

1 **Title:** Non-native oyster reefs mediate habitat use and foraging by fishes in a vegetated urban
2 estuary

3 Brad Martin¹, Charlie Huveneers¹, Simon Reeves^{1,2}, Ryan Baring¹

4 **1** *College of Science and Engineering, Flinders University, South Australia, 5042, Australia* **2** *The*
5 *Nature Conservancy Australia, Carlton, Victoria, 3053, Australia*

6 *Corresponding Author: Brad Martin, brad.martin@flinders.edu.au, Orchid-ID: 0009-0008-7429-
7 1724

8

9 **Conflict of Interest**

10 The authors declare that they have no conflicts of interest.

11 **Funding**

12 This work was supported by a Holsworth Wildlife Research Endowment from the Ecological Society
13 of Australia.

14 **Abstract**

15 Estuaries are important socio-ecological systems, often underpinned by the cooccurrence and
16 functions of habitat-forming organisms. Endemic habitat-formers, including mangroves, oysters,
17 and seagrass, can be indicators of healthy estuarine ecosystems by facilitating interactions and
18 processes established over millennia. However, the introduction of non-native habitat-formers
19 may alter the ecological communities and functions of these systems. Here, we assessed the
20 effects of introduced, reef-forming Pacific oyster *Magallana gigas*, on a temperate mangrove-
21 dominated estuary in Australia, investigating effects on intertidal fish and invertebrate
22 communities, benthic structure, and foraging behaviour. Firstly, we characterised the structural
23 traits and macrofaunal communities of bare sediment, mangrove *Avicennia marina*, and Pacific
24 oyster-mangrove dominated habitats using photo- and extractive-quadrats. The fish communities
25 associated with these habitats were then surveyed using unbaited remote underwater video
26 stations and fyke nets. Pacific oyster aggregations showed no impacts on mangrove
27 pneumatophore density or morphology, but facilitated higher sapling densities and enhanced
28 invertebrate biodiversity. Similarly, the oyster-mangrove habitat supported greater fish species
29 richness, higher counts of foraging behaviour, and larger small-bodied fishes, compared to the
30 other habitats. However, several other non-native species including exotic Gobiidae and European
31 green crabs *Carcinus maenas*, a declared noxious pest, were also facilitated by Pacific oyster
32 aggregations. Overall, we demonstrated that Pacific oyster-mangrove habitats generally enhanced
33 estuarine biodiversity, including fisheries-targeted species, but also facilitated other non-native
34 species. These outcomes highlight some of the ecological pros and cons of non-native oyster reefs,
35 and the complexity of managing estuarine systems where the co-occurrence of Pacific oysters and
36 native habitat-formers is globally increasing.

37 **Keywords:** biogenic, habitat-formers, facilitation, invasive species, mangroves, nekton, shellfish,
38 temperate

Introduction

In estuarine systems, habitat-forming, foundation species such as mangroves, seagrass, oysters and coral, can have a significant influence on community composition and ecosystem functioning (Dayton 1972; Angelini et al. 2011). This occurs from the direct modification of physical structure and biogeochemical processes by habitat-formers, and indirectly from the activities of organisms that they facilitate. Subsequently, habitat-formers serve a pivotal role in supporting valuable ecological services including fish production, nutrient cycling, and coastal protection (Barbier et al. 2011; zu Ermgassen et al. 2021). For example, mangroves protect coastal infrastructure and stabilise otherwise bare coastal margins (Marois and Mitsch 2015). They also sequester vast quantities of carbon, with an estimated 5.85 Pg of carbon stored by mangrove forests globally (Alongi 2020). Similarly, oyster reefs remove excess nitrogen via biofiltration (Ray and Fulweiler 2021) and are used as nursery habitats by fisheries-targeted nekton (Gilby et al. 2018; zu Ermgassen et al. 2021). Positive ecological functions can be further enhanced by the coexistence of multiple habitat-formers, which may interact to increase structural and functional heterogeneity, leading to facilitation cascades that enhance niche availability and species biodiversity (Thomsen et al. 2022). As an example of a facilitation cascade, intertidal bivalve recruitment and survival may be enhanced by the shading of saltmarsh plants, with in turn, benefit from greater sediment stabilisation and enrichment provided by the bivalves (Gagnon et al. 2020); with their cooccurrence facilitating enhanced invertebrate biodiversity (Angelini et al. 2015). Conversely, when a habitat-former is introduced outside its native range, it can have mixed and context-specific outcomes, including “negative” impacts such as declines in native species abundances, species diversity, ecosystem functions or services; or “positive” impacts, the opposite (Guy-Haim et al. 2018; Rilov et al. 2024).

Invasions by non-native species can significantly modify ecological communities and functions, often decreasing species abundance and diversity via negative interactions such as competition, predation, and altering environmental conditions (Gallardo et al. 2016). Non-native habitat-formers specifically, can have ecosystem-scale impacts by altering the physical and biochemical composition of habitats (Rilov et al. 2024). For instance, the non-native seagrass *Halophila stipulacea* has displaced native seagrasses in the Caribbean, altering invertebrate communities, and limiting nutrient availability (Muthukrishnan et al. 2020). Conversely, non-native habitat-formers may enhance biodiversity, including native (Rodriguez 2006), and other non-native

species (i.e. 'secondary invasions' O'Loughlin and Green 2017). For example, in Northern Europe, Pacific oysters *Magallana gigas* (formerly *Crassostrea*) have been found to enhance valuable ecosystem services (e.g. coastal protection, fisheries) generally without significant modification to community composition (Hansen et al. 2023). Zwerschke et al. (2019) proposed that non-native *M. gigas* reefs may restore the ecological functions of almost extinct native oysters *Ostrea edulis* in the region, with McAfee and Connell (2021) suggesting that the global spread of this invader potentially compensates for the worldwide loss of >85% of native oyster reefs (Beck et al. 2011).

Pacific oysters, endemic to the north-west Pacific, have been introduced deliberately for aquaculture, and unintentionally through shipping, and are now globally distributed on every continent except Antarctica (McAfee and Connell 2021). They are favoured in aquaculture because of their fast growth rate, high reproductive output, and relatively low disease mortality (Troost 2010). These traits have also led to the establishment of invasive *M. gigas* populations in 36 countries (Martínez-García et al. 2022), that are often difficult and costly to eradicate (Hansen et al. 2023). In the future, *M. gigas* may also spread to dominate most temperate coastlines (McAfee and Connell 2021), with projected climate change conditions favourable to their poleward expansion (King et al. 2021). This has created a dilemma for coastal management between encouraging non-native oyster production and restorative aquaculture (van der Schatte Olivier et al. 2020; Theuerkauf et al. 2022), versus mitigating the potential socioecological impacts of invasive wild oyster populations (Herbert et al. 2016).

Invasions by *M. gigas* are associated with mixed ecological outcomes, which are context and scale-dependent (McAfee and Connell 2021; Hansen et al. 2023). Outside their native range, they have been documented to outcompete and displace native bivalves (Padilla 2010), and facilitate other non-native species and diseases (Hansen et al. 2023). For example, in Argentina, exotic *M. gigas* reefs have been found to facilitate high densities of exotic and cryptogenic species that are absent from bare uninvaded control sites (Bazterrica et al. 2022). Conversely, non-native oysters have also been documented to facilitate similar invertebrate communities associated with native bivalve ecosystems in Northern Europe (Herbert et al. 2016; Hansen et al. 2023) and Australia (Wilkie et al. 2012). Manipulative trials in Sweden by Norling et al. (2015) indicated that *M. gigas* shells can provide greater fish and invertebrate habitat compared to native blue mussels *Mytilus edulis*. These examples indicate that the net impact of non-native oysters is likely to be complex,

and mediated by a combination of environmental conditions, habitat structural characteristics, and interactions with local biological communities.

Pacific oysters were deliberately introduced to temperate Australia in the 1940s to revitalise the oyster aquaculture industry, and they have since established invasive populations, primarily managed as an aquaculture biosecurity risk (Gillies et al. 2018). In Australian estuaries, *M. gigas* form dense aggregations on consolidated structures, including as secondary habitat-formers on the pneumatophores and trunks of the primary habitat-former, grey mangrove *Avicennia marina* (Wiltshire et al. 2010; Wilkie et al. 2012). Prior to the mid-20th century, this region once supported thriving native oyster reefs, but today, they are considered functionally extinct, with estimated losses of >99% of flat oyster *Ostrea angasi* reefs, and >90% of Sydney rock oyster *Saccostrea glomerata* reefs (Gillies et al. 2020). Subsequently, the establishment of non-native *M. gigas* reefs may provide an unintended offset to the loss of native oyster reefs in temperate Australia, contrary to contemporary models of habitat decline (Davis et al. 2011; McAfee and Connell 2021).

Despite the growing distribution of non-native oyster reefs worldwide, few studies have directly assessed how wild Pacific oyster *Magallana gigas* reefs influence higher trophic groups such as fishes (Hansen et al. 2023), which could be impacted from alterations to habitat structure and foraging opportunities (Gilby et al. 2018). Similarly, the ecological interactions and impacts of non-native oyster reefs in mangrove forest communities have been scarcely evaluated (i.e. Wilkie et al. 2012). To address these knowledge gaps, the community composition and ecological functions of non-native oyster-mangrove habitat, and uninvaded bare and structured control habitats, were investigated within a temperate Australian estuary. Specifically, it was hypothesised that established Pacific oyster aggregations alter the environmental conditions by significantly (1) limiting mangrove pneumatophore density and size; (2) increasing sediment organic matter through biodeposition and; (3) enhancing fish macrofaunal prey availability (e.g. richness, abundance, biomass). We also hypothesised that Pacific oyster-mangrove habitat would support (4) distinct fish and macrofauna community compositions and; (5) greater fish foraging behaviour. Thus, this study will provide critical insights for evaluating the ecological role of non-native oysters and understanding their interactions with estuarine vegetation, invertebrate, and fish communities.

129 **Methods**

130 **Location Description**

131 We conducted our study in the Port River-Barker Inlet Estuary, the largest temperate estuary in
132 Gulf St. Vincent, South Australia. As the main maritime port of Adelaide since 1837 (i.e. current
133 human population is 1.3 million people), the estuary has been highly modified with significant
134 declines in coastal vegetation and native shellfish ecosystems due to urbanisation, dredging,
135 pollution, and hydrological modification (Edyvane 1999). A range of non-native habitat-formers
136 including Pacific oysters and European fan worms *Sabella spallanzanii* have already established
137 self-sustaining populations in the estuary (Wiltshire et al. 2010). Pacific oysters occur in dense
138 intertidal aggregations on artificial structures (e.g. rock levees, pylons), and attached to *Avicennia*
139 *marina* and bivalve shells, forming biogenic oyster reef structures (pers. obs.).

140 The western shoreline of Torrens Island, which borders the main Port River channel (Fig. 1) is
141 characterised by heterogenous areas of bare sediment, fringing *Avicennia marina*, and oyster reefs
142 of pneumatophore-attached *M. gigas*. In March 2023, we surveyed these three habitats along a 2-
143 kilometre section of shoreline, with four replicate sites surveyed in each habitat (N=12) (Fig. 1).
144 Sites were randomly distributed along the shoreline to represent each habitat, with a minimum of
145 30 metres between sites. *Avicennia marina* and dead bivalve shells (e.g. cockles, oysters)
146 comprised the only available hard substrates for *M. gigas* settlement in this section of the estuary.

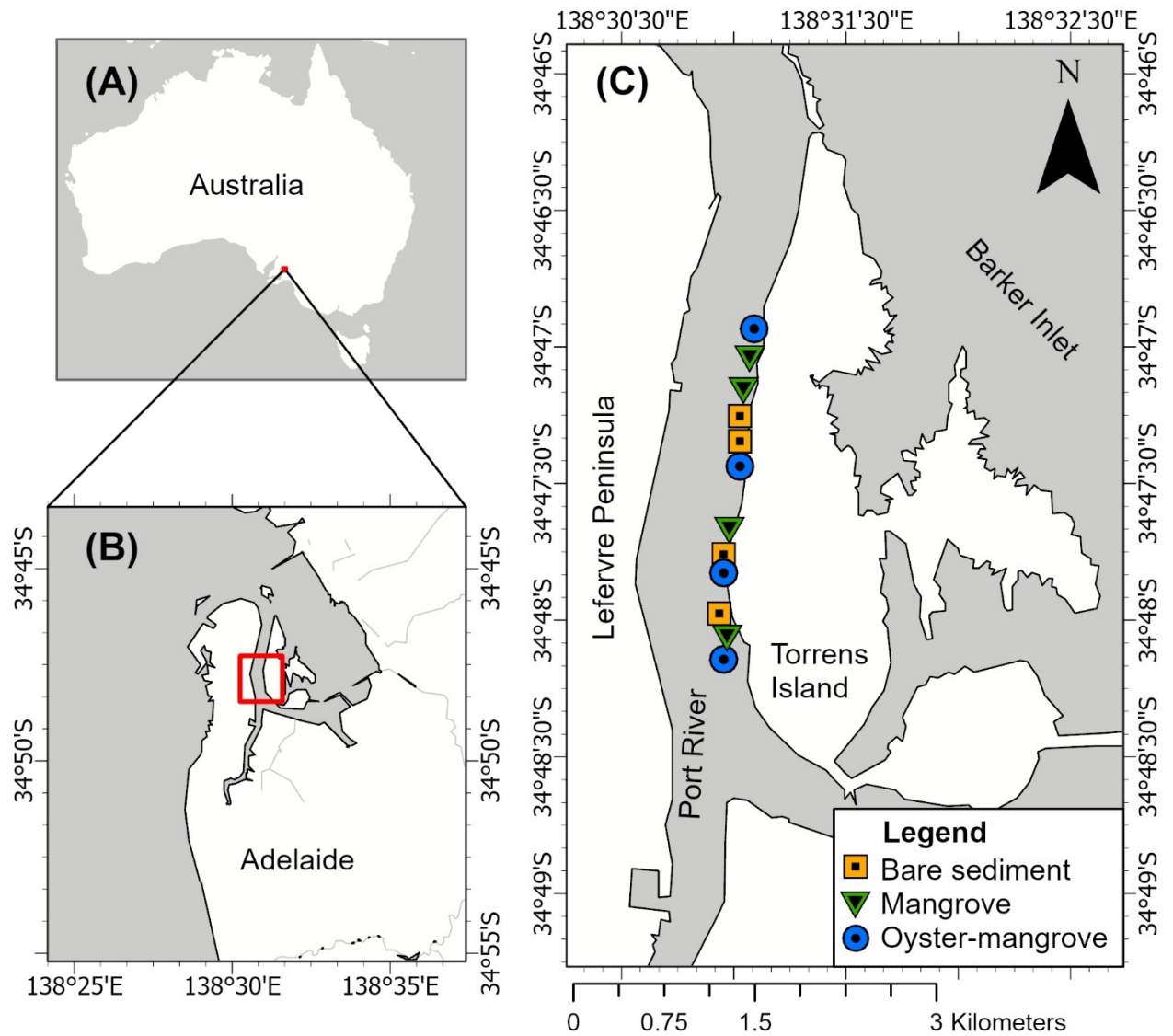


Figure 1. Location of (A) Port Adelaide in South Australia, (B) the Port River-Barker Inlet Estuary and (C) survey locations representing sites of the three habitat types.

Estimation of habitat characteristics and prey availability

We characterised the habitat of each site at low tide using eight (0.5 x 0.5 m) randomly placed photo-quadrats (N=96). We photographed each quadrat and analysed the photos in ImageJ (www.imagej.net) to estimate benthic cover composition (%), and densities of *A. marina* saplings and pneumatophores. Benthic cover categories consisted of bare sediment, cockle shell, mangrove structures, and Pacific oysters. Four photo-quadrats per site were extractively sampled to quantify the associated habitat structures and macrofaunal communities (N=48). Firstly, we measured the aboveground height and basal diameter of up to six randomly selected pneumatophores from each quadrat using vernier callipers (to within 0.1 mm). Next, we removed all oysters, associated macrofauna (epifaunal invertebrates and fish), and the top five centimetres of sediment within each quadrat for processing, as the oyster material was sometimes partially buried to this depth. This involved detaching any oysters and macrofauna from the surface of the pneumatophores, and removing the underlying sediment, which we then sieved *in situ* through a 1-millimetre sieve before being bagged, transported to the laboratory, and frozen (-20°C).

In the laboratory, we defrosted, rinsed, and sorted the retained material to assess the shell material and associated macrofauna. Firstly, we enumerated oysters and classified them as either alive juveniles (<25 mm), alive adults (>25 mm), dead cups (open shell without the top valve), or dead boxes (open shell with two articulated valves). To assess the size class distribution of *M. gigas*, we recorded the shell height (i.e. longest hinge-lip distance) of up to 20 alive juvenile and adult oysters per quadrat (to 0.1 mm). We measured the wet weight of (i) oyster and (ii) disarticulated cockle shell separately using an electronic scale (0.1 g) to estimate total biomass. Oyster biomass estimates included both the shell and wet meat weights as dead and alive oysters occurred together as clumped material, whereas cockle shells consisted of disarticulated and fragmented material. We inspected all shell material for macrofauna, which we enumerated, weighed (wet weight, 0.01 g), and identified to the lowest practical taxonomic level (Gowlett-Holmes 2008).

Fish community surveys

We surveyed the fish community including nektonic fish (teleosts and elasmobranchs), decapods, and cephalopods using a combination of non-extractive remote underwater video stations (RUVS) and extractive fyke nets, which were simultaneously deployed across sites (N=36). We

concurrently deployed pairs of RUVS and fyke nets across the twelve sample sites over two subsequent days of daylight high-tides, with sampling repeated across three sample periods (N=36) on a fortnightly basis. We positioned all survey gear at least 15 metres apart during daytime (8:00 to 16:00) high tides, in ≈ 1.5 metre depths, for a continuous soak-time of 90 minutes.

Each RUVS consisted of a single weight attached GoPro Hero 7/8 camera positioned 20 cm above the benthos. The RUVS were unbaited to avoid bait-biases and enable investigation of habitat selectivity and interactions of the observed species (Bradley et al. 2016). We annotated video records in EventMeasure (www.seagis.com) with all nekton counted and identified to the lowest taxonomic level (Gomon et al. 2008). Due to differences in recording duration across RUVS, we annotated the first 60-minutes of each video only, commencing 1-minute after deployment to allow disturbed sediment to settle. We calculated the maximum number of individuals of the same species present within a single frame from each video (MaxN), which is a commonly used conservative abundance metric (Whitmarsh et al. 2016). We also recorded fish foraging behaviour by counting the number of bite interactions observed between fish and the benthos.

We deployed unbaited fyke nets (0.4 m $\varnothing$ opening, fyke mesh size 1.2 mm²; with 2 m x 1.2 m wings; 4 m total length), with the net opening facing the shoreline to sample fish on the ebbing tide. We removed captured organisms from the net and placed them onto a scaled-grid where we photographed, enumerated, identified them to species level, then released them (except voucher specimens). From each fyke net deployment, we determined the length measurement of up to 20 individuals from voucher specimens and photographs in ImageJ as total length (fish), carapace length (decapods), or mantle length (cephalopods) (1.0 mm). For any unidentifiable fishes, we euthanised voucher specimens using an overdose of Aquí-S and transported them to the laboratory for identification and measurement.

Abiotic variables

We recorded water temperature (°C) using a multiparameter probe (Polaris C, Oxyguard), and salinity (PPT) using a handheld refractometer prior to each RUVS and fyke net deployment. We estimated distance to the estuary mouth to the nearest metre by recording the GPS coordinates of each survey site and measuring the contour along the river edge using Google Earth. Three replicate sediment samples (≈ 50 g) were collected from each site, transported to the laboratory and immediately frozen. We dried approximately 10 g of defrosted sediment from each sample at

60°C for at least 4 days, prior to incineration at 450 °C for 4 hours. We then calculated the percentage of sediment organic matter as the difference in weight between pre-combusted and post-combusted sediment.

Data analyses

We carried out all statistical analysis of the environmental and biological community variables in Rstudio (R Core Team 2024). We used Kruskal-Wallis chi-squared tests to assess differences in habitat characteristics from the photo- and extractive-quadrats, including (i) benthic cover (%); (ii) pneumatophore and sapling densities; (iii) pneumatophore morphology; (iv) shell weights, counts and heights; and (v) sediment organic matter (%). When significant ($p \leq 0.05$), we used Dunn's post-hoc tests for pairwise comparisons.

To evaluate the variables influencing the univariate macrofauna metrics (richness, density, biomass), we first tested collinearity between environmental predictors from the quadrats using the Pearson's correlation coefficient, with collinear predictors ($|r| > 0.7$) removed (**Appendix 1**). The reduced model of environmental predictors included distance to estuary mouth, pneumatophore count, sapling count, cockle shell (g), and oyster shell (g). We used generalised linear models (GLMs) to evaluate differences in the univariate macrofauna variables (e.g. species richness, biomass and densities) using the reduced model and habitat treatment categories. We assessed species richness using a Poisson distribution, whereas we used a Gamma (link function=log) for biomass and density to meet assumptions of normality and heteroscedasticity. We tested differences in the macrofaunal community composition by habitat type (fixed factor, three levels) with estuary mouth distance as a covariate using permutational multivariate analysis of variance (PERMANOVA) on the fourth-root transformed Bray-Curtis dissimilarity dataset, with subsequent post-hoc pairwise PERMANOVA tests conducted to assess significant habitat differences. We used a non-metric multidimensional scaling (nMDS) plot to visualise the dispersion of the macrofauna community structure.

We assessed differences in fish community composition using PERMANOVA tests of Bray-Curtis dissimilarity measures on the square-root transformed data obtained from the RUVS and fyke net surveys, respectively. We added a dummy value to the fyke net matrices to allow the inclusion of samples containing no fish. Each PERMANOVA included the habitat type (fixed factor; three levels), sample period (fixed factor; three levels) and estuary mouth distance as a covariate. We

240 used post-hoc pairwise PERMANOVA tests to examine significant habitat differences. We then
241 conducted Dufrene-Legendre indicator species analysis to identify the species contributing most to
242 differences between habitat types. We visualised habitat differences in the fish community using
243 Canonical Analysis of Principal (CAP) components with habitat relationships of the top indicator
244 species depicted as an overlay of Pearson's Correlation values.

245 We then used general linear models to assess changes in (1) abundances of fish species identified
246 from the indicator species analysis, (2) total abundance and (3) species richness, from each survey
247 method, (4) total observed fish bites from the RUVS observations and, (5) water quality
248 (temperature and salinity) across habitat types. The GLMs used the same factors and design as the
249 PERMANOVA tests and were followed by subsequent Tukey pairwise comparisons to investigate
250 significant habitat differences. We assessed the size-frequency distribution of all species measured
251 from the fyke nets using Kruskal-Wallis chi-squared tests, with Dunn's post-hoc tests carried out
252 on any fish species with evidence of habitat differences to investigate any size differences across
253 habitat types.

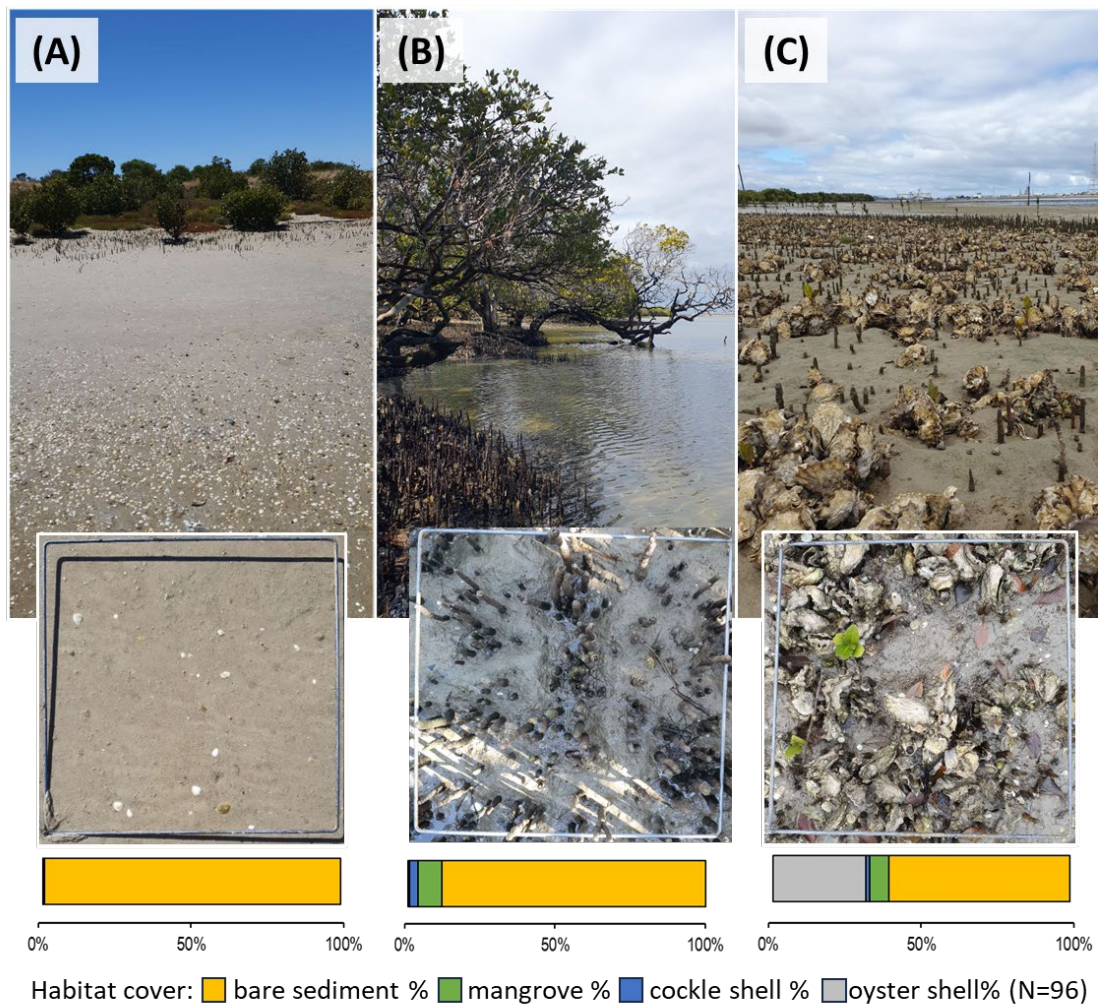
254

Results

Environmental characteristics

Benthic habitat characteristics provided evidence of notable structural differences between the habitat types, mostly between bare sediment and both mangrove and oyster-mangrove habitats. The benthic cover (%) significantly differed across habitat types for all categories ($p \leq 0.004$, Fig. 2), with pairwise tests indicating that bare sediment cover decreased with increasing biogenic structural cover categories (Table 1). The mangrove and oyster-mangrove habitats had similar proportions of cockle shell (%) ($p = 0.330$), and mangrove structure cover (%) ($p = 0.480$) due to the presence of *A. marina*, and did not differ in pneumatophore density and morphology (Table 1, Appendix 2). Both habitats contained densities of 254 ± 20 (mean $\pm$ standard error) pneumatophores per m^2 , with an above ground height and diameter of 89.4 ± 2.9 and 9.9 ± 0.2 mm, respectively (Table 1, Appendix 2).

High coverage (%) of *M. gigas* shells was unique to the oyster-mangrove habitat ($p \leq 0.001$, range: 10–77%, Table 1), representing an estimated biomass of 5 – 24 kilograms of oyster shell clumps per m^2 (Table 1). Seventy-three percent of the oysters were alive juvenile and adult oysters, up to 121 mm in shell height (Table 1, Appendix 3). Disarticulated cockle shells (*Katelysia* spp.) were present across all habitats, and ranged in quantity from 0 – 3.8 kilograms per m^2 , with larger quantities recorded from the oyster-mangrove habitat compared to the other two habitats ($p \leq 0.005$, Table 1). Oyster-mangrove habitat was also associated with the greatest densities of *A. marina* saplings, with up to 24 saplings per m^2 ($p \leq 0.037$, Table 1). The percentage of sediment organic matter was similar across habitats ($\chi^2 = 3.297$, $p = 0.192$), and ranged from 0.34 to 8.75% across site samples (Table 1). Measured water temperature and salinity was also similar across all habitats during the sampling periods ($p > 0.050$; 16.9–23.2°C and 35–44 ppt).



278

279 **Figure 2.** Representative images of the surveyed intertidal habitats characterised by either (A)
 280 bare sediment, (B) grey mangrove *Avicennia marina* pneumatophores, and (C) mangrove-attached
 281 Pacific oyster *Magallana gigas* reefs. Bottom images show examples of quadrats from each
 282 habitat. Horizontal bars represent benthic cover (%) estimated from the photo-quadrats for each
 283 habitat types (N=32 per habitat).

Table 1. Mean $\pm$ standard error (SE) and range (min–max) of habitat characteristics from the photo- and extractive-quadrats. This includes measurements associated with the biogenic structures of grey mangroves (*Avicennia marina*), Pacific oyster (*Magallana gigas*) and cockle shells (*katelaysia spp.*). Post-hoc tests denote significant results of Kruskal-Wallis tests and pairwise Dunn's post-hoc comparisons between habitat types ($p \leq 0.05$). Abbreviations: S=bare sediment, M=mangrove and OM=oyster-mangrove habitat.

Habitat characteristics	Bare sediment		Mangrove		Oyster-Mangrove		Post-hoc tests
	$\bar{x} \pm \text{SE}$	Range	$\bar{x} \pm \text{SE}$	Range	$\bar{x} \pm \text{SE}$	Range	
Photo-quadrats (N=96)							
Bare sediment %	99.43 ± 0.20	93.96 – 100	88.47 ± 1.58	58.43 – 97.97	60.82 ± 2.84	17.45 – 81.55	S>M>OM
Cockle shell %	0.48 ± 0.19	0 – 6.04	2.81 ± 1.25	0 – 38.15	1.51 ± 0.36	0 – 8.06	S<(M= OM)
Mangrove structures %	0.02 ± 0.02	0 – 0.56	8.08 ± 1.00	1.98 – 25.66	6.46 ± 0.68	1.11 – 15.51	S<(M= OM)
Oyster shell %	0.07 ± 0.07	0 – 2.38	0.63 ± 0.28	0 – 6.84	31.21 ± 2.87	9.97 – 76.93	S<M< OM
Biogenic cover % (shells & mangrove combined %)	0.57 ± 0.20	0 – 6.04	11.53 ± 1.58	2.02 – 41.57	39.18 ± 2.84	18.45 – 82.55	S<M< OM
Pneumatophore density .m ⁻²	-	-	250 ± 28	28 – 644	258 ± 27	60 – 624	M= OM
Sapling density.m ⁻²	0.1 ± 0.7	0 – 4	3 ± 4	0 – 12	6 ± 6	0 – 24	S<M< OM
Extractive-quadrats (N=48)							
Pneumatophore length (mm) (N=117)	-	-	86.13 ± 0.28 (n=98)	18 – 234	92.84 ± 4.33 (n=79)	24 – 224	M= OM
Pneumatophore diameter (mm) (N=117)	-	-	10.12 ± 0.28 (n=98)	5 – 20	9.58 ± 0.22 (n=79)	2.8 – 14	M= OM
Dead oyster density.m2	-	-	0.50 ± 0.50	0 – 8	169 ± 27	36 – 468	(S=M)< OM
Alive oyster spat density.m2	-	-	0.50 ± 0.50	0 – 8	190 ± 60	0 – 812	(S=M)< OM
Alive adult oyster density.m2	-	-	2.25 ± 1.09	0 – 12	254 ± 32	88 – 532	(S=M)< OM
Adult oyster height (mm)(N=335)	-	-	59.63 ± 10.12 (n=9)	25.6 – 110	61.49 ± 1.12 (n=326)	25.2 – 121	-
Disarticulated cockle shell g.m ⁻²	173 ± 66	0 – 948	392 ± 241	1 – 3,880	594 ± 103	56 – 1,704	(S=M)< OM
Oyster material g.m ⁻²	-	-	73 ± 40	0 – 536	13,146 ± 1,517	5,228– 24,176	(S=M)< OM
Percentage soil organic matter % (N=36)	0.97 ± 0.12	0.53– 1.75	2.17 ± 0.69	0.34 – 8.75	1.47 ± 0.28	0.53 – 1.75	S=M= OM

291 Macrofauna composition

292 We collected 11,500 macrofauna belonging to 64 species and 12 taxonomic classes from 48
 293 extractive quadrats. Nineteen species were found across all three habitat types, while 45 % of
 294 species were only found in one habitat type. Most macrofauna abundance was comprised of the
 295 minute air-breathing snails *Salinator fragilis* and *Hydrococcus brazieri* (33 %), and clams *Lasaea*
 296 *australis* and *Scintillua solida* (18 %). The most ubiquitous species consisted of *Polychaeta* spp.
 297 (ragworms), *Salinator fragilis* and *S. solida*, which occurred in >88 % of quadrats. In contrast, the
 298 intertidal snails *Austrocochlea constricta* and *Bembicium auratum* contributed the greatest
 299 combined biomass, representing 31 % of macrofauna weight. A variety of cryptogenic and non-
 300 native species including *Carcinus maenas* (European shore crabs), *Batrillaria australis* (mud
 301 creeper), and *Pyrazus ebenius* (Hercules club whelk) were also collected, with 96% of non-native
 302 macrofauna obtained from the oyster-mangrove habitat (Appendix 4).

303 Macrofauna richness, density, and biomass differed across habitats ($\chi^2 = 33.127$, $p < 0.001$, $\chi^2 =$
 304 18.975 , $p < 0.001$, $\chi^2 = 31.349$, $p < 0.001$, respectively), and were highest in the oyster-mangrove
 305 habitat (Table 2, Fig. 3). This habitat type supported at least twice the species richness (23.9 ± 1.2
 306 species), 1.8 times greater densities ($1,534 \pm 191$ individuals per m^2), and 7.6 times more
 307 macrofaunal biomass (426 ± 84 grams per m^2) than the other two habitats (Fig. 3). The mangrove
 308 habitat typically recorded greater richness and macrofauna biomass compared to the sand
 309 habitat, which in comparison, had higher density of macrofauna due to high abundances of minute
 310 air-breathing snails, but these were not significantly different (Fig. 3, Appendix 4, $p > 0.111$).

311 General linear models indicated that these trends were most strongly associated with habitat
 312 categories (Table 2, $p < 0.001$). Additionally, macrofauna richness generally decreased with
 313 increasing distance from the estuary mouth, whereas biomass increased with both
 314 pneumatophore density and organic matter (%) (Table 2). PERMANOVA tests provided strong
 315 evidence of habitat differences in the macrofauna community structure ($F = 20.457$, $p = 0.001$)
 316 with pairwise tests indicating differences between all three habitats ($p = 0.001$, Appendix 5).

317 Overall, the macrofauna samples from the oyster-mangrove habitat were most different from the
 318 sand and mangrove habitats, which shared a greater degree of similarity based on ellipse overlap
 319 (Fig. 4).

Table 2. Results of generalised linear models for macrofaunal richness, density, and biomass from the extractive quadrats (N=48) across habitat types. Bold font shows significant factors ($p \leq 0.05$). Abbreviations: DF = degrees of freedom.

Macrofauna Metric	DF	Deviance	P-value
Richness			
Intercept			
Habitat type	2	151.17	<0.001*
Estuary mouth dist.	1	4.94	<0.027*
Pneumatophores #	1	0.08	0.776
Saplings #	1	1.26	0.262
Oyster weight (g)	1	0.12	0.735
Cockle shell weight (g)	1	0.09	0.760
Soil organic matter (%)	1	3.67	0.056
Density -m ²			
Intercept			
Habitat type	2	10.178	<0.001*
Estuary mouth dist.	1	1.475	0.158
Pneumatophores #	1	1.742	0.125
Saplings #	1	0.005	0.936
Oyster weight (g)	1	0.433	0.444
Cockle shell weight (g)	1	0.001	0.974
Soil organic matter (%)	1	0.424	0.449
Biomass grams-m ²			
Intercept	2		
Habitat type	1	16.922	<0.001*
Estuary mouth dist.	1	0.052	0.398
Pneumatophores #	1	1.294	<0.001*
Saplings #	1	0.000	0.984
Oyster weight (g)	1	0.267	0.055
Cockle shell weight (g)	1	0.154	0.145
Soil organic matter (%)	1	1.851	<0.001*

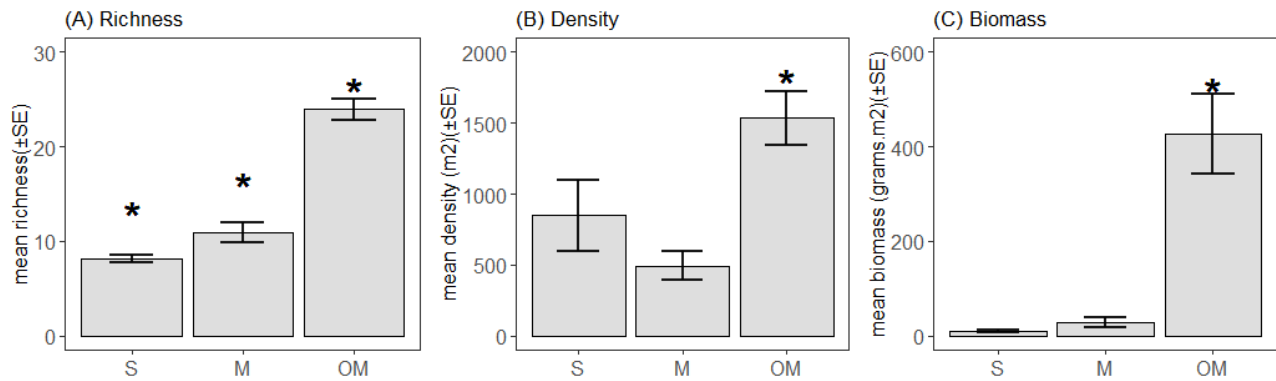


Figure 3. Mean $\pm$ standard error (SE) of macrofauna (A) richness, (B) density m^{-2} , and (C) biomass grams. m^{-2} from extractive quadrat surveys from the intertidal habitat types (N=48). Significant differences between habitats identified from Tukey pairwise comparisons are denoted by asterisk “*”. Abbreviations: S=bare sediment, M=mangrove and OM=oyster-mangrove habitat.

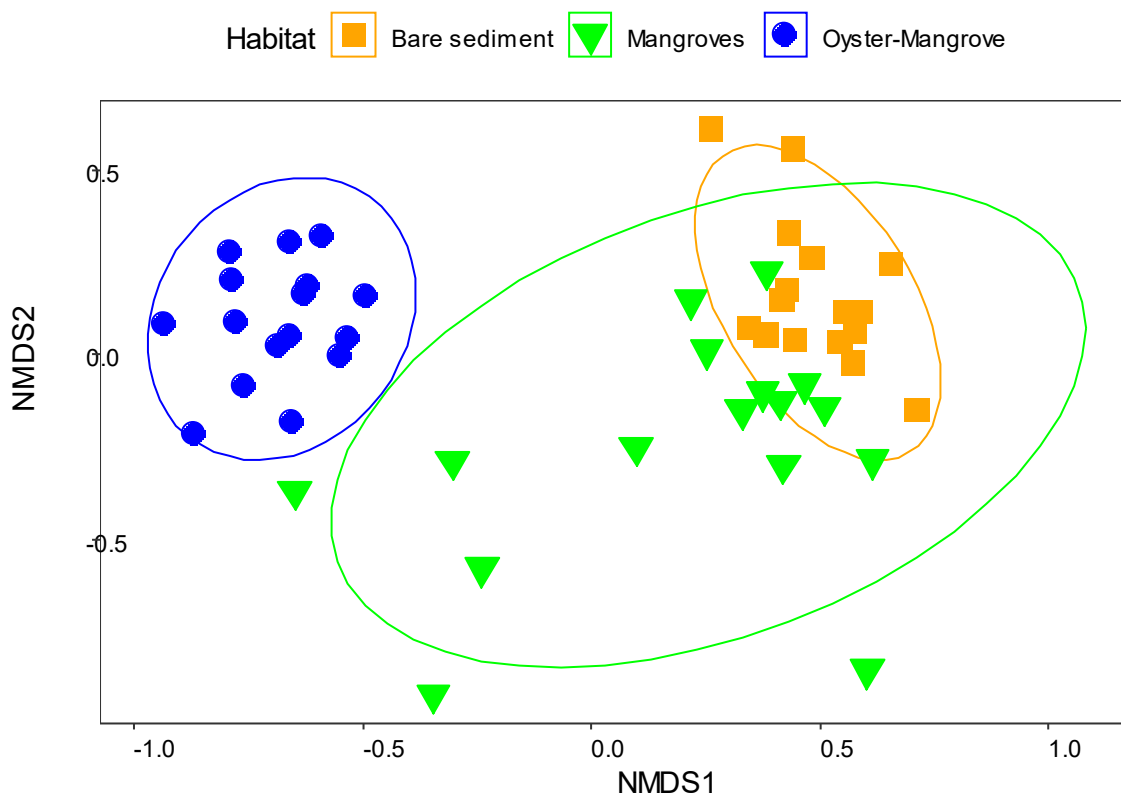


Figure 4. on-metric multidimensional scaling (NMDS) plot showing the macrofaunal community structure based on Bray-Curtis dissimilarities. Points represent individual quadrat samples colour coded by habitat type, with 95 % ellipses shown.

335 Fish communities from RUVS surveys

336 The unbaited video cameras detected 32 different nektonic species, consisting of 24 fishes, six
337 decapods, and one cephalopod, with a combined total MaxN of 3,641 organisms (Fig. 5, Appendix
338 6). Observed nekton were dominated by small pelagic fishes, *Atherinosoma microstoma*
339 (smallmouth hardyhead) and *Spratelloides robustus* (blue sprat), which comprised 66 % of
340 recorded nekton abundance, followed by *Sillaginodes punctatus* (King George whiting, 8.3 %).
341 Nektonic macroinvertebrates only made up 1.4 % of total MaxN. A total of 17 species were
342 associated with bare sediment sites, including 2 unique species to this habitat; 18 species were
343 associated with the mangrove sites with one unique species: and 29 species were observed from
344 the oyster-mangrove sites including 11 species that were unique. Fourteen species were observed
345 in all three habitat types. *Favonigobius lateralis* (southern longfin goby), *Acanthopagrus butcheri*
346 (black bream) and *S. punctatus* were the most ubiquitous species observed, occurring in >75 % of
347 videos.

348 There was strong evidence for habitat differences in the fish community structure recorded from
349 the RUVS ($F = 3.99$, $p < 0.001$), with similarities across the mangrove and oyster-mangrove habitats
350 ($p = 0.438$), which contrasted to the bare sediment habitats ($p \leq 0.024$) (Fig. 6, Appendix 5).
351 Similarly, habitat differences were also detected using GLM analysis of both the fish community
352 richness and abundance ($p = 0.005$, $p = <0.001$, respectively, Table 3). However, on average, the
353 oyster-mangrove habitat had much higher average fish richness (10.6 ± 0.9 species) and
354 abundance (148 ± 40.2 total maxN) detected from the RUVS, compared to the bare sand and
355 mangrove habitat (Fig. 7).

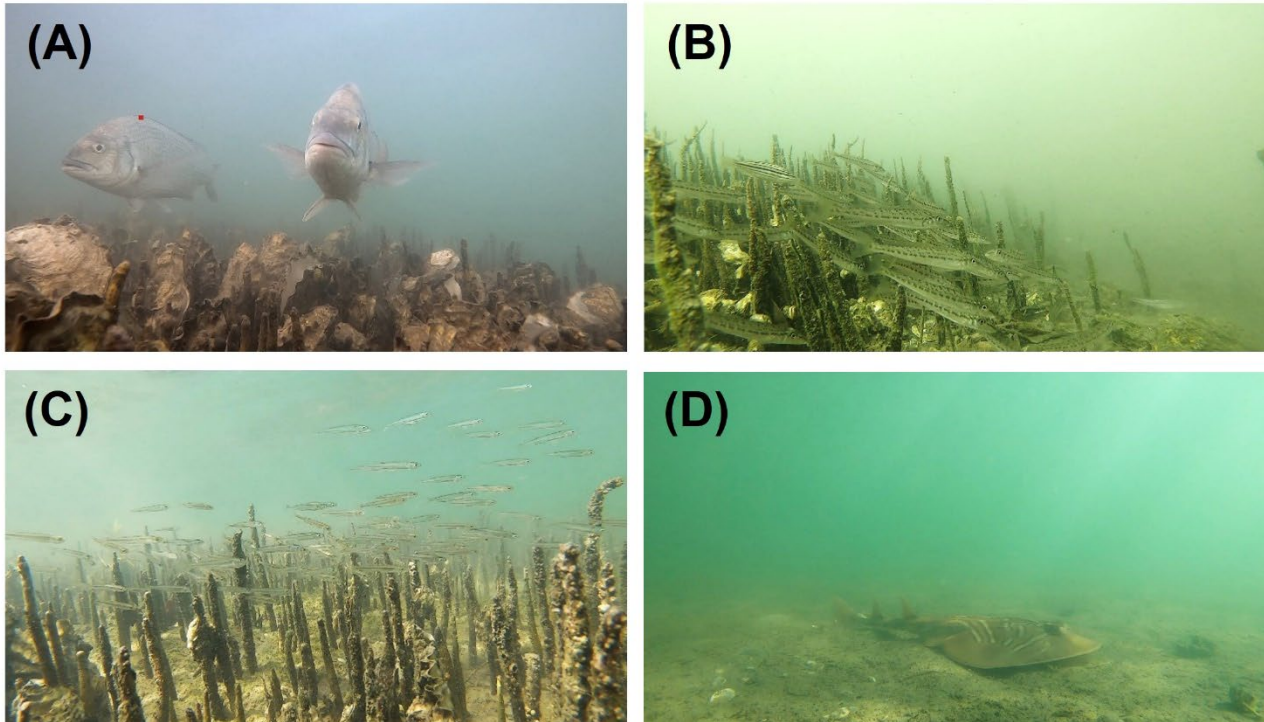


Figure 5. Examples of nekton observed from the RUVS, including (A) *Acanthopagrus butcheri*, black bream, (B) juvenile *Sillaginodes punctatus*, King George whiting, (C) *Atherinosoma microstoma*, small-mouthed hardyheads, and (D) *Trygonorrhina dumerilii*, Southern fiddler ray.

Table 3. Results from ANOVA multivariate generalised linear model for nekton richness, abundance, and fish bite counts from the fyke net and RUVS surveys. Factors in bold are significant with $p \leq 0.05$ denoted by '*'. Abbreviations: DF = degrees of freedom.

Unbaited cameras	DF	Deviance	p-value
Richness			
Habitat	2	10.45	0.005*
Sampling period	2	4.66	0.097
Mouth distance	1	1.51	0.219
Habitat*Sampling period	4	5.24	0.264
Abundance (total MaxN)			
Habitat	2	704.32	<0.001*
Sampling period	2	1063.89	<0.001*
Mouth distance	1	416.16	<0.001*
Habitat*Sampling period	4	200.79	<0.001*
Fish bites			
Habitat	2	181.63	<0.001*
Sampling period	2	167.41	<0.001*
Mouth distance	1	135.22	<0.001*
Habitat*Sampling period	4	119.10	<0.001*
Fyke nets	DF	Deviance	p-value
Richness			
Habitat	2	2.59	0.274
Sampling period	2	2.75	0.252
Mouth distance	1	2.76	0.009*
Habitat*Sampling period	4	4.77	0.311
Abundance (CPUE)			
Habitat	2	504.33	<0.001*
Sampling period	2	174.68	<0.001*
Mouth distance	1	145.70	<0.001*
Habitat*Sampling period	4	458.50	<0.001*
Water parameters	DF	Deviance	p-value
Water temperature (°C)			
Habitat	2	0.01	1.000
Sampling period	2	2.92	0.232
Mouth distance	1	0.43	0.510
Habitat*Sampling period	4	0.01	1.000
Salinity (PPT)			
Habitat	2	0.11	0.948
Sampling period	2	1.03	0.598
Mouth distance	1	0.54	0.462
Habitat*Sampling period	4	0.66	0.955

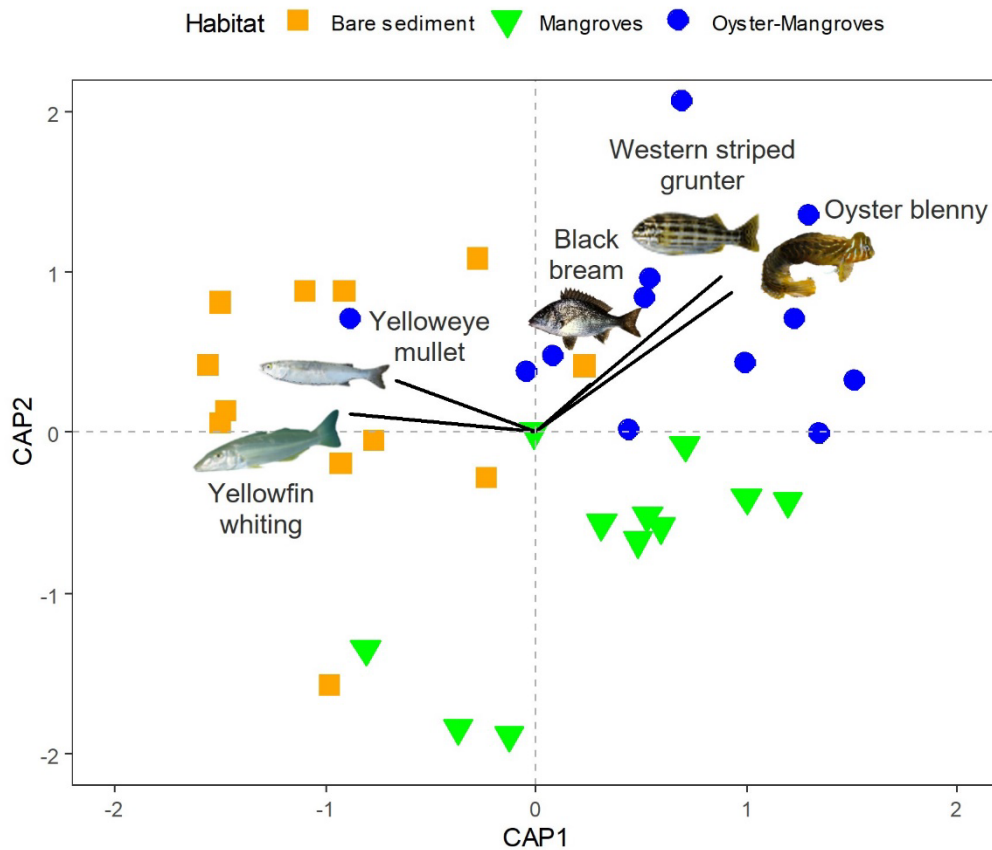


Figure 6. Canonical analysis of principal components (CAP) plot visualising nekton community composition (based on Bray-Curtis Similarity Index) from RUVS surveys of intertidal habitats. Vector overlays are Pearson correlations of indicator species identified from Dufrene-Legendre indicator species analysis.

Table 4. Indicator species analysis testing for the species that contributed most toward differences in nekton community structure between habitats.

Species	Group	Indicator value	p-value
Black bream	Oysters	0.48	0.038
Yellow eye mullet	Bare sediment	0.48	0.039
Western striped grunter	Oysters	0.55	0.003
Sand whiting	Bare sediment	0.59	0.001
Oyster blenny	Oysters	0.66	0.001

"Group" indicates the habitat for which that species is a significant indicator.

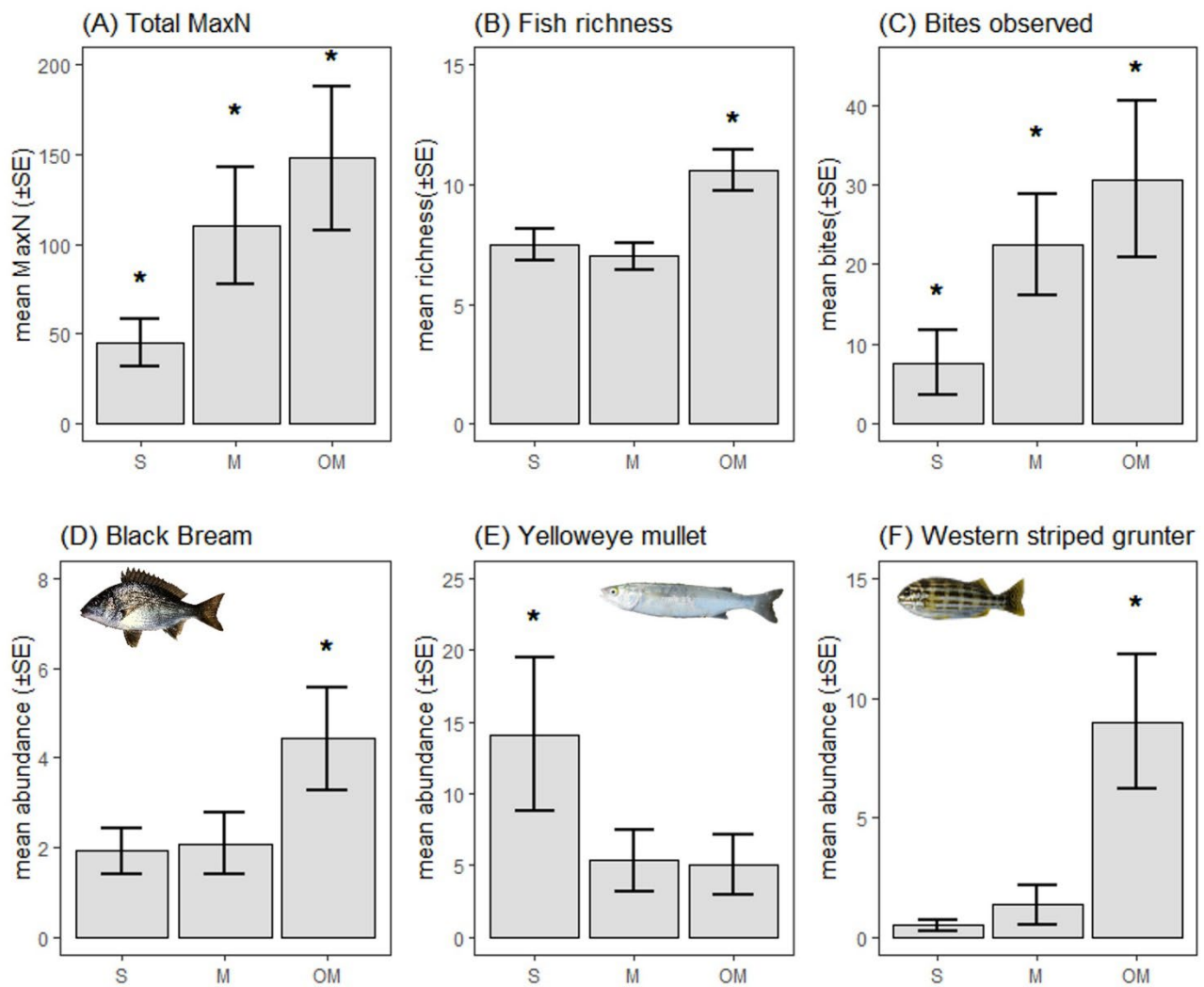


Figure 7. Average ($\pm$ SE) of (A) species richness, (B) nekton abundance (C) fish bites and the abundance of significant indicator species (D–F) from the intertidal habitats per RUVs video. Plots reflect the results of GLM analysis with significant differences between habitats identified from Tukey pairwise comparisons denoted by an asterisk “*”. Abbreviations: S=bare sediment, M=mangrove, and OM=oyster-mangrove habitat.

382 Influence of habitat type on estuarine fish

383 Differences in fish abundance, richness, and community composition across habitat types were
 384 driven by high numbers of cryptobenthic and demersal fish species in oyster-mangrove habitat
 385 (Fig. 5), including *Omobranchus anolius* (oyster blenny), *A. butcheri* and *Pelates octolineatus*
 386 (western striped grunter) which used areas of fringing *A. marina* mangroves associated with *M.*
 387 *gigas* aggregations (Table 4, Fig. 6), with higher detected abundances (Fig. 7). In contrast, bare
 388 habitat was characterised by schooling benthivores (Fig. 6), such as *Sillago schomburgkii* (yellowfin
 389 whiting) and *Aldrichetta forsteri* (yellow-eye mullet) (Table 4, Fig. 7A). The indicator test did not
 390 identify any nekton species that were strongly associated with the mangrove-dominated habitat
 391 (Table 4), likely driven by shared occurrence patterns across two or more habitats (Appendix 6).

392 Habitat foraging preferences

393 Foraging by fishes from the benthic habitat was observed from 730 bites from 10 different species
 394 over the study duration. The most frequent most foragers were *F. lateralis* and *S. punctatus*
 395 representing 37 % and 22 % of total observed bites, respectively. The number of fish bites varied
 396 by habitat type ($p = <0.001$), with more bites observed on average at the oyster-mangrove sites
 397 (30.7 ± 9.9 bites) compared to the mangrove (22.5 ± 6.3) or bare sediment (7.7 ± 4.0) sites ($p =$
 398 <0.001 , Table 3, Fig. 7C). Feeding behaviour was exhibited by five fish species at the mangrove and
 399 bare sediment habitats each, and nine species within the oyster-mangrove habitat.

400 Fish communities from fyke net surveys

401 Fyke nets caught 2,195 nektonic organisms representing 19 species divided amongst 14 fish, 4
 402 decapods, and 1 cephalopod (Appendix 6). Majority of animals caught consisted of *A. microstoma*
 403 (49 %), *F. lateralis*, (38 %) and *Gobiopertus semivestitus* (glassgoby, 5 %). Two non-native species,
 404 *Cryptocentroides gobioides* (crested oystergoby, $n=2$) and *Favonigobius exquisitus* (exquisite
 405 sandgoby, $n=1$), were also collected exclusively from the oyster-mangrove habitat. Of the caught
 406 fish species, 58 % were found across two or more habitats, with the total species richness varying
 407 across bare sand (9 spp.), mangrove (13 spp.) and oyster-mangrove (15 spp.) habitats.

408 Investigations of the fyke net surveys were unable to detect habitat differences in the community
 409 structure (PERMANOVA: $F = 0.710$, $p = 0.775$; CAP: Fig. 8A) or richness ($p = 0.274$; Table 3, Fig. 8C)
 410 with 3.6 ± 0.35 species caught on average per fyke net. Similarly, no species were identified as

411 indicator species (Dufrene-Legendre indicator species analysis) due to either insufficient sample
412 size or a shared occurrence across multiple habitats (Table 4, Appendix 6). In contrast, the catch-
413 per-unit-effort (CPUE) significantly varied between all habitats ($p < 0.001$) and was highest for
414 mangrove habitat (92.9 ± 45.5), followed by oyster-mangrove (65.0 ± 23.1), and bare sand ($25 \pm$
415 6.7) habitats (Fig. 8B).

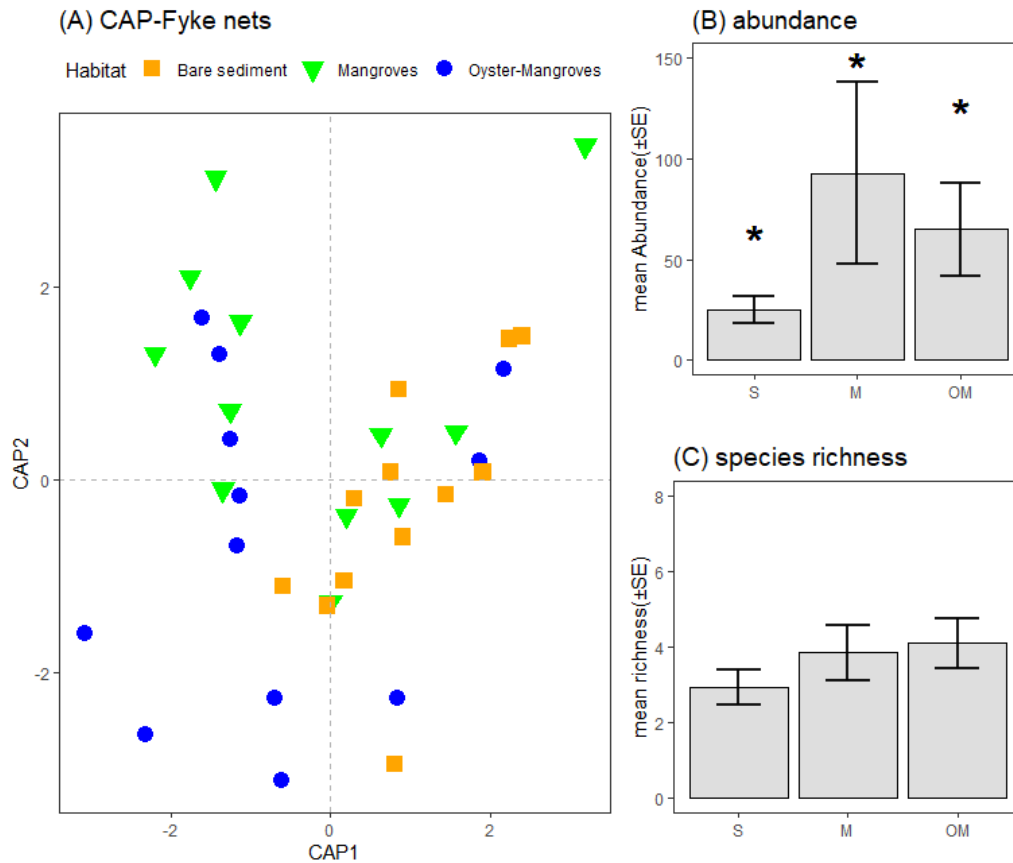


Figure 8. (A) canonical analysis of principal components (CAP) plot visualising nekton community composition (based on Bray-Curtis Similarity Index); and average ($\pm$ SE) (B) abundance and (C) species richness obtained from the fyke net surveys across intertidal habitat types. Plots reflect the results of GLM analysis with significant differences between habitats identified from Tukey pairwise comparisons denoted by an asterisk “*”. Abbreviations: S=bare sediment, M=mangrove and OM=oyster-mangrove habitat.

Fish length measurements

We measured the size of 386 individual nekton caught in the fyke nets from 19 species (Table 5). Adult fish primarily consisted of small-bodied Atherinidae and Gobiidae species, while we also caught juveniles of fisheries-targeted species, e.g., *S. punctatus* (range 72–120 mm total length) and *Portunus armatus* (blue swimmer crabs, range 4–25 mm carapace length). Significant differences in the size distribution between habitats were only identified for *F. lateralis* ($\chi^2 = 7.34$, $p < 0.03$), *A. microstoma* ($\chi^2 = 13.24$, $p < 0.002$), and *G. semivestitus* ($\chi^2 = 9.25$, $p < 0.01$). The oyster-mangrove habitat was associated with larger individuals (Mean: 30.8 ± 0.9 mm, 45.2 ± 1.6 mm, 16.4 ± 0.7 mm, respectively). On average, *Favonigobius lateralis* were smallest from the bare sand habitat (28.1 ± 0.9 mm), while smaller individuals of the other two species were associated with the mangrove habitat (36.8 ± 1.9 mm, 14.8 ± 0.34 mm, respectively) (Appendix 7). For the remaining species, there was insufficient evidence to indicate habitat differences in length measurements, which could be attributed to low sample size or similar length classes present across multiple habitats (Table 5).

Table 5. Total of the number of nekton (N) measured from each habitat, body length (millimetres) type (total length (TL), carapace length (CL) or mantle length (ML)) and range (min-max) for each species caught in the fyke nets from Torrens Island.

Species name	Length (mm)	Habitat type					
		Bare sediment		Mangrove		Oyster-Mangrove	
		Total N	Length Range	Total N	Length Range	Total N	Length Range
<i>Acanthopagrus butcheri</i>	TL					1	12.2
<i>Aldrichetta forsteri</i>	TL	6	85.0 – 120.6				
<i>Atherinosoma microstoma</i>	TL	65	14.4 – 79.4	85	12.0 – 73.0	78	11.0 – 77.0
<i>Bathygobius krefftii</i>	TL			2	42.0 – 54.0	6	47.2 – 58.0
<i>Cryptocentroides gobioides</i>	TL					2	32.0 – 44.0
<i>Diogenes senex</i>	CL	1	4.9 – 9.4	6	3.6 – 9.4	9	5.0 – 10.0
<i>favonigobius lateralis</i>	TL	107	13.6 – 63.2	134	13.0 – 57.9	145	12.0 – 63.1
<i>favonigobius exquisitus</i>	TL					1	57
<i>Gobiopterus semivestitus</i>	TL	44	12.8 – 18.4	46	11.0 – 23.3	25	11.0 – 24.0
<i>Kestratherina esox</i>	TL	7	48.0 – 81.0	5	65.7 – 84.9	21	43.4 – 84.8
<i>Neodax balteatus</i>	TL			1	67.0		
<i>Palaemon intermedius</i>	CL			1	3.0	1	7.0
<i>Pelates octolineatus</i>	TL					1	119.5
<i>Penaeus latisulcatus</i>	CL	1	8.0				
<i>Portunus armatus</i>	CL			10	4.0 – 19.0	27	6.0 – 25.5
<i>Pseudaphritis urvillii</i>	TL			1	121.0		
<i>Pseudogobius olorum</i>	TL			5	38.0 – 55.0	3	24.0 – 43.0
<i>Sillaginodes punctatus</i>	TL	13	73.9 – 117.5	6	85.0 – 120.0	1	72.0
<i>Xiphleptos notoides</i>	ML	2	5.0	1	11.0	7	4.0 – 11.0

443 Discussion

444 Despite the ecological risks posed by the spread of non-native habitat-formers globally (Rilov et al.
445 2024), such as Pacific oysters *Magallana gigas*, our knowledge on the interaction between non-
446 native oyster reefs and invaded ecological communities and functions is poor (Hansen et al. 2023).
447 However, endemic oysters reefs can support important ecological functions such as habitat
448 provisioning and fish production (Gilby et al. 2018; Connolly et al. 2024), that can be further
449 enhanced via facilitation cascades with other habitat-formers (Thomsen et al. 2022). We found
450 that despite its non-native status, oyster-mangrove habitat, formed from the nested cooccurrence
451 of wild Pacific oyster *M. gigas* and grey mangroves *Avicennia marina*, were generally more
452 biodiverse and supported higher fish foraging compared to habitats dominated by bare sediment
453 or grey mangroves alone. These results indicate that the oyster-mangrove habitat may enhance
454 the availability and range of ecological niches and functions, such as structural shelter and foraging
455 resources.

456 Pacific oyster habitat characteristics

457 Within the past decade, non-native Pacific oysters have extensively colonised the Port River-
458 Barker Inlet Estuary, transitioning from sparse individuals (Wiltshire et al. 2010) to dense biogenic
459 shellfish reefs containing up to 532 adults per m² and with over 24 kg per m² of oyster material, as
460 identified in our study. These Pacific oyster aggregations have modified the habitat characteristics
461 of colonised mangrove forests, establishing complex, biogenic shell matrices, potentially
462 comparable to oyster-mangrove habitats formed by other reef-forming oysters (e.g., McClenachan
463 et al. 2021; Martinez-Baena et al. 2022). The consolidated surfaces of mangroves can facilitate
464 secondary foundation species, such as epifaunal oysters, by provisioning settlement substrate
465 (Gagnon et al. 2020). Oyster reefs within mangrove forests then arise from successive recruitment
466 and shell accumulation, supported by intraspecific and interspecific facilitation interactions
467 (Reeves et al. 2020).

468 Despite high densities of Pacific oysters potentially affecting pneumatophore growth of mangroves
469 by limiting gas exchange (Cannicci et al. 2008), the oyster-mangrove habitat in the Port River-
470 Barker Inlet Estuary had similar pneumatophore density and morphology to mangrove habitats
471 without oysters. This could be due to oyster spat initially settling on already mature mangrove
472 root systems, with subsequent settlement preferencing the adult shells of established oyster reefs

(Bishop et al. 2012), rather than inhibiting establishing pneumatophores. Areas of extensive pneumatophores and disarticulated cockle shell that were free of oysters indicate that *M. gigas* spat are not substrate limited in our study area. The young age of the reefs (<10 years) means that negative interactions could also not occur until an oyster density threshold is surpassed, which may not manifest for decades (Bazterrica et al. 2022). Nevertheless, our study provides a baseline suitable for future assessments of these sites to understand long-term variability in the interactions and habitat characteristics of these habitat-formers.

Amounts of allochthonous material including disarticulated shell material and mangrove debris were found in greater quantities from the oyster-mangrove habitat. By modifying the benthic topography of the shoreline, the Pacific oyster clumps may trap and increase the retention of allochthonous material, including mangrove propagules (McClenachan et al. 2021), which could explain the greater abundance of *A. marina* saplings associated with the Pacific oysters across our study sites. Over longer timeframes, enhanced mangrove recruitment around the Pacific oyster aggregations may result in the expansion of the mangrove fringe to the deficit of the oysters, as observed in intertidal American oyster *Crassostrea virginica* reefs in the United States (McClenachan et al. 2021). Yet, despite the greater retention of plant material combined with oyster biodeposits, we did not detect significant differences in the percentage of soil organic matter between habitat types. This could be due to; rapid decomposition of material due to high macroinvertebrate densities in the oyster-mangrove habitat, resuspension and transport of fine organic material during tidal flushing, or confounding influences of microbial and microalgae mats across sites (Kristensen et al. 2008). Further investigations are therefore needed to understand how *M. gigas* may influence benthic processes and fluxes in organic matter.

Habitat value for fish and invertebrates

Our combination of extractive quadrats, RUVS, and fyke nets to survey dynamic intertidal habitats provided useful information about the habitat use of estuarine fish and macrofaunal communities. This is particularly practical for RUVS and fyke nets given that both approaches are used to assess the communities of intertidal shellfish ecosystems elsewhere in the world (e.g. Orfanidis et al. 2021; Martinez-Baena et al. 2022), but generally target different species and size classes. For example, unbaited RUVS are useful for monitoring large-bodied and juvenile fishes, and record their behaviour (Bradley et al. 2016; Sheaves et al. 2020). However, fyke nets may provide more accurate abundance estimates of small-bodied nekton compared to RUVS, with the extractive

sampling providing opportunities for accurate specimen identification and morphometric assessments (Orfanidis et al. 2021). Similarly, by sampling both the outgoing tide (i.e. RUVS and fyke nets) and at low tide using extractive quadrats, it's possible to infer the tidal movement of different species and identify resident species that are strongly associated with habitats throughout the tidal cycle. This approach is particularly relevant for intertidal ecosystems as transient species utilise habitats based on tidal accessibility and resources availability (Grabowski et al. 2005; Gilby et al. 2019). Additionally, multiple methods identified that distance from the estuary mouth was an important covariable for understanding patterns in fish and invertebrate communities, suggesting that environmental gradients or seascape composition may be influencing species distribution and behaviour (e.g. Jones et al. 1996). We recommend that practitioners assessing intertidal nekton communities consider the combined use of multiple sampling methods to obtain a holistic understanding of habitat use in future assessments of shellfish ecosystems.

Similar to previous studies in the Port River-Barker Inlet Estuary, we found that tidally inundated mangrove forests were associated with high numbers of demersal and small-bodied fishes (Bloomfield and Gillanders 2005; Henkens et al. 2022). Fish community composition from the RUVS was most similar between sites of mangroves with and without Pacific oyster aggregations. We hypothesise that this was driven by species-specific trends and some functional redundancy between habitats resulting from the shared structural dominance of *A. marina*. For example, small pelagic fishes (e.g., Atheriniformes) were common to both habitats and may access fringing mangroves for refugia at high tide (Henkens et al. 2022), with habitat differences only detected from the size classes. Conversely, cryptobenthic oyster blennies *O. anolius* and Gobiidae species were abundant in the oyster-mangrove habitat, consistent with previous studies that have identified their use of disarticulated bivalve shells as nesting sites and refugia throughout the tidal cycle (Hammer 2014; Martinez-Baena et al. 2022). Furthermore, high abundances of black bream and western striped grunters could be attributed to foraging behaviour, preferencing the oyster-mangrove habitat to feed on associated epibenthic invertebrates, particularly crustaceans and bivalves (Sarre et al. 2000; Potter et al. 2022). This was supported by the elevated prey availability and feeding behaviour observed at this habitat type. Contrary to fish dietary work by Henkens et al. (2022) in the Barker Inlet on mangrove habitats without oysters, our study identified that the intertidal mangrove habitats with oysters are providing important fish foraging grounds for some species. Trophic assessments such as stomach contents, predation assays, or stable isotope

analysis could therefore be valuable for understanding trophic linkages of these habitats and associated species (Martinez-Baena et al. 2023), including predation of Pacific oyster populations.

In contrast to other non-native species, invasions by bivalves generally facilitate enhanced biodiversity through positive ecological interactions such as increasing habitat complexity and ameliorating stresses (Guy-Haim et al. 2018). At the ecosystem-scale, oyster reefs are known to benefit fish and invertebrate communities by provisioning high value foraging and nursery habitat, and reducing abiotic and biotic stressors (e.g. predation, desiccation) (Reeves et al. 2020; zu Ermgassen et al. 2021). Our results concur with recent studies that have reported the positive effects of oyster reefs on fish and invertebrate communities in mangrove-dominated systems (e.g., Gilby et al. 2019; Martinez-Baena et al. 2022; Perry et al. 2023). For example, Perry et al. (2023) found that the fish species richness and harvestable fish abundance in structured habitats positively responded to oyster cover. Similarly, McAfee et al. (2016) found that oyster aggregations in mangrove forests facilitated elevated macrofaunal richness and abundances compared to mangroves without oysters. As microhabitats, the oyster aggregations enhance structural shelter, settlement surfaces, and enhance foraging opportunities for a range of macrofaunal grazers, detritivores, and mesopredators (Bishop et al. 2012; McAfee et al. 2016). These results can be attributed to facilitation cascades (Fig. 9) resulting from the combination of mangroves and oysters, which synergistically enhance the diversity and availability of niches, therefore elevating estuarine biodiversity (Thomsen et al. 2022). This indicates that non-native Pacific oysters in *A. marina* forests may provide beneficial functions, analogous to oyster-mangrove habitats formed by native oysters studied elsewhere.

Management implications of non-native oyster reefs

The facilitation interactions between *M. gigas* and other estuarine species identified in this study (Fig. 9) provides important evidence of the ecological benefits that may result from the establishment of non-native oyster reefs, including enhanced biodiversity and supporting fisheries-targeted species. While not quantified, these reefs may also support other valuable socioecological outcomes including nutrient sequestration, enhanced water visibility, and human shellfish harvesting (McAfee and Connell 2021; Hansen et al. 2023). Subsequently, in regions where *M. gigas* are naturalised, such as Northern Europe, the oysters have supported the development of new 'gastro-tourism' opportunities (Mortensen et al. 2019) and have been adopted in shoreline stabilisation structures (Walles et al. 2016). This has been partially supported by the functional

similarities of *M. gigas* to diminished native bivalves, and subsequent recovery of lost ecological functions (Zwerschke et al. 2019; McAfee and Connell 2021). As highlighted by Howie and Bishop (2021), non-native oysters may be considered for the restoration of ecological services, particularly in naturalised regions where analogous native species have failed to recover or adapt to modified environmental conditions. The broad environmental tolerance and high reproductive output of *M. gigas*, are traits favourable to establishing oyster reefs resilient to anthropogenic pressures such as climate change (Troost 2010). However, *M. gigas* may only partially restore functions of lost subtidal shellfish reefs (e.g. *O. angasi* in South Australia), and potentially establish novel, yet beneficial conditions in regions that historically lacked comparable habitats (Guy-Haim et al. 2018; McAfee and Connell 2021). In an anthropogenically changing world, the positive benefits of non-native habitat formers must increasingly be studied and considered to conserve and enhance ecological services (Rilov et al. 2024).

During our study, seven non-native and cryptogenic species were sampled exclusively or in greater numbers from the oyster-mangrove habitat, including the first confirmed specimens of the Hercules club whelk (*Pyrazus ebeninus*) and exquisite sandgoby (*Favonigobius exquisitus*) in South Australia. Thus, Pacific oyster aggregations may facilitate secondary invasions by other non-native species by creating favourable habitat conditions (Reise et al. 2023). For example, the European shore crab (*Carcinus maenas*) and crested oystergoby (*Cryptocentroides gobioides*) from eastern Australia are strongly associated with intertidal shellfish ecosystems in their native ranges (Troost 2010; Martinez-Baena et al. 2022), and therefore should respond positively to similar environmental conditions when introduced (O'Loughlin and Green 2017). The presence of non-native species alongside native counterparts at our study site could result in inter-specific competition of shared resources including prey, shelter, and nesting sites, and direct predation (Hammer 2014; Gallardo et al. 2016). Of particular concern are *C. maenas*, which may indirectly facilitate Pacific oysters by consuming their competitors, with a dietary preference for mussels over oysters (Joyce et al. 2020), posing a threat to the native *Brachidontes* and *Xenostrobus* mussels found at our sites (Campbell et al. 2019). Other potential socioecological impacts include changes in landscape aesthetics, channel navigation, and aquaculture interactions (e.g. competition, disease transmission, genetic exchange) (Herbert et al. 2016; Hansen et al. 2023). Potential declines in native species and ecological services following the establishment of *M. gigas* reefs and subsequent facilitation of other non-native species may provide justification for their mitigation and eradication.

The capacity for non-native habitat-formers to facilitate native and non-native species, and modify ecological services poses a management challenge for scientists and policymakers (Rilov et al. 2024). This is further complicated by the dual status of Pacific oysters as both an aquaculture species and marine pest (Herbert et al. 2016; Hansen et al. 2023). Cultivation of *M. gigas* outside their native range can support non-native reef establishment through repeated seeding and genetic enhancement from aquaculture stock (McAfee and Connell 2021). Furthermore, the widespread eradication and prohibition of *M. gigas* aquaculture to mitigate this vector for introduction is unlikely due the socio-economic impacts it would have on coastal communities (Herbert et al. 2016). It has also been recognised that once *M. gigas* populations attain reef-forming densities, biosecurity efforts are likely to incur high labour and financial costs with a low likelihood of complete eradication (Troost 2010; Hansen et al. 2023). Subsequently, management of non-native oyster reefs needs to be evidence-based with consideration of both favourable and undesirable socioecological outcomes within the local regional context (Martínez-García et al. 2022). For example, mitigating their expansion into vulnerable and protected ecosystems by regulating aquaculture permissions and implementing harvesting regimes (Hansen et al. 2023). In anthropogenically modified estuaries, however, we expect that non-native oyster reefs may provide more socioecological benefits compared to potential harm.

Conclusion

Non-native habitat-formers, such as the Pacific oyster *Magallana gigas*, can pose a significant socioecological challenge for managing coastal systems. In this study, we evaluated the ecological interactions of non-native *M. gigas* on mangrove forest biodiversity, particularly potential effects on the fish community. Our findings indicate that despite the non-native status of *M. gigas*, they can facilitate positive interactions with grey mangroves leading to subsequent enhancements in fish and invertebrate diversity, prey availability, and foraging opportunities. We also identified that the oyster-mangrove habitat supported fisheries-targeted species and may facilitate habitat conditions favourable to a greater range of species and functions. However, the oyster-mangrove habitat facilitated both native and non-native species, including previously undocumented species. Thus, we provide examples of the different ecological outcomes that can result the establishment of non-native habitat-formers, and potential impacts that may arise from the global expansion of non-native Pacific oyster reefs in vegetated coastal estuaries.

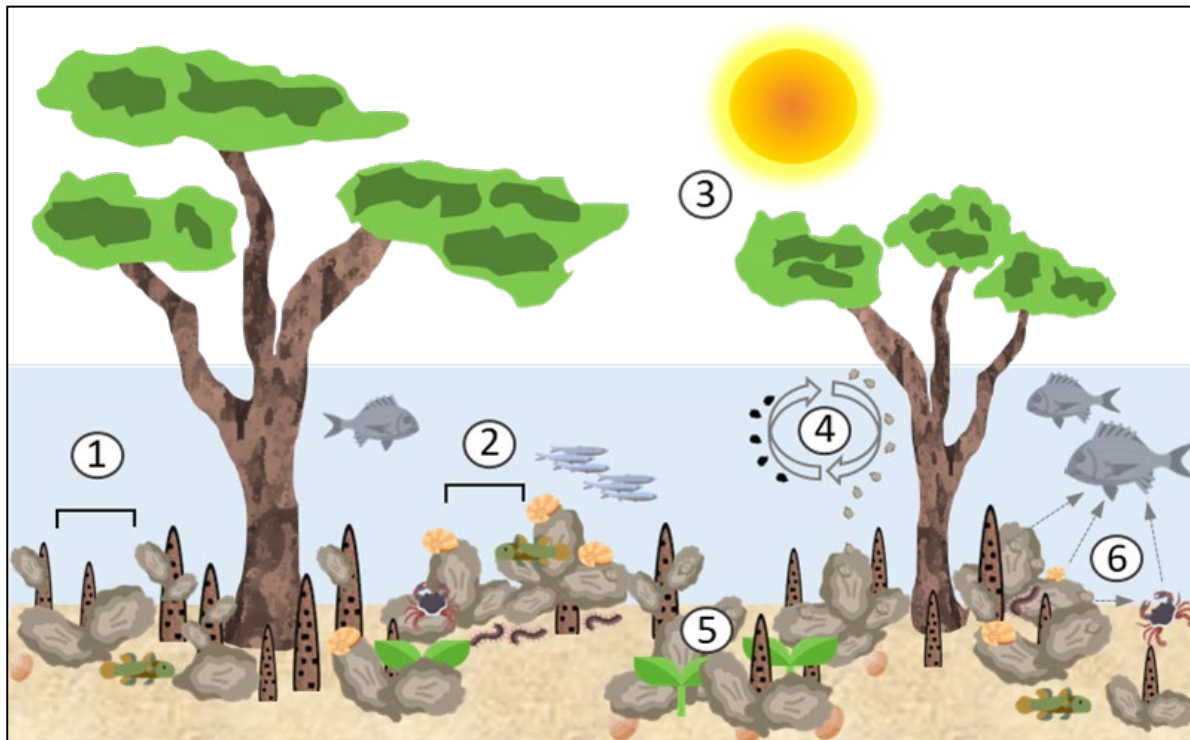


Figure 9. Schematic depiction of facilitation interactions identified from this study of grey mangroves (*Avicennia marina*) and Pacific oyster (*Magallana gigas*) communities: (1) mangroves provide hard substrate for secondary foundation species such as oysters, (2) producing structural habitat for invertebrates and fish of (3) reduced abiotic and biotic stressors. (4) oysters self-facilitate settlement cues for intraspecific recruitment, and (5) the shell clumps retain mangrove recruits, leaf litter and shell material. (6) fish and macrofauna foraging opportunities boosted by enhanced availability of food resources.

Acknowledgements

We thank volunteers for their support in the field and laboratory, particularly R. Tandon, E. Heathwood, and A. Grigson. Brad Martin recognises the support provided by a Holsworth Wildlife Research Endowment from the Ecological Society of Australia. We acknowledge and pay our respects to the Kurna People, Traditional Custodians of the Land and Sea Country where this research took place.

References

- Alongi DM (2020) Global significance of mangrove blue carbon in climate change mitigation. *Sci* 2: 67. doi:<https://doi.org/10.3390/sci2030067>.
- Angelini C, Altieri AH, Silliman BR, Bertness MD (2011) Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *BioScience* 61: 782-789. doi:<https://doi.org/10.1525/bio.2011.61.10.8>.
- Angelini C, van der Heide T, Griffin JN, Morton JP, Derksen-Hooijberg M, Lamers LP, Smolders AJ, Silliman BR (2015) Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. *Proceedings of the Royal Society B: Biological Sciences* 282: 20150421. doi:<https://doi.org/10.1098/rspb.2015.0421>.
- Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81: 169-193. doi:<https://doi.org/10.1890/10-1510.1>.
- Bazterrica MC, Hidalgo FJ, Rumbold C, Casariego AM, Jaubet ML, Merlo M, César I, Provenzal M, Addino M, Barón PJ (2022) Macrofaunal assemblages structure three decades after the first report of the invasive *Crassostrea gigas* reefs in a soft-intertidal of Argentina. *Estuarine, Coastal and Shelf Science* 270: 107832. doi:<https://dx.doi.org/10.1016/j.ecss.2022.107832>.
- Beck MW, Brumbaugh RD, Airolidi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay MC, Lenihan HS, Luckenbach MW, Toropova CL, Zhang G, Guo X (2011) Oyster Reefs at Risk and Recommendations for Conservation, Restoration, and Management. *BioScience* 61: 107-116. doi:<https://doi.org/10.1525/bio.2011.61.2.5>.
- Bishop MJ, Byers JE, Marcek BJ, Gribben PE (2012) Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves. *Ecology* 93: 1388-401. doi:<https://doi.org/10.1890/10-2296.1>.
- Bloomfield A, Gillanders B (2005) Fish and invertebrate assemblages in seagrass, mangrove, saltmarsh, and nonvegetated habitats. *Estuaries* 28: 63-77. doi:<https://doi.org/10.1007/BF02732754>.
- Bradley M, Baker R, Sheaves M (2016) Hidden Components in Tropical Seascapes: Deep-Estuary Habitats Support Unique Fish Assemblages. *Estuaries and Coasts* 40: 1195-1206. doi:<https://doi.org/10.1007/s12237-016-0192-z>.
- Campbell RT, Baring RJ, Dittmann S (2019) Cracking the cuisine: Invasive European shore crabs (*Carcinus maenas*) select a menu of soft-shelled mussels over cockles. *Journal of Experimental Marine Biology and Ecology* 517: 25-33. doi:<https://doi.org/10.1016/j.jembe.2019.05.011>.
- Cannicci S, Burrows D, Fratini S, Smith III TJ, Offenberger J, Dahdouh-Guebas F (2008) Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. *Aquatic Botany* 89: 186-200. doi:<https://doi.org/10.1016/j.aquabot.2008.01.009>.

- 681 Connolly R, Herrera C, Rasmussen J, Buelow C, Sievers M, Jinks K, Brown C, Lopez-Marcano S,
682 Sherman C, Martínez-Baena F, Martin B, Baring R, Reeves SE (2024) Estimating enhanced
683 fish production on restored shellfish reefs using automated data collection from
684 underwater videos. *Journal of Applied Ecology* 61: 633-646.
685 doi:<https://doi.org/10.1111/1365-2664.14617>.
- 686 Davis MA, Chew MK, Hobbs RJ, Lugo AE, Ewel JJ, Vermeij GJ, Brown JH, Rosenzweig ML, Gardener
687 MR, Carroll SP (2011) Don't judge species on their origins. *Nature* 474: 153-154.
688 doi:<https://doi.org/10.1038/474153a>.
- 689 Dayton PK (1972) Toward an understanding of community resilience and the potential effects of
690 enrichments to the benthos at McMurdo Sound, Antarctica. In: *Proceedings of the*
691 *colloquium on conservation problems in Antarctica*. Blacksburg, VA, 81-96 pp.
- 692 Edyvane K (1999) Coastal and marine wetlands in Gulf St. Vincent, South Australia: understanding
693 their loss and degradation. *Wetlands Ecology and Management* 7: 83-104.
694 doi:<https://doi.org/10.1023/A:1008481228129>.
- 695 Gagnon K, Rinde E, Bengil EGT, Carugati L, Christianen MJA, Danovaro R, Gambi C, Govers LL,
696 Kipson S, Meysick L, Pajusalu L, Tüney Kızılkaya İ, van de Koppel J, van der Heide T, van
697 Katwijk MM, Boström C, Pinto R (2020) Facilitating foundation species: The potential for
698 plant–bivalve interactions to improve habitat restoration success. *Journal of Applied*
699 *Ecology* 57: 1161-1179. doi:<https://doi.org/10.1111/1365-2664.13605>.
- 700 Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in
701 aquatic ecosystems. *Global Change Biology* 22: 151-163.
702 doi:<https://doi.org/10.1111/gcb.13004>.
- 703 Gilby BL, Olds AD, Henderson CJ, Ortodossi NL, Connolly RM, Schlacher TA, Grabowski J (2019)
704 Seascape context modifies how fish respond to restored oyster reef structures. *Ices Journal*
705 *of Marine Science* 76: 1131-1139. doi:<https://doi.org/10.1093/icesjms/fsz019>.
- 706 Gilby BL, Olds AD, Peterson CH, Connolly RM, Voss CM, Bishop MJ, Elliott M, Grabowski JH,
707 Ortodossi NL, Schlacher TA (2018) Maximizing the benefits of oyster reef restoration for
708 finfish and their fisheries. *Fish and Fisheries* 19: 931-947.
709 doi:<https://doi.org/10.1111/faf.12301>.
- 710 Gillies CL, Castine SA, Alleway HK, Crawford C, Fitzsimons JA, Hancock B, Koch P, McAfee D,
711 McLeod IM, zu Ermgassen PSE (2020) Conservation status of the Oyster Reef Ecosystem of
712 Southern and Eastern Australia. *Global Ecology and Conservation* 22:
713 doi:<https://doi.org/10.1016/j.gecco.2020.e00988>.
- 714 Gillies CL, McLeod IM, Alleway HK, Cook P, Crawford C, Creighton C, Diggles B, Ford J, Hamer P,
715 Heller-Wagner G, Lebrault E, Le Port A, Russell K, Sheaves M, Warnock B (2018) Australian
716 shellfish ecosystems: Past distribution, current status and future direction. *PLoS One* 13:
717 e0190914. doi:<https://doi.org/10.1371/journal.pone.0190914>.
- 718 Gomon MF, Bray DJ, Kuitert RH (2008) *Fishes of Australia's southern coast*. Chatswood, N.S.W. :
719 Reed New Holland, Musuem Victoria, Chatswood, N.S.W., pp.

- 720 Gowlett-Holmes KL (2008) A field guide to the marine invertebrates of South Australia.
721 Notomares, pp.
- 722 Grabowski JH, Hughes AR, Kimbro DL, Dolan MA (2005) How habitat setting influences restored
723 oyster reef communities. *Ecology* 86: 1926-1935. doi:<https://doi.org/10.1890/04-0690>.
- 724 Guy-Haim T, Lyons DA, Kotta J, Ojaveer H, Queirós AM, Chatzinikolaou E, Arvanitidis C, Como S,
725 Magni P, Blight AJ, Orav-Kotta H, Somerfield PJ, Crowe TP, Rilov G (2018) Diverse effects of
726 invasive ecosystem engineers on marine biodiversity and ecosystem functions: A global
727 review and meta-analysis. *Global Change Biology* 24: 906-924.
728 doi:<https://doi.org/10.1111/gcb.14007>.
- 729 Hammer MP (2014) Range Extensions for Four Estuarine Gobies (Pisces: Gobiidae) in Southern
730 Australia: Historically Overlooked Native Taxa or Recent Arrivals? *Transactions of the Royal*
731 *Society of South Australia* 130: 187-196.
732 doi:<https://doi.org/10.1080/3721426.2006.10887057>.
- 733 Hansen BW, Dolmer P, Vismann B (2023) Too late for regulatory management on Pacific oysters in
734 European coastal waters? *Journal of Sea Research* 191: 102331.
735 doi:<https://doi.org/10.1016/j.seares.2022.102331>.
- 736 Henkens J, Dittmann S, Baring R (2022) Nursery function of mangrove creeks in temperate
737 climates for estuarine fish. *Transactions of the Royal Society of South Australia* 146: 228-
738 248. doi:<https://doi.org/10.1080/03721426.2022.2035200>.
- 739 Herbert RJ, Humphreys J, Davies C, Roberts C, Fletcher S, Crowe T (2016) Ecological impacts of
740 non-native Pacific oysters (*Crassostrea gigas*) and management measures for protected
741 areas in Europe. *Biodiversity and Conservation* 25: 2835-2865.
742 doi:<https://doi.org/10.1007/s10531-016-1209-4>.
- 743 Howie AH, Bishop MJ (2021) Contemporary Oyster Reef Restoration: Responding to a Changing
744 World. *Frontiers in Ecology and Evolution* 9: 689915.
745 doi:<https://doi.org/10.3389/fevo.2021.689915>.
- 746 Jones GK, Baker JL, Edyvane K, Wright GJ (1996) Nearshore fish community of the Port River-
747 Barker Inlet Estuary, South Australia. I. Effect of thermal effluent on the fish community
748 structure, and distribution and growth of economically important fish species. *Marine and*
749 *Freshwater Research* 47: 785. doi:<https://doi.org/10.1071/mf9960785>.
- 750 Joyce PW, Dick JT, Kregting LT (2020) Lack of biotic resistance to an invasive bivalve irrespective of
751 season or hydrodynamic disturbance. *Journal of Experimental Marine Biology and Ecology*
752 528: 151382. doi:<https://doi.org/10.1016/j.jembe.2020.151382>.
- 753 King NG, Wilmes SB, Smyth D, Tinker J, Robins PE, Thorpe J, Jones L, Malham SK (2021) Climate
754 change accelerates range expansion of the invasive non-native species, the Pacific oyster,
755 *Crassostrea gigas*. *Ices Journal of Marine Science* 78: 70-81.
756 doi:<https://doi.org/10.1093/icesjms/fsaa189>.

- 757 Kristensen E, Bouillon S, Dittmar T, Marchand C (2008) Organic carbon dynamics in mangrove
758 ecosystems: a review. *Aquatic Botany* 89: 201-219.
759 doi:<https://doi.org/10.1016/j.aquabot.2007.12.005>.
- 760 Marois DE, Mitsch WJ (2015) Coastal protection from tsunamis and cyclones provided by
761 mangrove wetlands—a review. *International Journal of Biodiversity Science, Ecosystem*
762 *Services & Management* 11: 71-83. doi:<https://doi.org/10.1080/21513732.2014.997292>.
- 763 Martinez-Baena F, Lanham BS, McLeod IM, Taylor MD, McOrrie S, Luongo A, Bishop MJ (2022)
764 Remnant oyster reefs as fish habitat within the estuarine seascape. *Marine environmental*
765 *research* 179: 105675. doi:<https://doi.org/10.1016/j.marenvres.2022.105675>.
- 766 Martinez-Baena F, Raoult V, Taylor MD, Gaston TF, McLeod I, Bishop MJ (2023) Trophic Structure
767 of Temperate Australian Oyster Reefs Within the Estuarine Seascape: a Stable Isotope
768 Analysis. *Estuaries and Coasts* 46: 844-859. doi:[https://doi.org/10.1007/s12237-022-](https://doi.org/10.1007/s12237-022-01157-8)
769 [01157-8](https://doi.org/10.1007/s12237-022-01157-8).
- 770 Martínez-García MF, Ruesink JL, Grijalva-Chon JM, Lodeiros C, Arreola-Lizárraga JA, de la Re-Vega
771 E, Varela-Romero A, Chávez-Villalba J (2022) Socioecological factors related to aquaculture
772 introductions and production of Pacific oysters (*Crassostrea gigas*) worldwide. *Reviews in*
773 *Aquaculture* 14: 613-629. doi:<https://doi.org/10.1111/raq.12615>.
- 774 McAfee D, Cole VJ, Bishop MJ (2016) Latitudinal gradients in ecosystem engineering by oysters
775 vary across habitats. *Ecology* 97: 929-939. doi:<https://doi.org/10.1890/15-0651.1>.
- 776 McAfee D, Connell SD (2021) The global fall and rise of oyster reefs. *Frontiers in Ecology and the*
777 *Environment* 19: 118-125. doi:<https://doi.org/10.1002/fee.2291>.
- 778 McClenachan G, Witt M, Walters LJ (2021) Replacement of oyster reefs by mangroves:
779 Unexpected climate-driven ecosystem shifts. *Global Change Biology* 27: 1226-1238.
780 doi:<https://doi.org/10.1111/gcb.15494>.
- 781 Mortensen S, Dolmer P, Strand Å, Naustvoll L-J, Laugen AT (2019) Policy brief: the Pacific oyster—a
782 new Nordic food resource and a basis for tourism. *Nordic Council of Ministers*, pp.
- 783 Muthukrishnan R, Chiquillo KL, Cross C, Fong P, Kelley T, Toline CA, Zweng R, Willette DA (2020)
784 Little giants: a rapidly invading seagrass alters ecosystem functioning relative to native
785 foundation species. *Marine Biology* 167: 1-15. doi:[https://doi.org/10.1007/s00227-020-](https://doi.org/10.1007/s00227-020-03689-8)
786 [03689-8](https://doi.org/10.1007/s00227-020-03689-8).
- 787 Norling P, Lindegarth M, Lindegarth S, Strand Å (2015) Effects of live and post-mortem shell
788 structures of invasive Pacific oysters and native blue mussels on macrofauna and fish.
789 *Marine Ecology Progress Series* 518: 123-138. doi:<https://doi.org/10.3354/meps11044>.
- 790 O'Loughlin LS, Green PT (2017) Secondary invasion: When invasion success is contingent on other
791 invaders altering the properties of recipient ecosystems. *Ecology and evolution* 7: 7628-
792 7637. doi:<https://doi.org/10.1002/ece3.3315>.
- 793 Orfanidis GA, Touloumis K, Stenberg C, Mariani P, Stottrup JG, Svendsen JC (2021) Fish
794 Assemblages in Seagrass (*Zostera marina* L.) Meadows and Mussel Reefs (*Mytilus edulis*):

- 795 Implications for Coastal Fisheries, Restoration and Marine Spatial Planning. Water
796 (Switzerland) 13: 3268. doi:<https://doi.org/10.3390/w13223268>.
- 797 Padilla DK (2010) Context-dependent impacts of a non-native ecosystem engineer, the Pacific
798 oyster *Crassostrea gigas*. Integrative and comparative biology 50: 213-225.
799 doi:<https://doi.org/10.1093/icb/icq080>.
- 800 Perry HJ, Gaines LAG, Borland HP, Henderson CJ, Olds AD, Mosman JD, Gilby BL (2023) Identifying
801 optimal values of coastal habitat condition for management and restoration. Estuarine,
802 Coastal and Shelf Science 282: 108250. doi:<https://doi.org/10.1016/j.ecss.2023.108250>.
- 803 Potter IC, Kanandjembo A-R, Cottingham A, Rose TH, Linke TE, Platell ME (2022) A long-lived,
804 estuarine-resident fish species selects its macroinvertebrate food source based on certain
805 prey and predator traits. Estuarine, Coastal and Shelf Science 264: 107691.
806 doi:<https://doi.org/10.1016/j.ecss.2021.107691>.
- 807 R Core Team (2024) R: A language and environment for statistical computing. R Foundation for
808 Statistical Computing. 4.3.1 ed. R Foundation for Statistical Computing, Vienna, pp.
- 809 Ray NE, Fulweiler RW (2021) Meta-analysis of oyster impacts on coastal biogeochemistry. Nature
810 Sustainability 4: 261-269. doi:<https://doi.org/10.1038/s41893-020-00644-9>
- 811 Reeves SE, Renzi JJ, Fobert EK, Silliman BR, Hancock B, Gillies CL (2020) Facilitating Better
812 Outcomes: How Positive Species Interactions Can Improve Oyster Reef Restoration.
813 Frontiers in Marine Science 7: doi:<https://doi.org/10.3389/fmars.2020.00656>.
- 814 Reise K, Buschbaum C, Lackschewitz D, Thieltes DW, Waser AM, Wegner KM (2023) Introduced
815 species in a tidal ecosystem of mud and sand: curse or blessing? Marine Biodiversity 53: 5.
816 doi:<https://doi.org/10.1007/s12526-022-01302-3>.
- 817 Rilov G, Canning-Clode J, Guy-Haim T (2024) Ecological impacts of invasive ecosystem engineers: A
818 global perspective across terrestrial and aquatic systems. Functional Ecology 38: 37-51.
819 doi:<https://doi.org/10.1111/1365-2435.14406>.
- 820 Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and
821 why these impacts occur. Biological Invasions 8: 927-939.
822 doi:<https://doi.org/10.1007/s10530-005-5103-3>.
- 823 Sarre G, Platell M, Potter I (2000) Do the dietary compositions of *Acanthopagrus butcheri* in four
824 estuaries and a coastal lake vary with body size and season and within and amongst these
825 water bodies? Journal of Fish Biology 56: 103-122. doi:<https://doi.org/10.1111/j.1095-8649.2000.tb02089.x>.
- 827 Sheaves M, Bradley M, Herrera C, Mattone C, Lennard C, Sheaves J, Konovalov DA (2020)
828 Optimizing video sampling for juvenile fish surveys: Using deep learning and evaluation of
829 assumptions to produce critical fisheries parameters. Fish and Fisheries 21: 1259-1276.
830 doi:<https://doi.org/10.1111/faf.12501>.
- 831 Theuerkauf SJ, Barrett LT, Alleway HK, Costa-Pierce BA, St. Gelais A, Jones RC (2022) Habitat value
832 of bivalve shellfish and seaweed aquaculture for fish and invertebrates: Pathways,

- 833 synthesis and next steps. Reviews in Aquaculture 14: 54-72.
834 doi:<https://doi.org/10.1111/raq.12584>.
- 835 Thomsen MS, Altieri AH, Angelini C, Bishop MJ, Bulleri F, Farhan R, Frühling VM, Gribben PE,
836 Harrison SB, He Q (2022) Heterogeneity within and among co-occurring foundation species
837 increases biodiversity. Nature communications 13: 1-9.
838 doi:<https://doi.org/10.1038/s41467-022-29347-9>.
- 839 Troost K (2010) Causes and effects of a highly successful marine invasion: case-study of the
840 introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. Journal
841 of Sea Research 64: 145-165. doi:<https://doi.org/10.1016/j.seares.2010.02.004>.
- 842 van der Schatte Olivier A, Jones L, Vay LL, Christie M, Wilson J, Malham SK (2020) A global review
843 of the ecosystem services provided by bivalve aquaculture. Reviews in Aquaculture 12: 3-
844 25. doi:<https://doi.org/10.1111/raq.12301>.
- 845 Walles B, Troost K, van den Ende D, Nieuwhof S, Smaal AC, Ysebaert T (2016) From artificial
846 structures to self-sustaining oyster reefs. Journal of Sea Research 108: 1-9.
847 doi:<https://doi.org/10.1016/j.seares.2015.11.007>.
- 848 Whitmarsh SK, Fairweather PG, Huvaneers C (2016) What is Big BRUVver up to? Methods and uses
849 of baited underwater video. Reviews in Fish Biology and Fisheries 27: 53-73.
850 doi:<https://doi.org/10.1007/s11160-016-9450-1>.
- 851 Wilkie EM, Bishop MJ, O'Connor WA (2012) Are native *Saccostrea glomerata* and invasive
852 *Crassostrea gigas* oysters' habitat equivalents for epibenthic communities in south-eastern
853 Australia? Journal of Experimental Marine Biology and Ecology 420: 16-25.
854 doi:<https://doi.org/10.1016/j.jembe.2012.03.018>.
- 855 Wiltshire K, Rowling KP, Deveney MR (2010) Introduced marine species in South Australia: a
856 review of records and distribution mapping. SARDI Aquatic Sciences, Adelaide, pp.
- 857 zu Ermgassen PSE, DeAngelis B, Gair JR, zu Ermgassen S, Baker R, Daniels A, MacDonald TC,
858 Meckley K, Powers S, Ribera M, Rozas LP, Grabowski JH (2021) Estimating and Applying Fish
859 and Invertebrate Density and Production Enhancement from Seagrass, Salt Marsh Edge,
860 and Oyster Reef Nursery Habitats in the Gulf of Mexico. Estuaries and Coasts 44: 1588-
861 1603. doi:<https://doi.org/10.1007/s12237-021-00935-0>.
- 862 Zwerschke N, Eagling L, Roberts D, O'Connor N (2019) Can an invasive species compensate for the
863 loss of a declining native species? Functional similarity of native and introduced oysters.
864 Marine environmental research 153: 104793.
865 doi:<https://doi.org/10.1016/j.marenvres.2019.104793>.
- 866