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

2

3   Authors: I.M. McLeod[1], L. Bostrom-Einarsson[1] (co-first authors), C. Creighton[1], B. D'Anastasi[2,3],

4   B. Diggles[4], P.G. Dwyer[5], L. Firby[1], A. Le Port[1], A. Luongo[6], F. Martinez-Baena[6], S. McOrrie[7], G.

5   Heller-Wagner[8], C. Gillies[9].

6

7   1. TropWATER (Centre for Tropical Water and Aquatic Ecosystem Research), James Cook

8   University, Townsville, QLD 4811, Australia

9   2. College of Science and Engineering, James Cook University, Townsville, QLD 4811,

10   Australia

11   3. AIMS@JCU, James Cook University, Townsville, QLD 4811, Australia

12   4. DigsFish Services, Banksia Beach, QLD 4507, Australia

13   5. Aquatic Ecosystems, Department of Primary Industries Fisheries, 1243 Bruxner Hwy,

14   Wollongbar NSW 2477, Australia

15   6. Department of Biological Sciences, Macquarie University, NSW 2109, Australia

16   7. Port Stephens Fisheries Institute, New South Wales Department of Primary Industries,

17   Taylors Beach, NSW 2316, Australia

18   8. University of Tasmania, Tasmania, Australia

19   9. The Nature Conservancy, Carlton South, Vic. 3053, Australia

20

21   * Corresponding author - Ian McLeod ian.mcleod@jcu.edu.au

22

23   Keywords: oyster, reef, habitat, ecosystem services, productivity

24

25   Target journal Marine and Freshwater

Abstract

27 Estimates of the ecological and economic value of ecosystems can provide important

28 informationfor the prioritisation of conservation and restoration actions. Oyster reefs were

29 common in temperate and subtropical coastal waters but are now degraded or lost in most

30 areas. These reefs generally provide a suite of ecological services, such as habitat provision

31 and food supply for many other species, substrate stabilisation, and water quality

32 improvements. In Australia, there is growing interest in oyster reef restoration, but there are

33 knowledge gaps in regards to their habitat value and the ecosystem services they provide. Here

34 we estimate the density, biomass, productivity and composition of mobile macroinvertebrate

35 communities at eight remnant Sydney rock oyster (*Saccostrea glomerata*) reefs, and compare

36 these with adjacent 'bare' soft sediments which typically replace oyster reefs. The oyster reefs

37 had a distinct assemblage of macroinvertebrates, with 30% higher densities, five times the

38 biomass and almost five times the productivity of adjacent bare sediments. Infaunal

39 communities were twice as productive and crustacean communities were 13 times more

40 productive on oyster reefs compared to adjacent bare sediments. *S. glomerata* restoration

41 efforts may therefore enhance local secondary productivity in addition to other ecosystem

42 services provided by *S. glomerata* reefs.

43

Introduction

45 Bivalves such as oysters and mussels are ecosystem engineers that create, modify and

46 maintain habitat at a system-wide scale (Beck et al. 2009). At high densities, bivalves form reef

47 or bed structures comprised of living bivalves and dead shell accumulations (Gillis et al. 2018;

48 Beck et al. 2009). Formerly covering vast areas in temperate coastal waters, bivalve habitats

49 have collapsed globally (Lotze et al. 2006; Beck et al. 2011, Gillies et al. 2018). For example,

50 over 85% of oyster reefs have been lost or severely degraded by destructive fishing practices

51 (e.g. dredging), and water pollution and disease (Lotze et al. 2006; Beck et al. 2011). Bivalve

52 habitats provide a range of ecosystem services such as food provision, habitat for fish and

53 invertebrates, facilitation of fisheries productivity, water filtration, and shoreline protection

54 (Grabowski & Peterson 2007; Grabowski et al. 2012). These services have been valued

55 between USD$5500 and $99,000 per ha per year for the American oyster, *Crassostrea virginica*

56 (Grabowski et al. 2012). The diverse and abundant communities of invertebrates and fishes

57 supported by these ecosystems provide food for other species through predation on the

58 bivalves themselves, on other organisms inhabiting the reef and through the rich biodeposits

59 produced by their filter-feeding (Norling and Kautsky 2007; Engel et al. 2017). Many species

60 also use the structural complexity of the reefs as a refuge from predation and environmental

61 stresses (Coen et al. 2007, Commito et al. 2008, McAfee et al. 2016). Bivalve ecosystems,

62 particularly those occurring on soft sediments, provide a structurally complex network of hard

63 surface 'islands' amid a sea of sand or mud, increasing habitat diversity on a landscape scale

64 (Jones et al. 1997).

65

66 Bivalve restoration has been implemented in many areas with the goals of returning lost bivalve

67 ecosystems and their services (Brumbaugh and Coen 2009; La Peyre et al. 2014; Powers and

68 Boyer 2014). Restoration can be costly and decision makers need information about the impact

69 of restoration activities on ecosystem services to inform their decisions amongst competing

70 priorities for investment (Gillies et al. 2015; Grabowski et al. 2012). Qualitative predictions of

71 benefits, such as "improving biodiversity", may fail to convince managers to support restoration

72 projects (Powers & Boyer, 2014). Therefore, a quantitative approach should be taken when

73 possible (zu Ermgassen et al. 2016).

74

75   One way researchers and managers describe and compare the value of coastal habitats is

76   through their biological production (Fonseca et al. 2000, Peterson et al. 2003). Biological

77   production (productivity) can provide a proxy for overall ecosystems services because many

78   ecosystem services scale to increased biological production (Fonseca et al. 2000, Peterson et

79   al. 2008). Bivalve ecosystems have relatively low primary productivity compared to

80   photosynthesising habitats such as seagrass, saltmarshes meadows or macroalgae beds

81   (Lenihan & Peterson 1998, Coen et al. 2007). Bivalve ecosystems often provide habitat and

82   food for a biodiverse and productive macroinvertebrate community and these invertebrates

83   provide a pathway for energy and materials to flow from primary producers to predators such as

84   fishes (Edgar and Moore 1986; Taylor 1998; Cowles et al. 2009). Secondary production has

85   been used to quantify benefits of habitat restoration (French McCay & Rowe 2003, Peterson et

86   al. 2003). Production at the secondary trophic level may better represent habitat value because

87   it synthesizes contributions of local food production, food subsidies from other habitats, and the

88   protective benefits of habitat structure (Wong et al. 2011). Oyster reefs have high secondary

89   productivity due to the fast growth rates of the bivalves and the large communities of associated

90   organisms they support (Wong et al. 2011). Knowledge of the relative productivity of

91   macroinvertebrate communities could assist restoration practitioners communicate the value of

92   oyster reefs, by identifying these as areas of high productivity within an estuary likely to be

93   utilised by fish species of interest to fisheries managers and recreational and commercial

94   fishers.

95

96   In Australia, *Saccostrea glomerata* (Sydney rock oyster) formerly developed reef ecosystems

97   across its distribution from southern New South Wales to south east Queensland (Gillies et al.

98   2018). These reef ecosystems occurred in the intertidal zone to a depth of 8 m, with reefs

99   forming on hard substrates, sand and mud banks, or associated with mangroves (Gillies et al.

100   2018). In the mid-19th century reefs in New South Wales varied in area from 10 m^2 to greater

101   than 100,000 m^2 (Ogburn et al. 2007). Historically, *S. glomerata* reefs supported one of

102   Australia's largest maritime industries (1790 - 1900), a fishery which targeted oysters for their

103   food value and their shells, which were burned to produce lime for construction (Gillies et al.

104   2015; 2018). There was very little systematic recording of the extent of early harvests. However,

105   For example, the rock oyster (presumed to be dominated by *S. glomerata*) harvest in southeast

106   Queensland peaked in 1891 at 1890 tonnes, with over 200 people employed in the industry

107   (Gillies et al. 2015). The fishery generally used destructive harvest techniques such as dredging

108   and 'skinning', a process where schooners were berthed on intertidal oyster banks as oysters

109   and shells were shoveled onto the schooner until it was full (Ogburn et al. 2007; Gillies et al.

110   2015).

111

112   Despite the decline in the wild harvest of *S. glomerata* by the mid 1900's, the vast areas of

113   former reef have not naturally recovered and today *S. glomerata* are largely only present as

114   individual oysters or as relatively small patches within the intertidal zone across eastern and

115   southern Australia (Gillies et al. 2018). The lack of natural recovery has been attributed to the

116   effects of disease, invasive mud worms, pollution and smothering of adult and larval oyster

117   settlement habitat with large amounts of terrestrially-derived sediment (Kirby 2004; Ogburn et al.

118   2007; Beck et al. 2009; Diggles 2011). Not only is the spatial extent of these reefs greatly

119   reduced, but reefs appear to be absent from 96% of their historical vertical distribution,

120   persisting only in the mid-intertidal zone (Diggles 2013). Even in the intertidal zone, larger reefs

121   (10s - 100s of m^2) are now rare (Gillies et al. 2015; 2018). Consequently, *S. glomerata* reefs are

122   recognised as one of Australia's most imperiled marine habitats (Gillies et al. 2018) and have

123   been nominated as a threatened ecological community under Australia's Environment

124   Protection and Biodiversity Conservation Act 1999 (EPBC Act).

125

126 Interest in oyster reef restoration is gaining momentum in Australia, with restoration projects

127 starting or planned in every state (Gillies et al. 2015; 2018). Motivations for oyster reef

128 restoration in Australia include (1) assiting the recovery of a near extirpated ecosystem, (2)

129 improving local biodiversity in estuaries and (3) recovering ecosystem services, particularly fish

130 production. Quantifying the ecosystem service benefits and ecology of local bivalve reefs was

131 identified as one of 12 key actions to ensure the long-term success of bivalve restoration efforts

132 in Australia (Gillies et al. 2015). This study was designed to help fill this critical knowledge gap

133 by describing the structure of remnant *S. glomerata* reefs on soft sediments (sand and mud

134 banks) and their associated macroinvertebrate and fish communities. Given that

135 macroinvertebrates are important food sources for fishes, estimating their productivity will

136 provide information about how oyster reefs may support commercially and recreationally target

137 fish species.

138

139 The aims of this study were to (1) describe the structure of remnant *S. glomerata* reefs; (2)

140 estimate the composition, density, biomass and productivity of mobile invertebrate communities

141 associated with *S. glomerata* reefs and compare these with those supported by the 'bare' soft

142 sediments that have replaced them; (3) estimate the inhibition or facilitation of infauna under *S.*

143 *glomerata* reefs; (4) provide preliminary information about the fish communities supported by

144 intertidal *S. glomerata* reefs.

145

146 # Materials and Methods

147 ## Study sites

148 We sampled eight intertidal *Saccostrea glomerata* reefs growing either on sand banks (two sites

149 adjacent to North Stradbroke Island [27°29'S, 153°22'E]; and one site in Richmond River,

150 [28°50'S, 153°34'E]), or mud banks (three sites in Port Stephens [32°41'S, 152°01'E]; and two

151 sites in the Hunter River [32°53'S, 151°47'E]) along the east coast of Australia (Figure 1). Each

152 location was sampled once to describe the oyster reefs and their associated invertebrates

153 during 2016-17. We used satellite imagery (using Nearmap; www.nearmap.com.au) to measure

154 the approximate area of the sampled oyster reefs (Table 1).
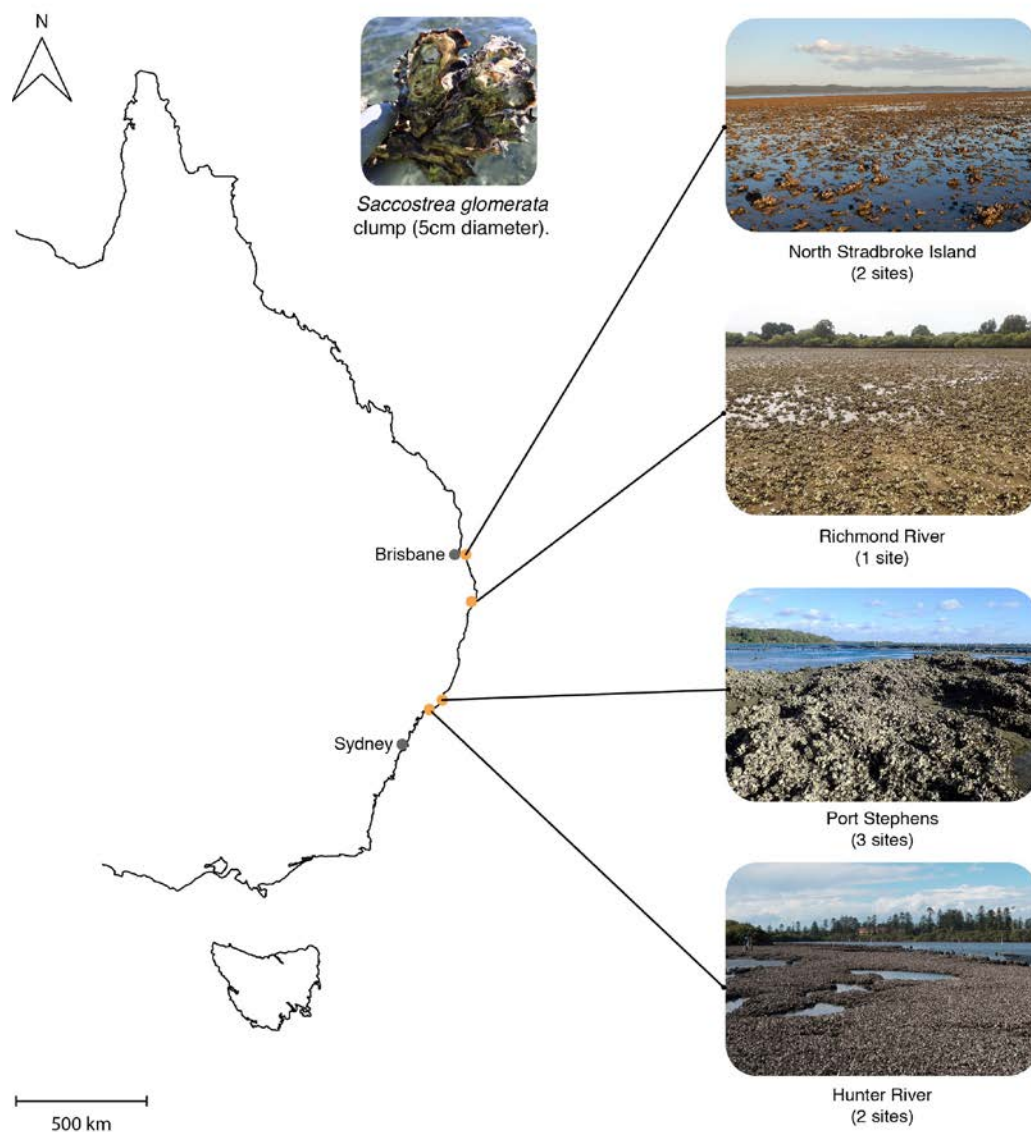
Figure 1 - Map of study locations (orange dots) of soft sediment oyster reefs along the east coast of Australia. Inset pictures depict the typical substrate of each reef. Base map produced using the 'oz' package in R (Venables and Hornick 2016). Image credits: North Stradbroke: B. D'Anastasi, Richmond River-P. Dwyer; Port Stephens, Hunter River: S. McOrrie.

Oyster reef descriptions

163   We estimated percentage cover of reef structure and densities of live oysters at each site.

164   Percentage cover was estimated from photographs of ten replicate 1 m^2 quadrats per site.

165   Quadrat placement was randomised using two independent random number tables to select

166   distance along and distance perpendicular to a transect tape laid across the longest edge of the

167   reef. Percentage cover was calculated for each quadrat by scoring benthic composition

168   (oyster/non-oyster) under twenty random points using ImageJ2 (Rueden et al. 2017). The

169   density of live oysters (<10mm were not included) was estimated by a smaller quadrat (25 cm x

170   25 cm) placed in the bottom left corner of each larger quadrat. Within this smaller quadrat, we

171   measured the maximum height of the oyster clumps above the substrate (at all sites except

172   Richmond River), and the longest axis of the shell was measured from a subset of a maximum

173   of 25 oysters.

174

175   To calculate the overall density of oysters at each site, we multiplied the average density of

176   oysters (m^{-2}) from the smaller quadrats, by the average percentage cover of the larger quadrats.

177   This was done to include sandy or muddy patches between high density clumps of oysters, and

178   thereby avoid artificially inflating the overall oyster density. We then isolated the quadrat with the

179   highest density within each site, and performed the same calculation to estimate the maximum

180   oyster density recorded (m^{-2}) at each site. To estimate the overall number of oysters per reef,

181   we used the oyster density for each site, multiplied by the total area of each oyster reef (Table

182   1).

183

Community structure, density, biomass, and productivity of mobile invertebrates

186

187   At each reef, mobile invertebrates were sampled from three habitats: (1) the oyster reef and

188   cultch (the mass of stones, broken shells, and grit from which an oyster reef is formed) above

189   the soft sediment substrate, (2) directly under the oyster reef to a depth of 10 cm, and (3)

190   adjacent soft sediment substrates including the surface and top 10 cm of sediment >2 m away

191   from the oyster reef. Samples were taken using a hand corer with 13 cm internal diameter. A

192   hand trowel was used to break off edges of the oyster reef if needed. Five samples of each

193   habitat type were taken at each site. Samples were preserved in 70% ethanol or 10% formalin

194   mixed with seawater within a few hours for later analysis.

195

196   To estimate the community composition, density, biomass and productivity of the mobile

197   invertebrates associated with the three habitats, samples were washed through a series of 11

198   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 sizes). The 1.4, 1.0,

199   and 0.5 mm size classes that were dominated by sand particles were subsampled up to 16

200   times. Invertebrates retained on the sieve classes 0.5-5.6 mm were identified to coarse

201   taxonomic levels (Class or Order) and counted. Larger invertebrates were identified to species

202   level. Sessile organisms were not included in this study. Water temperature was derived from

203   the Integrated Marine Observing System (IMOS 2017).

204

205   Oyster reef associated fishes and habitat

206   The abundance, density and composition of fish communities and associated habitats were

207   assessed at one location, North Stradbroke Island, over three days (16-18 May, 2017). Fish

208   were counted and identified to species level using underwater visual census (UVC) of belt

209   transects, 2 m x 25 m (n=34 belt transects in total). For each UVC, a point intercept method was

210   used at each meter along the transect and scored into broad benthic habitat types (oyster, shell,

211   sand, macroalgae, rubble, sponge, soft coral). Surveys were completed on snorkel (when water

212   level was <1 m) and SCUBA (when water level was ≥1 m). The position of each transect was

213   randomised using independent random number tables to determine the direction and distance

214   to travel to place the next transect.

215

Data analysis

217   Mobile invertebrates were sampled from three habitats: (1) the oyster reef (2) directly under the

218   oyster reef (3) adjacent soft sediment substrates. The oyster and under oyster habitats were

219   pooled (1 + 2) in subsequent analyses and compared to the adjacent bare substrates (3) to

220   show the overall effect of oyster presence. The net impact of oysters on the density, biomass

221   and productivity of fauna was thus assumed to be equal to 1+2-3. The exception to this was

222   when the under oyster (2) and adjacent bare substrates (3) were compared to describe the

223   influence of the presence of oyster reef on infaunal communities. Biomass and productivity of

224   mobile invertebrates (both expressed as ash-free dry weight [AFDW]) were estimated using the

225   general equations of Edgar (1990), which predict individual biomass as a function of sieve mesh

226   size, and productivity as a function of sieve mesh size and water temperature.

227

228   The differences in the mean density (m^{-2}), biomass (g AFDW m^{-2}) and productivity (g AFDW m^{-2},

229    $year^{-1}$) of mobile invertebrate between oyster habitats and adjacent bare sediment, and between

230   locations, were analysed using separate 2-way Analyses of Variance. All statistical analyses

231   were performed on data pooled per location. The model analysed the effects of Location

232   (Categorical factor, 4 levels: North Stradbroke Island, Port Stephens, Hunter River and

233   Richmond River), habitat type (Categorical, 2 levels: oyster habitat and adjacent bare sediment)

234   and the interaction between the two, on the response variable (density, biomass or productivity).

235   Non-significant 2-way interactions between the two explanatory variables were removed and the

236   data re-analysed with main effects only. Data were cube-root transformed to comply with

237 assumptions of homogeneity of variances and normality of residuals. Significant differences

238 were explored using Tukey's HSD post hoc test. All analyses were performed within the R

239 environment (R Core Team, 2017).

240

241 To investigate the difference in community composition without the influence of the numerically

242 dominant small (<2 mm) gastropods, these were removed and the analyses repeated. To

243 investigate the potential for a facilitation or inhibition effect of the presence of oyster reefs on

244 infauna directly under oysters we compared the under oyster habitat to adjacent bare sediments

245 in a separate analysis.

246

247 The diversity of mobile invertebrates was explored by classifying all organisms to taxonomic

248 Class, with the exception of the large and diverse Malacostraca class, which was further

249 subdivided into four taxonomic orders (Amphipoda, Brachyura, Isopoda and Decapoda). The

250 diversity of macroinvertebrate communities of the two main habitat types (oyster and adjacent

251 bare sediment) was compared using Simpson's Diversity Index, where a value of 0 indicates a

252 habitat with no diversity, and 1 a habitat with infinite diversity. Analyses were performed in R,

253 using the diversity() function within the vegan R package (Oksanen et al 2017).

254

255 To explore differences between the two habitat types in multivariate space, we performed a

256 Principal Component Analysis of the pooled counts of the 10 most common mobile invertebrate

257 taxa at each Site and Location (n=8 across the 4 locations). Because smaller size classes were

258 dominated by gastropods, we conducted analyses of the combined data set, as well as the

259 dataset excluding mobile invertebrates <2 mm. The two first principal components were

260 displayed for each analysis (Figure 4). Because crustaceans >1 mm are an important food

261 source for fishes (Edgar & Shaw 1995), we isolated these from the data and performed a

262 separate analysis of their density, biomass and productivity across the two habitat types using a

263   Student's T-test. A linear regression was performed to analyse the relationship between the

264   density of fishes and substrate types.

265   Results

266   Oyster reef descriptions

267   The eight reefs investigated were spread across four locations, spanning 620 km along the east

268   coast of Australia (Figure 1). The reefs varied in size, substrate type and oyster density (Table

269   1). The reefs in the Hunter River and Port Stephens were characterised by discrete reefs

270   growing on mud with relatively high vertical height and very high oyster densities (up to 740

271   oysters m^{-2}). Richmond River had a lower oyster density, less vertical height (I. McLeod, pers.

272   obs.) and more isolated clumps of oysters, growing on muddy sand (Figure 1). The two oyster

273   reefs at Peel Island, North Stradbroke Island were vast and had low oyster density (up to 70 ind.

274   m^{-2}), and oysters mostly grew in isolated clumps on sand, with less vertical height compared to

275   the other locations (Figure 1). The scattered, low density nature of North Stradbroke oyster

276   reefs made it difficult to determine their boundaries, giving us less confidence in these

277   estimates. To avoid artificially inflating calculations of total oyster abundance on these two sites,

278   they were therefore excluded from reef-size estimates.

279

280

281
282
283
284
285
286
287   **Table 1** - Oyster reef site descriptions, based on 1 m^{-2} quadrats, at North Stradbroke Island (two
288   sites), Richmond River (one site), Port Stephens (three sites) and Hunter River (two sites), on

289 the east coast of Australia. Maximum values for each measure are highlighted in green and
290 minimum values in blue.

Location	Site	Substrate	Area (m^2)	Average Benthic Oyster reef cover (%) *	Mean density of oysters (m^{-2} ±SEM)	Max Density of oysters (m^{-2})	Number of oysters on reef (millions)	Average size of oysters ±SEM (mm)	Average Vertical height (mm)
North Stradbroke Island	Peel Island 1	Sand	99770[+]	23	68.4 ±6.1	209.8	+	33.0 ± 0.7	59.3
North Stradbroke Island	Peel Island 2	Sand	250752 +	12.8	10.2 ±3.3	69.6	+	27.3 ± 1.3	25.2
Richmond River	1	Muddy sand	7,493	39.4	168.9 ±2.1	264.8	3.2	31.5 ±0.8	N/A
Port Stephens	1	Mud / shell	2,704	59.3	209.7 ±8.6	673.6	1.0	34.9 ±1.1	53.6
Port Stephens	2	Mud / shell	1,458	65.0	740.5 ±15.8	1591.2	1.7	37.6 ±0.9	113.7
Port Stephens	3	Mud / shell	5,199	43.3	353.3 ±16.3	1004.6	4.2	40.4 ±1.2	95.3
Hunter River	1	Mud / shell	4,486	64.4	605.9 ±9.7	978.9	4.2	39.2 ±0.8	143.8
Hunter River	2	Mud / shell	2,896	64.5	601.6 ±11.1	1135.2	2.7	41.3 ±0.9	93.2

291 * The average benthic cover of oysters includes live oyster and shell, as it was not possible to
292 discriminate these from the photo. Vertical height data was not collected at Richmond River.

293 [+] The low density of oysters in North Stradbroke sites made estimates of area using satellite data
294 unreliable. To avoid artificially inflating the estimates, we did not include these estimates in calculations of
295 oyster numbers.

296

Density, biomass, and productivity of mobile invertebrates

298

299 Oyster habitat supported significantly higher density, biomass and productivity of mobile invertebrates

300 compared to adjacent bare sediments. The density of mobile invertebrates was 30% higher in oyster

301 habitat, compared to adjacent bare sediments (Figure 2b, mean density: *oyster habitat* 6151 invertebrates

302 m^{-2} ± 1596 SEM, *non-oyster habitat* 4609 ± 1645). The density of mobile invertebrates was significnatly

303 different between both main effects (2-way ANOVA, Main factor: *Habitat* df=(1, 875), F= 68.53, p<0.001,

304 *Location* df=(3, 875), F= 35.64, p<0.001). The elevated density of invertebrates was characterised by

305 high numbers of gastropods in the smaller size-classes (<2mm) in the North Stradbroke sites (Figure 2a).

306 Without the influence of these smaller size classes, mobile invertebrate density of oyster reef habitat, was

307 893 ind^{-1} m^{-2} (14.5% of total individuals ≥2 mm) and adjacent bare habitats 173 ind^{-1} m^{-2} (3.8% of total

308 individuals ≥2 mm). The removal of size classes <2mm revealed a significant 2-way interaction between

309 the main factors, indicating that the difference in the density of invertebrates on the two habitat types was

310 not consistent across the four study sites, and (2-way Anova, *Habitat x Location*= df=(3, 632), F= 3.6,

311 p=0.01).

312

313 Oyster habitat supported over five times the biomass of mobile invertebrates (mean biomass: *oyster reef*

314 10.13 g AFDW m^{-2} ± 0.7 SEM, *adjacent bare sediments* 1.8 ± 0.04, Figure 2d) and almost five times the

315 productivity (mean productivity: *oyster reef* 32.0 g AFDW m^{-2} year^{-1} ± 2.3 SEM, *adjacent bare sediments*

316 6.9 ± 1.1, Figure 2f) compared to adjacent bare sediments. The biomass patterns were driven by

317 significant differences in biomass between oyster reef and adjacent bare sediments, and between

318 locations (2-way ANOVA, Main factor: *Habitat* df=(1, 875), F= 232.43, p<0.001, *Location* df=(3, 875), F=

319 19.92, p<0.001). The magnitude of the difference in productivity on oyster reefs compared to adjacent

320 bare sediments varied between locations. This is reflected in a significant two-way interaction between

321 the two main factors in the model (Habitat and Location; 2-way ANOVA, df= 3, 872, F= 3.51, p=0.02).

322
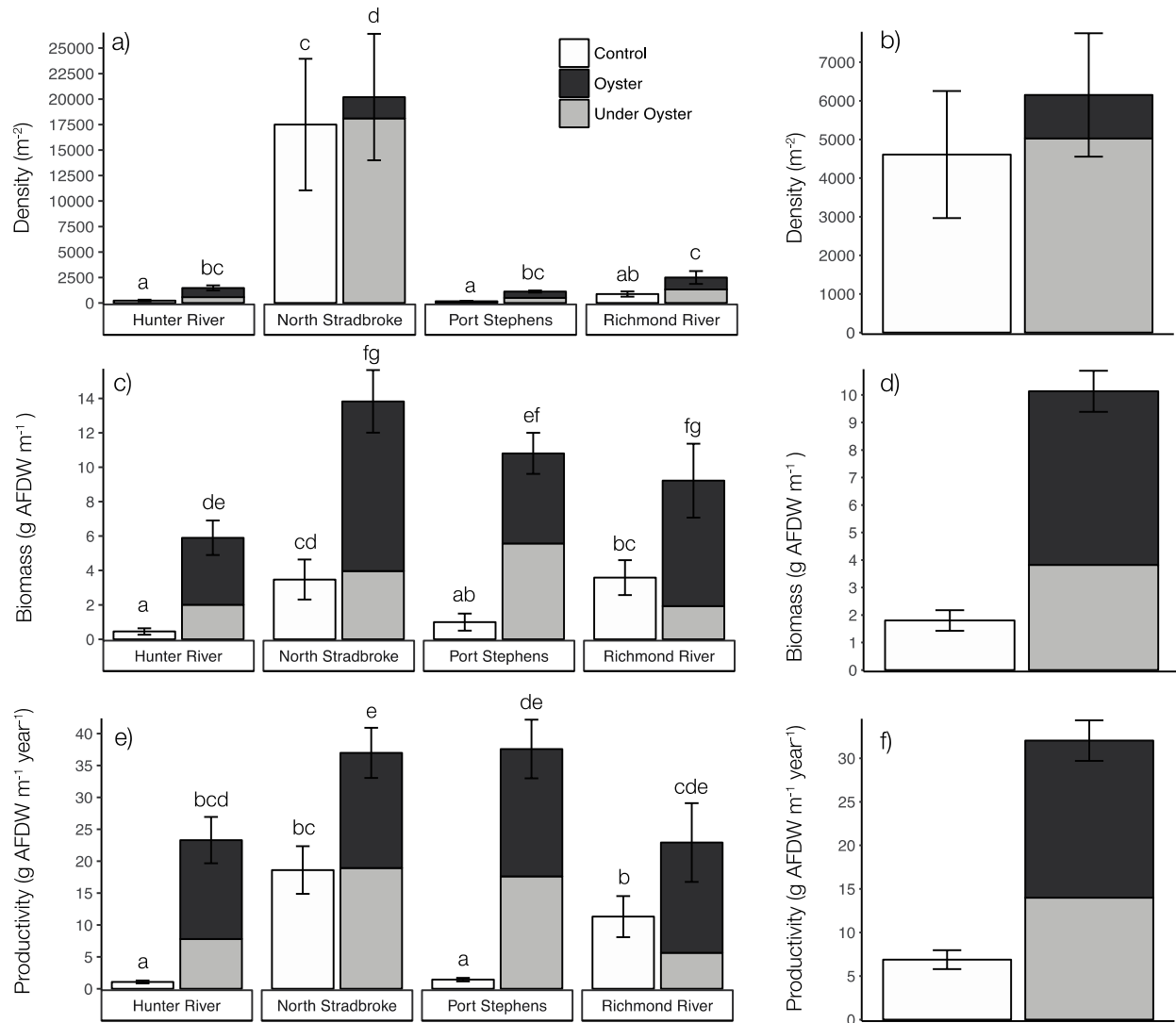
Figure 2: Mean density (a, b), biomass (b,c) and productivity (e,f) of the mobile invertebrate assemblage associated with oyster habitat (oyster and under oyster, black and grey respectively) compared to adjacent soft sediment substrate oysters (Control, white). The left column (a,c,e) depicts values per location, while the right column (b,d,f) displays mean values across all locations. The main effects of habitat and location were significantly different for density and biomass (a,c), and the interaction between the two was significant for productivity (e), however we have chosen to keep figures consistent for ease of comparison between the three variables (density, biomass and productivity). Letters reflect significant groupings in Tukey's Post-hoc test, based on the simplest significant model (i.e. interaction or main effects only), error bars represent SEM.

334   Species composition of mobile invertebrates
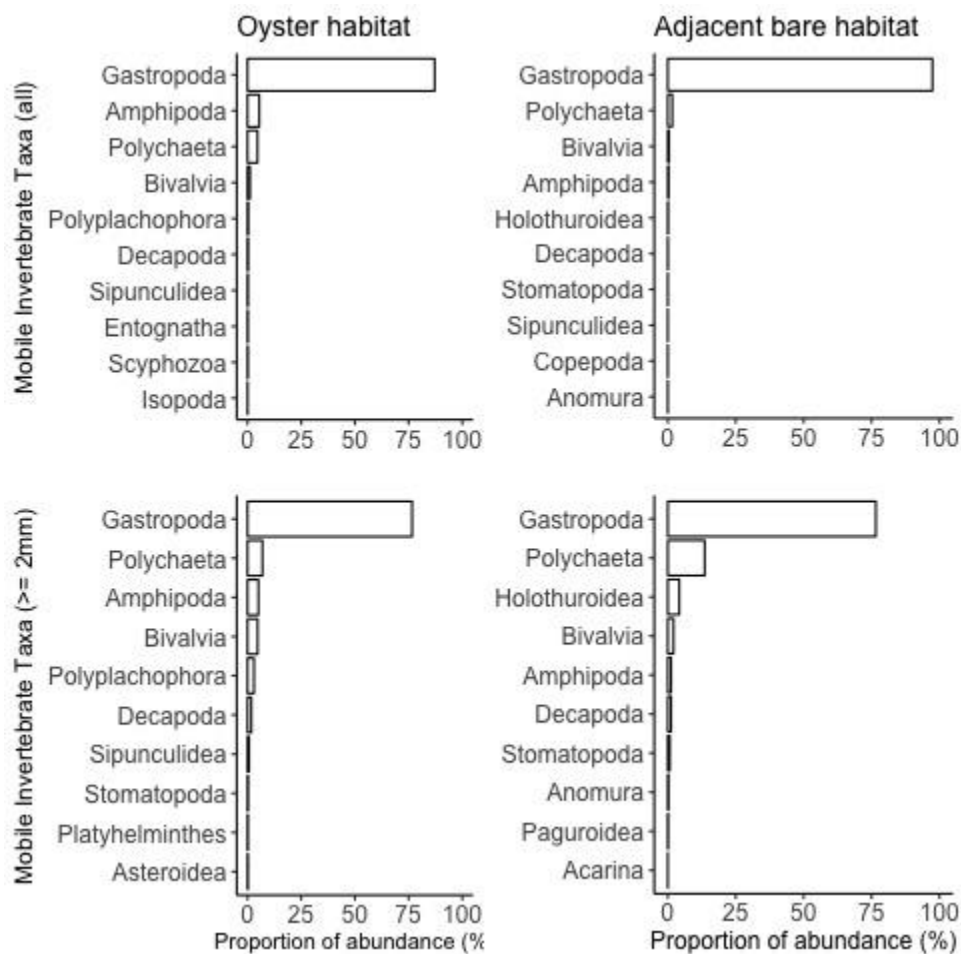
335

336   **Figure 3:** The diversity of all invertebrate taxa (a,b) and invertebrates ≥ 2 mm (c,d) associated with oyster
337   habitat (associated with oysters, and underneath oyster clumps) and adjacent bare sediment habitat.
338   Samples were identified to nearest taxonomic Class, except for the abundant class Malacostraca which
339   was further separated into Orders (Amphipoda, Decapoda and Isopoda).
340

341   Oyster reefs supported a higher level of biodiversity (Simpson's D=0.22) than the adjacent bare

342   sediments (D=0.05). Although both habitats were dominated by gastropods, oyster reefs

343   supported higher densities of a wider range of other taxa (e.g: Amphipoda, Polychaeta and

344   Bivalvia), compared to adjacent bare sediments, which were inhabited almost exclusively by

345   gastropods, with a relatively low proportion of other taxa (Figure 3). However, removal of small

346   gastropods from analyses revealed that oyster reefs (D=0.38) and adjacent bare sediments

347   (D=0.35) supported similar levels of biodiversity (Figure 3 c and d), but under oyster habitat was

348   more biodiverse (D=0.12) than the adjacent bare substrate habitat (D=0.05).

349

350   Oyster reefs supported 14 times the density of crustaceans >1 mm (average density of

351   crustaceans >1 mm on *oyster habitat* 804.2 m^{-2} ± 206 SEM, *adjacent bare sediment* 56.5 m^{-2} ±

352   18 SEM, Student's T-test, t=7.14, df=158, p<0.001), nine times the biomass, and a 13 times

353   higher productivity on oyster reefs, compared to adjacent bare sediments (average biomass of

354   crustaceans >1 mm on *oyster reefs* 5.7 g AFDW m^{-2} ±1.5 SEM, *adjacent bare sediments* 0.6 g

355   AFDW m^{-2} ± 0.26 SEM, Student's T-test, t=6.4, df=158, p<0.001). Average productivity of

356   crustaceans >1 mm on *oyster reefs* was 10.5 g AFDW m^{-2} ± 1.6 SEM, *adjacent bare sediment*

357   0.8 g AFDW m^{-2} ± 0.28 SEM, Student's T-test, t=8.2, df=158, p<0.001).

358

359   Principal component analyses revealed habitat type (oyster versus adjacent bare soft sediment)

360   had a greater influence on differences in the mobile invertebrate communities, than geographic

361   distance (up to 100s of kilometres away) (Figure 4a). When the numerically dominant smaller

362   size classes (<2 mm) were removed from the data set, the separation between oyster reefs and

363   adjacent bare sediments increased (Figure 4b).
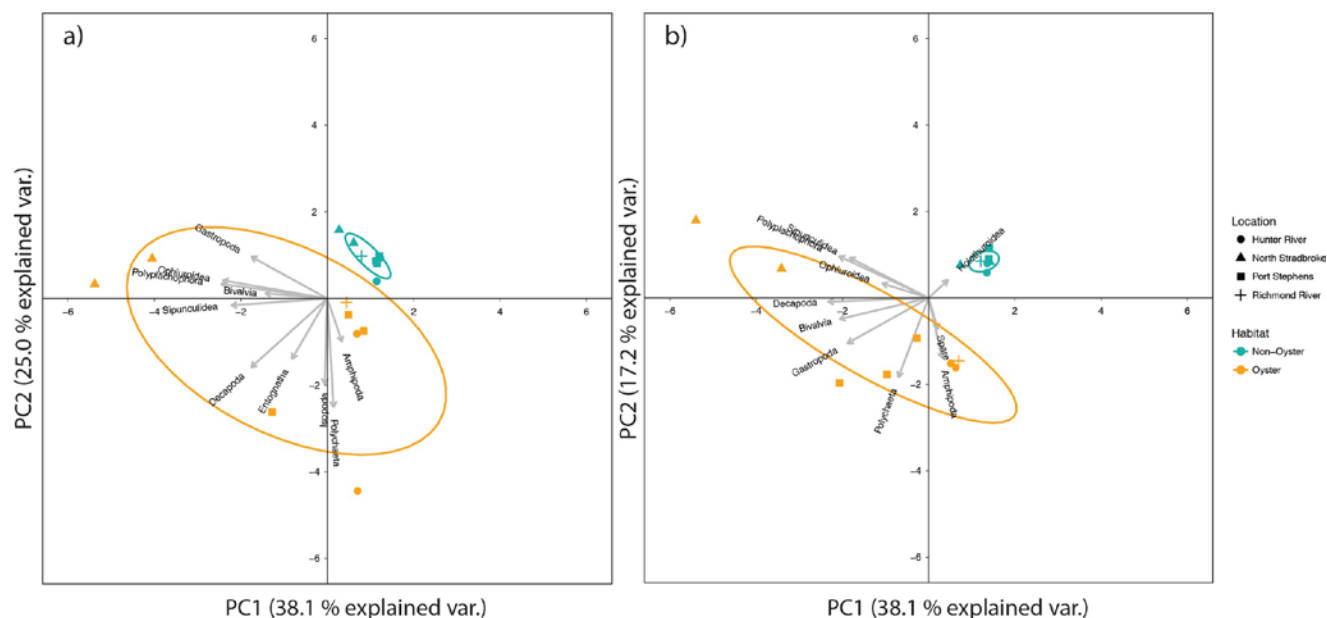
Figure 4: Principal component analysis of (a) the overall invertebrate assemblage, and (b) invertebrates ≥2mm associated with oyster reefs and adjacent soft sediment habitats. Data points represent individual sites within each location. Oyster habitat includes oyster and under oyster samples.

Oyster reef associated fishes

Overall, we observed five species of fishes associated with oyster reefs at North Stradbroke

Island, at an overall average density of 1.0 fish $m^{-2} \pm 0.1$ SEM. The four most abundant species

were from the Gobiidae (gobies) and Blennidae (blennies) Families (Figure 5). There was no

significant relationship between the density of fish and the percentage of live oysters or oyster

shell.

376
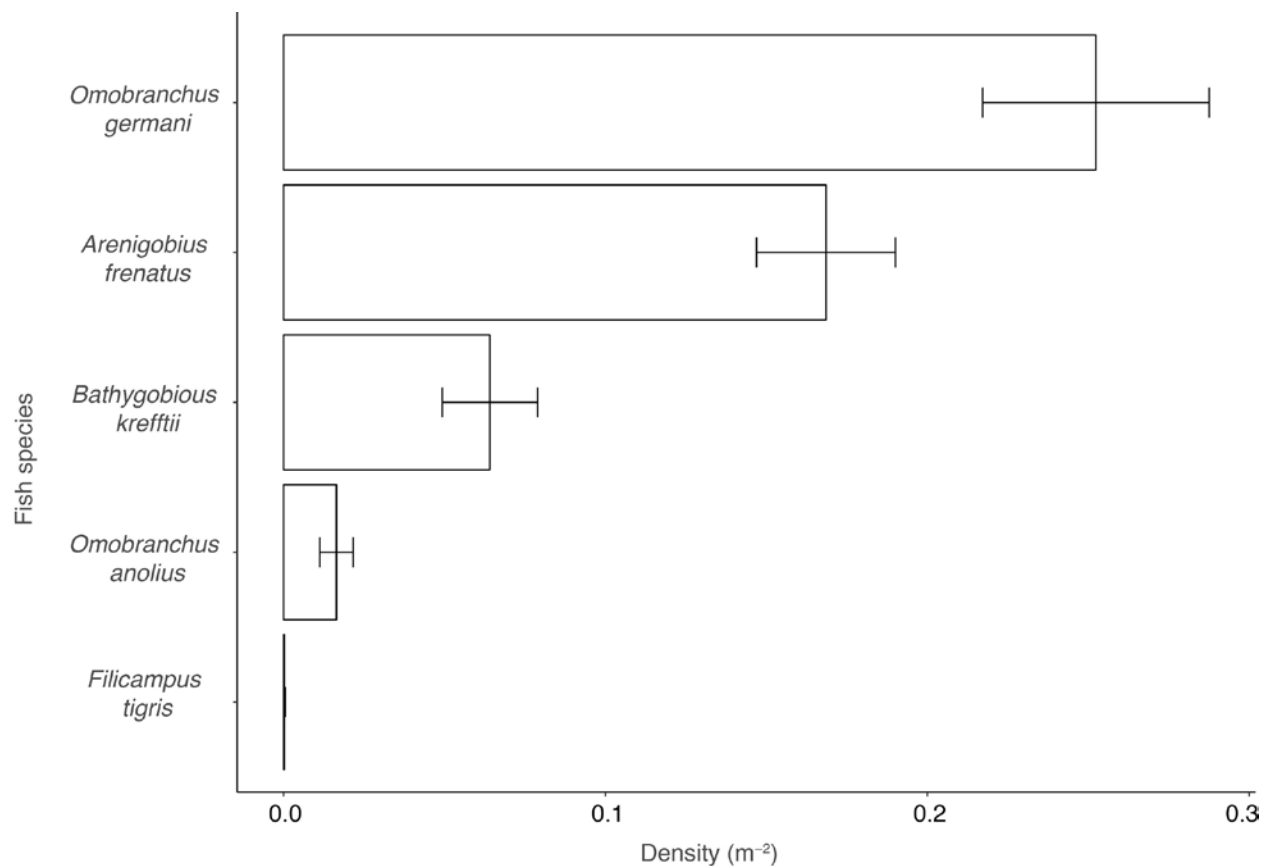
Figure 5: The average density (m^{-2}) of five fish species associated with soft sediment intertidal oyster reefs at North Stradbroke Island.

379

Discussion

This study has shown that *Saccostrea glomerata* reefs support diverse and productive mobile

invertebrate communities. Historically, *S. glomerata* reefs were a common intertidal and subtidal

habitat type in Australia, but these have largely been replaced by bare sediments. Our study

shows that these soft sediment habitats, although important and productive habitats in their own

right, support less biodiversity and are less productive than the oyster reefs they have replaced.

386

387 **Oyster reefs structure**

388

389 Oyster density and reef structure differed markedly between the four study locations. The reefs

390 in Hunter River and Port Stephens were smaller in overall area, yet supported higher densities

391 of oysters on discrete reefs that were visibly elevated above the surrounding bare muddy

392 substrate. In contrast, the reef at Richmond River, and the two reefs around North Stradbroke

393 Island were larger but had lower densities of oysters, in scattered clumps, distributed over a

394 sandy substrate. Overall the sites in Port Stephens and the Hunter River supported oyster

395 densities between 200 and 600 oysters per meter. These reefs seem to be in relatively good

396 condition compared to those at North Stradbroke (10-68 m^{-2}). However, these densities are all

397 likely to be substantially lower than historical estimates. For example, New South Wales reefs

398 varied in area from 10m^2 to 100,000m^2 and were described as "close set clumps of five or six

399 oysters thick all over the bed, averaging 18 mature oysters besides spat of every 5 square

400 inches (5570 oysters per m^2) over an unbroken bed of shell" (Oyster Culture Commission 1887).

401 Due to the scattered, low density nature of the less discrete reefs in North Stradbroke and

402 Richmond River it was difficult to define their boundaries using aerial imagery and therefore we

403 have less confidence in these reef-area estimates. Furthermore, these extant reefs are likely to

404 be different in structure to the now functionally extinct subtidal reefs. Regardless, these remnant

405 reefs are valuable as they provide the only extant reference sites to use for structuring

406 restoration targets and may be good candidate sites for restoration and further research into

407 ecosystem services.

408

409
410 **Habitat value for invertebrates**

411

412 Our study demonstrates that *S. glomerata* reefs host a diverse assemblage of mobile

413 invertebrates with a higher density, biomass and productivity compared to nearby bare

414   sediment, which typically replaces these reef ecosystems when they become degraded or

415   extinct. Overall, the density of mobile invertebrates was a third higher associated with oyster

416   reefs. However, densities of invertebrates larger than or equal to 2 mm were over five times

417   higher associated with oyster reefs than adjacent bare sediments. These data demonstrate that

418   oyster reefs are a more valuable habitat for these larger invertebrates than soft sediment

419   habitats. This is also supported by our findings that oyster reefs were five times more productive

420   compared to adjacent bare sediment. The magnitude of difference in productivity between

421   oyster habitat and adjacent bare sediment differed between locations. Adjacent bare sediments

422   at the two locations characterised by muddy substrates, Port Stephens and Hunter River, were

423   much less productive than the sandy substrates of North Stradbroke and Richmond River,

424   which supported comparatively higher levels of productivity.

425

426   Bivalve habitats have been shown to be highly productive habitats relative to other less-

427   structured estuary habitats (Wong et al. 2011; McLeod et al. 2013; Coen & Humphries 2017)

428   Overall, the level of secondary productivity within the remnant intertidal *S. glomerata* reefs

429   examined in this study (overall mean 30.2 g AFDW m^{-2} year^{-1}), are comparable to those

430   estimated for other sub-tropical and temperate marine systems, like subtidal rocky reefs (20.1 g

431   AFDW m^{-2} year^{-1}, Cowles et al. 2009), and urchin barrens (30 gAFDW m^{-2} , Taylor 1998).

432   Ferrano and Cole (2007) used benthic macroinvertebrate diversity, density and biomass to rank

433   habitat value in Wilapa Bay, Washington, USA and found that oyster reefs were more

434   ecologically valuable, in terms of providing habitat for macroinvertebrates, than salt marsh, mud

435   shrimp habitat, bare mud / sand and ghost shrimp habitat. Similarly, Hosack et al. (2006) found

436   that epifaunal density was higher in seagrass and oyster reef habitats and lowest in bare mud. It

437   should be noted that we did not estimate the secondary productivity of the oysters themselves,

438   which is likely to be a large proportion of the total productivity of this habitat. Indeed, Bahr

439   (1976) demonstrated that oysters comprised the majority (circa 95%) of the total secondary

440   productivity of an oyster reef. Future research estimating the total productivity of natural *S.*

441   *glomerata* reefs would allow for direct comparisons with other systems.

442

443   The biodiversity of oyster-associated mobile invertebrate assemblages in this study was greater

444   than the surrounding bare sediments, consistent with other bivalve habitat such as *Perna*

445   *canaliculus* (green-lipped mussel) beds (Mcleod et al. 2013). As expected for a habitat spread

446   across a wide range of sites with different environmental conditions, the species assemblages

447   were different at each site. However, strikingly, the mobile invertebrate assemblages of oyster

448   habitat was more similar between oyster habitat separated by 100s of kilometres, compared to

449   adjacent bare sediment at the same site. This indicates that oyster reefs are a unique

450   ecosystem despite local environmental effects.

451

452   It has been hypothesised that bivalve aggregations may negatively affect infaunal communities

453   through the build up of an anoxic layer of biodeposits (Creese et al. 1997), or through the

454   predation of infaunal larvae via filter feeding (Commito & Boncavage 1989). In contrast, we

455   found evidence of greater infaunal biomass and/or productivity under oysters compared to

456   adjacent bare sediment. Norkko et al. (2006) found also found a higher density and abundance

457   of infauna near the suspension-feeding bivalve *Atrina zelandica*. Norling & Kautsky (2007)

458   showed that blue mussel (*Mytilus edulis*) biodeposits supplied up to 31% of the energy

459   demands of an associated macroinvertebrate community on the west coast of Sweden. Overall,

460   it is likely that the role of bivalves and their biodeposits in the facilitation or inhibition of infauna

461   varies depending on bivalve density and environmental conditions.

462

463   **Habitat value for fish**

464   Five species of small fishes were found associated with the intertidal *S. glomerata* reefs around

465   North Stradbroke Island at high tide. The fish communities were dominated by two Blenniidae

466   species and two Gobiidae species, small fishes that grow to a maximum size of around 10 cm

467   and are common in shallow structured environments (Froese and Pauly 2018). Fish

468   communities are highly dynamic, and it is likely that increasing the spatial and temporal scale of

469   these surveys would increase the number of species identified. Indeed, ongoing work, using

470   unbaited video techniques detected 20 species of fish associated with *S. glomerata* reefs in

471   south eastern Australian estuaries (Martinez-Baena, unpublished data). Also, underwater visual

472   census methods have well-known biases because many fish species are diver-averse and small

473   species may hide in the substrate and not be counted. Therefore, these results should be

474   considered a preliminary estimate of the fish communities associated with *S. glomerata* reefs.

475

476   The fish species we detected are not targeted by recreational or commercial fishers. However,

477   they may be prey for larger, targeted fish species and therefore involved in transferring energy

478   between trophic levels. Associated macroinvertebrates also contribute important trophic

479   linkages (Grabowski et al. 2005). Furthermore, crustaceans ($\geqq 1$ mm) are a primary food source

480   of small fishes (fish weighing 0.1-100 g, Edgar & Shaw 1995). Crustaceans from these size

481   classes were 14 times more numerous, and 13 times more productive on oyster reefs that in

482   adjacent bare sediments. Together, these lines of evidence suggest that *S. glomerata* reefs

483   could be an important habitat supporting biodiversity and productivity at higher trophic levels in

484   Australian estuaries. In North America, oyster reefs have been shown to provide important

485   habitat for recreationally and commercially valuable fish species (reviewed in Grabowski et al.

486   2012) and support fish communities that are higher in abundance nearby sand flats (Lenihan et

487   al. 2001) or muddy substrates (Humphries et al. 2011).

488

489   **Restoration for ecosystems services**

490   Quantification of ecosystem services is increasingly valuable for conservation and restoration

491   decision-making. Restoration of bivalve habitats historically focussed on supporting bivalve

492   fisheries by replacing habitat or directly reseeding reefs or beds (Shulte 2017; McLeod et al. *in*

493   *press*). In recent decades the focus has shifted to bring back threatened or locally extinct

494   bivalve habitats and valuing their role in supporting biodiversity (Shulte 2017; Bersoza

495   Hernández et al. 2018. Large-scale bivalve restoration projects are now being implemented to

496   return lost ecosystem services. For example, 142 hectares of oyster reefs have been restored in

497   Harris Creek, Chesapeake Bay with the goals of restoring water filtration and fin fish and

498   invertebrate fishery production (McLeod et al. *in press*). The present study provides some

499   information about the habitat value of *S. glomerata* reefs in Australia. Further work into the

500   productivity of targeted fish and invertebrate species associated with Australian oyster reefs,

501   and their economic value, would provide vital information for decision makers to help weigh the

502   costs and benefits of restoration projects, Tools such as the oyster calculator developed by The

503   Nature Conservancy (http://oceanwealth.org/tools/oyster-calculator/) allows managers to set

504   restoration objectives based on desired ecosystem services, such as water filtration or fisheries

505   production for American oysters. Future work in Australia should focus on parameterising a

506   similar calculator for Australian oyster species, by building on the present work with estimates of

507   fish and invertebrate growth and survival data, coupled with local hydrological information to

508   predict the functional benefits of reef restoration.

509
510   **Conclusion**
511
512   In this study we have demonstrated that *Saccostrea glomerata* reefs support diverse and

513   productive mobile invertebrate communities. Interest in shellfish habitat restoration is increasing

514   in Australia (Gillies et al. 2018), with restoration trials in most states. *S. glomerata* reef

515   restoration trials have begun along Australia's east coast motivated by the potential of bringing

516   back a reduced or locally extinct ecosystem and its services Our study lends support for the

517   potential of oyster reef restoration to re-establish the productivity of invertebrates and support

518   local fisheries productivity in Australia.

519

520

References

522
523 Bahr LM (1976) Energetic aspects of the intertidal oyster reef community at Sapelo Island,
524 Georgia (USA). Ecology 57: 121−131
525
526 Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ,
527 Hancock B, Kay M, Lenihan H, Luckenbach MW, Toropova CL, Zhang G (2009) Shellfish reefs
528 at risk: a global analysis of problems and solutions. The Nature Conservancy, Arlington VA
529
530 Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C,et al. (2011) Oyster
531 Reefs at risk and recommendations for conservation, restoration, and management. BioScience
532 61:107−116
533
534 Bersoza Hernández, A., Brumbaugh, R.D., Frederick, P., Grizzle, R., Luckenbach, M.W.,
535 Peterson, C.H., Angelini, C. (2018) Restoring the eastern oyster: how much progress has been
536 made in 53 years? Frontiers in Ecology and the Environment, 16 (8), pp. 463-471
537
538 Brumbaugh RD, Coen LD (2009) Contemporary approaches for small-scale oyster reef
539 restoration to address substrate vs recruitment limitation: a review and comments relevant for
540 the Olympia oyster, *Ostrea lurida* (Carpenter, 1864). Journal of Shellfish Research 28, 147-161
541
542 Coen LD, Brumbaugh RD, Bushek D, Grizzle R, Luckenbach MW, Posey MH, Powers SP,
543 Tolley SG (2007) Ecosystem services related to oyster restoration. Mar Ecol Prog Ser 341:303-
544 307
545
546 Commito JA, Boncavage EM (1989) Suspension feeders and coexisting infauna: an
547 enhancement counterexample. J Exp Mar Biol Ecol 125:33-42
548
549 Commito JA, Como S, Grupe BM, Dow WE (2008) Species diversity in the soft-bottom intertidal
550 zone: biogenic structure, sediment, and macrofauna across mussel bed spatial scales. J Exp
551 Mar Biol Ecol 366:70-81
552
553 Cowles A, HeWitt JE, Taylor RB (2009) Density, biomass and productivity of small mobile
554 invertebrates in a wide range of coastal habitats. Mar Ecol Prog Ser 384:175-185
555

556 Creese R, Hooker S, De Luca S, Wharton Y (1997) Ecology and environmental impact of
557 *Musculista senhousia* (Mollusca: Bivalvia: Mytilidae) in Tamaki Estuary, Auckland, New
558 Zealand. N Z J Mar Freshw Res 31:225-236
559
560 Diggles BK (2011) Historical epidemiology indicates water quality decline drives loss of oyster
561 (*Saccostrea glomerata*) reefs in Moreton Bay, Australia. N Z J Mar Freshw Res 47:561-581
562
563 Diggles, B. K. 2013. Historical epidemiology indicates water quality decline drives loss of oyster
564 (Saccostrea glomerata) reefs in Moreton Bay, Australia. New Zealand Journal of Marine and
565 Freshwater Research 47:561–581.
566
567 Edgar GJ (1990) The use of the size structure of benthic macrofaunal communities to estimate
568 faunal biomass and secondary production. J Exp Mar Biol Ecol 137:195-214
569
570
571 Edgar DJ, Moore PG (1986) Macro-algae as habitats for motile macrofauna. Monogr Biol 4:255-
572 277
573
574 Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish
575 assemblages in southern Australia II. Diets of fishes and trophic relationships between fishes
576 and benthos at Western Port, Victoria. J Exp Mar Biol Ecol 194:83-106
577
578 Engel, FG., Javier Alegria, Rosyta Andriana, Serena Donadi, Joao B. Gusmao, Maria A. van
579 Leeuwe, Birte Matthiessen, and Britas Klemens Eriksson. 2017. "Mussel Beds Are Biological
580 Power Stations on Intertidal Flats." Estuarine, Coastal and Shelf Science 191 (May): 21–27.
581
582 Fonseca MS, Julius BE, Kenworthy WJ (2000) Integrating biology and economics in seagrass
583 restoration: How much is enough and why? Ecol Eng 15:227−237
584
585
586 French McCay DP, Rowe JJ (2003) Habitat restoration as mitigation for lost production at multiple
587 trophic levels. Mar Ecol Prog Ser 264:233−247
588
589 Froese, R. and D. Pauly. Editors. 2018. FishBase. Electronic publication. www.fishbase.org,
590 (Accessed April:2018)
591
592 Ferraro SP, Cole FA (2007) Benthic macrofauna-habitat associations in Willapa Bay, Washington,
593 USA. Estuarine, Coastal and Shelf Science 71:491-507.
594
595 Gillies CL, Creighton C, McLeod IM (2015) Shellfish reef habitats: a synopsis to underpin the
596 repair and conservation of Australia's environmentally, socially and economically important bays
597 and estuaries. Report to the National Environmental Science Programme, Marine Biodiversity
598 Hub. Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER) Publication,
599 James Cook University, Townsville

600
601
602 Gillies, C. L., I. M. McLeod, H. K. Alleway, P. Cook, C. Crawford, C. Creighton, Ben Diggles, J.
603 Ford, P. Hamer, G. Heller-Wagner, E. Lebrault, A. Le Port, K. Russell, M. Sheaves, and B.
604 Warnock. 2018. Australian shellfish ecosystems: Past distribution, current status and future
605 direction. PLoS ONE 13:e0190914.
606
607
608 Grabowski JH, Peterson CH 2007. Restoring oyster reefs to recover ecosystem services. In
609 Cuddington K, Byers JE, Wilson WG, Hastings A eds. Ecosystem engineers: concepts, theory
610 and applications. Netherlands, Elsevier/Academic Press. Pp. 281 298.
611
612
613 Grabowski JH, Brumbaugh RD, Conrad RF, Keeler AG, Opaluch JJ, Peterson CH, Piehler MF,
614 Powers SP, Smyth AR (2012) Economic valuation of ecosystem services provided by oyster
615 reefs. Bioscience 62:900-909
616
617 Hosack GR, Dumbauld BR, Ruesink JL, Armstrong DA (2006) Habitat associations of estuarine
618 species: comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea*
619 *gigas*) habitats. Estuar Coast 29: 1150−1160
620
621 Jones C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as
622 physical ecosystem engineers. Ecology 78, 1946-1957
623
624 Lenihan, H. S., C. H. Peterson, J. E. Byers, J. H. Grabowski, G. W. Thayer, and D. R. Colby.
625 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress.
626 Ecological Applications 11:764–782.
627
628 Coen, L.D., Humphries, A.T. 2017. Oyster-generated marine habitats: Their services,
629 enhancement, restoration and monitoring (2017) Routledge Handbook of Ecological and
630 Environmental Restoration, pp. 27
631
632 Humphries, A. T., M. K. La Peyre, M. E. Kimball, and L. P. Rozas. 2011. Testing the effect of
633 habitat structure and complexity on nekton assemblages using experimental oyster reefs.
634 Journal of Experimental Marine Biology and Ecology 409:172–179.
635
636 IMOS 2017, IMOS - SRS Satellite - SST L3S - 01 day composite - day time, URL:
637 https://portal.aodn.org.au/search, Accessed: 28 November 2017.
638
639 Kirby MX (2004) Fishing down the coast: historical expansion and collapse of oyster fisheries
640 along continental margins. Proceedings of the National Academy of Sciences of the United
641 States of America 101:13096-13099
642

643 La Peyre MK, Furlong J, Brown LA, Piazza BP, Brown K (2014) Oyster reef restoration in the
644 northern Gulf of Mexico: extent, methods and outcomes. Ocean & Coastal Management 89:20–
645 28
646
647 Lenihan HS, Peterson CH (1998) How habitat degradation through fishery disturbance
648 enhances impacts of hypoxia on oyster reefs. Ecol Appl 8:128−140
649
650 Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC,Kidwell SM, Kirby MX,
651 Peterson CH, Jackson JB (2006) Depletion, degradation, and recovery potential of estuaries
652 and coastal seas. Science 312:1806–1809
653
654 McAfee D, Cole VJ, Bishop MJ (2016) Latitudinal gradients in ecosystem engineering by oysters
655 vary across habitats. Ecology 97:929-939
656
657 McLeod I.M., Parsons D.M., Morrison M.A., Van Dijken S.G., Taylor R.B., 2013. Mussel reefs on
658 soft sediments: a severely reduced but important habitat for macroinvertebrates and fishes in
659 New Zealand. NZ Journal of Marine and Freshwater Research 48, 48-59
660
661 Norkko A, Hewitt JE, Thrush SF, Funnell GA (2006) Conditional outcomes of facilitation by a
662 habitat-modifying subtidal bivalve. Ecology 87(1): 226-234
663
664 Norling P, Kautsky N (2007) Structural and functional effects of Mytilus edulis on diversity of
665 associated species and ecosystem functioning. Mar Ecol Prog Ser 351:163-175
666
667 Ogburn DM, White I, Mcphee DP (2007) The disappearance of oyster reefs from eastern
668 Australian estuaries-impact of colonial settlement or mudworm invasion? Coast Manage 35:271-
669 287
670
671 Oksanen, Jari, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan
672 McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H.
673 Stevens, Eduard Szoecs and Helene Wagner (2017). vegan: Community Ecology Package. R
674 package version 2.4-4. https://CRAN.R-project.org/package=vegan
675
676 Oyster Culture Commission (1877) Report of the Royal Commission. New South Wales,
677 Sydney. 101pp.
678
679 Peterson MS, Comyns BH, Hendon JR, Bond PJ, Guff GA (2000) Habitat use by early life-
680 history stages of fishes and crustaceans along a changing estuarine landscape:
681 differences between natural and altered shoreline sites. Wetlands Ecol Manag 8:209−219
682
683 Peterson CH, Kneib RT, Manen CA (2003) Scaling restoration actions in the marine
684 environment to meet quantitative targets of enhanced ecosystems services. Mar Ecol Prog Ser
685 264:173−175
686

687   Peterson CH, Able KW, DeJong CF, Piehler MF, Simenstad CA, Zedler JB (2008) Practical
688   proxies for tidal marsh ecosystem services: application to injury and restoration. Adv Mar Biol
689   54:221−266
690
691   Powers SP, Boyer KE (2014) Marine Restoration Ecology, Ch. 22. In: Bertness MD, Bruno JF,
692   Silliman BR, and Stachowicz JJ (eds) Marine community ecology and conservation. Sinauer
693   Associates, Sunderland, MA
694
695   R Core Team (2017). R: A language and environment for statistical computing. R Foundation for
696   Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
697
698   Rueden, C. T.; Schindelin, J. & Hiner, M. C. et al. (2017), "ImageJ2: ImageJ for the next
699   generation of scientific image data", BMC Bioinformatics 18:529, doi:10.1186/s12859-017-1934-
700   z.
701
702   Schulte DM (2017) History of the Virginia oyster fishery, Chesapeake Bay, USA. Frontiers in
703   Marine Science 127.
704
705   Taylor RT (1998) Density, biomass and productivity of animals in four subtidal rocky reef
706   habitats: The importance of small mobile invertebrates. Mar Ecol Prog 172:37-51
707
708   Wong, M. C., C. H. Peterson, and M. F. Piehler (2011). Evaluating estuarine habitats using
709   secondary production as a proxy for food web support. Marine Ecology Progress Series
710   440:11–25.
711
712   zu Ermgassen PM, Hancock B, DeAngelis B, Greene J, Schuster E, Spalding M, Brumbaugh R
713   (2016) Setting objectives for oyster habitat restoration using ecosystem services: A manager's
714   guide. The Nature Conservancy, Arlington VA
715
716
717

718

719