



# De novo reefs: Fish habitat provision by oyster aquaculture varies with farming method

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**ABSTRACT:** Aquaculture industries have the capacity to produce positive ecosystem service benefits, such as the provision of habitat to wild animals. Oyster cultivation is the oldest and largest aquaculture industry in south-eastern Australia. Oyster spat are grown to marketable size in rack-and-rail ('racks') or longline-and-basket ('baskets') configurations, which add structure to estuarine waters. This study assessed: (1) how the fish communities associated with oyster farms vary with production method; (2) how communities of fish utilise oyster infrastructure, as compared to adjacent natural habitats; and (3) whether oyster infrastructure can serve as de facto oyster reefs by supporting similar fish communities. Remote underwater video surveys, conducted during summer and winter of 2 study years, revealed that fish observations and species richness were generally greater for rack than basket cultivation. Both types of oyster farms supported at least as many species of fish as adjacent natural habitats, including oyster reef, seagrass, mangrove and bare sediment. Fish communities were, in general, most similar between racks and baskets and most dissimilar between racks and bare sediments. Oyster farms supported species of fish otherwise limited to habitats with wild oysters, and unique harvested fish species were observed more frequently at racks. Fish use of oyster-growing infrastructure for foraging and shelter mirrored use of natural biogenic habitats. Overall, this study suggests that the oyster aquaculture infrastructure can support fish communities with species composition similar to those of natural biogenic habitats, although this service is dependent on farming method. Ecosystem services provided by aquaculture should be considered in estuarine habitat enhancement, conservation and restoration.

**KEY WORDS:** Estuary · Fish · Habitat · Seagrass · Oyster · Reef · Remote underwater video · RUV · Shellfish · Artificial structure

## 1. INTRODUCTION

There is increasing recognition that agro- as well as natural ecosystems can provide ecosystem services that extend far beyond the provision of the goods for which they were established (Alleway et al. 2019, van der Schatte Olivier et al. 2020). Besides food production, coastal aquaculture has the capacity to produce a range of other provisioning (e.g. production of raw materials, pharmaceuticals), as well as regulating

(e.g. wave attenuation, carbon sequestration, water filtration), cultural (e.g. tourism, recreation, employment) and supporting services (e.g. habitat provision, genetic diversity) (Alleway et al. 2019, Gentry et al. 2020, Theuerkauf et al. 2022). Provision of these services is likely dependent on the biological and physico-chemical environment in which the aquaculture is occurring, farm design, operational standards, stocking densities, stock rotation and maintenance (Alleway et al. 2019, Gentry et al. 2020, Theuerkauf

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et al. 2022). As aquaculture industries continue to expand in the coastal zone, there is a need to actively plan aquaculture sites with the objective of enhancing services (over and above food production) that benefit a range of coastal stakeholders (Froehlich et al. 2017, Theuerkauf et al. 2019).

The pens, cages, baskets and other infrastructure utilised by aquaculture operations provide food and habitat to fish communities (Dealteris et al. 2004, Glenn 2016, Callier et al. 2018). These structures provide substrate for attachment and growth of fouling organisms which, in turn, can provide food and shelter to finfish (Tallman & Forrester 2007, van der Schatte Olivier et al. 2020). Fish may also be attracted or repelled by the cultivated species itself, according to whether it is a predator or prey item or a species that modifies the availability of resources (e.g. organic matter; Callier et al. 2018). Consequently, aquatic farms can support similar abundances of fish and invertebrates as natural habitats (Tallman & Forrester 2007, Glenn 2016, Mercaldo-Allen et al. 2020, Shinn et al. 2021). The role of aquaculture farms in providing habitat may be particularly important in environments where conditions no longer support complex natural habitats (e.g. oyster and coral reefs, seagrass, mangroves, saltmarsh) or where these habitats have been damaged or degraded by human activities (Nell 2001, Buestel et al. 2009, Schulte 2017).

Oyster reefs were once an abundant and conspicuous component of estuarine and coastal seascapes globally, but largely due to historical overharvesting, have been reduced to <15% of their 1700–1800s abundance (Beck et al. 2011, Zu Ermgassen et al. 2012). This loss has not only resulted in the widespread closure of wild-harvest oyster fisheries once supported by this habitat, but also loss of other associated ecosystem services, including provision of habitat to fish and invertebrates, nutrient cycling, water filtration, shoreline stabilisation and wave attenuation (Grabowski & Peterson 2007, Gillies et al. 2018). The oyster aquaculture industries that have replaced wild harvest are generally situated in intertidal or shallow-water estuarine environments in which oyster reefs and other structured marine habitats (e.g. seagrass) were once common but have similarly faced decline (Walker & McComb 1992, Orth et al. 2006). Oysters produced in hatcheries, or wild caught in estuaries, are typically grown in cages, racks, trays and baskets to marketable size. This infrastructure may be suspended above unvegetated soft-bottom or seagrass beds and located within an estuarine mosaic habitat that, depending on geographic location, may include remnant (i.e. persisting or recovered) oyster reefs,

seagrass beds, mangrove forests, saltmarshes and/or mud/sand flats.

The infrastructure provided by oyster farms can support communities of invertebrates and fishes with similar, or in some instances, greater biomass and abundance than adjacent habitats, including rocky reef, seagrass beds, mudflats and oyster reefs (Glenn 2016, Coe 2019, Mercaldo-Allen et al. 2020, 2021, Muething et al. 2020, Munsch et al. 2021). However, how this service of oyster farms varies as a function of farming methodology is poorly understood (but see Theuerkauf et al. 2022 for a meta-analysis addressing this question). Differential effects of farm gear may be expected both as a direct effect of variation in their structure as well as their positive or negative effects on adjacent, ecologically connected habitats, underlying habitats and the extent to which they modify environment conditions such as flow and wave exposure (Dumbauld et al. 2009). For example, whereas racks have been demonstrated to produce negative impacts on underlying seagrass through shading (Forrest et al. 2009, Skinner et al. 2014), similar impacts have not been reported for baskets (Bulmer et al. 2012). Understanding how farming methodology influences the provision of habitat to fish is critical in designing multi-purpose aquaculture facilities that provide supporting, provisional and regulating benefits that extend beyond the primary goal of food production (Alleway et al. 2019, van der Schatte Olivier et al. 2020).

Here, we determined the habitat value for fish communities of 2 different off-bottom oyster farming methods: the traditional rack-and-rail method ('racks') and the modern longlines-with-baskets ('baskets') method, that are set within a mosaic of natural habitats (remnant oyster reefs, seagrasses, mangroves and bare sediment) in Australian waters. To assess whether these farming methods can serve as *de facto* habitats in terms of fish provisioning, the fish communities of both farming methods were compared to those of adjacent remnant oyster reefs, seagrasses, mangroves and bare sediment. We hypothesised that farms using baskets would support a more abundant and species-rich fish community than the farms using racks because they have less impact on the seagrass habitats directly below and, as a result, add additional habitat structure. Consequently, we also expected that farms using baskets would support fish communities that are more similar to those of seagrass beds, which are able to persist below their structures, than other adjacent natural habitats. By contrast, we expected that farms using racks would support fish communities that are more similar to those of oyster reefs

than the other habitats, as they provide a large area of hard structure over bare sediment, which may attract fish species common in oyster reefs. We further expected that feeding activity of fish would be proportionately higher on rack infrastructure and at oyster reefs than in other habitats, due to the greater availability of hard substrate for development of fouling communities on which fish can feed.

## 2. MATERIALS AND METHODS

### 2.1. Study location

The study was conducted at 2 sites within the Port Stephens estuary in New South Wales (NSW), Australia: Corrie Island (32° 40' 41" S, 152° 7' 16" E) and Soldiers Point (32° 42' 14" S, 152° 3' 28" E; Fig. 1). Both sites (0.5 to 1 km<sup>2</sup> in area) comprised a mosaic of intertidal and shallow habitats (mean low water

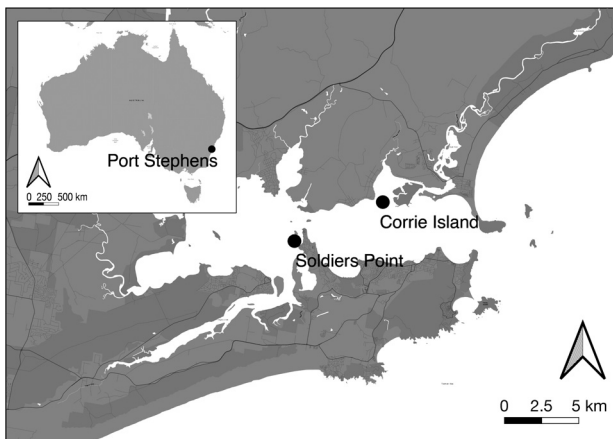


Fig. 1. Sampling sites in Port Stephens estuary, New South Wales, Australia

[MLW] +0.6 to -2.0 m) in which oyster aquaculture overlapped with natural oyster reefs, seagrass beds, mangroves and bare sediment habitats. Remnant intertidal oyster reefs (MLW +0.6 to -0.1) were formed of live Sydney rock oysters *Saccostrea glomerata* that had settled onto a dead shell base to create 3-dimensional structures (reef patches) that extended 53–500 mm above the sediment surface, with a cover of 43–65% of live oysters (McLeod et al. 2020). Reef patches varied in size (7 to 1300 m<sup>2</sup>) and were interspersed within a soft sediment matrix covering an area ranging from 8000 to 9000 m<sup>2</sup>. Oyster reefs were surrounded by intertidal to shallow subtidal (MLW +0.1 to -0.1) soft sediment flats, predominantly a mixture of sand and mud, which covered an area of at least 400 m<sup>2</sup>. Seagrass beds were continuous patches of shallow subtidal (MLW -0.5 to -2.0) *Posidonia australis*, covering a minimum area of 100 000 m<sup>2</sup>, and mangrove forests (MLW +0.6 to +0.2) were dominated by mature grey mangroves *Avicennia marina* of at least 9600 m<sup>2</sup>.

At each site, oyster farms using rack-and-rail and longlines-with-basket cultivation systems were present. Racks consisted of mesh-covered trays of oysters sitting on 2 parallel wooden rails, and basket systems consisted of baskets with oysters attached to horizontal longlines (Fig. 2) (Nell 1993, 2001). Intertidal racks were historically the dominant method of oyster cultivation in NSW estuaries because the low tide drying of oysters reduces infestation by mud-worm (*Polydora* spp.) and other fouling organisms (Nell 1993, 2001). However, in recent years, cultivation has shifted to floating baskets due to a desire to reduce shading impacts to seagrass and to increase growth rates through a greater immersion time (Nell 2001). At Corrie Island, baskets were situated above unstructured bare sediment (extending from MLW +0.6

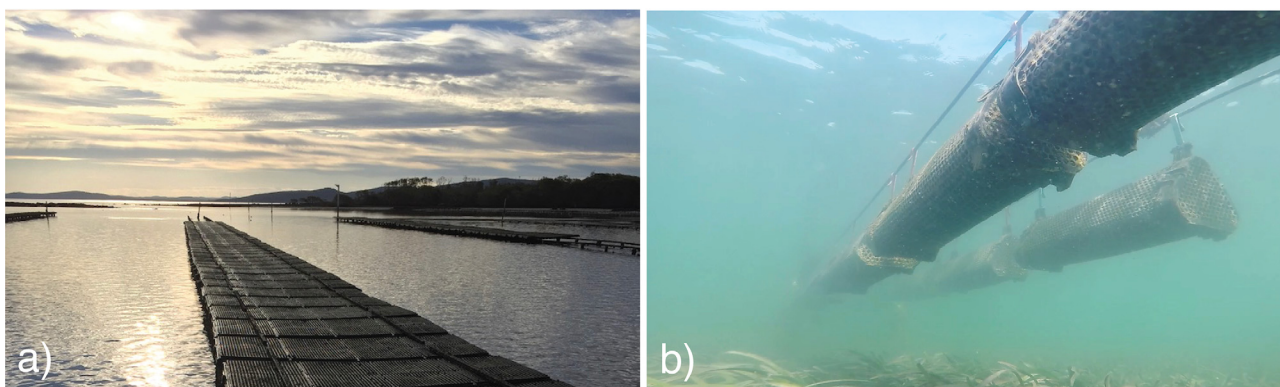


Fig. 2. Examples of oyster farm (a) rack-and-rail and (b) longlines-and-basket infrastructure in Port Stephens, New South Wales, Australia (source: F. Martínez-Baena)

to +0.4), while at Soldiers Point, they were positioned above a continuous patch of seagrass (*P. australis*) (MLW +0.6 to –2.0). At both sites, racks were situated within seagrass beds (*P. australis*; MLW +0.6 to –2.0), although the area directly underneath each rack was denuded of seagrass and instead comprised sediment with a mix of shell and wood debris and winter growth of *Sargassum* sp. All sampling occurred during daylight hours within 1.5 h of the high tide, when all habitats were covered by 1–3 m of water.

## 2.2. Sampling

Sampling of each site was conducted on 3 days during the winter and the summer of 2 consecutive years (2017–2019). Within seasons, sites were sampled on different, temporally interspersed days when wind speeds were less than 10 knots. On each day of sampling, 4 unbaited remote underwater cameras (GoPro hero 4, Silver Edition) were haphazardly deployed within each of the 6 habitats (2 farm types, 4 natural habitats) per site, to give a total of 24 simultaneously deployed cameras per site. Cameras were deployed with a minimum distance of 10 m from each other, when possible, in different patches of the same habitat, and at least 20 m from other habitats. Cameras faced toward the habitat they were targeting and faced away from the sun to eliminate glare. Each camera was mounted on a metal frame that held it 25 cm off the sediment surface, ensuring unobstructed fields of view. Cameras recorded video footage for 1 h and 25 min, with the first and last 5 min of each video excluded from analysis, to eliminate disturbances caused by the deployment and retrieval. This left 75 min of footage per camera deployment for analysis. Visibility was measured at each site on each day with a turbidity tube, consisting of a 1.2 m long and 4.5 cm diameter sealed polycarbonate tube with a Secchi disc at the bottom. The tube was filled with water and visibility was categorised as either: <0.8, 0.8–1, 1–1.1 or >1.2 m. Sampling did not proceed when visibility was less than 0.8 m.

## 2.3. Video analysis

Raw footage from each camera deployment was compiled into a 75 min video and colour-enhanced with Adobe After Effects and Adobe Encoder (Adobe®). To quantify fish communities and behaviour, each video was then reviewed using Event-Measure software (SeaGIS).

To compare fish communities among habitats, for each video, we calculated species richness, total observations of fish individuals and total observations of fish individuals grouped by species. Species richness was the total number of different species recorded per camera. The number of observations was determined by summing the total number of times a fish entered the frame, for a given camera, across all species. To avoid over-inflating observations for highly mobile reef species, individual fish that swam into and out of the frame multiple times within a span of 20 s (apparent by their exit/entrance from a similar point in the frame) were counted only once. To reduce the influence of shoaling species (i.e. species that are found in groups comprising many individuals) on analyses, we counted any group of individuals of the same species that entered a frame simultaneously as one observation. This ensured that species had comparative weighting in terms of their observations. Observations were considered as a relative measure of the presence of the species within the habitat (Lanham et al. 2021) and were used instead of the relative abundance measure MaxN (Cappo et al. 2004).

To assess any differences in how fish used the habitats, every fish that appeared in a frame was assigned 1 of 4 main behaviours: passing, wandering, feeding and chasing. An individual was counted as ‘passing’ when it passed with a constant speed through the habitat and no interest was shown in it. ‘Wandering’ was scored when the fish changed constantly in speed and direction with an apparent interest in the habitat, whether looking for food, refuge or just swimming slowly around the habitat. ‘Feeding’ was recorded when an individual was directly feeding in the habitat, on another animal, alga or plant, or just picking at the substrate. ‘Chasing’ was reported when an individual actively chased another individual of the same or a different species. Scoring of behaviours was annotated with each fish observation captured in EventMeasure and then reported in a similar fashion as were observations, with the exception that if different individuals within a shoal exhibited different behaviours, an observation per behaviour was noted for that shoal.

## 2.4. Data analysis

Differences in fish community structure were assessed using permutational multivariate analysis of variance (PERMANOVA; in PRIMER v.7.0.11, Anderson et al. 2008) with Bray-Curtis dissimilarities calcu-



lated for the matrix of species observations. The analysis, run on untransformed data, had 5 factors: Habitat (6 levels, fixed: racks, baskets, oyster reefs, seagrass, mangroves and bare); Site (2 levels, random: Corrie Island and Soldiers Point); year (2 levels, random: 1 and 2); season (2 levels, fixed: winter and summer); and day (3 levels and random, nested within year  $\times$  season  $\times$  site). A dummy variable of 1 was added to each sample prior to analysis to facilitate inclusion of samples containing no fish (Clarke et al. 2006). Statistically significant interactions (at  $\alpha = 0.05$ ) were further examined using pairwise *a posteriori* PERMANOVAs. Where the number of possible permutations of the data was less than 100, *a posteriori* tests used Monte-Carlo p-values (Anderson et al. 2008).

A distance-based redundancy analysis (Legendre & Anderson 1999) was used to identify the fish species that contributed most to the relationships between significant factors. A Bray-Curtis similarity matrix was also produced using the 'capscale' function ('vegan' package v. 2.5-7 in R v. 4.0.2, Oksanen et al. 2020, R Core Team 2019). Significant factors in the previous PERMANOVA were included in the model and a permutational test assessed statistical significance of canonical axes produced by the dbRDA, and the triplot was made. For clarity, only species that were positioned  $\pm 0.5$  along either axis were plotted.

Univariate linear mixed effects models using square-root transformed data ('lme4' package v. 1.1-27.1 in R, Bates et al. 2015) were used to evaluate the following metrics: (1) total number of fish observations; (2) total species richness; (3) species-specific observations of 5 abundant fish species of commercial or recreational value that were found in the study: yellowfin bream *Acanthopagrus australis*, luderick *Girella tricuspidata*, silverbiddy *Gerres subfasciatus*, whiting *Sillago ciliata* and mulloway *Argyrosomus japonicus* (NSW DPI 2020); (4) the relative percentage of total feeding observations per sampling day; (5) the relative percentage of total wandering observations per sampling day; and (6) the relative percentage of total passing observations per sampling day. Chasing behaviour was not analysed, as it was determined to be a behaviour that commonly occurred at scales greater than the habitat observed by a camera. These models included the same 5 factors as the community analyses but with Year, Season and Site treated as fixed effects because linear mixed effects models require at least 5 'levels' for a random intercept to achieve a robust estimate of variance (Harrison et al. 2018). Day, which was nested in Site, Season and Year, was considered a random factor, with all possi-

ble combinations of this with the other factors producing 24 levels. After running a full model with all factors and their interactions, we tested the significance of the fixed factors and their interactions with an ANOVA and the significance of the random factors using the 'ranova' function ('LmerTest' package v.3.1-3 in R, Kuznetsova et al. 2017). After each analysis, models were checked visually to confirm that in all instances their residuals conformed with the assumptions of normality. Post hoc pairwise comparisons identified sources of any significant effect of habitat using the 'emmeans' function ('emmeans' package v.1.7.1-1 in R, Lenth 2021). Where habitat displayed a significant interaction with other factors, we tested for differences between habitats within levels of the other factors.

### 3. RESULTS

A total of 510 videos, totalling 586.5 h of footage, could be analysed, after cameras that had failed to record, had tipped over or had footage that was obstructed in some way were excluded. Of the analysed videos, 96 focussed on the farms with baskets, 95 on the farms using racks, 83 on the oyster reefs, 82 on the seagrass, 79 on the mangroves and 75 on the bare sediment.

#### 3.1. Fish community structure

A total of 90 species of fish from 51 families were observed in this study (Table S1 in the Supplement at [www.int-res.com/articles/suppl/q014p071\\_supp.pdf](http://www.int-res.com/articles/suppl/q014p071_supp.pdf)). Fifty species were associated with racks, of which 10 were unique to this habitat; 45 with baskets, of which 3 were unique; 54 with oyster reefs of which 6 were unique; 43 with seagrasses, of which 8 were unique; 29 with mangroves, of which 1 was unique; and 36 with bare sediment, of which 3 were unique. A total of 11 species were observed across all 6 habitats (Table S2).

In general, racks and baskets supported more similar fish communities than other habitat contrasts, and racks and bare sediments were the most dissimilar (Table S3). In summer, communities at each site did not significantly differ between baskets and racks, and at Corrie Island did not differ between racks and oyster reefs. In winter, communities at both sites were statistically indistinguishable between mangroves and oyster reefs and at Soldiers Point between seagrass and baskets. Additionally, mangroves and

oyster reefs also supported similar fish communities at Corrie Island in the second year. In all other instances, fish communities significantly differed among habitats, within each site, season and year (Table S3).

The 3 species that contributed most to differences in community structure among habitats were yellowfin bream, oyster blenny *Omobranchus anolius* and luderick (Fig. 3). Bream, oyster blenny and rotund blenny *O. rotundiceps* were species that characterised oyster reefs and mangroves, while luderick were associated with racks and baskets. Stripey *Microcanthus strigatus*, silverbiddy and three-barred porcupinefish *Dicotylichthis punctulatus* were associated with racks, baskets and oyster reefs. Trumpeter *Pelates sexlineatus* was one of the species most frequently observed in seagrass, but was also associated with oyster farms (Fig. 3).

The total number of fish observations was generally greater for racks than baskets except for Corrie Island in the summer of the first year and Soldiers Point in the summer of the second year, when racks and baskets had similar observations (4-way interaction among habitat, site, season and year; Fig. 4; Table S4). In summer, racks and oyster reefs generally had similarly high observations, that were greater than those in other natural habitats (seagrass, mangrove, bare sediment). However, at Corrie Island in the second year, oyster reefs had fewer observations than racks. In winter, racks generally supported more observations than baskets, and more than oyster reefs, which was the natural habitat with generally highest observations during this season. In general, fewer fish observations were made for baskets than oyster reefs, and this number was similar to that in other structured mangrove and seagrass habitats which was greater than that in bare sediment (Fig. 4; Table S4).

Species richness generally did not differ between racks and baskets, except in summer at Corrie Island, where racks had greater richness (3-way interaction between habitat, site and season; Fig. 5; Table S5). Species richness was also generally similar between farms and natural habitats. Racks only had a higher species richness than natural habitats in summer at Corrie Island, and generally supported similar richness to structured natural habi-

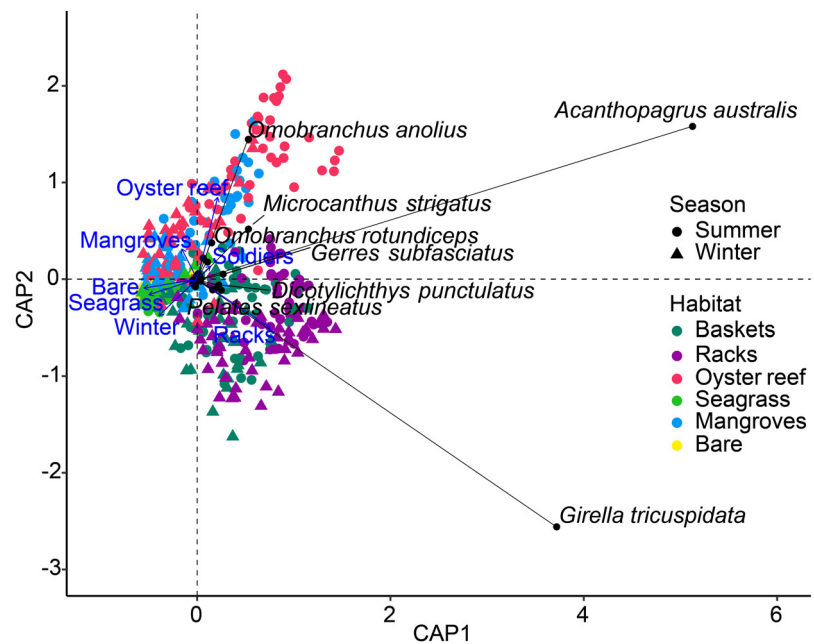


Fig. 3. Distance-based redundancy analysis triplot of transformed fish observations data across 4 habitats, sites and seasons. Species exceeding a critical value of  $\pm 0.5$  on one of canonical axes CAP1 and CAP2 axes are indicated. Points represent individual videos

tats, including oyster reefs. At Corrie Island, baskets had a similar species richness to oyster reefs in both summer and winter, but at Soldiers Point, baskets had lower species richness than oyster reefs in both seasons (Fig. 5; Table S5).

### 3.2. Species-specific distributions

The commercially and recreationally important species yellowfin bream, luderick, silverbiddy, whiting and mulloway together accounted for 72 % of the total number of observations recorded in this study.

Bream were the most common fish, accounting for 42 % of total fish observations. Bream were observed more often in association with racks than baskets, with racks generally having similar numbers of observations to oyster reefs (3-way interaction among habitat, site and season; Fig. 6; Table S6). Baskets generally supported similar numbers of bream as in mangroves and greater numbers than at seagrass or bare sediment (Fig. 6).

Luderick accounted for 24 % of total fish observations and were more frequently observed in farmed than natural habitats, and among racks than baskets, although the latter difference was not always significant (4-way interaction among habitat, site, season and year; Table S7, Fig. S1).

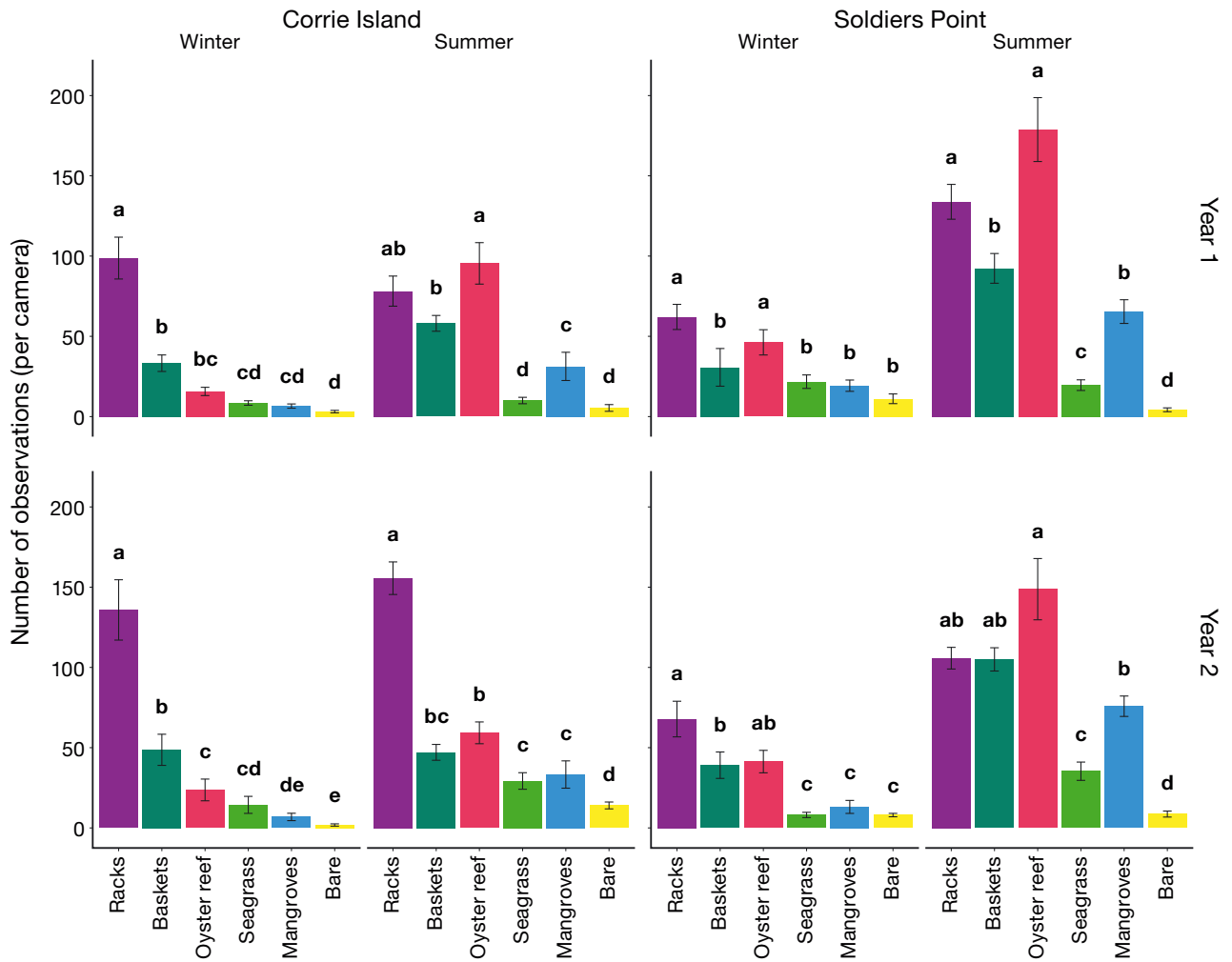


Fig. 4. Mean ( $\pm$ SE) fish observations, per habitat site, season and year as documented by 75 min remote underwater video deployments ( $n = 48$ ). Letters above columns denote treatments that were significantly different (at  $\alpha = 0.05$ ) within each year, site and season by estimated marginal means

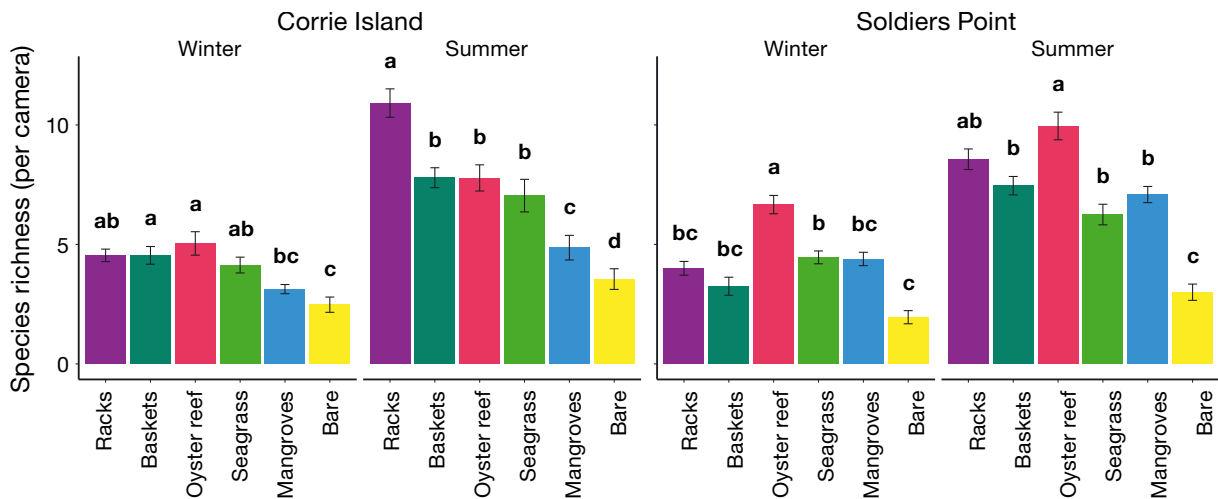


Fig. 5. Mean ( $\pm$ SE) species richness per habitat, site and season as documented by 75 min remote underwater video deployments. Data are averaged across the 2 study years, as these did not significantly differ, with 4 cameras deployed on 3 replicate days of each season and year, to give  $n = 24$ . Letters above columns denote treatments that were significantly different (at  $\alpha = 0.05$ ) within each site and season by estimated marginal means

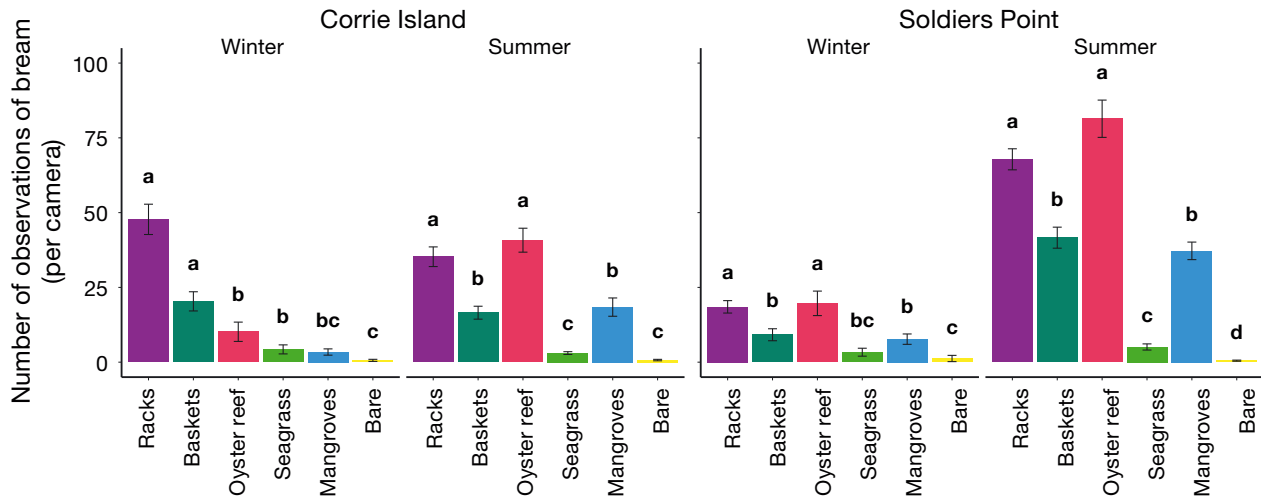


Fig. 6. Mean ( $\pm$ SE) observations of bream as documented by 75 min remote underwater video deployments. Data are averaged across the 2 study years, as these did not significantly differ, with 4 cameras deployed on 3 replicate days of each season and year, to give  $n = 24$ . Letters above columns denote treatments that were significantly different (at  $\alpha = 0.05$ ) within each site and season by estimated marginal means

Silverbiddy accounted for 3% of the total fish observations. In winter, the number of silverbiddy observed did not differ among any of the habitats, but in summer, racks had greater observations than any of the other habitats (interaction present between habitat and season; Table S8, Fig. S2).

Whiting, which accounted for 3% of fish observations, were generally more abundant in bare sediment than in any of the other habitats (Table S9, Fig. S3). Of the remaining 5 habitats, racks and baskets generally supported the next greatest number of whiting observations, although this varied with season and year (Fig. S3).

Mulloway accounted for 0.74% of the total observations and displayed the greatest habitat and site fidelity over each season and year of the 5 species examined (4-way interaction among habitat, site, season and year; Table S10, Fig. S4). Mulloway were exclusively found at Corrie Island and generally only around racks, with the exception of a few observations recorded in seagrass in winter of the first year (Fig. S4).

### 3.3. Fish behaviour

Wandering accounted for 80% of documented fish behaviours, feeding for 11%, passing for 8% and chasing for 1%. Among the 90 species recorded in this study, 84 species exhibited wandering behaviour, 40 species exhibited feeding behaviour, and 51 species exhibited passing behaviour. The relative percentage of fish that were observed wandering

was generally greater in structured natural habitats (i.e. seagrass, mangrove, oyster reef) and oyster farms (both rack and baskets), among which there were few differences, than in unstructured (bare) habitats (Fig. 7; Table S11). The relative percentage of observations attributed to feeding behaviour only differed among habitats and sites in winter (3-way interaction between habitat, site and season; Fig. 7; Table S12). At Corrie Island in winter, a greater percentage of fish were observed feeding on oyster reefs and baskets than on seagrass or bare sediment, although these percentages did not significantly differ from mangroves and racks. At Soldiers Point, the highest percentage of fish feeding was observed on bare sediment, though this was only significantly greater than feeding percentages observed for racks and baskets, but not the other natural habitats. The percentage of fish observed passing was greater for bare sediment than the other habitats at each of the sites and in both seasons (3-way interaction between habitat, site and season; Fig. 7; Table S13).

## 4. DISCUSSION

In Australia, and globally, oyster reefs have been greatly reduced over the last 2 centuries, primarily due to over-harvest and destructive fishing practices that removed live oysters and the reef shell matrix, but also due to diseases (Beck et al. 2011, Zu Ermgassen et al. 2012, Gillies et al. 2018). In environments where natural ecosystems have been destroyed, damaged or degraded, off-bottom aquaculture infra-



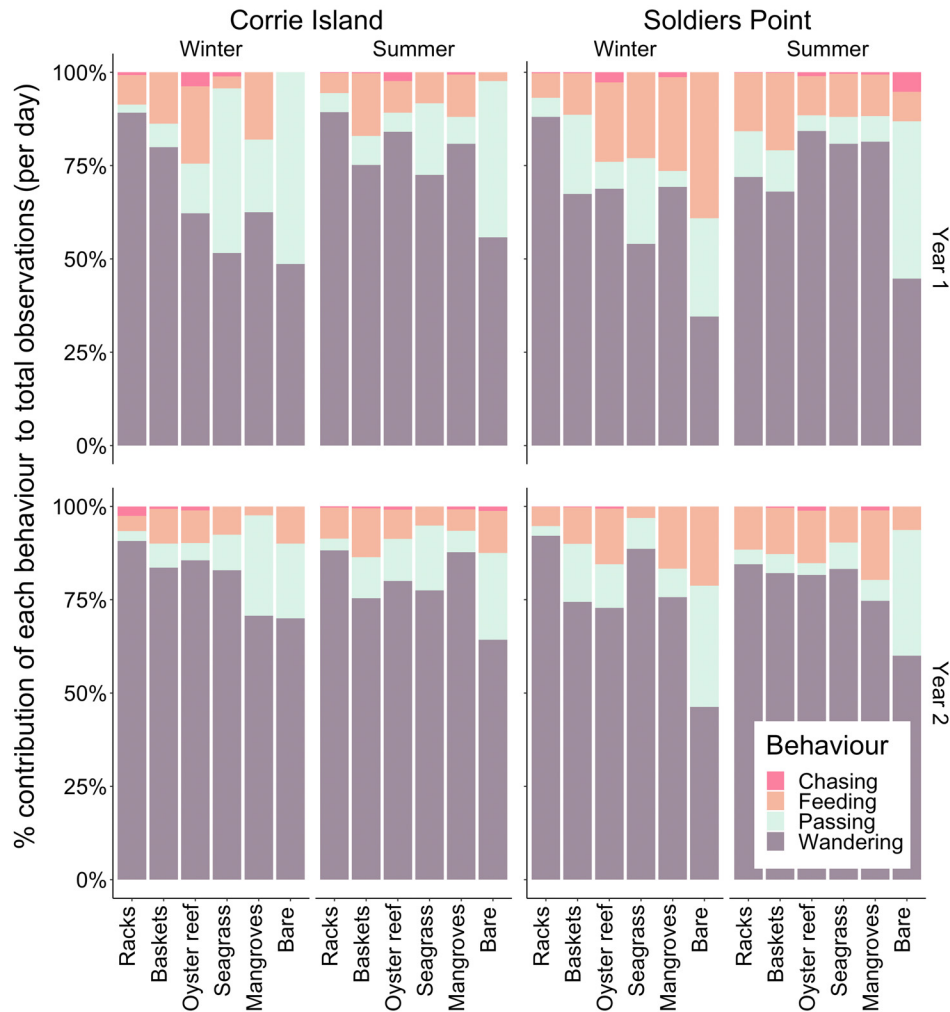


Fig. 7. Mean percentage contribution of each behaviour to total observations recorded during 75 min remote underwater video deployments for each habitat, site, season and year ( $n = 64$ )

structure can serve as important habitat to wild organisms, and there is growing evidence that off-bottom shellfish aquaculture can provide important fish habitat (Dealeris et al. 2004, Mercaldo-Allen et al. 2020, 2021, Muething et al. 2020, Ferriss et al. 2021) and trophic resources (Lefcheck et al. 2019). Yet, uncertainty surrounding the impact of farm and infrastructure type on habitat provisioning functions remains a major knowledge gap which could inhibit the development of multifunctional shellfish aquaculture. We found that both rack and basket oyster farms supported fish communities that were generally more diverse than those in adjacent unstructured open sediment habitats and often more diverse than those in adjacent complex biogenic estuarine habitats. Although the 2 types of oyster farms displayed fish communities more similar to one another than to adjacent natural habitats, more fish were generally observed at racks than baskets. Fish appeared to use

oyster farms for feeding and shelter in similar ways to adjacent natural structural habitats, and more frequently than unstructured habitat, where fish were more commonly observed just passing through without any interaction. The similarity between fish communities and their behaviourally inferred engagement with racks and remnant oyster reefs suggests that appropriately designed oyster farms could serve some of the habitat functions of oyster reefs in areas where oyster reefs have been driven to functional extinction (Gillies et al. 2020).

In NSW, the depletion of natural oyster reefs was followed by the rise of oyster aquaculture, often in areas once supporting natural oyster reefs (Nell 1993). Oyster farming remains the largest aquaculture industry in NSW, spanning 41 estuaries, 3200 leases and 4300 ha (Schrobback et al. 2014, NSW DPI 2017). The similarity in fish communities between remnant oyster reefs and oyster racks suggests that

this increase in oyster infrastructure has supported species that are associated with oyster reefs, despite degradation of this primary habitat (Beck et al. 2011, Gillies et al. 2018). Important crypto-benthic fish like oyster gobies and blennies found only on oyster reefs or in mangrove forests inhabited by oysters, were also found around racks and baskets. While there is growing interest and investment in oyster reef restoration in Australia (Gillies et al. 2015, McAfee et al. 2020), it is possible that in environments unsuitable for oyster reef restoration (e.g. as a consequence of conflicting human uses of estuaries, or unstable bottom types), oyster farms may provide many of the same habitat functions (Lefcheck et al. 2021). However, further studies addressing the extent to which 'enhancement' reflects increased fisheries production, as opposed to attraction of fish away from neighbouring habitats, would first be required. Artificial structures may act as ecological 'traps', with negative ecological consequences, if the species they attract suffer reduced fitness (Swearer et al. 2021).

Despite the similarities in species of fish that are associated with oyster racks and reefs, there were also notable differences. In particular, mulloway and luderick were more frequently observed around racks than oyster reefs. The differing utilisation of the 2 habitats by these species may reflect differences in food availability as well as habitat quality. Mulloway feed on juvenile fishes and crustaceans, such as shrimp, that can be locally enhanced by shellfish farming (Hosack et al. 2006, Taylor et al. 2006a, Dumbauld et al. 2015). Luderick feed on macroalgae such as *Enteromorpha* spp. and *Ulva* spp., that foul low intertidal and shallow subtidal hard substrate such as that provided by the wooden beams and posts of rack-and-rail farms (Anderson & Connell 1999, Forrest et al. 2009). These macroalgal species are rare on intertidal reefs that are subject to drying at low tide (F. Martínez-Baena pers. obs.). Additionally, mulloway and luderick, which can exhibit strong site fidelity to subtidal reefs (Ferguson et al. 2013) and/or habitat features (Taylor et al. 2006b), may be responding to the availability of permanently inundated habitat beneath racks. Individuals associated with intertidal oyster reefs, by contrast, would need to migrate to deeper habitats at low tide.

The greater number of observations, and in some instances species, associated with racks than baskets, may have reflected differences in the habitat structure created by the 2 farming methods, their environmental context and their effect on the surrounding habitat. As compared to the relatively slender construct of longlines, flat racks introduce a

greater surface area of artificial habitat. The greater surface area of racks may allow colonisation by a greater biomass of epibenthic and encrusting organisms which in turn provide greater habitat area and foraging opportunities to fish (Dealteris et al. 2004, Ozbay et al. 2014, McLeod et al. 2020, Mercaldo-Allen et al. 2020).

Differences in the fish communities between the 2 farming methods may also relate to differences in their degree of shading and/or effects on underlying benthic habitat. Shading can prevent survival of seagrasses on the substrate below human infrastructure (Thorne 1998, Ferriss et al. 2019). Along with habitat damage through boat mooring scars, shading, primarily from piers and jetties, has been cited amongst the factors leading to *Posidonia australis* seagrass decline in NSW, where the ecological communities formed by *P. australis* are listed as endangered in 6 estuaries (Fitzpatrick & Kirkman 1995, Glasby & West 2015, Evans et al. 2018). Besides this indirect effect of shading on fish communities, shading by piers and over-water artificial structures may produce direct negative effects on fish communities, diminishing abundances and richness (Southard et al. 2006, Able et al. 2013, Munsch et al. 2017). Nonetheless, a certain degree of shading created by some natural habitats, such as mangroves, can have positive effects on fish communities, especially juvenile fish looking for refuge and shelter (Cocheret de la Morinière et al. 2004, Ellis & Bell 2004, Verweij et al. 2006). As racks are formed by mesh-like plastic trays, a degree of light is able to enter through them at all times, which can be similar to the degree of shading created by a mangrove forest canopy (Fig. 8). Minimising negative impacts to remnant seagrass beds is a key consideration in selecting among aquaculture methods, and has contributed to a shift by the industry from rack to basket cultivation (Bulmer et al. 2012).

Differences in the habitat directly below oyster infrastructure may also have contributed to differences in fish communities observed between the 2 farming methods. The underlying habitat found beneath the racks was mostly bare, in some instances also with seasonal *Sargassum* spp. algae, and with woody and shell debris. By contrast, the underlying habitat beneath baskets was seagrass, bare or bare with woody and shell debris. As predicted from differences in the underlying habitat, the fish communities and richness associated with baskets were generally more similar to those of seagrass habitats than were the communities associated with racks. However, fish observations were higher for baskets than seagrass, perhaps reflecting the additional complex-



Fig. 8. Photographs of (a) mangrove forests and (b) rack aquaculture systems at Port Stephens (source: F. Martínez-Baena)

ity that baskets add to the underlying habitat. Previous studies have likewise found similar invertebrate and fish communities between seagrasses and longline farms and between seagrasses and longlines with flipbag farms (Coe 2019, Muething et al. 2020, Munsch et al. 2021), although in some instances, longlines supported higher abundances but lower richness of fish than seagrass habitats (Dealteris et al. 2004, Glenn 2016).

Despite mangroves also providing a greater extent of hard substrate and habitat complexity and similar shading as racks, our study found greater fish observations and richness in oyster farms than mangroves. Few other studies have compared ecological communities among oyster farms, natural oyster reefs and mangroves, which remains a major research gap. Erbland & Ozbay (2008) compared macrofaunal communities between oyster cages and a restored oyster reef, finding higher richness and abundances in oyster cages. Although not directly considering oyster reefs, Mercaldo-Allen et al. (2020) found similarities in the finfish communities of an oyster farm and an adjacent rocky reef. The structural complexity of oyster farms may benefit finfish populations by increasing the abundance of, and therefore feeding opportunities on, invertebrates living on or below the racks and/or by providing fish with refuge from larger predators (O'Beirn et al. 2004). Further studies would be required to disentangle the mechanisms by which the 2 farm types support differing fish communities, and to distinguish between their role in attracting fish away from other neighbouring habitats versus enhancing fisheries productivity. These might in-

clude isotopic studies, documenting trophic linkages, movement studies involving acoustic tagging, as well as demographic studies, documenting population structure, using direct (otoliths) or indirect (size) aging techniques.

Previous studies that have found that shellfish farms can provide food and habitat to commercially important fish have come predominantly from Europe and the Americas (Dealteris et al. 2004, Erbland & Ozbay 2008, Muething et al. 2020, Ferriss et al. 2021, Theuerkauf et al. 2022). This study similarly documents that oyster farms provide important fish habitat in Australia. The role of oyster farms in providing habitat to fish extended beyond small benthocryptic species to commercially and recreationally important species that used farms as sites for foraging and refuge. Bream, luderick, silverbiddy, whiting and mulloway, which collectively account for 21% of the total commercial and recreational estuarine fisheries landings by weight in NSW (NSW DPI 2003, 2020), were observed in greater or equal numbers on rack and basket farms than in adjacent natural habitats (or specifically in just racks as was the case for mulloway). Local recreational community groups are aware of the value of oyster aquaculture infrastructure as hotspots for fishing (F. Martínez-Baena pers. obs.), but further evidence of the benefits of oyster aquaculture for enhancing recreational fishing activities is needed.

The majority of environmental studies on aquaculture industries continue to focus on negative impacts associated with intensive operations (Gentry et al. 2020). Our study contributes to a growing body of

research demonstrating that aquaculture, and specifically, shellfish cultivation, can provide considerable environmental benefits (Froehlich et al. 2017, Alleway et al. 2019, Gentry et al. 2020, van der Schatte Olivier et al. 2020, Theuerkauf et al. 2022). Our study supports claims and empirical evidence from meta-analyses that these benefits will likely depend on farming practice (Alleway et al. 2019, Gentry et al. 2020, Theuerkauf et al. 2022), and in the case of fish habitat benefits, are particularly enhanced for raised racks (Theuerkauf et al. 2022). Here, rack and basket farms supported distinct fish communities despite being situated alongside one another. However, our study was limited to 2 locations in a single estuary. The patterns described herein would benefit from investigation of similar habitats in other locations and environmental contexts. Further monitoring is also required to establish which aspects of these farming practices lead to the differences observed in the fish communities they support. This will involve experiments that directly manipulate key structural attributes of the differing farming methods, as well as environmental factors such as shading, availability of prey resources, flow and characteristics of adjacent habitats that may be differentially modified by alternate farming practices.

As efforts to repair lost marine habitats scale up, there is need to recognise the importance of aquaculture infrastructure as a part of the estuarine seascape. Building knowledge of the relationship between farm design and the provision of ecosystem services is essential for optimising positive environmental effects of aquaculture infrastructure, and producing synergies with habitat restoration (Gentry et al. 2020). This will require understanding environmental thresholds (e.g. of shading) beyond which degradation of underlying habitat occurs, and the tradeoffs between provision of artificial habitat structure and such impacts. In some instances, gear selection may be coupled with rotational farming methods to maximise environmental benefits and minimise impacts. In other instances, where rotational farming methods may not be viable, the positioning of the infrastructure within the estuarine seascape, and for off-bottom cultivation, the specific underlying habitat, will be key to minimise the impacts and maximise these benefits. In areas where racks and baskets are common oyster aquaculture methods, we recommend the installation of racks on top of bare soft sediment areas and replacement of racks with baskets in areas with underlying seagrass beds, so as to avoid shading impacts and maximise habitat value. As a result, the habitat value of both underlying habitats

can be preserved, whilst enhancing structural complexity. This knowledge will enable policy and management practices to be developed that not only maximise aquaculture production, but also promote environmental stewardship and production of associated wild fisheries.

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