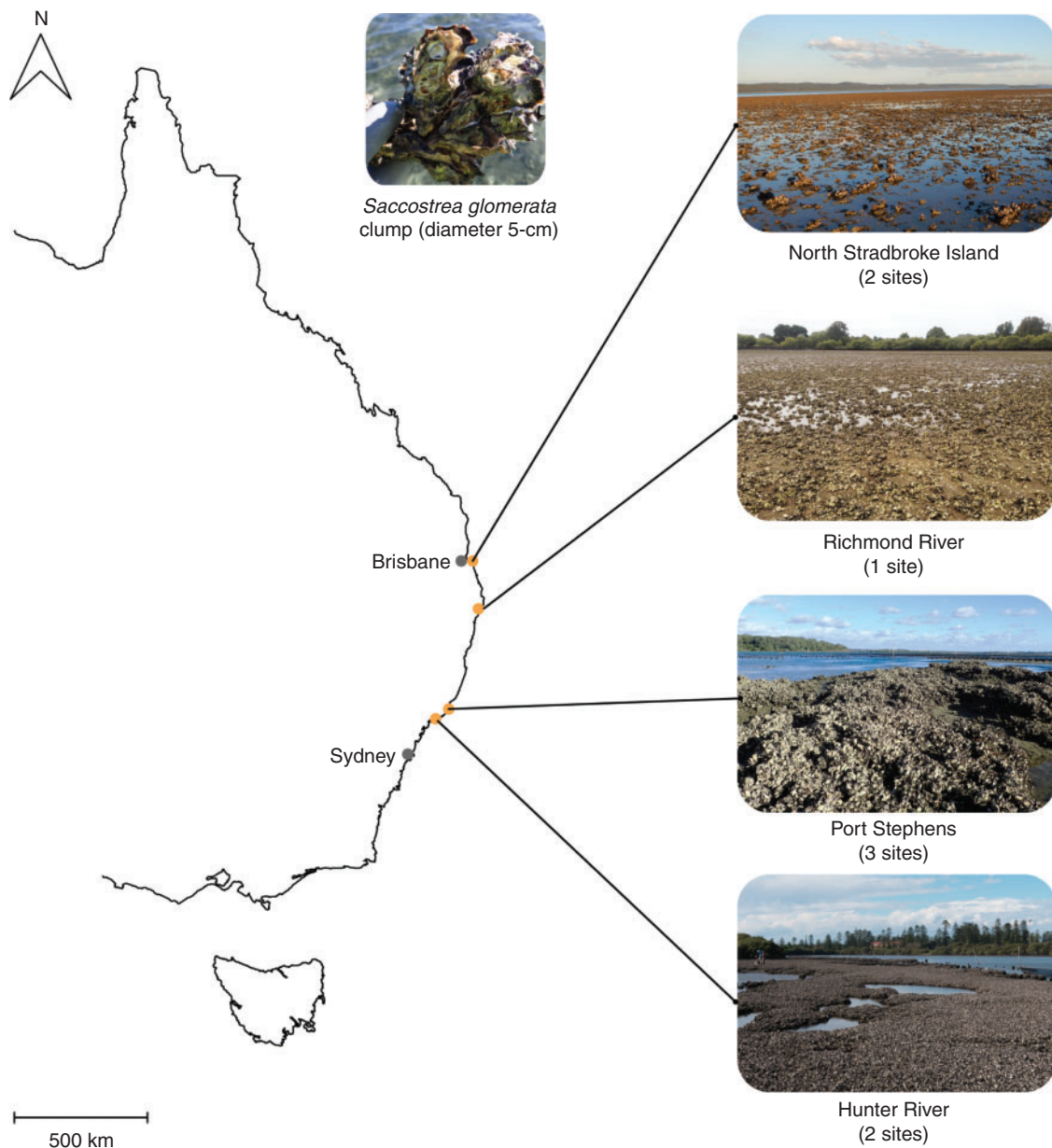


Fig. 1. Map of study locations (orange dots) along the east coast of Australia. Photographs show the typical substrate of each reef. Photographs courtesy of B. D'Anastasi (North Stradbroke), P. Dwyer (Richmond River) and S. McOrrie (Port Stephens and Hunter River).

Materials and methods

Study sites

Four locations with intertidal *S. glomerata* reefs were identified along the east coast of Australia (Fig. 1; North Stradbroke Island: 27°29'S, 153°22'E; Richmond River: 28°50'S, 153°34'E; Port Stephens: 32°41'S, 152°01'E; Hunter River: 32°53'S, 151°47'E). Multiple sites were sampled in each location when more than one reef was present (two sites adjacent to North Stradbroke Island, one site in Richmond River, three sites in Port Stephens and two sites in the Hunter River). The North Stradbroke and Richmond River sites were characterised by oysters

growing on sand banks, whereas at the Port Stephens and Hunter River sites oyster reefs were located on mud banks. Each location was sampled once during 2016–17 (Richmond River, November 2016; Port Stephens and Hunter River, April 2017; North Stradbroke, May 2017). The area of the sampled oyster reefs was estimated using satellite imagery (using Nearmap; see www.nearmap.com.au, accessed 17 November 2017; Table 1).

Oyster reef structure

The percentage cover of reef structure and density of live oysters were estimated at each site. Percentage cover was estimated from

Table 1. Oyster reef site descriptions, based on 1-m² quadrats, at North Stradbroke Island (two sites), Richmond River (one site), Port Stephens (three sites) and Hunter River (two sites), on the east coast of Australia

Unless indicated otherwise, data are given as the mean \pm s.e.m.; N/A, not applicable

Location	Site	Substrate	Area (m ²)	Oyster reef cover (%)	Oyster density (individuals m ⁻²)	Maximum density of oysters (m ⁻²)	Number of oysters on reef ($\times 10^6$)	Maximum length of oysters (mm)	Vertical height (mm)
North Stradbroke	1	Sand	N/A	23	68.4 \pm 6.1	209.8	N/A	33.0 \pm 0.7	59.3 \pm 11.0
	2	Sand	N/A	12.8	10.2 \pm 3.3	69.6	N/A	27.3 \pm 1.3	25.2 \pm 10.3
Richmond River	1	Muddy sand	7493	39.4	168.9 \pm 2.1	264.8	3.2	31.5 \pm 0.8	N/A
Port Stephens	1	Mud, shell	2704	59.3	209.7 \pm 8.6	673.6	1.0	34.9 \pm 1.1	53.6 \pm 18.4
Port Stephens	2	Mud, shell	1458	65.0	740.5 \pm 15.8	1591.2	1.7	37.6 \pm 0.9	113.7 \pm 22.0
Port Stephens	3	Mud, shell	5199	43.3	353.3 \pm 16.3	1004.6	4.2	40.4 \pm 1.2	95.3 \pm 21.6
Hunter River	1	Mud, shell	4486	64.4	605.9 \pm 9.7	978.9	4.2	39.2 \pm 0.8	143.8 \pm 45.8
Hunter River	2	Mud, shell	2896	64.5	601.6 \pm 11.1	1135.2	2.7	41.3 \pm 0.9	93.2 \pm 13.3

photographs of 10 replicate 1-m² quadrats per site. Quadrat placement was randomised using two independent random number tables to select distance along and perpendicular to a transect tape laid across the longest axis of the reef. Percentage cover was calculated from the quadrat photographs by scoring benthic composition (oyster or non-oyster) under 20 random points using the software package ImageJ (see <https://imagej.net>, accessed 18 November 2017; Rueden *et al.* 2017). The density and size of live oysters was estimated by placing a smaller quadrat (25 cm²) in the bottom left corner of each larger quadrat. Within this smaller quadrat, the maximum height of the oyster clumps above the substrate (at all sites except Richmond River) and the longest axis of the shell from a subset of a maximum of 25 oysters were measured, and all oysters ≥ 10 mm were counted.

To calculate the overall density of oysters at each site, the average density of oysters (m⁻²) from the smaller quadrats was multiplied by the average percentage cover of the larger quadrats. This was done to include sandy or muddy patches between high-density clumps of oysters, and thereby avoid artificially inflating the overall oyster density for the reef. Then, the quadrat with the highest oyster density within each site was isolated, and the same calculation was performed to estimate the maximum oyster density recorded (m⁻²) at each site. To estimate the overall number of oysters per reef, the average oyster density for each site was multiplied by the total area of each oyster reef (Table 1).

Macroinvertebrate community structure, density, biomass and productivity

At each reef, macroinvertebrates were sampled from two habitats: (1) the oyster reef above the soft sediment substrate, plus the sediment directly under the oyster reef to a depth of 10 cm ('oyster habitat'); and (2) adjacent soft sediment substrates including the surface and top 10 cm of sediment > 2 m away from the oyster reef ('adjacent bare sediment'). Samples were taken using hand corers with an internal diameter of 13 cm. A hand trowel was used to break off edges of the oyster reef if needed. Five samples of each habitat type were taken at each site. Samples were preserved in 70% ethanol or 10% formalin mixed with seawater within a few hours for later analysis.

Results from other studies (e.g. Creese *et al.* 1997; Norkko *et al.* 2006) have suggested that the presence of oysters can affect the infaunal community in one of two ways: (1) the nutrient rich biodeposits produced by oysters could increase microbial activity, leading to an anoxic environment, which would inhibit infaunal communities; or (2) the increased nutrients could facilitate the presence of infauna by providing extra nutrients without creating anoxic conditions. In order to test for the presence of inhibition or facilitation, we separated the oyster samples into two groups, namely the above-surface macroinvertebrates associated with the oyster reef and the infauna collected underneath the oyster reef. These were then compared to the infauna from adjacent bare sediment. This subdivision of samples was only used to explore infaunal facilitation or inhibition; all other analyses used the complete samples of oysters habitat *v.* adjacent bare sediment.

To estimate the community composition, density, biomass and productivity of macroinvertebrates associated with oyster habitat and adjacent bare sediment, samples were washed through

a series of 11 sieves (22.4-, 16.0-, 11.2-, 8.0-, 5.6-, 4.0-, 2.8-, 2.0-, 1.4-, 1.0- and 0.5-mm mesh). The 1.4-, 1.0- and 0.5-mm size classes that were dominated by sand particles were subsampled up to 16 times. Invertebrates retained on the 0.5- to 5.6-mm sieve classes were identified to coarse taxonomic levels (Class or Order) and counted. Larger invertebrates (>5.6 mm) were identified to species level and counted. Community biomass and productivity were estimated using the empirically derived equations of Edgar (1990), which predict individual biomass as a function of sieve mesh size, and productivity as a function of sieve mesh size and water temperature as described in the data analysis section below. Sessile organisms such as barnacles or algae were not included in this study. Water temperature was derived from the Integrated Marine Observing System (see <https://portal.aodn.org.au/search>, accessed 28 November 2017).

Data analysis

The biomass (Eqn 1) and productivity (Eqn 2) of macroinvertebrate communities were estimated using the empirically derived equations of Edgar (1990) as follows:

$$\log(B) = -1.01 + 2.64 \times \log(S) \quad (1)$$

where B is faunal ash-free dry weight (AFDW; mg) and S is sieve size (mm).

$$P = 0.0049 \times B^{0.80} \times T^{0.89} \quad (2)$$

where P is the production of an individual macrobenthic animal ($\mu\text{g day}^{-1}$), B is body size ($\mu\text{g AFDW}$) and T is water temperature ($^{\circ}\text{C}$). Validation exercises have shown that estimates from Edgar's equations are similar to those from other empirical models and direct measurements (Cowles *et al.* 2009).

The differences in the mean density (m^{-2}), biomass (g AFDW m^{-2}) and productivity ($\text{g AFDW m}^{-2} \text{ year}^{-1}$) of macroinvertebrates between oyster habitats and adjacent bare sediments, as well as between locations, were analysed using separate mixed-effects models (to account for an unbalanced dataset between sites and locations). The mixed-effects models included a random intercept and site and quadrat or core within site as random effects. The model analysed the effects of location (categorical factor, four levels: North Stradbroke, Port Stephens, Hunter River and Richmond River), habitat type (categorical, two levels: oyster habitat and adjacent bare sediment) and the interaction between the two on the response variable (density, biomass or productivity). Data were cube-root transformed to comply with assumptions of homogeneity of variances and normality of residuals. The significance of differences was explored using Tukey's least-squares means *post hoc* test. All analyses were performed within the R environment (R Foundation for Statistical Computing, Vienna, Austria, see <https://www.R-project.org/>, accessed 15 July 2018), using the *nlme* (ver. 3.1-131, J. Pinheiro, D. Bates, S. DebRoy, D. Sarkar, and R Core Team, see <https://CRAN.R-project.org/package=nlme>, accessed 18 June 2019) and *lsmeans* (ver. 2.30-0, see <https://cran.r-project.org/web/packages/lsmeans/lsmeans.pdf>, accessed 15 July 2018; Lenth 2016) packages.

Further exploration of the dataset required grouping and subdivision as follows. The net effect of oyster habitat on the

density, biomass and productivity of mobile macroinvertebrates was assumed to be equal to the contribution of oyster habitat minus the contribution from adjacent soft sediment. To investigate the potential for a facilitative or inhibitory effect of the presence of oysters on infauna directly under oysters, we compared the under-oyster habitat to adjacent bare sediments in a separate analysis. Because crustaceans >1 mm have been described as an important food source for fishes (Edgar and Shaw 1995), we isolated these from the data and performed a separate analysis of their density, biomass and productivity across the two habitat types using the same linear mixed-effects models as above.

The diversity of macroinvertebrates was explored by classifying all organisms to taxonomic Class, with the exception of the large and diverse Malacostraca Class, which was further subdivided into four taxonomic orders (Amphipoda, Isopoda, Brachyura and other Decapoda). The diversity of macroinvertebrate communities of oyster habitat and adjacent bare sediment was compared using Simpson's diversity index, where a value of 0 indicates a habitat with no diversity and 1 indicates a habitat with infinite diversity. Analyses were performed in R using the *diversity()* function within the *vegan* R package (ver. 2.4-4, J. Oksanen, F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Stevens, E. Szoecs, and H. Wagner, see <https://CRAN.R-project.org/package=vegan>, accessed 20 March 2019). To explore which taxa may be driving differences between oyster habitat and bare sediments, a principal component analysis (PCA) was performed of the pooled counts of the 10 most common macroinvertebrate taxa at each site and location ($n = 8$ across the four locations).

Full model outputs for all analyses are presented in Tables S1–S5 of the Supplementary material to this paper, whereas raw count data of macroinvertebrates are available in Tables S5–S6 of the Supplementary material.

Where appropriate data are given as the mean \pm s.e.m.

Results

Oyster reef structure

The eight oyster reefs explored in this study were spread across four locations, spanning 620 km along the east coast of Australia (Fig. 1). Size, substrate type and oyster density varied among these reefs (Table 1). The Hunter River and Port Stephens locations were characterised by discrete reefs ranging in area from 1458 to 7493 m^2 , with mean vertical height per site ranging from 53 to 144 mm above the surrounding mud substrate (with a maximum height of 500 mm at Port Stephens). Oyster densities ranged from 169 to 740 oysters m^{-2} at the Hunter River and Port Stephens sites (Table 1; Fig. 1). Richmond River had an average of 169 oysters m^{-2} , with more isolated clumps of oysters growing on muddy sand (Table 1; Fig. 1). The two oyster reefs at North Stradbroke Island were vast and had lower oyster density (10–68 individuals m^{-2}), with oysters forming isolated clumps on sand, with less vertical height compared with the other locations (Table 1; Fig. 1). The scattered, low-density nature of North Stradbroke oyster reefs made it difficult to determine their boundaries in satellite imagery, and we therefore excluded reef size estimates at North Stradbroke from the analysis.

Macroinvertebrate community structure, density, biomass and productivity

The density of macroinvertebrates differed significantly between locations (linear mixed-effects model, Location $F_{3,4} = 26.6$, $P = 0.004$). However, visual inspection of PCAs indicated that habitat type (oyster habitat *v.* adjacent bare sediment) had a greater effect on differences in the macroinvertebrate communities than location (Fig. 2a). Indeed, macroinvertebrate density was 37% higher in oyster habitat compared with adjacent bare sediments (pooled all sites mean (\pm s.e.m.) density $69\,400 \pm 18\,790$ *v.* $50\,696 \pm 19\,226$ invertebrates m^{-2} respectively, Fig. 3a, b), but the difference between habitats was not statistically significant. This is likely driven by high numbers of gastropods in the smaller size classes (<2 mm), primarily in the North Stradbroke sites. We subsequently removed the <2-mm size class and re-ran the analysis. Excluding size classes below 2 mm revealed a significant interaction between habitat and location on the macroinvertebrate density (Habitat \times Location $F_{3,67} = 8.0$, $P = 0.0001$). This suggests that although there is an effect of habitat on macroinvertebrate density (mean density 7330 ± 495 *v.* 1382 ± 316 individuals m^{-2} in oyster habitat and adjacent bare sediments respectively), the magnitude of this effect differs between locations (Fig. 3a). This was evident when visualised using PCAs because the clustering of oyster habitats and adjacent bare sediments was more pronounced in this reduced dataset (Fig. 2b). Overall, the oyster habitats exhibited more variability (less clustering) than the adjacent bare sediments, presumably because of the low diversity of taxa recorded at the latter (Fig. 2a, b).

Overall, oyster habitat supported over fivefold the biomass of macroinvertebrates than adjacent bare sediment (114.3 ± 8.1 *v.* 19.8 ± 4.4 g AFDW m^{-2} respectively, Fig. 3c, d). Similarly, oyster habitat supported macroinvertebrate communities that were almost fivefold as productive as those of adjacent bare sediment (361.3 ± 23.6 *v.* 75.7 ± 17.6 g AFDW m^{-2} year $^{-1}$ respectively, Fig. 3e, f). Biomass and productivity patterns were driven by significant interactions between the fixed factors habitat and location (linear mixed effects model, Location \times Habitat, biomass $F_{3,67} = 4.3$, $P = 0.008$; productivity $F_{3,67} = 7.9$, $P = 0.0001$), and were not affected by the inclusion or exclusion of macroinvertebrates <2 mm.

Infaunal macroinvertebrate communities directly underneath oysters had, on average, 9% higher density and twice the biomass and productivity of adjacent bare sediment (mean density $55\,291 \pm 17\,834$ *v.* $50\,696 \pm 19\,226$ invertebrates m^{-2} respectively, Fig. 3a, b; mean biomass 42.04 ± 4.41 *v.* 19.8 ± 4.4 g AFDW m^{-2} respectively, Fig. 3c, d; mean productivity 154 ± 17 *v.* 75.7 ± 17.6 g AFDW m^{-2} year $^{-1}$ respectively, Fig. 3e, f). There were significant interactions between the main factors for biomass and productivity (linear mixed effects models: biomass $F_{3,68} = 6.8$, $P < 0.001$; productivity $F_{3,68} = 6.8$, $P < 0.001$), and a significant effect for location on invertebrate density ($F_{3,4} = 24.7$, $P = 0.005$).

The net benefit of oyster habitat on macroinvertebrate communities can be expressed as the overall density, biomass and productivity of macroinvertebrates associated with oyster habitat minus that present in adjacent bare sediment. The presence of oyster reefs increased the overall average density

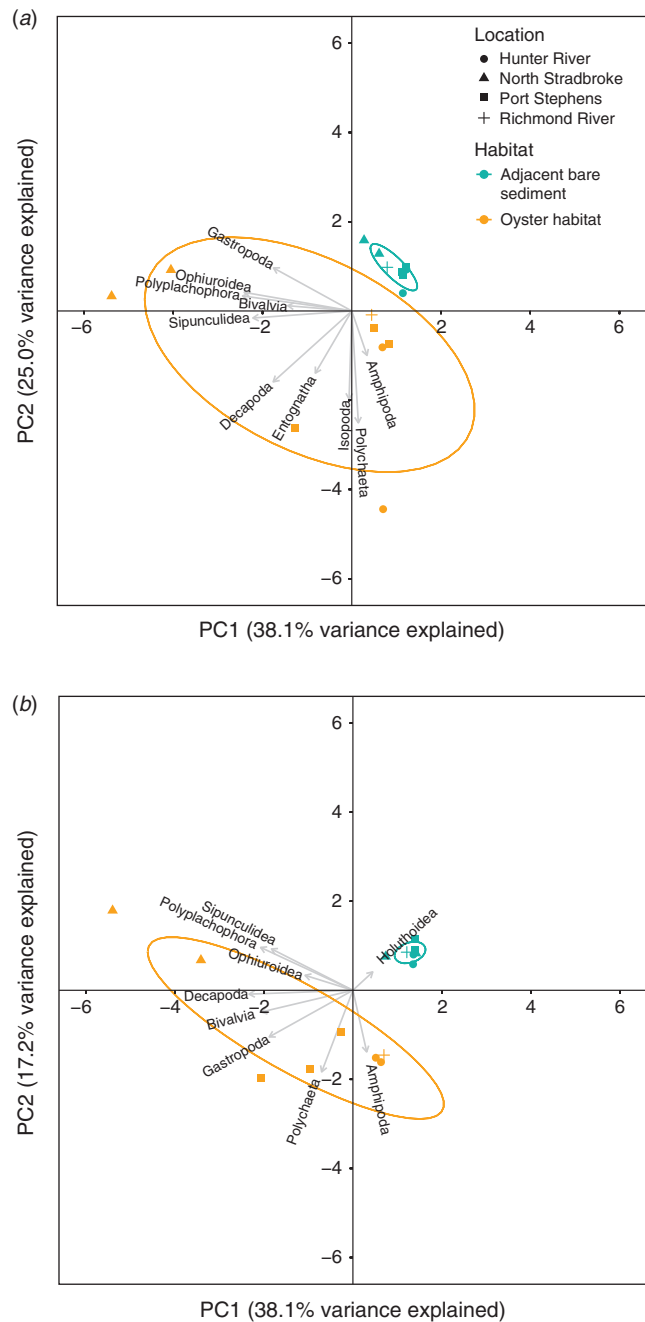


Fig. 2. Principal component (PC) analysis of (a) the overall macroinvertebrate assemblage and (b) macroinvertebrates ≥ 2 mm associated with oyster habitat and adjacent soft sediment habitats. Data points represent individual sites within each location. Oyster habitat includes oyster and under-oyster samples.

of macroinvertebrates by $17\,400 \pm 1\,673$ invertebrates m^{-2} , increased biomass by 94 ± 8 g AFDW m^{-2} and increased productivity by 283.7 ± 30.1 g AFDW m^{-2} year $^{-1}$. The net effect of oyster reefs varied between locations, but was consistently positive (Table S4).

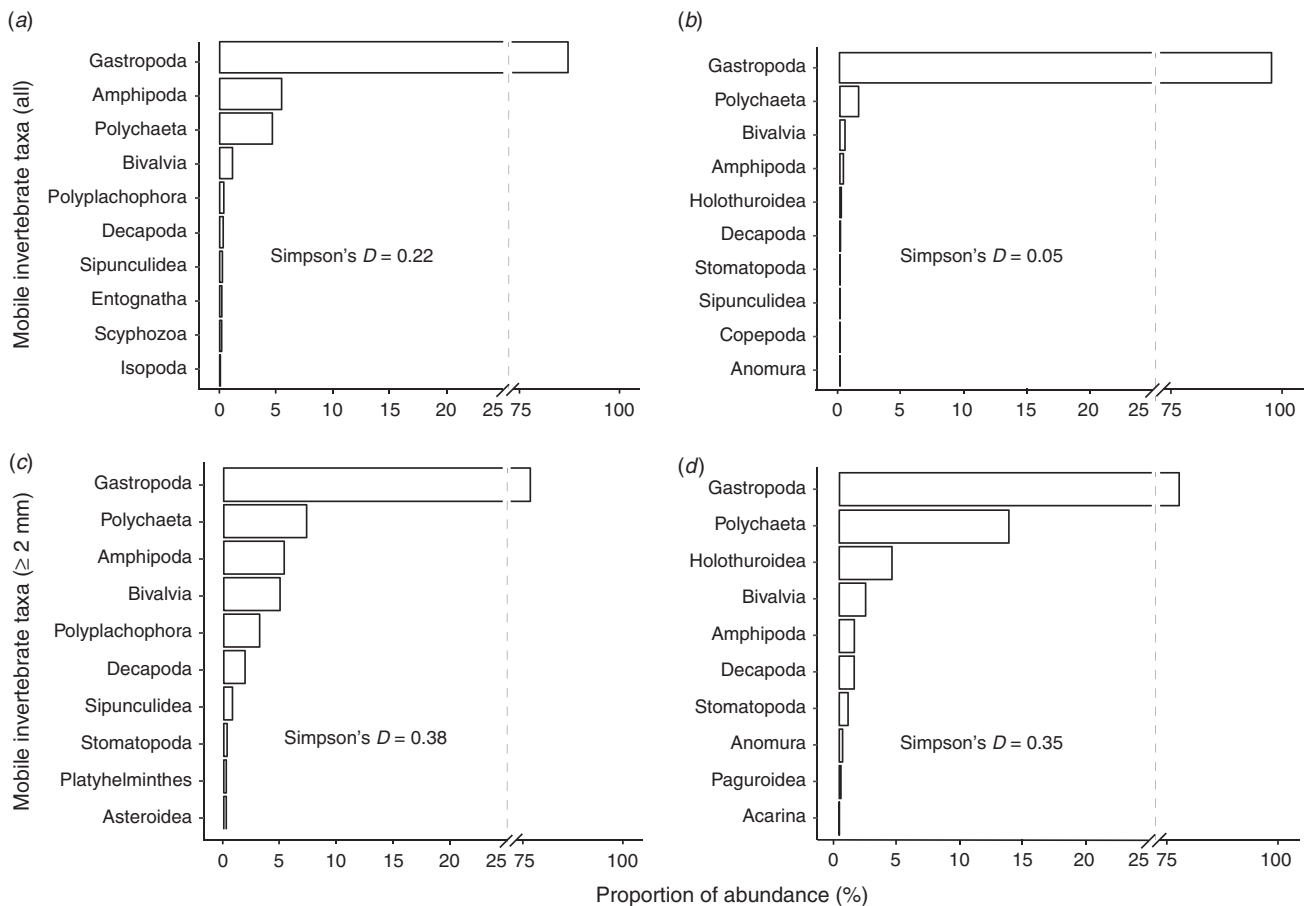


Fig. 3. Mean (a, b) density, (b, c) biomass and (e, f) productivity of the macroinvertebrate community associated with oyster habitat (oyster and under oyster; black and grey shading respectively) compared to adjacent bare sediments (control; white). (b, d, e) Data pooled for all sites. Data show the mean \pm s.e.m. Letters above columns reflect significant groupings in Tukey's *post hoc* test, based on the simplest significant model (i.e. interaction or main effects only). AFDW, ash-free dry weight.

Diversity index

Oyster habitat supported a higher level of biodiversity (Simpson's $D = 0.22$, Fig. 4a) than the adjacent bare sediments ($D = 0.05$, Fig. 4b). Although both habitats were dominated by gastropods, oyster habitat supported higher densities of a wider range of other taxa (e.g. Amphipoda, Polychaeta and Bivalvia) than adjacent bare sediment (Fig. 4a, b). Overall, oyster habitats supported macroinvertebrates from 20 different taxa, whereas invertebrates from adjacent bare habitat belonged to 12 different taxa (Tables S5–S6). When taxa ≥ 2 mm were removed, the diversity was similar between the two habitat types (Fig. 4c, d). Independently, infaunal communities beneath oyster habitat were more diverse ($D = 0.12$) than the infauna from adjacent bare substrate habitat ($D = 0.05$). It should be noted that these analyses pooled species into broad taxonomic groups and further detailed research into the biodiversity supported by oyster habitat is underway. All macroinvertebrate data including the species composition of individuals > 5.6 mm is available in Tables S5–S6.

Oyster habitat supported 14-fold the density of crustaceans > 1 mm than adjacent bare sediment (1650 ± 336 v. $113 \text{ m}^{-2} \pm 27 \text{ m}^{-2}$ respectively; linear mixed-effects model, Habitat \times Location $F_{3,67} = 11.3$, $P < 0.0001$), 9-fold the biomass

of crustaceans > 1 mm (11.7 ± 2.8 v. 1.2 ± 0.5 g AFDW m^{-2} respectively; linear mixed-effects model, Habitat \times Location $F_{3,67} = 4.6$, $P < 0.01$) and 13-fold higher productivity of crustaceans > 1 mm (21.5 ± 2.8 v. 1.6 ± 0.5 g AFDW m^{-2} respectively; linear mixed-effects model, Habitat $F_{3,67} = 51.3$, $P < 0.0001$; Location $F_{3,4} = 3.8$, $P > 0.05$).

Discussion

This study revealed that *S. glomerata* oyster reefs support diverse and productive mobile macroinvertebrate communities. Historically, *S. glomerata* reefs were a common intertidal and subtidal habitat type in Australia, but have largely been replaced by bare sediments (Gillies *et al.* 2018). The present study shows that soft sediments, although important and productive habitats in their own right, support macroinvertebrate communities that are less biodiverse and productive than those associated with the oyster reefs they have replaced.

Oyster reefs structure

Oyster density and reef structure differed between the four study locations. The reefs in Hunter River and Port Stephens

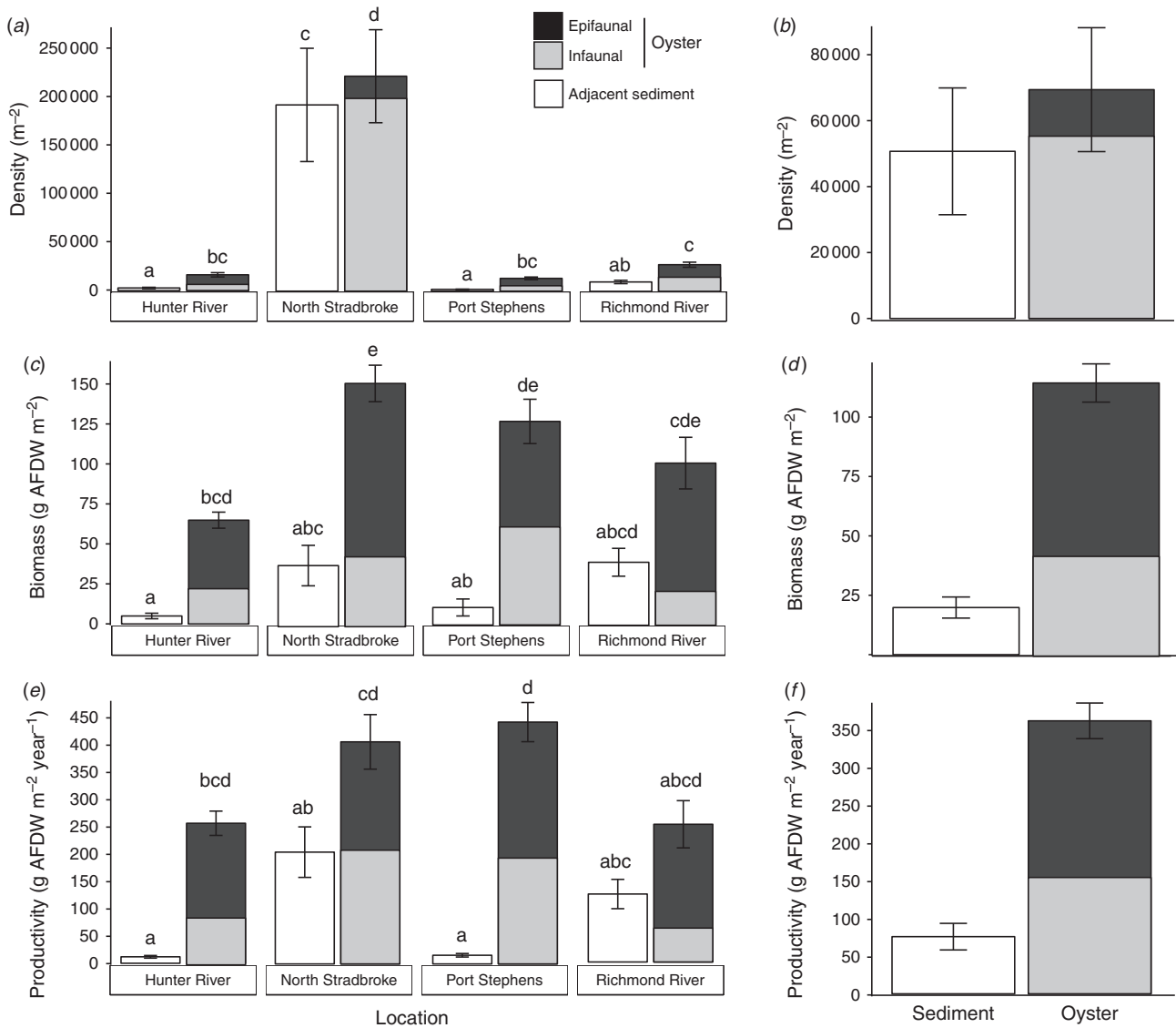


Fig. 4. Proportion and diversity of (a, b) all invertebrate taxa and (c, d) invertebrates ≥ 2 mm associated with oyster habitat (a, c; associated with oysters and underneath oyster clumps; $n = 80$ cores total) and adjacent bare sediment habitat (b, d; $n = 40$ cores). Note that the x-axis is broken for visualisation purposes.

were smaller in overall area and supported greater densities of oysters in discrete reefs that were visibly elevated above the surrounding bare muddy substrate. In contrast, the reefs at Richmond River and North Stradbroke Island were larger in overall area but had lower densities of oysters, often located in scattered clumps, fairly evenly distributed over a sandy substrate. Overall, the sites in Port Stephens, Hunter River and Richmond River supported relatively high oyster densities (160–600 m⁻²), whereas North Stradbroke supported oysters at densities an order of magnitude lower (10–68 m⁻²).

The oyster density estimates recorded in this study are considerably lower than historical accounts, but are similar to other contemporary estimates (e.g. Bishop *et al.* 2010; Wilkie

et al. 2013). Historically, oyster reefs in NSW covered areas ranging from 10 to 100 000 m² and were described as:

close set clumps of five or six oysters thick all over the bed, averaging 18 mature oysters besides spat of every 5 square inches [5570 oysters m⁻²] over an unbroken bed of shell [Oyster Culture Commission 1877].

Our method of using satellite imagery to define the edges of oyster reefs was only suitable for well-defined reef structures and we were unable to accurately detect the edges of low-density reef-sand matrices. Future studies may need to consider the use of global positioning system (GPS) in the field to more accurately measure the edges of lower-density reef systems.

Habitat value for macroinvertebrates

This study demonstrates that *S. glomerata* reefs support a diverse assemblage of macroinvertebrates with a greater density, biomass and productivity than nearby bare sediments. Although the overall density of macroinvertebrates associated with oyster habitat and adjacent bare sediment was similar, this was largely driven by high numbers of small gastropods <2 mm, in particular at North Stradbroke sites. In the absence of gastropods, oyster habitat generally supported over fivefold the densities and biomass of other macroinvertebrates. Oyster reefs are known to provide refuge from predators and heat stress and support productivity through the provision of hard substrate and food (McAfee and Bishop 2019), which can account for higher densities of invertebrates compared with unstructured habitats. Despite the magnitude of difference in productivity between oyster habitat and adjacent bare sediment differing between locations, this pattern was consistent across all four locations assessed, despite differences in latitude and sediment type. This interaction was largely driven by differences in the infaunal community of adjacent bare habitats between locations rather than differences in the productivity of oyster reefs themselves between locations. Adjacent bare sediments at the two locations characterised by muddy substrates, Port Stephens and Hunter River, were much less productive than the sandy substrates of North Stradbroke and Richmond River, which supported comparatively higher levels of productivity. This could be driven by differences in the sediment grain size, nutrient levels and differences in oxygen availability. However, these were not measured in the present study and other factors, such as latitude or temperature, are likely to also affect these factors. Further, each reef was only sampled at a single time point. Future research may benefit from including more environmental variables and accounting for seasonal variation in their study design.

Oyster and other shellfish reefs have been shown to be highly productive habitats relative to other less-structured habitats (Wong *et al.* 2011; McLeod *et al.* 2014; Coen and Humphries 2017). Wong *et al.* (2011) used estimates of secondary productivity of natural habitats in North Carolina in the US and ranked habitats (in decreasing order of productivity) as oyster reefs > saltmarsh > seagrass > intertidal flat and subtidal flats. Similarly, Ferraro and Cole (2007) used benthic macroinvertebrate diversity, density and biomass to rank habitat value in Willapa Bay (WA, USA) and found that oyster reefs were more ecologically valuable, in terms of providing habitat for macroinvertebrates, than salt marsh, mud shrimp habitat, bare mud or sand and ghost shrimp habitat. The level of secondary productivity of macroinvertebrates within the remnant intertidal *S. glomerata* reefs examined in the present study (overall mean 361.3 g AFDW m⁻² year⁻¹), was higher than that estimated by Wong *et al.* (2011) for intertidal oyster reefs in North Carolina, but those authors did not include the infaunal productivity below the oyster reef in their estimates (from 140.2 to 256.1 g AFDW m⁻² year⁻¹, calculated from their overall secondary productivity estimates and estimates of the oyster component of this). It should be noted that we did not estimate the secondary productivity of the oysters themselves, which is likely to be a large proportion of the total productivity of this habitat. Future

research estimating the total productivity of natural *S. glomerata* reefs would allow for direct comparisons with other systems.

The biodiversity of macroinvertebrate assemblages associated with oyster habitat was greater than that of the surrounding bare sediments in this study, consistent with previous studies (for a review, see McLeod *et al.* 2019). As expected for a habitat spread across a wide range of sites with different environmental conditions, the species assemblages were different at each site. However, the macroinvertebrate assemblages of oyster habitat were more similar between oyster habitat separated by hundreds of kilometres than with adjacent bare sediment at the same site. This indicates that oyster reefs are a unique ecosystem despite local environmental effects.

Bivalve aggregations can negatively affect infaunal communities through the build-up of an anoxic layer of biodeposits (Creese *et al.* 1997), or through the predation of infaunal larvae by filter feeding (Commito and Boncavage 1989). We found evidence of greater infaunal biomass and productivity under oysters compared with adjacent bare sediment. Similarly, Norkko *et al.* (2006) found a higher density of infauna near the suspension-feeding bivalve *Atrina zelandica*, whereas Norling and Kautsky (2007) demonstrated that biodeposits from the blue mussel *Mytilus edulis* supplied up to 31% of the energy demands of an associated macroinvertebrate community on the west coast of Sweden. Overall, it is likely that the role of bivalves and their biodeposits in the facilitation or inhibition of infauna varies depending on bivalve density and environmental conditions. Indeed, we found that although the facilitative effect of oysters was negligible on the sandy sites (North Stradbroke and Richmond River), it was substantial in the muddy sites of Port Stephens and Hunter River. These differences were correlated with oyster density, suggesting a critical mass of oysters may be required to have a facilitative effect, although these differences could also be related to other environmental variables, such as water flow.

Macroinvertebrates contribute important trophic linkages in marine systems (Grabowski *et al.* 2005). For example, crustaceans (>1 mm) are a primary food source of small fishes weighing 0.1–100 g (Edgar and Shaw 1995). In the present study, crustacean communities from these size classes were 14-fold more numerous and 13-fold more productive on oyster habitat than in adjacent bare sediment. Together, these lines of evidence suggest that *S. glomerata* reefs could be an important habitat supporting biodiversity and productivity at higher trophic levels in Australia. In the US, oyster reefs are known to provide important habitat for recreationally and commercially valuable fish species (for a review, see Grabowski *et al.* 2012) and support fish communities that are higher in abundance than nearby sand flats (Lenihan *et al.* 2001) or muddy substrates (Humphries *et al.* 2011). Peterson *et al.* (2003) estimated that oyster reef restoration in the south-east US leads to increases in local fish and large mobile decapod productivity of ~260 g m⁻² year⁻¹ of restored reef, estimated to be worth US\$4123 ha⁻¹ year⁻¹ for local fisheries (Grabowski *et al.* 2012).

Restoration for ecosystems services

Quantification of ecosystem services (both ecological and economic) is increasingly valuable for conservation and

restoration decision making. Restoration of oyster reefs historically focused on supporting reefs fisheries by replacing habitat or directly reseeding reefs or beds (Schulte 2017; McLeod *et al.* 2019). In recent decades, the focus shifted to bringing back threatened or locally extinct habitats and valuing their role in supporting biodiversity (Schulte 2017; Bersoza Hernández *et al.* 2018). Large-scale restoration projects are now being implemented to return lost ecosystem services. For example, 142 ha of oyster reefs has been restored in Harris Creek (Chesapeake Bay, USA), with the goals of improving water quality through their filtration and increasing local fish and non-oyster invertebrate fishery production (McLeod *et al.* 2019). The present study provides some information about the habitat value of remnant *S. glomerata* reefs in Australia. Given the degraded state of remnant intertidal oyster reefs and the current absence of subtidal reefs in Australia, these calculations are likely an underestimate of the potential benefits from oyster habitat restoration. Further work into the productivity of targeted fish and invertebrate species associated with Australian oyster reefs, and their economic value, would provide vital information for decision makers to help weigh the costs and benefits of restoration projects. Tools such as the oyster calculator developed by The Nature Conservancy (see <http://oceanwealth.org/tools/oyster-calculator>, accessed 15 June 2019) allow managers to set restoration objectives based on desired ecosystem services, such as water filtration or fisheries production for American oysters. Future work in Australia should focus on parameterising a similar calculator for Australian oyster species by building on the present work with estimates of fish and invertebrate growth and survival data, coupled with local hydrological information to predict the functional benefits of reef restoration.

Conclusion

S. glomerata oyster reefs support diverse and productive macroinvertebrate communities. Interest in oyster reef restoration is increasing in Australia (Gillies *et al.* 2018) and *S. glomerata* reef restoration trials have begun along Australia's east coast, motivated by the potential of bringing back a reduced or locally extinct ecosystem and its services. This study provides evidence that oyster reefs in Australia are productive marine ecosystems and their restoration may be a useful tool for increasing secondary productivity.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

This work was supported by the Marine Biodiversity Hub, a collaborative partnership supported through funding from the Australian Government's National Environmental Science Programme (NESP) Marine Biodiversity Hub (<http://www.nespmarine.edu.au/>, accessed 15 February 2019), The Nature Conservancy's Great Southern Seascapes program (<http://www.natureaustralia.org.au/our-impact/oceans/>, accessed 15 February 2019), the Thomas Foundation (<http://thomasfoundation.org.au/>, accessed 15 February 2019) and the New South Wales Department of Primary Industries.

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Handling Editor: Antony Knights