

OYSTERS AS FISH HABITAT

A seascape perspective

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*Submitted in fulfilment of the requirements for the degree of Doctor of
Philosophy*

December 2020

*A mi abuela, mi tita Manoli,
mis hermanas y mis padres:
en cielo y tierra.*

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Summary

Intertidal oyster reefs were once a widespread and conspicuous habitat of temperate and subtropical Australian estuaries. These reefs covered vast areas and formed complex three-dimensional structures providing a myriad of regulating and provisioning services. Today, oyster reefs are considered functionally extinct, occupying less than 5% of their distribution prior to industrialisation. Historic overharvest using destructive fishing practices and more recent water pollution and disease have placed this important habitat at the brink of national extinction.

With growing recognition of the plight of oyster reefs in Australia, interest and investment in oyster reef conservation and restoration has grown. Yet despite the importance of understanding the ecological role of oyster reefs in setting restoration targets in Australia, their ecology remains largely unexplored. Furthermore, it is unclear how oyster farms, which were established in response to the collapse of wild oyster fisheries, replicate some of the ecological functions of natural reefs, and consequently may serve as *de novo* reefs in areas where oyster reefs cannot be restored.

This thesis investigated the role of remnant intertidal Sydney rock oyster (*Saccostrea glomerata*) reefs and oyster farms in providing food, habitat and a nursery to fish. Remnant oyster reefs and oyster farms are located within a mosaic of other natural biogenic habitats, such as mangroves, seagrasses and bare sediment, among which fish may migrate tidally, seasonally or ontogenetically. Consequently, this study compared the fish communities of oyster reefs and farms with those of adjacent habitats. Within oyster farms, it also compared fish utilisation of two of the most extensively used cultivation methods: rack-and-rail and longlines-with-baskets.

This study found that despite their degraded state, remnant oyster reefs were key habitats to fish within the temperate estuarine seascape, providing food, refuge and shelter, and serving as a nursery to juvenile fish. As expected, based on their structural differences, oyster reefs consistently supported more species and greater observations of both adults and juveniles

when compared to bare sediment. However, oyster reefs also supported at least as many species, individuals and juveniles, and in many instances more, than other biogenic habitats, broadly regarded as essential fish habitats. Several recreationally or commercially fished species utilised multiple habitats, but displayed unique behavioural profiles on oyster reefs. A stable isotope study demonstrated that the role of oyster reefs extended beyond habitat attraction, to trophically underpinning estuarine food webs. Oyster farms in many instances supported higher richness and observations of fish than natural habitats, and similar richnesses and observations to oyster reefs, particularly in the case of rack-and-rail farms. This challenges the view that aquaculture negatively impacts ecosystem services.

Overall, this thesis demonstrates the crucial role oyster reefs play as fish habitat within the temperate estuarine seascape of south-eastern Australia. The knowledge generated by this study will serve as a baseline against which to establish realistic conservation and restoration objectives and will assist in identifying those settings in which restoration may reap greatest ecological benefits.

Declaration

I declare that the work presented in this thesis entitled "Oysters as fish habitat: a seascape perspective", is my own work and has not been previously submitted, partly or wholly, for another degree or diploma in any university or institution. All components of this thesis are original material composed by the author. Any additional assistance I received have been acknowledged in the Statement of contributions to chapters section.

Research conducted under Animal Ethics ARA 2017/010

Francisco Martínez-Baena

Sunday, 6 December 2020

Contributions

CHAPTER 1: GENERAL INTRODUCTION

I performed the literature review and writing of Chapter 1, with constructive feedback from my supervisor, Melanie Bishop.

CHAPTER 2: REMNANT OYSTER REEFS AS FISH HABITAT: A SEASCAPE PERSPECTIVE

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This chapter has been prepared for submission to *Marine Ecology Progress Series*.

Personal contribution to Chapter 2: Concept and design – 80%, Data collection = 90%, Data analysis and interpretation= 70%, Chapter drafting – 100%, Critical revision – 40%.

Brendan S. Lanham assisted with data analysis and interpretation, fieldwork logistics and critical revision. Ian M. McLeod and Matthew D. Taylor assisted with critical revision, and Matthew D. Taylor also assisting with fieldwork logistics. Stephen McOrrie and Alyssa Luongo assisted with fieldwork logistics and data collection. Melanie Bishop assisted with the concept and design, data interpretation and critical revision.

This research was presented at three conferences: 1) Australian Shellfish Reef Restoration Network & 19th International Conference on Shellfish Restoration. Adelaide, South Australia, 2018; 2) Macquarie University Department of Biological Sciences Annual High Degree Research Conference, Sydney, New South Wales, 2018; 3) The Australian Marine Sciences Association (AMSA) Conference, Fremantle, Western Australia, 2019.

This research has won two prizes: Best presentation award (Runner up), Macquarie University Department of Biological Sciences Annual High Degree Research Conference, Sydney, New South Wales, 2018 and AMSA NSW Branch Travel award for the Australian Marine Sciences Association (AMSA) Conference, Fremantle, Western Australia, 2019.

CHAPTER 3: REMNANT OYSTER REEFS AS NURSERY HABITAT FOR FISH: A FORGOTTEN COMPONENT OF THE ESTUARINE SEASCAPE NURSERIES

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Personal contribution to Chapter 3: concept and design – 80%, Data collection = 90%, Data analysis and interpretation= 70%, Chapter drafting – 100%, Critical revision – 40%.

Brendan S. Lanham assisted with data analysis and interpretation, fieldwork logistics and critical revision. Ian M. McLeod and Matthew D. Taylor assisted with critical revision, and Matthew D. Taylor also assisted with fieldwork logistics. Stephen McOrrie assisted with fieldwork logistics and data collection. Melanie Bishop assisted with the concept and design, data interpretation and critical revision.

This research was presented at Macquarie University Department of Biological Sciences Annual High Degree Research Conference, Sydney, New South Wales, 2019.

CHAPTER 4: TROPHIC STRUCTURE OF TEMPERATE AUSTRALIAN REMNANT OYSTER REEFS WITHIN THE ESTUARINE SEASCAPE: A STABLE ISOTOPE ANALYSIS

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Personal contribution to Chapter 4: concept and design – 90%, Data collection = 90%, Data analysis and interpretation= 60%, Chapter drafting – 100%, Critical revision – 40%.

Vincent Raoult assisted with data analysis and interpretation and critical revision. Ian M. McLeod, Matthew D. Taylor and Troy Gaston assisted with critical revision, and Matthew D. Taylor also assisting with fieldwork logistics and data collection. Melanie Bishop assisted with the concept and design and critical revision.

This research received the Holsworth Wildlife Research Endowment Grant of the Ecological Society of Australia in 2018 and 2019 with the consecutive Matching Grant Program of the Department of Biological Sciences at Macquarie University.

CHAPTER 5: DE-NOVO REEFS: FISH HABITAT PROVISION BY OYSTER AQUACULTURE VARIES WITH FARMING METHOD

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Personal contribution to Chapter 3: concept and design – 60%, Data collection = 90%, Data analysis and interpretation= 80%, Chapter drafting – 100%, Critical revision – 40%.

Brendan S. Lanham assisted with data analysis and interpretation, fieldwork logistics and critical revision. Ian M. McLeod assisted with concept and design and critical revision, Matthew D. Taylor assisted with critical revision, and assisted with fieldwork logistics. Stephen McOrrie assisted with fieldwork logistics and data collection. Melanie Bishop assisted with the concept and design, data interpretation and critical revision.

This research was presented at two conferences: 1) the NSW Oyster Conference in Forster, NSW, 2018 and 2) Macquarie University Department of Biological Sciences Annual High Degree Research Conference, Sydney, New South Wales, 2020, and will be presented at the upcoming Australian Marine Sciences Association (AMSA) Conference, Sydney, 2021.

CHAPTER 6: GENERAL DISCUSSION

I wrote Chapter 6, with constructive feedback from my supervisor, Melanie Bishop.

Acknowledgements

I have to say that I wasn't expecting "Acknowledgements" to be the most difficult part of the PhD, there are so many people to thank, and I feel so grateful and extremely happy for this entire experience. First and foremost, I would like to thank my family, for always giving me the opportunity and unconditional support to embark on all the adventures of my life no matter how far away these adventures have taken me from you, I think of you all every day, and I am eternally grateful for it. To my nephew and nieces, Alberto, Paula and Elena, I hope I can pass my love for nature to you and inspire you to seek your own adventures one day. My partner (and now fiancé), for being so supportive and keeping my sane, you truly have been my Kryptonite over these last four years, and I don't have enough words to express how thankful I am. My parents in-law, Antonia and Idelfonso for their continuous interest and support in all my PhD experiences and for taking time during their holidays in Australia to come with me to field sites and cook delicious food for me and my volunteers. Truly, my family rocks.

My supervisor, Mel Bishop, thank you for giving me this incredible opportunity and for being so dedicated even in, what I believe was one the most precious moments of a person's life, that is giving birth to two beautiful children. Thank you for being there 24/7, and for boosting my research career, you have been an incredible supervisor, role model and inspiration to me. The success of this PhD has been because of you. My co-supervisors, Ian McLeod and Matt Taylor, I feel incredible lucky for having you throughout these four years, you have been so important for me. All your mentorship, support, research suggestions, and time have been so valued for me. Ian, I have been so inspired and motivated by you and you have been so important in the early development of this PhD and in coaching me through these early days.

My labmates, colleagues, friends and now family, Maria Vozzo, Kate Dodds and Viv Cumbo. You have been so special in so many ways, and I am so grateful for crossing paths with you, you have mentored and supported me in every step of the PhD, and I learnt so much from

your experiences and hardwork, I truly admire you. Ramila, I loved having you as my desk mate, always lightening up the day, being able to listen and offering great advice, your empathy has meant a lot to me.

To my collaborator and friend Brendan Lanham, I think he didn't know what he was getting into when I visited him for the first time in UNSW. I am so happy that I found you and so grateful for you being by my side at every step of my PhD. My success is your success, and I hope that we can continue doing great research in the future. Similarly, my collaborator and friend Alyssa Luongo, you have been extremely important for the development and success of this PhD, you have been my rock and without you this PhD wouldn't have been what it is now. My loyal volunteers Steph Bagala and Justin McNab, you guys have made my fieldwork unforgettable, so lucky to have found you too.

Huge thanks to everyone who helped me so much at the Port Stephens NSW Fisheries Institute, especially Steve McOrrie, for accompanying me throughout all field seasons and being the best skipper I could ever find, chatting with you and learning from your incredible knowledge of oyster reefs and NSW estuaries have been one of the best experiences of this PhD. To Wayne O'Connor, Mike Dove, Ian Lyall, Kylie Russell, Vicky Cole, you all have been so good to me and are incredible role models I aspire to be like you one day. To the oyster aquaculture tech staff: Kyle, Brandt and Wally, thank you for assisting me and being so interested on this PhD.

All my gorgeous colleagues and postgraduate friends that I have crossed paths during these four years: Mitch Gibbs, Giulia Ferretto, Lou Tosetto, Joni Pini-Fitzsimmons, Giulia Filippini, Derrick Cruz, Emily Junk, Laura Martina, Kaja Wierucka, Amy Rose, Sebastian Vadillo, Paula Sgarlata, Rick Leong, Tegan Furchert, Alice Howie, Juan Muelbert, Tristan Guillemin and I am sure I am forgetting hundreds of you, I really can't wait to see your next adventures. All the AMSA councillors and MQ Marine board and the senior researchers, academics and early career researchers that have been looking out for me, Chris Gillies, Jane Williamson, Katie Dafforn, Adriana Vergés, Will Figueira, Ana Bugnot, Ziggy Marzinelli, Mariana Mayer-Pinto, Troy Gaston, Vincent Raoult, Dom McAfee, Simon Reeves, Simon Branigan, Ben Gilby and many more, I truly admire you all.

To the Macquarie admin team, the field and vehicle managers Nick Harris and Tarun Rajan, you guys are the best. The Sydney Institute of Marine Sciences crew as well, thank you for helping me with the fantastic time that I had doing my lab work there.

This PhD has been very special to me, and all these people (and many more) are responsible for having lived a dream come true.

Chapter 1: General Introduction



1.1 ESTUARIES

Estuaries are transitional ecosystems, that lie at the interface between land and sea (Potter et al. 2010, Elliott & Whitfield 2011). Estuarine environments are strongly shaped by their connectivity to both marine and freshwater environments, with hydromorphology (Elliott & Whitfield 2011), salinity and physicochemical characteristics, geomorphological features, river flow, tidal and wave influences key environmental drivers governing the ecological function of these (Elliott & Whitfield 2011, Tweedley et al. 2019). Many of these key drivers display strong gradients along estuaries and coastlines, and consequently estuaries display considerable variability at spatial scales of meters to hundreds of kilometres. Within estuaries, environmental conditions are also highly temporally variable, at time scales of tides, days, seasons and years (Potter et al. 2010, Elliott & Whitfield 2011).

The high degree of environmental variability within estuaries necessitates that estuarine organisms are physiologically or behaviourally adapted to fluctuating environments (Elliott & Whitfield 2011, Elliott & Quintino 2019). As many organisms are not able to survive in these variable conditions, estuarine ecosystems are generally taxonomically less diverse than other adjacent marine ecosystems. Nonetheless, the resilience required by estuarine organisms means that many display a high tolerance for and capacity to recover from adverse environmental conditions (Elliott & Whitfield 2011). Paradoxically, estuaries are, by contrast, one of the most productive ecosystems on earth (Wolanski & Elliott 2016). The variability and complex physicochemical interactions occurring in estuarine ecosystems create a wide range of niches in which euryoecious biota can thrive, resulting in high densities and abundances of individuals, including those of ecologically, recreationally and commercially important species (Elliott & Whitfield 2011, Potter et al. 2015, Elliott & Quintino 2019).

Some of the valuable organisms that are found in estuaries are ecosystem engineers. Ecosystem engineers are able to physically engineer the ecosystem, through their burrowing, provision of complexity, sediment-trapping, rock-boring, and modification of hydrological systems. In modifying estuarine abiotic conditions, they have a large influence on other species, ecological processes and overall estuarine functioning (Jones et al. 1996, Gutiérrez et al. 2011). Estuarine ecosystem engineers provide coastal protection and erosion control, water purification and nutrient supply, maintenance of fisheries, carbon sequestration, recreation and tourism activities as well as education and research opportunities (Barbier et al. 2011, Gutiérrez et al. 2011, Boerema & Meire 2017). Ecosystem engineers in estuarine systems encompass all kinds of life forms (from microbes to vertebrates) and are responsible for the formation of the major estuarine habitats, such as seagrasses beds, saltmarshes, mangroves, kelp forest and biogenic reefs. These habitats are formed by one or several ecosystem engineers, and the

engineered structures created by these, considerably impact the abiotic system, for example by changing erosion and sedimentation, light and oxygen availability, temperature, moisture, water flow, and hard substrate for attachment (Gutiérrez et al. 2011). The modification of abiotic factors by ecosystem engineers, ameliorates environmental stressors, facilitating further settlement of other ecosystem engineers and species that would have not being able to survive in previous conditions, and that depend on them for substrate, refuge and food supply (Thomsen et al. 2010, Gutiérrez et al. 2011, van der Zee et al. 2015).

1.2 THE ESTUARINE SEASCAPE

Estuarine biogenic habitats are distributed spatially according to gradients in abiotic factors, the environmental tolerances of the key habitat-forming organisms and the facilitation cascades and interactions that help to sustain these (Gutiérrez et al. 2011). As a result, estuarine habitats are spatially distributed as a mosaic of habitat patches embedded in a sediment matrix, with patches varying in size, shape, spatial arrangement and proximity. This spatially heterogeneous mosaic of habitat patches is described as seascape (Boström et al. 2011). The habitat patches found in a seascape are functionally connected by biotic and abiotic flows (Boström et al. 2011), with the connectivity among patches determined by their identity, proximity, spatial configuration and size (Boström et al. 2011). The estuarine seascape habitat mosaic generates valuable ecosystem services that have been largely quantified (Pinto et al. 2010, Barbier et al. 2011, Boerema & Meire 2017), but can exceed those provided by individual habitat units (Olds et al. 2016, Olson et al. 2019, Ortodossi et al. 2019, Swadling et al. 2019).

The principles of landscape ecology are instructive in understanding the estuarine 'seascape'. Terrestrial ecologists have long considered how the pattern of and interactions among habitats shape ecological processes (Pickett & Cadenasso 1995, Cushman et al. 2010, Baguette et al. 2013). Landscape ecology combines spatial approaches, such as the geography and geometry of habitats, and functional ecology, to understand the causes and ecological consequences of spatial patterns in the environment (Pittman et al. 2011). Important considerations in landscape ecology are the context in which habitats are found, as their local conditions are influenced by the attributes of the surroundings (Bell et al. 1991, Pittman 2017). Three main metrics used in landscape ecology to quantify spatial patterns and the relationship between spatial structure, ecological function and landscape change are: (1) landscape composition, (i.e. the abundance and variety of patch types, without reference to spatial attributes of the geometry); (2) configuration (i.e. the spatial arrangement of individual patches and

mosaics of patches); and (3) fractal dimension (i.e. the shape complexity of a patch or landscape; (Wedding et al. 2011, Turner & Gardner 2015).

Increasingly the principles of landscape ecology have also been applied to marine ecosystems through the field of seascape ecology. Starting with its application to the theory of island biogeography (MacArthur et al. 1967), 'seascape ecology' has since grown (Pittman 2017) and been applied to shallow water benthic environments such as seagrass meadows, saltmarshes, coral reefs, and mangroves, in tropical and temperate systems, but rarely extended to shellfish reefs (Boström et al. 2011). Studies on these habitats have demonstrated the importance of spatial patterning metrics, such as patch size, patch shape, and edge effects in determining faunal communities (Richards et al. 2016, Dunbar et al. 2017, Gittman et al. 2017, Shinomiya et al. 2017, Mahoney et al. 2018). Studies have also revealed the importance of the identity of adjacent patches in shaping highly mobile nektonic communities and in determining key ecosystem services such as fisheries productivity and habitat provision (Boström et al. 2011).

A concept derived from seascape ecology is the seascape nursery (Nagelkerken et al. 2015). A seascape nursery is a spatially explicit unit consisting of a mosaic of habitat patches that are functionally interconnected (Nagelkerken et al. 2015). In contrast to the traditional nursery concept that considers habitats individually (Beck et al. 2001) the seascape nursery concept considers that multiple habitats may work together to contribute to the recruitment of organisms from juvenile to adult populations (Nagelkerken et al. 2015, Sheaves et al. 2015). They may do so by each serving as nurseries that vary in time and space in terms of their relative importance, by serving as multiple habitats for juveniles that migrate tidally, diurnally or ontogenetically between these, or by together forming corridors from juvenile to adult populations habitats (Nagelkerken et al. 2015, Sheaves et al. 2015). The seascape nursery concept has been successfully applied to the study of tropical and temperate systems, with the focus being mainly on shallow vegetative habitats within a seascape mosaic (Lefcheck et al. 2019, Olson et al. 2019, Berkström et al. 2020, Fulton et al. 2020).

Despite the increasing application of seascape concepts to the study of vegetated aquatic habitats, they are less frequently applied to biogenic reefs and macroalgal systems (Boström et al. 2011, Lefcheck et al. 2019). This is the case of oyster reefs, which despite their current status as functionally extinct in many areas of the globe, have a relatively unexplored role in the estuarine seascape (Beck et al. 2011, Boström et al. 2011). Several studies have pointed to a key role for oyster reefs in providing important ecosystem services and overall estuarine functioning (Lehnert & Allen 2002, Shervette & Gelwick 2008, Abeels et al. 2012, Grabowski et al. 2012). High structural complexity, high vertical relief and the formation of extensive habitat patches are attributes of oyster reefs that suggest that they may be important components of the overall ecological

functioning of the estuarine seascape, and seascape nursery (Grabowski et al. 2008, Humphries et al. 2011, Lefcheck et al. 2019). Thus, further studies on the role of oyster reefs in the seascape complex are needed, especially considering ongoing estuarine modification and degradation (Boström et al. 2011).

1.3 ESTUARINE DEGRADATION

The myriad of ecosystem services provided by estuaries, their proximity to fresh water sources along with their sheltered waters that provide ideal ports, has made estuaries favoured areas for human settlement. Humans have settled on estuaries since the beginning of civilization, and consequently, many of the world's largest urban areas are situated in estuarine and coastal areas. In 2005, 61% of the world's population lived in coastal and estuarine areas and 71% of the population within 50 km of an estuary (Agardy et al. 2005, O'Higgins et al. 2010, Day et al. 2012). Intensive anthropogenic development in coastal areas is causing severe degradation of estuaries, producing changes in their geomorphology (e.g. from draining and filling areas, dredging channels for navigation, and developing drainage systems), their chemical composition (e.g. from pollutants, water extraction, flow modification) and their ecosystems (e.g. from overharvest of species, species introductions, and habitat degradation and loss) (Cooper 2003, O'Higgins et al. 2010, Day et al. 2012). As a consequence, it is estimated that of historical ranges, >65% of seagrass, 25 -50% of saltmarsh, 35% of mangrove forests and >85% of shellfish reefs have been destroyed globally (Lotze et al. 2006, Valiela et al. 2009, Beck et al. 2011, Mcowen et al. 2017). Habitat loss and degradation of these ecosystem engineers is diminishing the ecosystem services and impacting the facilitation cascades provided by these, consequently disrupting the links with surrounding habitats and affecting the estuarine ecological function as a whole (Boström et al. 2011, Gutiérrez et al. 2011). These impacts have not only affected the overall health of estuaries, but also the human populations that rely on them. Such impacts include health risks associated with pollution, loss of human lives and assets as a consequence of reduced nature-based coastal protection against storms surges, hurricanes and sea level rise, and decreases in food provision, as well as cultural impoverishment (Stronge et al. 2005, Gutiérrez et al. 2011, Day et al. 2012).

In the last couple of decades, there has been a growing recognition of the essential ecological role estuarine and coastal systems play, the magnitude of their degradation and the need for ecosystem-based management, conservation and restoration (McLeod et al. 2005, Lotze et al. 2006, Lotze et al. 2011, Delacámara et al. 2020). Pursuing estuarine and coastal habitat recovery and restoration is a complex and difficult task that requires consideration of physical (e.g. natural hydrodynamics, sediment dynamics,

de-linearizing coasts and inland waterways), chemical (contaminants, nutrients) as well as broader connectivity issues (need for habitat patch complexity connected across landscapes, catchments, and seascapes) (Geist & Hawkins 2016). Despite the complexity that entails habitat recovery and restoration, progress in the field through the last decades has been promising (Geist & Hawkins 2016). The literature focussed on coastal and estuarine habitat recovery and restoration has surged considerably, at a rate of 15.4 %/year, since 1980, accumulating promising evidence of success and elucidating trajectories and drivers of ecosystem recovery (Duarte et al. 2013a). Despite this expansion in the literature, most habitat restoration studies have been concentrated in the western hemisphere, with little to no research on coastal habitat restoration found elsewhere, suggesting that there is a pressing biological need for restoration research and transference of knowledge geographically (Zhang et al. 2018). In Australia, restoration of marine environments has largely been “off the radar”, with few projects reaching the size required to appreciably improve ecosystem services at landscape scale (Gillies et al. 2015b). Nonetheless, local interest and recognition in habitat restoration is rapidly growing (Creighton et al. 2019), and a number of large restoration projects are now underway (McAfee et al. 2020a), with baselines for estuarine and coastal habitat restoration being set across the country (McLeod et al. 2019, Wood et al. 2019, McAfee et al. 2020b, Tan et al. 2020).

1.4 OYSTER REEFS

Oysters are ecosystem engineers, that form complex habitat, that supports dense and diverse communities of fish and invertebrates (Coen et al. 1999, Beck et al. 2011). Oysters are gregarious settlers that form habitat when successive generations recruit on top of one another to form complex structures. Aggregations of oysters accumulate sediment in the interstitial spaces, burying older oysters that disarticulate once they die, becoming the skeletal core of the reef along with the accumulated sediment and biodeposits (Powell et al. 2006, Rodriguez et al. 2014). Depending on the vertical growth of the consolidated structure, these oyster formations can vary in height from beds with low vertical relief, extending a few centimetres above the bottom, to reefs with high vertical relief, extending as much as several meters above the bottom, and creating complex three dimensional structures (Coen & Grizzle 2007).

The complex three dimensional structures created by oyster reefs provide a myriad of ecosystem services (Coen et al. 2007, Grabowski & Peterson 2007, Grabowski et al. 2012). These services include: (1) production of oysters; (2) water filtration and concentration of biodeposits; (3) provision of habitat; (4); sequestration of carbon; (5) augmentation of fishery resources; (6) stabilization of sediment and benthic intertidal

habitat and (7) increase of seascape diversity (Coen et al. 2007, Grabowski & Peterson 2007). Oyster reef have served as an important food source to coastal civilizations throughout history, with shellfish middens dating back to 6000 years (Gillies et al. 2018), and spanning America, Europe and Australia (MacKenzie et al. 1997, Kirby 2004). Oyster reefs provide important food resource to a wide variety of estuarine species, from diatoms to fish. Some species consume the reef forming bivalves themselves (Thomson 1954, Anderson & Connell 1999), while others consume the rich biodeposits that these bivalves excrete (Norling & Kautsky 2007). Additionally, the structural complexity of oyster reefs provides nursery, resting and refuge to species at a range of scales. The interstitial spaces within the shell matrix are used as microhabitat for resident infauna, epifauna (Summerhayes et al. 2009, McLeod et al. 2020) and juvenile and small cryptic fish (Harding & Mann 2000). At the seascape-scale, oyster reef complexity provides habitat to larger organisms that may move among habitats seeking not only food, but also shelter (Harding & Mann 2001, Lehnert & Allen 2002, Joyce 2011, Kingsley-Smith et al. 2012, Hanke et al. 2017).

Oyster reefs were once a dominant habitat of subtropical to temperate estuaries and coastal areas across the globe (Beck et al. 2011), ranging in size from 10 to 100 000 m² (Oyster Culture Commission 1877), and comprising oyster densities of 10m⁻² to 1000 m⁻² (DeAlteris 1988). Today, less than 15% of reefs present prior to industrialisation remain, with the condition of many remnant oyster reefs being poor (Beck et al. 2011) and the habitat declared functionally extinct in many parts of the globe (Ogburn et al. 2007, Beck et al. 2011, Gillies et al. 2018). The plight of oyster reefs can largely be attributed to their historic overharvest, using destructive fishing practices, but also more recently urbanisation and declining water quality and disease (Beck et al. 2011). Global demand for oysters, for food and lime, increased rapidly in the 16th and 17th centuries, accompanying the pattern of human coastal population growth (MacKenzie et al. 1997, Kirby 2004). With increased shellfish demand came the development of intensive techniques to collect shellfish such as dredging, which removes not only live oysters but also the shell base on which reefs grow (MacKenzie et al. 1997, Gillies et al. 2018). Dredging became widespread in the 18th century and led to the depletion of many shellfish reefs, and the reduction of oyster populations across the world (MacKenzie et al. 1997, Gillies et al. 2018). More recently, sedimentation, nutrient loading, diseases and water pollution have contributed to the overall depletion of shellfish reefs.

In recent decades, there has been an expansion of research into current and past reef distributions, ecological function and ecosystem services (Luckenbach et al. 1999, Beck et al. 2011, Chakraborty 2017, Gillies et al. 2018, Fitzsimons et al. 2019, Pogoda 2019). This research has generated awareness of the extent of the loss of oyster reefs and their ecosystem services, and generated interest and investment in oyster reef restoration (Coen et al. 2007, Grabowski & Peterson 2007, Grabowski et al. 2012, La Peyre et al.

2014). Services such as coastal protection, water filtration, and habitat provision to commercially valuable fish and crustaceans, have become primary motivations for many restoration projects (Fitzsimons et al. 2019). It is estimated that the economic value of these services provided by oyster reefs range from US\$5500 to US\$99,000 per hectare per year and that the median restoration investment is recovered within 2 – 14 years (Grabowski et al. 2012). Since the 1990s, hundreds of small to medium scale reef restorations have been attempted, especially in USA, with limited success due to lack of post-construction monitoring and adaptive management, a failure to control harvest pressures on restored reefs and a lack of coordination among agencies involved (Kennedy et al. 2011). Recently, successful restoration efforts are scaling up worldwide, with lessons learned from previous attempts, and management frameworks developed through restoration guidelines (Kennedy et al. 2011, Baggett et al. 2015, Fitzsimons et al. 2019).

In Australia, two of the most common endemic reef forming species are the Sydney rock oyster (*Saccostrea glomerata*, Gould 1850) and the flat oyster (*Ostrea angasi*, G. B. Sowerby II, 1871). The distribution of the Sydney rock oyster extends northwards along the east Australian coastline, from approximately 25°17'S, through northern Australian and down the western Australian coast to 25°S latitude (Ogburn et al. 2007). This species is mainly found in the mid intertidal to low subtidal, and besides forming reefs, it also abundant on sheltered rocky shores and mangrove forests, where it attaches to the hard substrate provided by rock, as well as mangroves tree trunks and roots (Gillies et al. 2015a). The flat oyster is primarily subtidal, extending down to depths of up to 40 m, and is distributed along the southern coast of Australia from New South Wales (30°5'S latitude approximately) to Western Australia (31°50'S latitude approximately), including Tasmania and Victoria (Ogburn et al. 2007, Gillies et al. 2015a).

Once predominant features on the Australian landscape, oyster reefs comprised of one or both species have been depleted across their latitudinal range with only 1% of the *O. angasi* and 8% of the *S. glomerata* reefs remaining (Gillies et al. 2018, Gillies et al. 2020). It is only in the past 15 years that the full extent of oyster reef loss has been recognised across the country (Alleway & Connell 2015, Gillies et al. 2018, Gillies et al. 2020). This has stimulated oyster reef restoration pilots and recent investment in several large-scale projects, with on-ground and planning phases in place (Gillies et al. 2018, Gillies et al. 2020, McAfee et al. 2020a, McAfee et al. 2020b). Still, knowledge on the ecological function of remnant oyster reefs and their ecosystem services remains largely unexplored, despite being key to the success of shellfish reef restoration efforts (Gillies et al. 2015a). Previous studies on remnant oyster reefs in Australia have been limited to assessments of oyster reef condition and their provision of habitat to invertebrates (McLeod et al. 2020). Among the key knowledge gaps for Australian oyster reefs are: recruitment, growth and expansion; their fisheries productivity and role as habitat for

fish; their ecological connectivity with other estuarine habitats; and their provision of shoreline stabilisation and filtration services. In Australian estuaries, oyster reefs commonly exist alongside seagrass beds, mangrove forests, unvegetated sediments and/or saltmarsh. Given the oligotrophic status of many east Australian estuaries as compared to the US estuaries in which the bulk of oyster reef research has been done (Scanes et al. 2007), and the differing environmental context, studies are needed that specifically assess the role of remnant oyster reefs in Australian estuarine seascapes. As successful restoration efforts are increasing worldwide, collating and sharing knowledge from monitoring studies and successful and failed restoration attempts internationally is key to making advances, leveraging knowledge and showcasing a powerful front in international oyster reef conservation, recovery and restoration.

1.5 OYSTER AQUACULTURE

Oyster farming is one of the oldest forms of aquaculture, with various oyster aquaculture methods dating back over two millennia (Botta et al. 2020). Nonetheless, in many parts of the world, it was not until the collapse of wild oyster populations in the 17th century that systematic oyster cultivation and accompanying policy and management were developed (Nell 2001, Buestel et al. 2009, Schulte 2017, Gillies et al. 2018). Since then, oyster production worldwide has fluctuated, largely due to disease outbreaks, but with sustained growth from the 1950s due to innovations in transportation, larval culture and selective breeding techniques (Botta et al. 2020).

In Australia, systematic oyster cultivation began in New South Wales (NSW) and southern Queensland with the farming of the Sydney rock oyster around 1870 with the use of wooden sticks, rock culture and bottom culture as early methods used to catch and grow oysters (Nell 1993). Since then, farming of other species began, including several attempts of farming the native flat oyster in Victoria, Tasmania and South Australia after their natural reefs became exhausted, and the introduction of the Pacific oyster (*Crassostrea gigas*) for farming purposes in 1960s (Nell 2001). Over this period, the oyster industry has fluctuated in production with the introduction of different off-bottom culture techniques, peaking in the 1970s at 14 million dozen or 8400 t (wet weight including shell) (Nell 2001, Schrobback et al. 2014). Production has since decreased slightly, though the oyster industry remains the largest aquaculture industry in NSW, spanning 41 estuaries, 3200 leases and 4300 hectares (Schrobback et al. 2014, DPI 2017). Off-bottom oyster infrastructure has been extensively placed within shallow water unvegetated and seagrass habitats, or in areas where Sydney rock oyster reefs were once common. Among some of the off-bottom cultivation methods used in NSW, rack-and-rail and longlines-and-baskets are widely used (Nell 1993, 2001). Rack-and-rail

methods consist of trays (covered or uncovered with a plastic mesh or frame) that sit on parallel wooden or plastic rails at a constant height, usually mid-intertidally. Longlines-and-baskets consist of horizontally suspended plastic tubes clipped on parallel longlines attached to wooden or plastic sticks (Nell 2001).

Previous ecological studies on oyster aquaculture have focused on negative impacts that can occur under scenarios of poor management, including overstocking, and inappropriate positioning of infrastructure in poorly flushed or semi-enclosed embayments (Forrest et al. 2009, Han et al. 2017, Gentry et al. 2019). Such impacts can include local phytoplankton depletion, excessive sediment organic enrichment, disruption of local hydrodynamics and benthic community impacts and habitat fragmentation (Oo & Oo 2016). Rack-and-rail culture have received special attention regarding the negative impacts they can cause on seagrass beds beneath the infrastructure. Long-term shading of seagrass from racks results in lower seagrass productivity, density and leaf growth, preventing survival, and ultimately causing habitat fragmentation (Thorne 1998, Madigan et al. 2000, Forrest et al. 2009). Studies on other culture methods such as longlines-and-baskets have, however, determined that their impacts on seagrass are negligible (Bulmer et al. 2012, Smith et al. 2018).

Recently, there has been a shift in the perception of aquaculture as environmentally damaging, to consider the positive ecosystem services that it may, to the contrary, facilitate under well-managed circumstances (Alleway et al. 2019, Gentry et al. 2019, van der Schatte Olivier et al. 2020). The ecosystem services provided by shellfish aquaculture can extend far beyond their primary purpose of provisioning, to include regulating, habitat, supporting and cultural services (Alleway et al. 2019). These services may include many of those provided by natural oyster reefs, such as water filtration and denitrification, sediment stabilisation and erosion control, and creation of habitat (Grabowski et al. 2012, Alleway et al. 2019). Thus, in areas where natural shellfish ecosystems have been degraded or depleted (Beck et al. 2011), shellfish aquaculture serve as a valuable surrogate habitat maintaining similar services to these provided by lost natural habitats (Alleway et al. 2019).

One of the valuable ecosystem services oyster aquaculture may provide is habitat to fish and invertebrates (Alleway et al. 2019, Gentry et al. 2019). The hard farming infrastructure can be used by benthic organisms as attachment space and by nektonic species, such as macroinvertebrates and fish as shelter, refuge and foraging areas (Alleway et al. 2019). In the USA, abundances and richnesses of organisms are in some instances comparable between oyster farms and other adjacent natural habitats (Glenn 2016, Muething 2018, Coe 2019, Mercaldo-Allen et al. 2019). In Australia, the ecosystem services provision by oyster aquaculture infrastructure still remain uncertain. As oyster reef restoration efforts are increasing throughout the country (Gillies et al.

2018, McAfee et al. 2020b), there is a need to understand the value of oyster aquaculture as surrogate habitat in areas where reef restoration may not be feasible. Furthermore, understanding the interactions among aquaculture infrastructure and adjacent natural habitats and their benthic and nektonic communities would contribute to better management of the industry to minimise its impacts and maximise the regulating and provisioning services it can provide.

1.6 THESIS OUTLINE

Given the current status of Sydney rock oyster reefs as Critically Endangered (Gillies et al. 2020) and the growing interest and investment in their conservation and restoration, it is a priority to quantify the ecological functions and services provided by remnant reefs. Understanding the functions and services of remnant reefs is critical for establishing baselines and targets against which oyster reef conservation and restoration can be assessed. This thesis aimed to describe the general role of remnant oyster reefs and oyster aquaculture infrastructure as fish habitat in New South Wales, Australia. Using a seascape perspective, it compared fish communities between remnant oyster reef and aquaculture infrastructure, and adjacent and highly ecologically valued habitats, such as seagrasses, mangroves and bare sediment areas. Sampling addressed not only compositional differences in fish communities but also differential utilisation of the habitats for feeding and refuge. As remnant Sydney rock oyster reefs and oyster infrastructure are set mainly in the intertidal and thus are primarily used by fish at high tide, understanding patterns at the seascape level is critical.

The four data chapters of this thesis cover different key aspects of the role of remnant oyster reefs and oyster aquaculture infrastructure in providing fish habitat. In **chapter 2**, I describe the fish community that utilises remnant oyster reefs and adjacent seagrass, mangrove and bare sediment in two estuaries of New South Wales, Botany Bay and Port Stephens, over summer and winter of two consecutive years, using remote underwater cameras. Specifically I aimed to determine (1) whether the fish communities utilising remnant oyster reefs would differ from the fish communities utilising the adjacent seagrasses, mangroves and bare sediment habitats, (2) whether the number of fish observations and diversity found in remnant oyster reefs differ to those in adjacent habitats, (3) whether the fish species utilising oyster reefs display different behaviours when compared to adjacent habitats and (4) whether the number of observations of important recreationally and commercially valuable fish species found in remnant oyster reefs is different to that found in adjacent habitats. Previous studies, mainly in the US, have demonstrated the importance of oyster reefs as essential fish habitat, especially

for recreationally and commercially valuable species (Harding & Mann 2001, Lehnert & Allen 2002, Peterson et al. 2003). These studies generally documented higher fish densities and richnesses in oyster reefs than bare unstructured habitats and a potential increase in fisheries productivity with increasing reef restoration efforts (Peterson et al. 2003).

Fish utilisation of remnant oyster reefs may be a consequence of their natural structural complexity that can offer shelter, nesting areas, an attachment substrate or refuge; or may be linked to the different trophic pathways underpinned by oyster reefs. Some species of fish directly consume reef forming bivalves, or their excreted biodeposits, while others feed on organisms that reside on or within the reef matrix. In **chapter 3**, I use stable isotope analysis to ascertain whether estuarine species are using remnant oyster reefs as foraging grounds or whether they are simply attracted to their structural complexity. Specifically, I determine (1) whether species that utilise remnant oyster reefs as primary habitats (reef residents) and species that use them transiently (reef transients) are using oyster reefs as foraging grounds by any of the aforementioned possible trophic pathways, (2) the trophic levels of the resident and transients species, and (3) whether there is an overlap between the trophic niches of the resident and transient fish community, when grouped by their respective feeding guilds. Stable isotopes have been used to determine the trophic structure and transfer of organic matter from lower to higher trophic levels in marine ecosystems (Schaal et al. 2008, Layman et al. 2012). Thus, I expect to elucidate the extent to which organisms are using remnant oyster reefs as feeding grounds and whether remnant oyster reefs are contributing to the enhancement of the estuarine food web. The results from this chapter contribute to growing evidence of the key role of remnant oyster reefs as fish habitat and suggest that the conservation and restoration of this habitat does not only attract fish, but underpins fish productivity by providing a feeding ground.

In **chapter 4**, I delve deeper into the role of remnant oyster reefs as fish habitat, assessing the nursery value of remnant oyster reefs as compared to other adjacent estuarine habitats in the seascape mosaic. Specifically, I explore (1) whether the number of juvenile fish observations in remnant oyster reefs is greater than adjacent estuarine habitats, (2) whether the number of juvenile observations of recreationally and commercially valuable species is greater in remnant oyster reefs than other adjacent habitats, (3) whether the ratio of juvenile to adult fish observations differs between oyster reefs, and adjacent seagrass, mangrove and bare sediment habitats and (4) whether juvenile fish display different behaviours among remnant oyster reefs and adjacent habitats. Nursery habitats and nursery seascapes are critical areas for the survival and growth of juveniles and provide important migration routes to adult habitats (Beck et al. 2001, Lefcheck et al. 2019). Consequently, nurseries underpin recruitment to and the productivity of adult populations and the overall survival of the species (Beck

et al. 2001, Nagelkerken et al. 2015, Lefcheck et al. 2019). Estuaries have long been recognised as providing important nursery habitats to fish (Beck et al. 2001, Lefcheck et al. 2019). Within these, oyster reefs have been proposed as potential important nursery areas, but yet, few studies have attempted to quantify their nursery role (Beck et al. 2001, Lehnert & Allen 2002, zu Ermgassen et al. 2016, Lefcheck et al. 2019). In Australia, the nursery role of remnant oyster reefs still remains uncertain. This chapter quantifies for the first time the nursery role of oyster reefs within the estuarine seascape nursery.

Despite oyster farming being one of the most important aquaculture industries in New South Wales (DPI 2020), it is often viewed as a consumer of natural goods and services rather than a provider of these (Alleway et al. 2019). In **chapter 5**, I determine the habitat provision for fish communities of two methods of oyster aquaculture widely used in New South Wales: rack-and-rail and longlines-and-baskets. Specifically, I determine (1) whether the two farming methods provide habitat to distinct fish communities, (2) whether these farming methods provide habitat to a similar or different fish community when compared to the adjacent natural habitats and (3) whether these methods can act as de-facto oyster reefs in areas where they cannot be successfully restored. A growing number of studies suggest that shellfish aquaculture infrastructures can serve as important fish habitat (Erbland & Ozbay 2008, Bourdon 2015, Glenn 2016, Muething 2018, Coe 2019, Mercaldo-Allen et al. 2019), challenging the view that aquaculture generally degrades ecosystem services (Alleway et al. 2019, van der Schatte Olivier et al. 2020). In ascertaining how farming method influences habitat provision to fish, this study will help farmers and coastal managers develop strategies that maximise positive benefits and minimize negative impacts of aquaculture on ecosystem services.

Understanding the role of remnant oyster reefs and oyster aquaculture infrastructure as fish habitat will help to strengthen the business case for oyster reef conservation and restoration while promoting sustainable and extensive oyster aquaculture. Grabowski et al. (2012) estimated that a hectare of oyster reefs in the US would present a commercial fish value of US\$4123 per year in 2011 dollars, and that this value would vary depending on the amount of existing oyster reef present in a given estuary. Determining and quantifying the value of oyster reefs as fish habitat, among other ecosystem services, provides stakeholders and coastal managers both an economic justification and a stronger decision-making framework for prioritizing further ecosystem-based management actions (Grabowski et al. 2012). As restoration efforts are increasing in Australia, it is a priority to build knowledge on the current status of the services provided by our remnant oyster reefs, such as fish habitat and fisheries productivity, and communicate this knowledge to guide restoration (Gillies et al. 2015b).

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Chapter 2: Oyster reefs as fish habitat

A SEASCAPE PERSPECTIVE

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2.1 ABSTRACT

Estuarine ecosystems comprise a mosaic of biogenic and abiogenic habitat patches, that provide food and habitat for fishes and invertebrates, many of which migrate among habitats. Oyster reefs were once an important component of temperate estuarine seascapes, but historic overharvest, pollution and disease have rendered them functionally extinct across much of their former range. As interest in oyster reef conservation and restoration grows, there is a need to understand the communities of fish associated with oyster habitats across a range of habitat contexts, and how these communities compare to those of other estuarine habitats. We used remote underwater video (RUV) sampling in two estuaries in New South Wales, Australia, to compare fish communities between remnant oyster reefs and adjacent mangroves, seagrasses and bare sediment. At high tide, these oyster reefs provided habitat to a unique and diverse fish community with generally higher fish observations and species richness than not only bare sediments but also adjacent structured habitats. Seagrasses were the exception, having a similar species richness of fish to oyster reefs, but a significantly lower relative abundance. Oyster reefs were similarly important as adjacent biogenic habitats in providing a range of exploited fish species with food and shelter. Resolving the linkage between oyster reefs and exploited fish species within the broader seascape provides important background for building a business case for oyster reef restoration, and identifying scenarios in which oyster reef restoration is likely to yield greatest benefit.

Keywords: Oyster, reef, habitat, fish, seascape, ecology, ecosystem services, RUV.

2.2 INTRODUCTION

Estuaries are among the world's most productive ecosystems (Ducrotoy et al. 2019), comprised of mosaics of shallow-water habitats that support diverse communities (Lenihan et al. 2001, Skilleter & Loneragan 2003). In particular, complex biogenic habitats such as oyster reefs, seagrass, mangroves and saltmarsh support a wide range of vertebrate and invertebrate species as nurseries, providing nurseries, foraging habitats, refugia from environmental stressors and predators, and attachment space (Beck et al. 2001, de la Moriniere et al. 2003, Beck et al. 2011, Humphries & La Peyre 2015, McLeod et al. 2020). Such habitats are often described as key estuarine fish habitats, and their loss or degradation may constrain the productivity of many coastal fisheries (Beck et al. 2001). These habitats are functionally interconnected, and the

degradation of one of them is likely to impact surrounding habitats and disrupt linkages throughout the entire estuarine ecosystem (Boström et al. 2011).

Despite the inherent connectivity of estuarine habitats, most research has focused on the value of individual habitats to fish communities, or compared the role of individual structured to unstructured habitats. Among these, vegetated estuarine habitats, such as seagrass beds (Campagne et al. 2015, Ruiz-Frau et al. 2017, Nordlund et al. 2018), mangroves (Kelleway et al. 2017, Himes-Cornell et al. 2018), and saltmarshes (McKinley et al. 2020) have received particular research attention. These structured vegetated habitats generally support greater abundances and richnesses of fish than unstructured habitat (Gilby et al. 2018a, Ruesink et al. 2019, Zarco-Perello & Enriquez 2019) as well as greater foraging, shelter and nursery functions (Whitfield 2017, Lefcheck 2019). These functions of structured habitats reflect the greater prey and resource availability, decreased predator foraging efficiency and dampened environmental stressors within them (Harding & Mann 2001, Jackson et al. 2001, Laegdsgaard & Johnson 2001, Lehnert & Allen 2002, Minello et al. 2003, Tolley & Volety 2005). However, it is less clear the extent to which the various structured habitat support distinct fish communities to one another and how individual species of fish differentially utilise these habitats for foraging, resting and sheltering activities.

Oyster reefs are historically abundant components of temperate and sub-tropical estuaries and coastal environments worldwide, that suffered greater than 85% decline at many locations since the 1800s, primarily due to destructive fishing practices such as dredging, along with pollution and disease (Beck et al. 2011, Gillies et al. 2018). Oyster reefs form on soft bottoms when successive generations of oysters recruit on one another to form dense, three dimensional aggregations. These aggregations trap sediment and organic matter in their interstitial spaces and, as newly recruited oysters grow, older oysters are buried below, dying and disarticulating to form the dense shell matrix that forms the inner core of the reef (Powell et al. 2006). Studies, mostly from the USA and mostly looking into restored and/or subtidal oyster reefs, have demonstrated the importance of oyster reefs in underpinning fisheries productivity, nutrient cycling, shoreline stabilisation and maintenance of water clarity, with an estimated economic value ranging from US\$5500 to US\$99,000 per hectare and year (Grabowski & Peterson 2007, Grabowski et al. 2012, Pierson & Eggleston 2014). As the historical significance of oyster reefs is increasingly recognised, there is growing interest in oyster reef restoration around the world (Gillies et al. 2015a, Fitzsimons et al. 2019, McLeod et al. 2019). In Australia, little is known about the benefits habitat repair might confer to fisheries (Alleway & Connell 2015, Gillies et al. 2015a, Gilby et al. 2018b, Crawford et al. 2019).

Remnant intertidal oyster reefs, though extremely scarce particularly in Australia (Gillies et al. 2018), provide the unique opportunity to study the ecological structure and function of this habitat. Within estuaries, remnant oyster reefs typically exist alongside structured (e.g., seagrass beds, marshlands and mangroves, rocky reefs and oyster reefs) and non-structured (e.g., mudflats, bare sediments) habitats, contributing to the estuarine seascape mosaic. It is unclear to what extent remnant intertidal oyster reefs support ecosystem functions that are unique versus redundant to these other habitats. Historically, the great majority of research on fish habitat has focused on the ecology of single estuarine habitats or compared structured to non-structured habitats. These studies have generally found greater abundances and richnesses of fish in structured than unstructured habitat, reflecting greater prey and resource availability, decreased predator foraging efficiency and dampened environmental stressors in structured habitats (Harding & Mann 2001, Jackson et al. 2001, Laegdsgaard & Johnson 2001, Lehnert & Allen 2002, Minello et al. 2003, Tolley & Volety 2005). However, it is less clear the extent to which the various structured habitats support distinct fish communities and how individual species of fish differentially utilise these habitats for foraging, resting and sheltering activities. Those studies that have developed a seascape approach to studying oyster reefs have generally compared their communities to seagrass and/or saltmarshes, but not mangroves. Moreover, such comparisons have generally only been performed on restored intertidal oyster reefs (Grabowski et al. 2005, Gregalis et al. 2009), oyster aquaculture (Hosack et al. 2006, Glenn 2016), or subtidal remnant oyster reefs (Nevins et al. 2014, Glenn 2016). There is a need to describe the importance of intertidal remnant oyster reefs to estuarine fish communities, and how their habitat provision overlaps with, and differs from other adjacent and highly productive habitats, such as mangroves, seagrasses and sandflats (Beck et al. 2011, Gillies et al. 2018). Furthermore, for species that utilise multiple habitats of the estuarine seascape, there is need to understand how their behaviours, and hence habitat uses, differ between these.

This study compared the role of remnant intertidal Sydney rock oyster (*Saccostrea glomerata*, Gould, 1850) reefs as fish habitat to adjacent seagrasses (*Posidonia australis*, Hooker, 1858), mangroves (*Avicennia marina*, (Forssk) Vierh, 1907) and bare sediments. Specifically, it tested the hypotheses that 1) remnant oyster reefs will support distinct fish communities to other estuarine habitats; 2) remnant oyster reefs will support fish abundances and diversity that are equal to or greater than other structured habitats; 3) fish utilising remnant oyster reefs will display distinct behavioural profiles in this habitat as compared to the other habitats in which they are found; 4) behavioural analysis will reveal that fish utilise oyster reefs for foraging and as habitat; and 5) oyster reefs will provide habitat to both juvenile and adult fishes.

2.3 METHODS

2.3.1 Experimental design

Two estuaries in New South Wales (Australia) were sampled; Botany Bay and Port Stephens (Figure 2.1). Within each estuary, two study sites were sampled, in Botany Bay, the study sites were situated in Quibray Bay ($34^{\circ}0'58.08''\text{S}$, $151^{\circ}10'45.78''\text{E}$) and Carters Island ($34^{\circ}0'40.35''\text{S}$, $151^{\circ}8'47.32''\text{E}$). In Port Stephens, study sites were Corrie Island ($32^{\circ}40'41.26''\text{S}$, $152^{\circ}7'16.09''\text{E}$) and Soldiers Point ($32^{\circ}42'14.34''\text{S}$, $152^{\circ}3'28.26''\text{E}$; Figure 2.2). Each study site contained remnant oyster reefs, seagrass beds, mangroves and bare sediment co-occurring in habitat mosaics at a depth of 1-3 m below mean high water, and within an area of 0.5 to 1 km². Remnant oyster reefs comprised Sydney rock oyster (*S. glomerata*) aggregations that extended 53 to 500 mm in height above the surrounding soft sediment substrate (McLeod et al. 2019). Seagrasses beds were predominantly composed by thick and continuous aggregations of *Posidonia australis* and mangrove habitats were predominantly composed by mature grey mangroves, *Avicennia marina* (Figure 2.1).

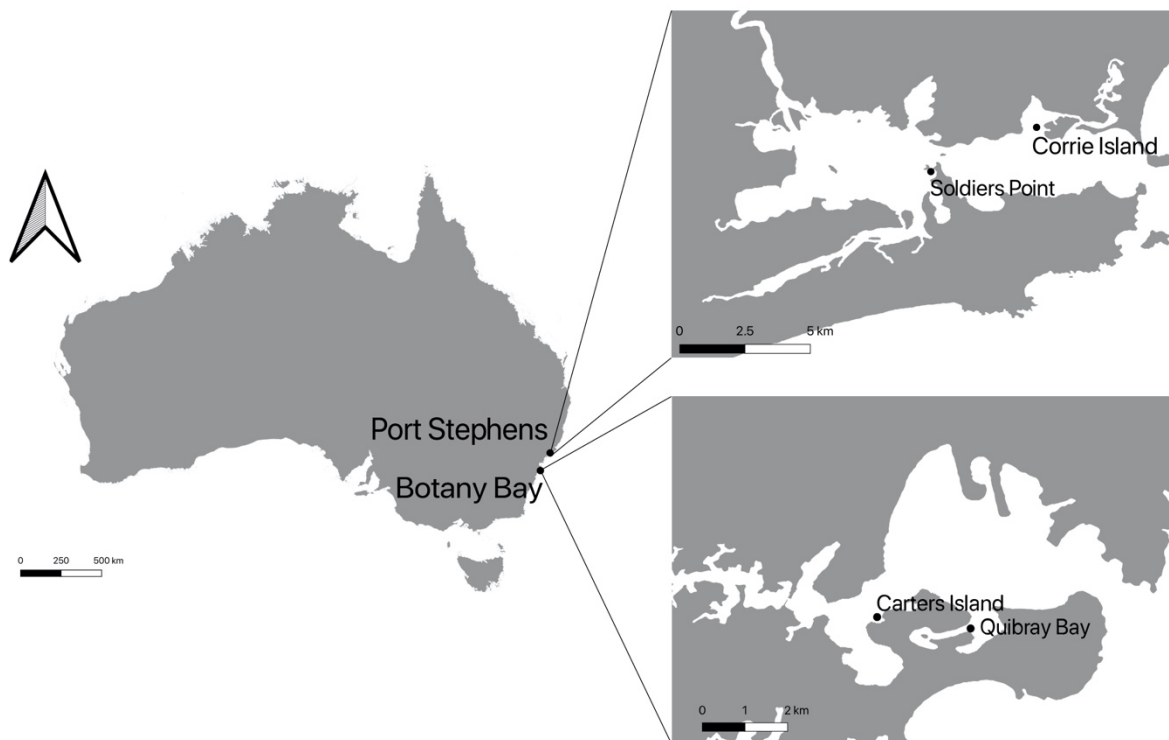


Figure 2.1: Locations of the estuaries and study sites within these: Carters Island and Quibray Bay for Botany Bay, and Soldiers Point and Corrie Island for Port Stephens.

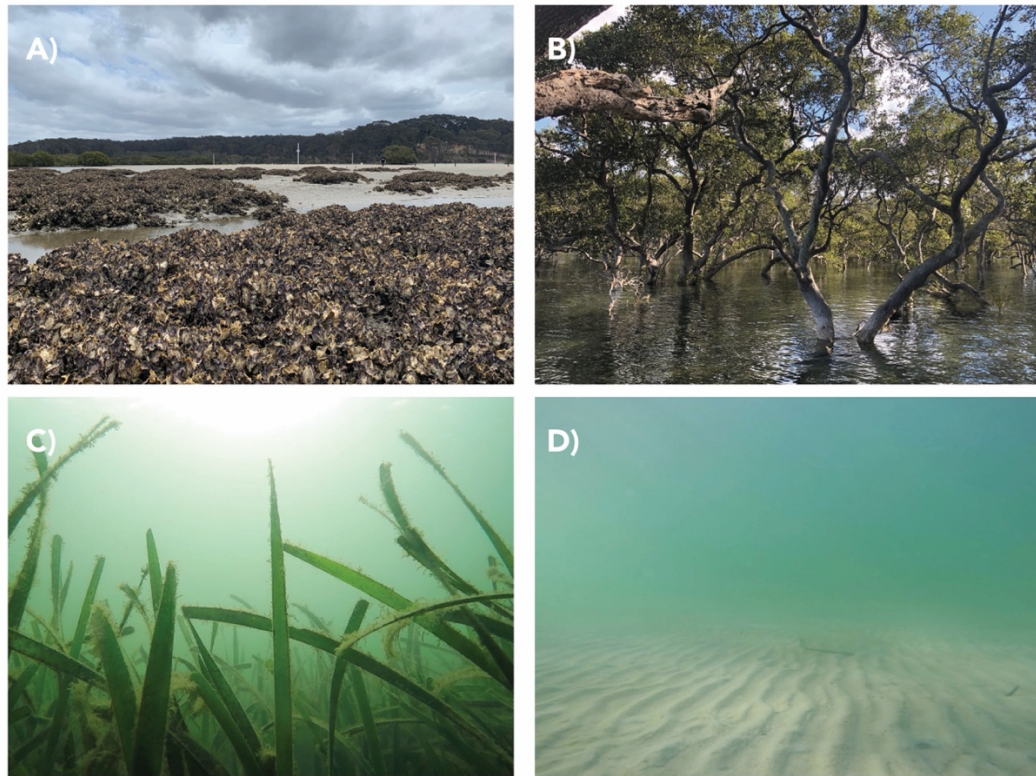


Figure 2.2: Photographs of study habitats. A) Remnant intertidal Sydney rock oyster reefs at low tide, B) grey mangrove forests at mid tide, C) seagrasses beds and D) bare sediment flats. Photographer: F. Martínez-Baena

2.3.2 Sampling

Sampling of each of the study sites was conducted over two consecutive years (December 2017- February 2019), in the austral summer and winter during daylight hours and within 1.5 hours of high tide. Within each season, sampling was replicated on three days. On each day, fish communities of the four habitat types (oyster reefs, seagrasses, mangroves and bare sediments) were surveyed simultaneously using unbaited remote underwater video (RUV) cameras (GoPro Hero 4 Silver Edition). Within each habitat, four cameras were haphazardly deployed at least 5 m apart and at least 20 m from adjacent habitats. This design gave a total of 16 simultaneously recording cameras per site. Cameras were positioned such that they faced towards the targeted habitat and away from the sun to avoid shadowing which may impede fish identification. Cameras were attached to a metal stand positioned 25 cm off the seabed, with a float-line attached to assist in retrieval and were left recording for 85 minutes. After recording, the first and last 5 minutes of each video were deleted to eliminate deployment disturbances on the fish community, leaving 75 minutes of footage per camera to analyse. At each sampling date, we measured the visibility within each habitat with a

turbidity tube. This comprised a methacrylate tube of 1.2 m length and 4.5 cm diameter that had a Secchi disc and capped discharge pipe at one end and was open at the other. The tube was filled with water from each sampling site and water was discharged from the tube until the Secchi disk was seen from the top. The maximum depth of overlying water at which the Secchi disk was still visible was then measured. Visibility was categorised as either: <0.8, 0.8-1.0, 1.0-1.2, or >1.2 m. Sampling did not proceed if visibility was less than 0.8 m.

2.3.3 Video analysis

Prior to analysis, Adobe After Effects (2020, Adobe®) was used to edit footage into a 75-minute video that was then colour balanced. Each video was then processed using EventMeasure software (SeaGIS Pty. Ltd.) to quantify fish communities and their behaviour.

To characterise fish communities associated with each of the habitat types, for each video, we determined the species richness, total observations of all fishes and by species (hereafter referred to as observations), and of juveniles and adults separately. Adults and juveniles were distinguished based on their morphological features, and their observations were analysed separately, as well as combined, so as to assess the differential use of habitats by these two groups. Species richness was the total number of species recorded by a single camera, on a given day. Observations were recorded by species as the total number of times that species entered the frame of a single camera, on a given day. Observations are a good indicator of habitat use (i.e., whether fish were resident or transient (Lanham 2019)) and total observations (summed across species, for a single camera) was used instead of indicators of relative abundance (i.e., MaxN; Cappo et al. (2004)), that were developed specially for baited underwater remote cameras (BRUV) studies. In order to avoid double counting, if an individual entered the frame, and re-entered again from the same side it left, within a span of 20 seconds, that individual was not counted the second time. To eliminate any bias towards species that shoal (i.e. are found in groups comprising many individuals), we counted a shoal of individuals of the same species as one observation, such that they had the same weighting as species that do not shoal. This was to prevent these species that naturally form big groups from dominating analyses.

To assess differences in fish behaviour among habitats, we scored the behaviour of each individual, per frame. Fish were assigned one of four behaviours: passing, wandering, feeding or chasing. A fish was scored as 'passing' where it passed through the frame at constant speed, without displaying any detectable interest in the habitat. It was scored as 'wandering' when it slowed down to investigate a specific area of the habitat, perhaps looking for food, or swam slowly around the habitat. 'Feeding' was scored when a fish

directly fed on the habitat, or on another species. 'Chasing' was documented when a fish actively chased or was chased by conspecifics or other species. In assessments of behaviour (as per observations) a shoal was considered as equivalent to one individual. Where individuals of the same shoal displayed different behaviours, we assigned one observation per different behaviour observed within the shoal.

2.3.4 Data analysis

Differences in fish communities among habitats were assessed using permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008). The analysis was run on Bray Curtis dissimilarity measures, produced using untransformed observations data to which a dummy variable of one had been added (to allow inclusion of samples containing no fish, Clarke et al. 2006). It included the factors: Habitat (4 levels, fixed: Oyster reefs, Seagrass, Mangroves and Bare), Estuary (2 levels, random: Botany Bay and Port Stephens), Site (2 levels, random: nested within each estuary), Year (2 levels, random: 1 and 2), Season (2 levels, fixed: Winter and Summer), and Day (3 levels and random, nested within Year x Season x Site). The sources of statistically significant (at $\alpha = 0.05$) differences among habitats (generally apparent within levels of the other factors) were examined using a *posteriori* pairwise PERMANOVAs. Due to the small number of permutations of the data that could be generated for a *posteriori* tests, these used Monte-Carlo p-values (Anderson et al. 2008).

A distance-based Redundancy Analysis (dbRDA, (Legendre & Anderson 1999)) was used to ordinate community data and identify species contributing most to dissimilarities in fish community structure among samples. The dbRDA used Bray-Curtis dissimilarity measures, calculated using the "capscale" function of the Vegan package (Oksanen 2015) in R (R Core Team, 2019). To select the species most closely correlated with dissimilarity measures, significant factors from the PERMANOVA analysis were included and permutational tests assessed statistical significance of each axis and marginal terms, and a triplot was made. For clarity, only species that were positioned +/- 0.5 along either axis were plotted.

Univariate Linear Mixed Effects Models were run within the package "lmer4" (Bates et al. 2015) on the following metrics calculated for each camera: (1) the total number of fish observations, (2) the total species richness, (3) observations of adults, (4) observations of juveniles, the percent contribution of each of (5) feeding, (6) wandering, and (7) passing behaviour to total observations per camera and (8) the total observations by species of taxa identified by dbRDA as good discriminators between oyster reefs and other habitats or highest observations in the study. Chasing behaviour was reported but not analysed as the scale at which this behaviour occurs is frequently cross-habitat. The model, utilised by each of these analyses, included the factors: Habitat, Season, Estuary,

Site (nested with Estuary) and Year. These were each considered as fixed factors because Linear Mixed Effects Models require at least five “levels” for a random intercept to achieve a robust estimate of variance (Harrison et al. 2018). To account for the spatio-temporal effects, the factors Day, nested in Site, Season, Estuary and Year were treated as random effects with 48 levels, combined. Data followed typical distributions for counts, so were square root transformed to produce the Gaussian distribution, required by the model. After running our model, we performed an ANOVA of the fixed effects using the “anova” function and tested the significance of the random effects by using the function “ranova” from the “lmerTest” package (Kuznetsova et al. 2017). We also checked that model assumptions, including normality of data, were met by visual inspection of the model residuals. Pairwise comparison tests with Tukey’s p-value adjustments examining sources of significant interactions were performed using Estimated Marginal Means (EMMs) within the “emmeans” package (Lenth et al. 2020).

2.4 RESULTS

Once videos with recording issues were excluded, a total of 740 RUVs were analysed including 188 deployments on the oyster reef, 186 on the seagrass, 187 on the mangroves and 179 on the bare sediment, encompassing 925 hours of analysable footage.

2.4.1 Species composition

A total of 92,524 fish observations were made across the 740 RUVs, representing 99 species, belonging to 49 families (Appendix A, Table A.1). A total of 66 species were seen on oyster reefs, of which 14 species were unique to this habitat; 60 species were associated with seagrasses, including 22 unique species; 43 species were seen on bare sediment including five that were unique; and 40 species were found in mangroves of which two were unique to this habitat. Yellowfin bream (*Acanthopagrus australis*) was the most observed species in oyster reefs and mangroves, luderick (*Girella tricuspidata*) the most observed species in seagrass and whiting (*Sillago ciliata*) the most observed species in bare sediment (Appendix A, Table A.1). Twelve species, including yellowfin bream, luderick and whiting, were common to all four habitats. When separated into adults and juveniles, adults of 90 species were identified that accounted for 83% of total observations and juveniles of 37 species, accounting for 17% of observations.

2.4.2 Fish community differences among habitats

Multivariate analyses revealed that the fish community displayed differences among habitats that varied with season and among sites (sig. Season x Site(Estuary) x Habitat interaction, Appendix A, Table A.3a). In general, differences among habitats were more pronounced in summer than in winter (*a posteriori* tests, Appendix A, Table A.3b). In summer, at three of the four sites, the four habitats each supported distinct communities. At the fourth site, Carters Island, Botany Bay, the fish communities of bare sediments did not significantly differ from those of seagrasses or mangroves, but all other pairwise comparisons were significant. By contrast, in winter, at the two Port Stephens sites, oyster reefs supported similar fish communities to mangrove, but all other habitats differed. In Botany Bay, conversely, oyster reefs and mangroves were the only two habitats to differ at Carters Island in winter. At Quibray Bay in winter all but the seagrasses and bare sediments, and seagrasses and oyster reefs comparisons were significant.

Inspection of dbRDA revealed clear differences among the fish community between each of the habitats except for oyster reefs and mangroves, which grouped together (Figure 2.2). *Pelates sexlineatus* (trumpeter), *Meuschenia trachylepis* (yellow-finned leatherjacket), *Rhabdosargus sarba* (tarwhine), *Acanthaluteres spilomelanurus* (bridled leatherjacket), *Sphyræna obtusata* (striped seapike) characterised seagrass fish communities, while *Sillago ciliata* (sand whiting) characterised bare sediment, and *A. australis* (yellowfin bream, hereafter referred to as bream), *Omobranchus anolius* (oyster blenny), *Omobranchus rotundiceps* (rotund blenny), *Microcanthus strigatus* (stripey) and *Mugil cephalus* (sea mullet) characterised oyster reef and mangrove habitats.

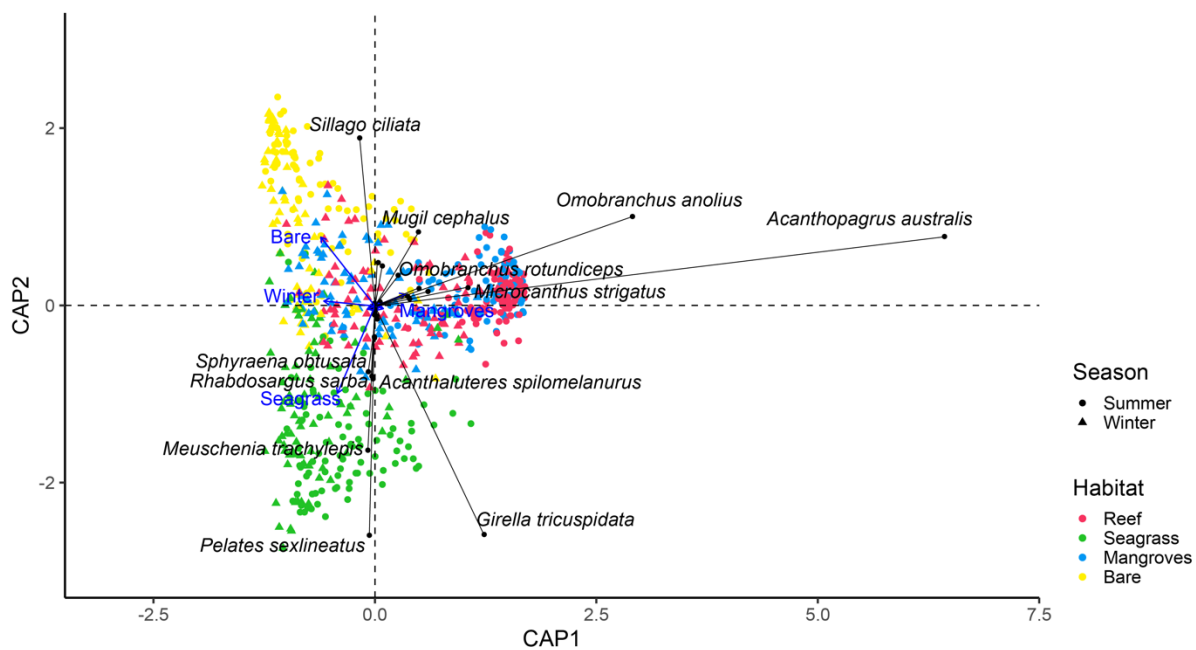


Figure 2.3: Distance-based Redundancy Analysis (dbRDA) triplot of transformed fish observations data, across four habitats, four sites and two seasons. Species exceeding a critical value of ± 0.5 on one of the axes are indicated. Points represent individual cameras ($n = 740$).

2.4.3 Fish observations and species richness among habitats

Multivariate differences in community structure could, in part, be attributed to site- and season-dependent effects of habitat on fish observations and richness, which also showed yearly differences (Appendix A, Tables A.4a, A.5a). As with community data, these metrics generally displayed greater differences among habitats in summer than winter (Appendix A, Tables A.4b, A.5b). In summer, at all sites and in both years, oyster reefs had a significantly greater number of fish observations (Appendix A, Tables A.4, Figure 2.4) than any of the other habitats. In winter, the number of fish observations in oyster reefs was also generally greater than in any of the other habitats, but this difference was not statistically significant for some sites and years (Appendix A, Table A.4b). Species richness of fish (Appendix A, Tables A.5, Figure 2.5) in summer of both years followed a similar pattern to fish observations, with oyster reefs having a greater or similar richness when compared to the other structured habitats and higher richness when compared to unstructured bare sediments. In winter of both years, richness differences across habitats were less accentuated, with oyster reefs and seagrass having generally similar richness to one other and higher or similar richness when compared to other habitats. The pattern of greater numbers of fish observations in oyster reef than other habitats was also displayed when adults and juveniles were analysed separately, with greater seasonal variation in juveniles (Appendix A, Table A.6, A.7).

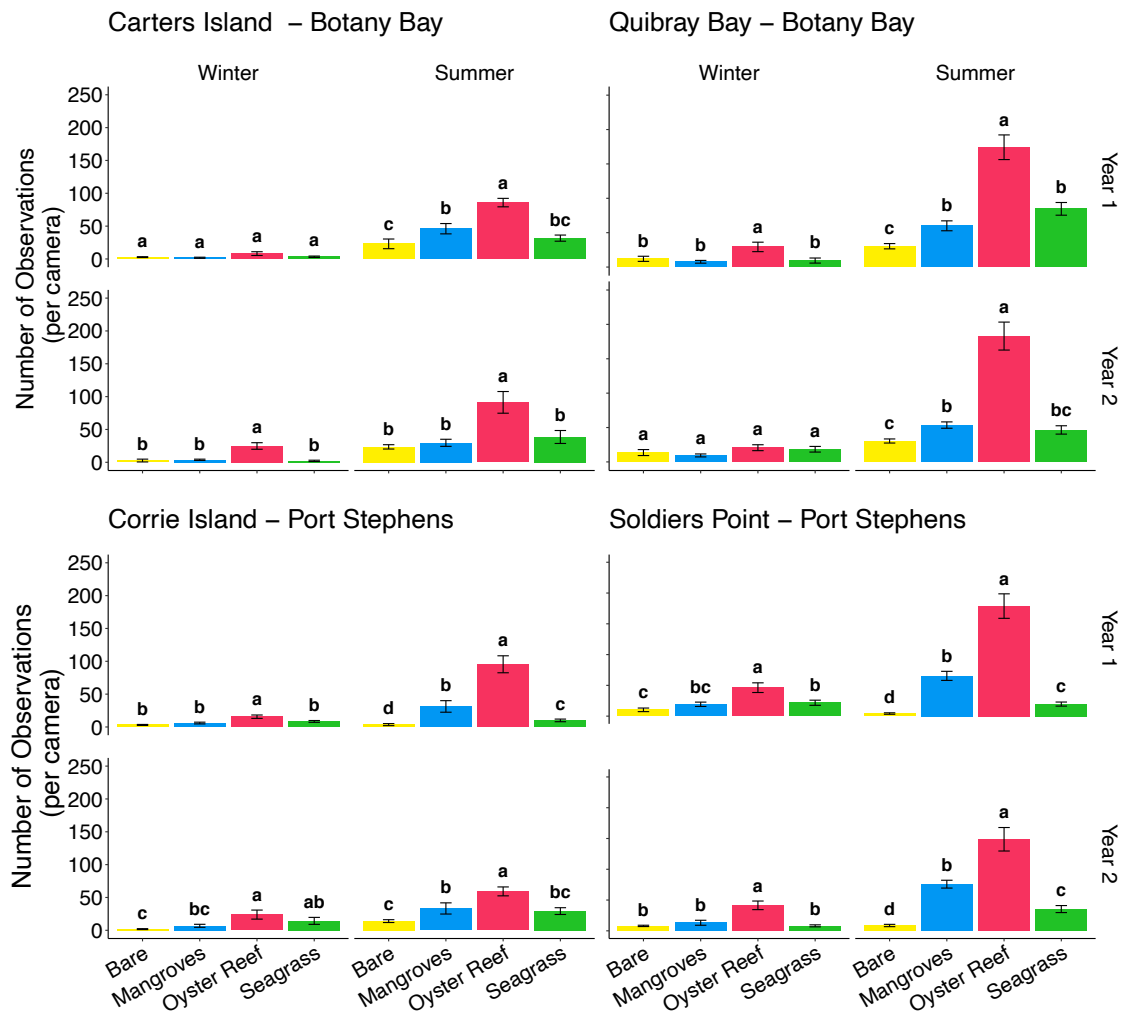


Figure 2.4: Mean ($\pm$ SE) fish observations, per habitat, site, season, and year, as documented by 75 min Remote Underwater Video deployments, $n = 64$ (when cameras are pooled for each Habitat $\times$ Site $\times$ Season $\times$ Year combination). Different letters above columns denote Habitats that were found to significantly differ at $\alpha = 0.05$ using estimated marginal means pairwise comparisons by season within each site and year.

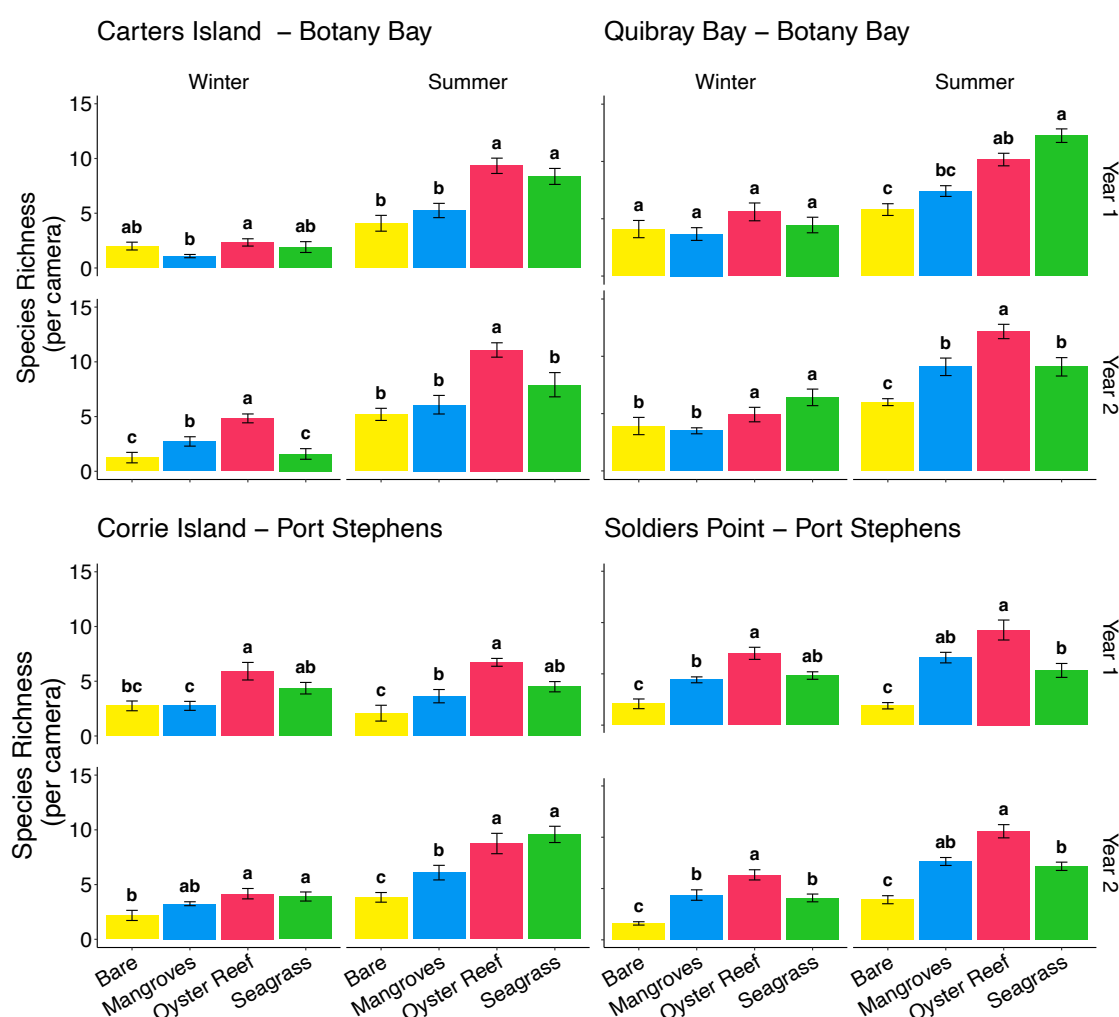


Figure 2.5: Mean ($\pm$ SE) species richness of fish, per habitat, site, season, and year, as documented by 75 min Remote Underwater Video deployments, $n = 64$ (when cameras are pooled for each Habitat $\times$ Site $\times$ Season $\times$ Year combination). Different letters above columns denote Habitats that were found to significantly differ at $\alpha = 0.05$ using estimated marginal means pairwise comparisons by season within each site and year.

2.4.4 Species-specific observations among habitats

Together, bream, luderick, tarwhine, whiting and four mullet species -- sea mullet, goldspot mullet, sand mullet (*Myxus elongatus*), and flat-tail mullet (*Paramugil georgii*) -- accounted for 59% of the total number of fish observations in the study, and were key contributors to differences in fish communities among habitats (Figure 2.3).

Bream was the most commonly observed species, accounting for 36% of total observations. Observations of bream varied according to the interacting effects of Year, Season and Habitat (Appendix A, Table A.8a). Differences in bream observations among

habitats were generally stronger in summer than winter. In general, for both years, more bream were observed in oyster reefs than any other habitat (Appendix A, Figure A.1), followed by mangroves, with seagrass and bare sediment generally displaying the fewest bream observations (Appendix A, Table A.8b). Within oyster reefs, 9% of bream were feeding, 84% were wandering, 6% were passing and <1% were chasing (Appendix A, Table A.2).

Luderick, the third most encountered species (13% of total observations), also displayed site- and season-specific patterns of difference in observations among habitats within years (Appendix A, Table A.9a). In Botany Bay, luderick were observed in all four habitats, with observations generally greater in oyster reef than in bare or mangrove habitat, with oyster reef also having greater than or equal observations to seagrass (Appendix A, Figure A.2, Table A.9b). Generally, luderick observations in Port Stephens were greater in each of oyster reef and mangroves (which in most instances did not significantly differ) than in bare sediment, from which they were completely absent, and from seagrass where they were absent or rare (Appendix A, Figure A.2, Table A.9b). Within oyster reef, 16% of luderick observations were of individuals feeding, 72% wandering, 10% passing and 3% chasing (Appendix A, Table A.2).

Tarwhine accounted for 1% of the total number of observations in the study. Though displaying differences in observations among habitats that were dependent on the three-way interaction between site, season and year, more tarwhine were generally observed in seagrass than the other habitats, in which they were rare (Appendix A, Figure A.3, Table A.10). Sand whiting, which contributed to 3% of total observations, was generally more abundant in the bare than the other habitats (Appendix A, Figure A.4, Table A.11), the latter of which displayed few differences which, when apparent, were season- and year-specific.

The Mugilidae family (comprising four species) collectively accounted for 6% of total observations. Mullet observations were generally greater in oyster reef than the other habitats, with some exceptions (Appendix A, Figure A.5, Table A.12a). Differences in mullet observations among the other habitats were more spatially and temporally variable, with no consistent pattern apparent between sites or through time (Appendix A, Figure A.5, Table A.12b). Within oyster reef, 13% of mullet were feeding, 59% were of wandering, 28% were passing and <1 % were chasing (Appendix A, Table A.2).

2.4.5 Fish behaviour differences among habitats

Of the fish observed by this study, 13% of their observations were classified as passing, 74% as wandering, 12% as feeding and 1% as chasing. The percentage of fish that were feeding was similar across the four habitats surveyed, ranging from 10% in seagrass to

12% in mangroves (Figure 2.6, Appendix A, Tables A.13). The percentage of fish that were wandering and passing, by contrast, varied according to the three-way interaction between Habitats, Seasons and Years (Figures 2.7, 2.8, Appendix A: Tables A.14, A.15). The percentage of fish that were wandering was generally greater in the three structured habitats -- oyster reef, mangroves and seagrass -- than on bare sediment. Exceptions were winter of year one and summer of year two, where this percentage did not significantly differ between bare sediment and seagrass. The percentage contribution of passing to total observations displayed the reverse trend to wandering, with generally higher percentages in the bare sediment than in other habitats.

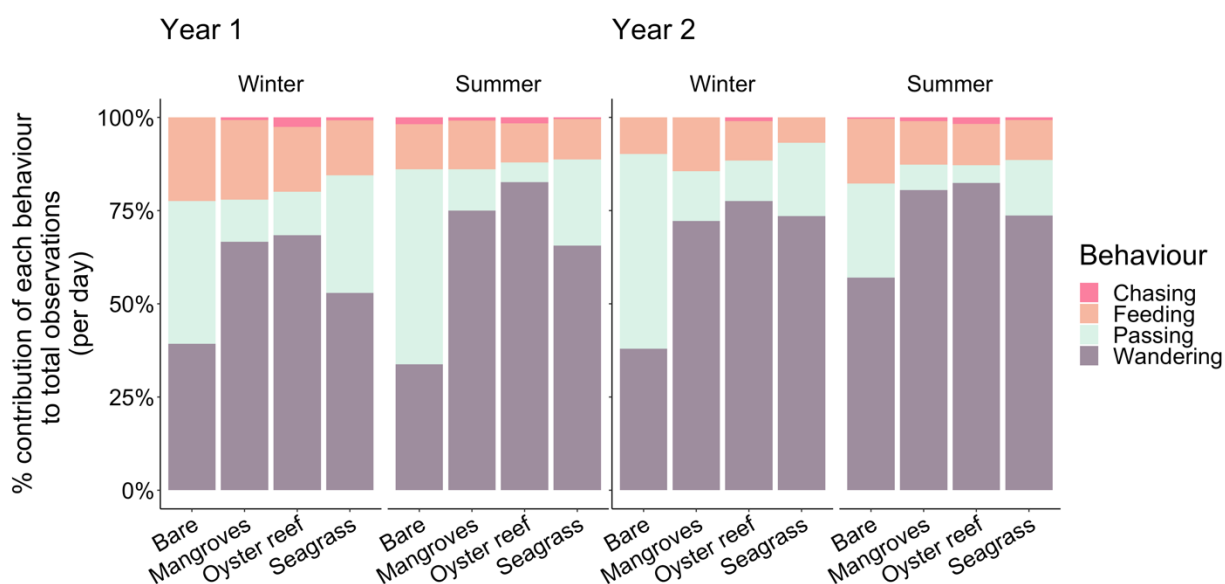


Figure 2.6: Mean ($\pm$ SE) percentage contribution of feeding to total observations recorded during 75 min Remote Underwater Video deployments, $n = 16$ (when days are pooled for each Habitat combination). Different letters above columns denote Habitats that were found to significantly differ at $\alpha = 0.05$ using estimated marginal means pairwise comparisons.

2.5 DISCUSSION

This is the first study to compare the fish communities of remnant intertidal oyster reefs with those of other structured estuarine habitats in south-eastern Australia. We found that remnant oyster reefs were habitat to a greater range of fish species, present at higher or similar abundance, than other key habitats of the estuarine seascape, several of which are considered nursery habitats (Beck et al. 2001, Lefcheck et al. 2019). Our observations of fish behaviour suggested that oyster reefs are utilised at high tide as

foraging grounds and protective habitat by a unique fish community that includes important recreational and commercial fish species.

2.5.1 Oyster reef fish community

Despite the proximity of remnant oyster reefs to other biogenic habitats comprising the estuarine seascape, oyster reefs supported fish communities distinct from those found in bare sediments, seagrass beds and mangrove forests. This difference in fish communities among habitats was particularly pronounced in summer when the overall richness and abundance of fish was greatest, though differences among habitats were apparent throughout the year. The fish communities associated with oyster reefs were most similar to those associated with mangrove forests. This may be explained by the role of mangrove pneumatophores in supporting oysters as a secondary habitat-forming species (Hughes et al. 2014), such that there was some overlap in the structural habitat and prey resources provided. Nevertheless, this result adds to growing evidence that even proximate estuarine biogenic habitats are functionally distinct in terms of the habitat they provide to fish (Hindell & Jenkins 2004, Green et al. 2009, Gain et al. 2016, Ruesink et al. 2019)

Differences between oyster reefs and other biogenic habitats in fish community composition were in part, driven by cryptic species, such as blennies and gobies. These groups have also been found to display a high degree of site fidelity to remnant and restored oyster reefs elsewhere (Tolley & Volety 2005, Grabowski & Peterson 2007, Gain et al. 2016, Gilby et al. 2018b, Crawford et al. 2019, Harding et al. 2019). As oyster reefs grow by accretion, dead disarticulated oysters and trapped sediment remain as the main structural component of the reef, leaving interstitial spaces between shells. These spaces can serve as microhabitats not only for epifaunal (Summerhayes et al. 2009) and infaunal invertebrates (McLeod et al. 2020), but also for juvenile and small cryptic fish (Harding et al. 2019).

Additionally, larger facultative species, such as bream and mullet, strongly influenced the fish community composition on oyster reefs. Behavioural observations of these species suggest that this association was due to both the food and habitat resources provided by oyster reefs (Norling & Kautsky 2007, Abeels et al. 2012, Quan et al. 2012, Hoellein et al. 2014, Engel et al. 2017, McLeod et al. 2020). Bream congregate around structurally complex habitats, such as oyster reefs and seagrass meadows, to feed on oyster spat, other epibenthic invertebrates and fish (Brook et al. 2018, Olds et al. 2018, Taylor et al. 2018). Late-stage juvenile and adult mullet feed mainly on detritus and benthic microalgae, together with foraminiferans, filamentous algae, protists, meiofauna and small invertebrates (Thomson et al. 1963, Blaber 1976, Lawson & Jimoh 2010). Such resources can also be enhanced by oyster reefs (Norling & Kautsky 2007,

Southwell et al. 2017, McLeod et al. 2020). Oysters provide nutrient rich biodeposits through their filter feeding. This biodeposition leads to organic enrichment of the reef environment, and surrounding bare sediment which in turn promotes growth of microphytobenthos, and secondary production of invertebrates and fish (Quan et al. 2011, Abeels et al. 2012, Engel et al. 2017).

2.5.2 Fish utilisation of oyster reefs

Although a large number of studies have compared fish communities between oyster reefs and other estuarine habitats (Lehnert & Allen 2002, Grabowski & Peterson 2007, Humphries et al. 2011, Humphries & La Peyre 2015, Gain et al. 2016), few of these have attempted to partition the role of oyster reefs into structural versus trophic (Abeels et al. 2012, Quan et al. 2012, Gain et al. 2016, Pfirrmann & Seitz 2019). Moreover, the role of oyster reefs as nursery habitat remains largely unexplored (Lefcheck et al. 2019).

Our analyses of fish behaviour and of adult and juvenile groups provided some insight into the potential structural, trophic and nursery habitat roles of oyster reefs. In our videos, we directly observed fish feeding on oysters and other invertebrates, providing evidence for an important trophic role for oysters (Quan et al. 2011, Abeels et al. 2012). The proportion of fish feeding was similar between oyster reefs and seagrass and mangroves, all of which are broadly regarded as important fish foraging grounds (Abrantes et al. 2015, Sheaves et al. 2016, Whitfield 2017). Predation, stomach content and stable isotopes studies would be required to fully understand the trophic role of remnant east Australian oyster reefs, which may also stimulate detrital pathways through filter-feeder biodeposition (Norling & Kautsky 2007, Hoellein et al. 2014).

A higher proportion of fish were also found wandering (i.e. swimming slowly) around oyster reefs, mangroves and seagrasses than in bare sediments. This suggests fish are displaying some fidelity and residency within structured habitats, including oyster reefs, rather than simply swimming through (Lowry et al. 2017, Taylor et al. 2018). Based on the behavioural sightings from our remote underwater videos, wandering behaviour can be related to foraging, seeking refuge or simply resting, and further studies are needed to investigate site fidelity within these habitats and how seeking refuge and resting can be related to this behaviour.

Our results are also suggestive that oyster reefs may serve as important nursery habitats. We observed not only more adults but also juveniles on oyster reefs than in mangrove and seagrass habitats the latter two of which are widely regarded as important nursery habitats (Whitfield 2017, Lefcheck et al. 2019). Yet whilst our study clearly shows that remnant oyster reefs provide habitat to a wide range of juvenile fish species, studies employing more explicit life-stage characterisation are required to better understand

ontogenetic movements and putative nursery function of oyster reefs within the estuarine seascape (Beck et al. 2001, Lefcheck et al. 2019).

2.5.3 Connectivity of oyster reefs with other estuarine habitats

Despite differences in the structure of fish communities among habitats, there was considerable overlap in the overall assemblage by the most observed species in the study that, in turn, were species with high commercial and recreational interest. For example, although most abundant on oyster reefs, bream, luderick and mullet were also found in other habitats. Fish may display tidal, seasonal and/or ontogenetic shifts among habitats in the estuarine seascape for foraging, refuge and/or reproduction, and many obligately or facultatively use multiple habitat types to complete their life history (Sheaves 2009, Gilby et al. 2018a). That single species utilise multiple habitats illustrates the importance of considering habitat location, habitat connectivity and a seascape ecology perspective when monitoring different habitat ecosystem services, such as habitat value for nektonic species (Gilby et al. 2018a, Gilby et al. 2019b).

Ecological connectivity can be influenced by the spatial arrangement, size and quality of habitat patches within the system, as well as other environmental factors (Boström et al. 2011, Olds et al. 2016, Gilby et al. 2019a). Our study did not explicitly examine how the fish communities of oyster reefs vary according to their proximity to other estuarine habitats, or the size and quality of these. Nevertheless, within estuaries we found variation between study sites in the magnitude of differences in fish communities among habitats. While differences in environmental context may have contributed to this site-scale variability (Bradley et al. 2019), each site was defined by a different arrangement of the four habitats, with different patch sizes, habitat conditions and distances between patches. Further studies are needed in order to disentangle how seascape context influences the role of oyster reefs in estuarine settings.

2.5.4 Conclusions

Our study provides the first insight into the potential value of remnant oyster reefs as fish habitat in south-eastern Australia and builds upon previous studies on their habitat value to invertebrates (McLeod et al. 2020, Cole et al. 2021). Our results point to a role for oyster reefs in providing food and habitat to fish, which in some cases (and at most times of the year) may exceed that of other estuarine biogenic habitats. The results also suggest a potential role for oyster reefs serving as nursery habitats. Commercially and recreationally fish are an important component of the estuarine fish community supported by oyster reefs such that the conservation and restoration of these habitats may be expected to bolster fisheries production. Nevertheless, the considerable overlap in species between oyster reefs and adjacent habitats indicates that the habitat

context in which oyster reefs are reconstructed will play a major role in determining the net ecosystem and fisheries benefits of oyster reef restoration. The need for a seascape approach to oyster reef restoration is clear (Gilby et al. 2018b), and this needs to be supported by studies synthesising fish movements, habitat mapping, trophic analysis, and observations of the assemblage. This will ultimately support intertidal Sydney rock oyster restoration strategies that optimise fisheries outcomes.

2.6 ACKNOWLEDGMENTS

We thank the Department of Biology from Macquarie University for their support through the Macquarie University Research Excellence Scholarship (MQRES), the NSW Department of Primary Industries Fisheries Department and University of New South Wales for their support on equipment and logistics. Thank you to Wayne O'Connor, Michael Dove, Ian Lyall and Kylie Russell for their support and assistance and we would like to thank our fieldwork manager Nick Harris and volunteers Steph Bagala and Justin McNab for their continuous assistance with the fieldwork. We acknowledge and pay our respect the Dharawal, Dharug, Eora and Worimi nations, Traditional Custodians of the lands on which this study has taken place and whose cultures have nurtured and conserved estuarine habitats.

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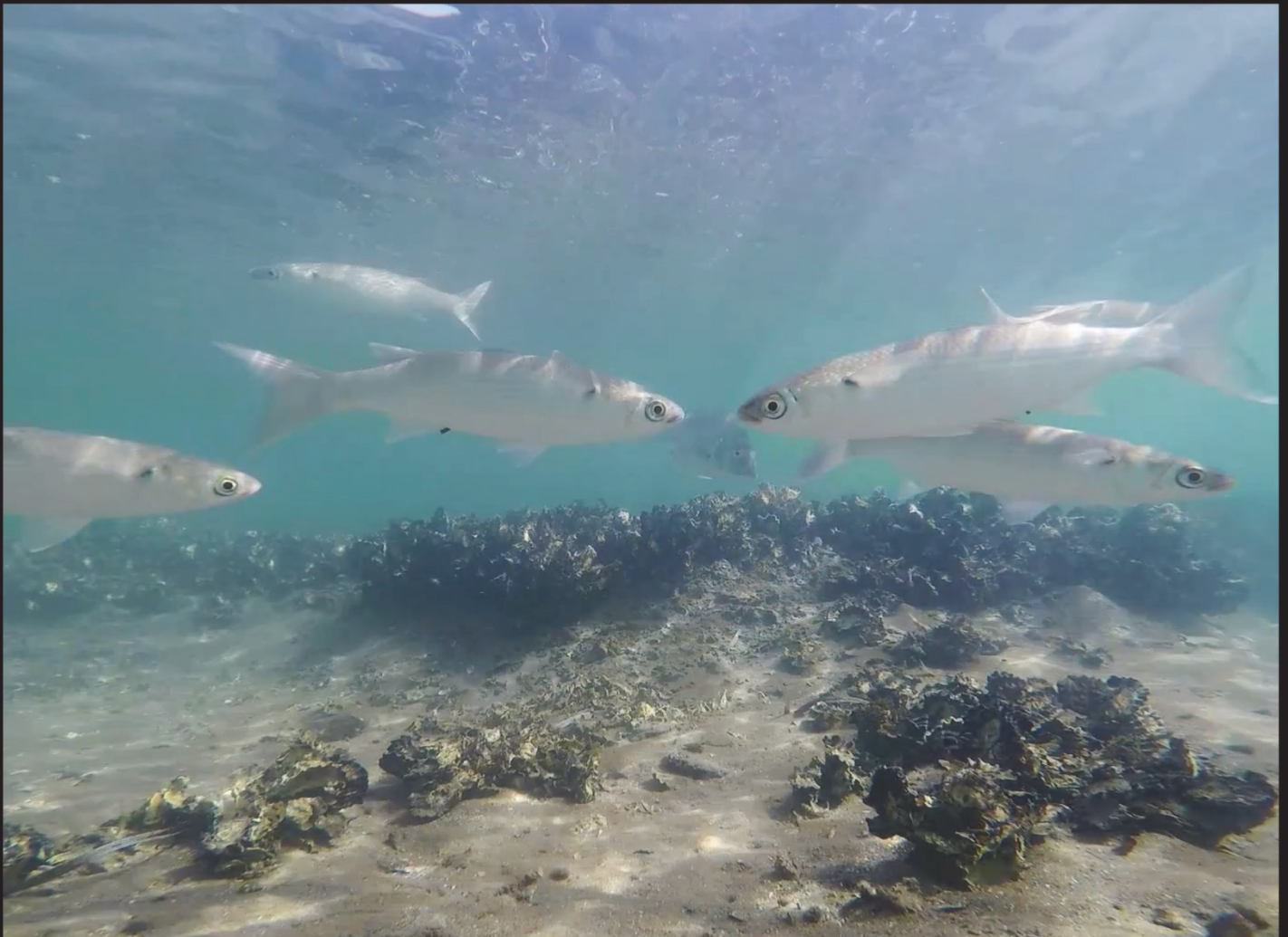
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Chapter 3: Trophic structure of oyster reefs

A STABLE ISOTOPES ANALYSIS

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3.1 ABSTRACT

Oyster reefs, once a dominant habitat of temperate and subtropical estuaries, have globally been reduced to <15% of their pre-industrialisation abundance. Remnant oyster reefs support dense and diverse communities of invertebrates and fish, and there is growing interest in restoring this important habitat to enhance fisheries productivity. Whether construction of new oyster reefs will enhance or simply redistribute existing fisheries productivity depends on their trophic role – which, to date, is unknown for east Australian estuaries. In this study, conducted in Port Stephens, New South Wales, Australia, we used stable isotope analysis to determine trophic linkages among remnant oyster reefs and their resident and transient species. Specifically, we identified whether the potential trophic linkages could be arising directly, from the consumption by higher trophic levels of reef-forming bivalves, or indirectly, from uptake of oyster-generated organic matter found in the sediment and consumption of reef-dwelling organisms. Our results suggest oyster reefs are contributing to the trophic ecology of both resident and transient species, both through direct predation on the oysters and other reef forming bivalves, but also indirectly through consumption of benthic organic matter found on the reefs grounds, and of prey species that reside in oyster reefs. These results suggest that the construction of new oyster reefs will not simply attract species away from existing habitats in the estuarine mosaic, but will likely enhance productivity by broadening the resource base. Studies are now needed to quantify the extent to which oysters enhance productivity across a range of habitat settings.

3.2 INTRODUCTION

Estuaries are among the most productive ecosystems on Earth, but also among the most heavily impacted by coastal development and climate change (Stronge et al. 2005). In severe cases, anthropogenic disturbances have pushed many estuarine habitats to the edge of extinction (Lotze et al. 2006). Among these, oyster reefs were once a dominant estuarine habitat globally with reefs ranging from 10 to 100 000 m² in size (Oyster Culture Commission 1877), but historic overharvest coupled with more recent declines in water quality and proliferation of diseases have rendered them functionally extinct throughout much of their range (Beck et al. 2011, Gillies et al. 2018). In Australia, it is estimated that only 10% of the oyster reefs that were present prior to industrialisation currently remain, and the habitat has been almost completely lost from some estuaries (Gillies et al., 2018).

Oysters are important habitat forming organisms, and along with the reefs they form support important ecosystem services, such as water filtration, sediment stabilisation, and fisheries productivity (Grabowski & Peterson 2007, Bateman & Bishop 2017). Some studies indicate that the diverse range of organisms associated with oyster reefs sustain complex food webs that support higher trophic levels than surrounding habitats (Wrast 2008, Quan et al. 2012). By intercepting suspended particles and nutrients before they enter microbial loops or are exported, oyster reefs promote the transfer of energy from primary producers to fishes, crabs, and higher-order predators (Quan et al. 2011, Abeels et al. 2012). Among the species that benefit from this transfer are not only those that directly feed on oysters (Tolley & Volety 2005), but also the associated resident fauna that live within the reef complex (McLeod et al. 2020).

Previous studies have described the role of remnant oyster reefs in supporting invertebrate communities (McLeod et al. 2020), in regulating nutrient dynamics and in mediating benthic-pelagic coupling (Newell 2004, Dame 2011). In Australia, it is unclear the extent to which nektonic relationships with the habitat are based on trophic linkages versus structural habitat associations. Trophic linkages associated with oysters may be related to two main trophic pathways: (1) an indirect pathway originating from biodeposits produced by reef forming species and (2) a direct pathway through predation. The indirect pathway involves the production of biodeposits from oyster reef forming species. These biodeposits are generated through excretion of faeces and pseudo faeces, that results in organic matter enrichment in nearby sediments (Castel et al. 1989, Leguerrier et al. 2004). The nutrients from the biodeposits can be utilised by microphytobenthos (Miller et al. 1996, Prins et al. 1997) and detritivorous species as a food source (Quan et al. 2011). The direct pathway involves predation on oysters, their larvae, juvenile stages and the epifauna that live in the reef complex. Direct predation on oysters by gastropods (Wright et al. 2018), crabs (Carroll et al. 2015, Scherer et al. 2017) and fish (Anderson & Connell 1999) is a key factor limiting oyster recruitment, settlement, survivorship and hence spatial distribution within estuaries (Fodrie et al. 2014, Hanley et al. 2016, Strain et al. 2018a), but also promotes trophic energy transfer within estuarine systems. Elucidating the extent to which these pathways are important and sustain higher trophic levels in estuarine systems is key for quantifying the role of oyster reefs within the estuarine seascape. The extent to which remnant oyster reefs trophically support nektonic species, especially exploited species, will contribute to the increasing evidence that these habitats are essential for fishes (Peterson et al. 2003), and further underline the need for their conservation and restoration.

In Australia stable isotopes have been used to investigate trophic ecology and productivity of other key estuarine biogenic habitats such as mangroves, seagrasses and saltmarshes (Mazumder et al., 2011, Selleslagh et al., 2015; Taylor et al., 2018, Raoult et al., 2018, Hewitt et al., 2020). These studies most often use isotopes of C and N

(Bouillon et al. 2011, Franca et al. 2011, Selleslagh et al. 2015) to measure links between epibenthic producers, lower level consumers and mobile consumers such as fishes by determining the degree to which isotope signatures are transferred through food webs (Peterson 1999). Stable isotope ratios of C and N are able to discriminate among various primary producers that support food webs in several coastal habitats and relative trophic levels of consumers (Fry & Sherr 1984, Peterson et al. 1985, Bustamante & Branch 1996, Riera & Richard 1996), as these isotopes enrich between trophic levels in a relatively predictable manner (Kelly 2000). While $\delta^{15}\text{N}$ values show a stepwise enrichment between 2 – 5‰ with each trophic level and can indicate a consumer's trophic position, $\delta^{13}\text{C}$ values show less change through trophic transfer but are useful indicators of dietary sources of carbon (Layman et al. 2012). Together, C and N isotopes provide a powerful tool to infer transfer of organic matter in ecosystems such as oyster reefs (Schaal et al. 2008).

In this study we used stable isotopes analysis to determine whether the habitat role of intertidal oyster reef forming species, the Sydney rock oyster (*Saccostrea glomerata*) and the hairy mussel (*Trichomya hirsuta*), is explicitly limited to a structural role or to direct or indirect trophic linkages with other consumers. Specifically we (1) determine the contribution of these reef forming species as a trophic resource to the diet spectrum of the oyster reef community through the two main trophic pathways: direct prey items and indirectly from the sediment integration of oyster reef biodeposits using Bayesian stable isotope mixing models; (2) establish the trophic levels of the oyster reef community; and, (3) examine whether the isotopic niche of the oyster reef forming species is unique in relation to other species, or whether there is a niche overlap between animals that use the oyster reefs as primary habitat (reef residents), or as facultative habitat (reef transients), grouped by their respective feeding guilds.

3.3 METHODS

3.3.1 Study area

Sampling occurred on the southern side of Dowadee Island in Soldiers Point, Port Stephens, New South Wales, Australia (32°42'14.34"S, 152° 3'28.26"E). The study site contained one of the largest natural remnant intertidal *Saccostrea glomerata* oyster reef in New South Wales set alongside a complex habitat mosaic of unvegetated sand and mud bottom, intertidal *Avicennia marina* mangrove, and subtidal mixed seagrass beds of *Posidonia australis* and *Zostera muelleri*, all within a 166 m² area. Previous sampling of oyster reef, seagrass, mangrove and unvegetated habitats at this site revealed that it

supported a diverse range of invertebrates and fish species, including cryptic, as well as predatory species. The site was characterised by semidiurnal tides and was situated 12.63 km from the estuarine mouth.



Figure 3.1: Map including the location of the study site at Port Stephens estuary in NSW.

3.3.2 Sample collection and processing

To ascertain the isotopic structure of the estuarine habitat mosaic, stable isotope analyses were conducted on pelagic and benthic organic matter (the latter collected from oyster reef and mangroves habitat), 6 primary producers as well as 35 consumers, 16 of which were invertebrates and 19 of which were fish (Appendix B, Table B.1). Targeted species represented the most abundant primary producers at our study site, as well as invertebrate and fish species often encountered in this seascape (McLeod et al. 2020, Chapter 2). All sampling occurred in April and May of 2018 (i.e. the Austral autumn) during daylight hours, with the exception of gill nets that were set overnight.

Benthic organic matter (hereinafter referred after as BOM and containing detritus, sediment and other biological material), primary producers, cryptic fish and invertebrates were collected at low tide. BOM was collected by scraping the top 5 cm of sediment from 6 replicate patches in each of oyster reef and mangrove sediments using a plasterer's spatula. Seagrasses (*Posidonia australis*, *Zostera muelleri*) and algae (*Hormosira banksii*, *Sargassum* sp. were sampled by collecting a single leaf or thallus

from ten different individuals. For mangroves (*Avicennia marina*) we collected 7 leaves, each from a separate tree, as well as 5 pneumatophores. Epiphytes were removed from seagrass blades and algal thalli prior to their analysis. Epiphytes removed from the ten *P. australis* samples were retained for analysis. The reef-building Sydney rock oyster and hairy mussel, associated invertebrates and cryptic fish were collected from reefs using hand corers ($n = 12$) of 13 cm diameter and 15 cm height, randomly positioned across the oyster reef. Target species were separated from sediments and other animals by washing the contents of each core over a 0.5 mm mesh sieve. Each BOM, algal, seagrass or mangrove sample was considered a replicate in stable isotope analyses. For oysters, mussels, cryptic fish and invertebrates, individuals were considered as replicates (see Appendix B, Table B.1 for a list of replication by target species/source).

Suspended organic matter (hereafter referred to as SOM, and containing zooplankton, detritus and other biological material), fishes, large crustaceans and cephalopods were sampled at high tide. SOM was collected with a plankton net (200 μ m mesh size) towed for 2 min at high tide within the area of study. Towing was repeated five times. Small pelagic fishes and cephalopods were captured using beach seine nets (mesh size = 2 mm; length = 8 m) at low tide on *Zostera* beds adjacent to the oyster reef. Large crustaceans (i.e. blue swimmer crabs) were captured using crab pots that were 90cm in diameter, 50cm in height, and with 50 mm mesh. Nine crab pots were deployed daily on three days for four hours, checked and redeployed for another 4 hours. Larger fish species were captured using multi-mesh monofilament nylon gill nets. Two gill nets were used over three days. Gill nets were deployed for four hours and then retrieved, with target species euthanized with slurry ice and non-targeted species released. For SOM, each plankton tow was considered a replicate. For all other organisms, individuals were replicates (Appendix B, Table B1).

3.3.3 Sample processing

Samples of primary producers and epiphytes were rinsed with deionized water, cleaned of epiphytes and detritus then frozen at -80°C for 24 hours before freeze-drying samples and grinding them to a fine and homogeneous powder with an oscillating mill (MM400). Sediment samples for analysis of BOM were washed over nested 4-mm, 1-mm, 0.5-mm and 0.25-mm sieves. Material and microorganisms retained on the finest size sieve was considered benthic organic matter (BOM; see Loneragan et al. (1997)) and processed similarly to primary producers.

For larger animals (e.g. shrimp, larger crabs, fishes), which could be dissected, stable isotope analyses were conducted on lean muscle tissue (Bodin et al. 2007). For smaller animals, the animal was either analysed whole (polychaetes, small crabs) or following the removal of exoskeletons and digestive tracts (gastropods, small shrimp).

Carbonate contamination and high lipid concentrations of the samples can alter $\delta^{13}\text{C}$ values and bias isotopic results (Ng et al. 2007, Logan et al. 2008, Franca et al. 2011). For small animals with calcareous structures that could not be removed, acidification protocols (following Kolasinski et al. (2008), Mateo et al. (2008), Mazumder et al. (2010)) were performed prior to $\delta^{13}\text{C}$ analysis. The acidification protocol involved drying the samples at 65°C for 24 hours, homogenizing them to a fine powder and then treating them with 2M HCl for 24 hours, or until no more bubbling was seen. Following acid treatment, deionized water was added to the sample and it was centrifuged for 5 min (3600 rpm), with the supernatant discarded. For samples of individuals that had to be analysed as a whole, or for which lean muscle could not be retrieved or their tissue contained naturally high lipid concentrations, suggested by C:N ratios as a proxy for lipid content (Logan et al. 2008), a lipid removal protocol (based on the Stable Isotope Laboratory of the Doñana Biological Station, Spain) was also added. The lipid removal protocol involved drying samples at 70°C for 24 hours, grinding samples to a fine powder then immersing samples with a 2:1 (v:v) solution of chloroform:methanol and vortexing them for a 3 minutes. Following 24 hr of lipid extraction, samples were centrifuged (750 rpm for 10 min) and the supernatant was removed, before the lipid extraction protocol was repeated. Following the two rounds of lipid extraction, the remaining solid residue was rinsed with deionized water, shaken in vortex for a few minutes, then centrifuged for 10 minutes at 12000 rpm, with the supernatant removed. Samples were repeatedly washed and centrifuged until the supernatant was clear, indicating the absence of chloroform:methanol. These processes described above have the potential to impact the isotopic composition (Pinnegar & Polunin 2002, Sweeting et al. 2006). As a result, a set of untreated sub-samples were analysed separately for $\delta^{15}\text{N}$. The subsample assigned to $\delta^{15}\text{N}$ analysis was frozen at -80°C freezer, freeze-dried and ground into a fine powder (as per primary producer and BOM samples).

After processing, subsamples were taken from homogenised samples, with their size determined using the Sample Weight Calculator from the University of California Davis Stable Isotope, according to the tissue/matter type. Subsamples were weighed and packaged into tin capsules then shipped to the University of California Davis Stable Isotope Facility for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Isotope ratios were calculated relative to the international standards, Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$ and are reported in the conventional delta (δ) per mil (notation ‰).

3.3.4 Data analysis

All data analysis was performed using R v. 4.0.0 (R Core Team, 2019).

Species were grouped according to known feeding habits and their degree of association with oyster reef habitats. Feeding habits were evaluated through a review of the published literature (Bray & Gomon 2018, Atlas of Living Australia 2019, Froese & Pauly 2019), and six main groups were identified: carnivores, omnivores, planktivores, grazers, deposit feeders and filter feeders. Species' habitat use was designated as either "reef former" (Sydney rock oysters and hairy mussels), "reef resident", or "reef transient" based on observational data obtained by McLeod et al. (2020) and Chapter 2. Reef resident species were the group of species utilising oyster reefs as their primary habitat and they are present on oyster reefs in significantly higher densities than on the adjacent habitats. By contrast, reef transient species were the group of species that have a primary habitat other than oyster reef, for example seagrass, mangrove, or bare sediments, but use oyster reefs intermittently for feeding or refuge.

Bayesian stable isotope mixing models run using the MixSIAR package (Stock & Semmens, 2016) determined the relative contributions of dietary sources of the species sampled. Before each Bayesian mixing models was run, we ensured that all assumptions for these models were met (Phillips et al. 2014). These analyses utilised tailored source groups (as per Parnell et al., 2010; Phillips et al., 2014), defined by a literature review on the feeding habits, the species feeding guild and the spatial disposition of their isotopic signatures bound within the sources considered, and assessed visually from the MixSIAR isoscape plots (Phillips & Gregg 2003). Sources that spatially overlapped and had $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ values that did not significantly differ (ANOVA, Appendix B, Table B.2), were grouped *a posteriori* where possible to decrease the number of sources to $n + 1$ (where n is the number of isotopic tracers, which is C and N in our case; (Brett 2014). Source group values were included in the analysis as raw data rather than mean $\pm$ SD to increase model accuracy. The analyses used trophic enrichment factors, estimated by averaging across published values for a given taxon, identified from a literature search (Appendix B, Table B.3). Prior to each analysis, Markov Chain Monte Carlo (MCMC) parameters for all models were set to "normal" mode and assumptions were checked using Gelman-Rubin and Geweke diagnostic tests. If chains did not converge successfully, models were run again with MCMC parameters set to "long" mode, until all chains successfully converged (Stock & Semmens, 2016). If a mixing model for a certain species did not meet these requirements, the species was removed from the analysis.

The trophic position (TP) of each consumer was estimated using the "tRophicPosition" package in R (Quezada-Romegialli et al., 2018). Posterior TP modes for each consumer

were calculated under the “two baselines model”, where a mixing model is included to discriminate among two main sources of C and N. In our case, a combination of the signatures of C3 + C4 plants and BOM, and two equations, one per $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were used. A trophic enrichment factor (TEF) value for each species was estimated by averaging literature values for species or equivalent functional group (Appendix B, Table B.3). The model baseline trophic level was set to 1.

For each of the three main groupings of species – reef forming species, reef residents and reef transients – we used the package “SIBER” (Jackson et al., 2011) to calculate the Bayesian standard ellipse area (SEA_B) as a measure of isotopic niche for each feeding guild present (filter feeders, deposit feeders, grazers, planktivores, omnivores and carnivores). Isotopic niche is the total amount of isotopic space exploited by a particular consumer and, thus, is a proxy for trophic diversity (isotopic width) (Albo-Puigserver et al. 2015). Additionally, we calculated niche overlap and compared it between: (1) the two reef forming species, the Sydney rock oyster and the hairy mussel, (2) reef forming species as a group and each of the resident and transient feeding guild communities and (3) the total convex hull area of the reef forming species as a group, the reef resident community and the reef transients community using “nicheROVER” (Swanson et al. 2015). To determine niche overlap among communities, we firstly obtained the distribution of convex hull areas (TA) from posterior distributions of the means for resident and transient groups, and secondly, calculated the probability of overlap between them. The mode and 95% credibility intervals (CI) were reported for all measurements.

3.4 RESULTS

Primary producer $\delta^{13}\text{C}$ signatures ranged from $-11.4 \pm 2.1\text{‰}$ for the group containing seagrasses, epiphytes and the alga, *Hormosira*, to $-27.0 \pm 1.8\text{‰}$ for the more depleted C4 plant species group of *Avicennia*. $\delta^{15}\text{N}$ signatures for primary producers ranged from $8.1 \pm 0.5\text{‰}$ for SOM-Sargassum to $4.6 \pm 0.9\text{‰}$ for BOM.

Among consumers, a total of 19 species were grouped as resident species, with $\delta^{13}\text{C}$ signatures ranging from $-19.4 \pm 1.2\text{‰}$ for the transient pelagic Port Jackson glassfish *Ambassis jacksoniensis* to $-10.9 \pm 0.6\text{‰}$ for the benthic rotund goby *Omobranchus rotundiceps*. Reef resident $\delta^{15}\text{N}$ signatures ranged from 7.2 ± 0.4 for the furry-clawed crab *Australoplax tridentata* to $13.6 \pm 1.6\text{‰}$ for adult stage bream, *Acanthopagrus australis*. A total of 15 species formed the group of transient species with $\delta^{13}\text{C}$ signatures ranging from $-18.6 \pm 0.1\text{‰}$ for the ghost shrimp *Trypaea australiensis* to $-12.6 \pm 1.3\text{‰}$

for the light-blue soldier crab *Mictyris longicarpus*. Reef transient $\delta^{15}\text{N}$ signatures ranged from $13.1 \pm 0.3\text{‰}$ for the dusky flathead *Platycephalus fuscus* to $6.1 \pm 0.5\text{‰}$ for *M. longicarpus* (Appendix B, Table B.1, Figure 3.2).

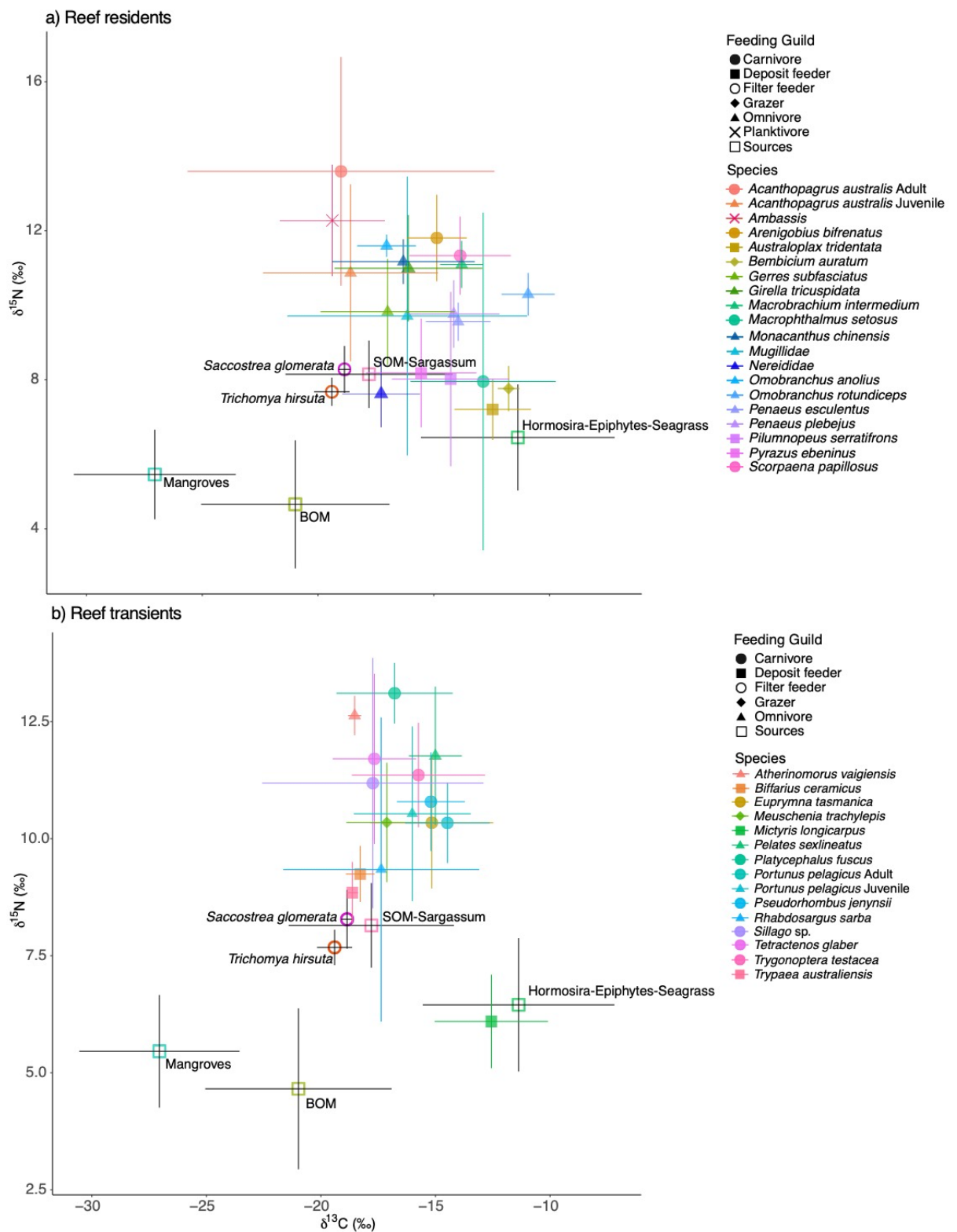


Figure 3.2: Mean ($\pm$ SD) carbon and nitrogen isotope values of primary producers, reef forming species, (a) reef residents and b) reef transient species represented by their feeding guilds.

3.4.1 Oyster reef contribution to diets of reef residents and reef transients

The group containing bivalves (reef forming species) and Nereididae polychaetes was the main resource (>40% contribution) for four species of reef resident (all omnivorous fish) and six species of reef transient (three carnivores: one crustacean and two fish species, and three omnivores: one cephalopod and two fish species) (Figure 3.3, Appendix B, Table B.4).

The benthic organic matter group (BOM) was the primary resource, with > 40% contribution, to seven species of reef residents, including two fish (omnivores), three crustaceans (deposit feeders), one gastropod (deposit feeder) and one polychaete (omnivore). BOM was not found to be a key contributor to the diet of any of the reef transients, with its greatest contribution for this group ranging between 31-33% for two species of fish (Figure 3.3, Appendix B, Table B.4).

Of the remaining resources, the group comprising suspended particulate organic matter (SOM) and Sargassum was the primary resource for two species of reef residents (two omnivorous crustaceans) and three species of transients (two deposit feeder crustaceans and one grazer fish). The group of primary producers, Hormosira-Epiphytes-Seagrasses, was the main resource for three reef resident species (one grazer gastropod, one deposit feeder crustacean and one omnivorous fish). The crustacean-gastropod resource group was the primary resource (>40%) for two reef residents (two carnivorous fish species) and one transient carnivorous fish. The source group of fish-cephalopods only had a major contribution as a resource for the adult (carnivorous) and juvenile (omnivorous) stage of one crustacean species. The mangrove group was not an important resource (i.e. > 40% contribution) for any of the species collected, only contributing between 35-37% of two deposit feeder crustacean species (Figure 3.3, Appendix B, Table B.4).

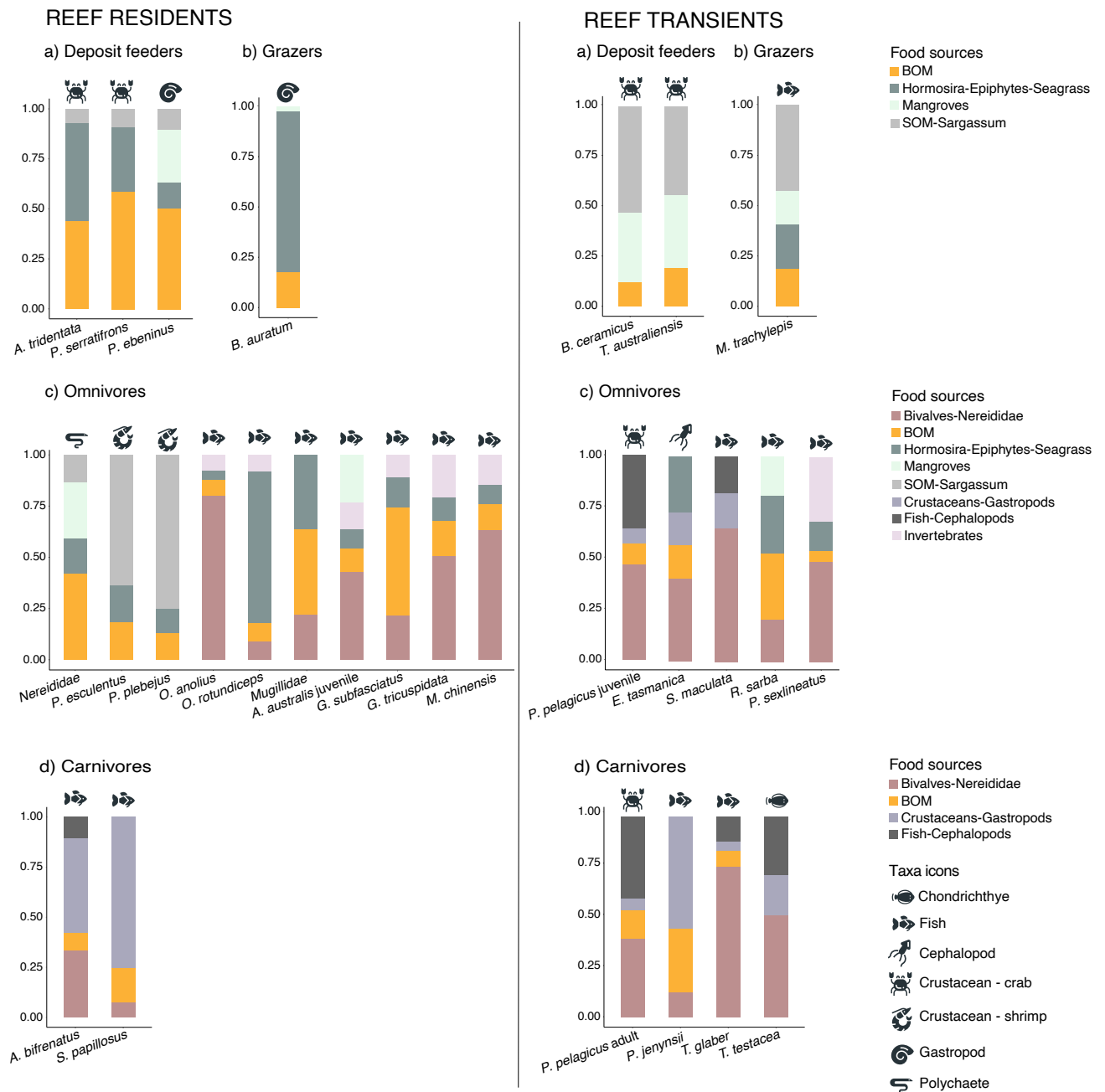


Figure 3.3: Stacked bar plots showing mean proportionate contributions of resources to taxa, grouped by feeding guild and reef relationship (resident or transient), as determined using Bayesian mixing models.

3.4.2 Trophic structure of the oyster reef seascape

Trophic positions, estimated using a Bayesian trophic position model, ranged from 1.01 (CI: 1 - 1.13) for Soldier crabs (*M. longicarpus*) to 2.75 (CI: 2.42 - 3.09) for dusky flathead (*P. fuscus*) (Figure 3.4). Most species fell between trophic levels 1 and 2, including the

two reef forming species, Sydney rock oysters and hairy mussels, which had trophic positions of 1.43 (CI: 1.13 - 1.81) and 1.44 (CI: 1.11 - 1.8), respectively (Appendix B, Table B.1).

Among the 21 reef residents, 12 species (10 macroinvertebrate and two fish) were assigned to the first trophic level, with TPs ranging from 1.17 (CI: 1.01 - 1.52) for Neredidae polychaetes to 1.97 (CI: 1.6 - 2.17) for the shrimp, *Penaeus plebejus*. A total of nine species (one macroinvertebrate and eight fish species) were assigned to the second trophic level, with TPs ranging from 2.17 (CI: 1.56 - 2.32) for the rotund blenny, *O. rotundiceps*, to 2.69 (CI: 2.35 - 3.21) for adult bream, *A. australis* (Appendix B, Table B.1).

Among reef transients, five species (three macroinvertebrate and two fish species) were included in the first trophic group, with TPs ranging from 1 (CI: 1 - 1.13) for the soldier crab, *M. longicarpus*, to 1.95 (CI: 1.62 - 2.26) for the leatherjacket fish, *Meuschenia trachylepis*. The second trophic group comprised 9 species (two macroinvertebrate and seven fish species), with TPs ranging from 2.10 (CI: 1.74 - 2.33) for the cephalopod *Euprymna tasmanica*, and 2.10 (CI: 1.69 - 2.43) adult blue swimmer crabs, *Portunus pelagicus*, to 2.75 (CI: 2.42 - 3.09) for the flathead fish, *P. fuscus* (Appendix B, Table B.1).

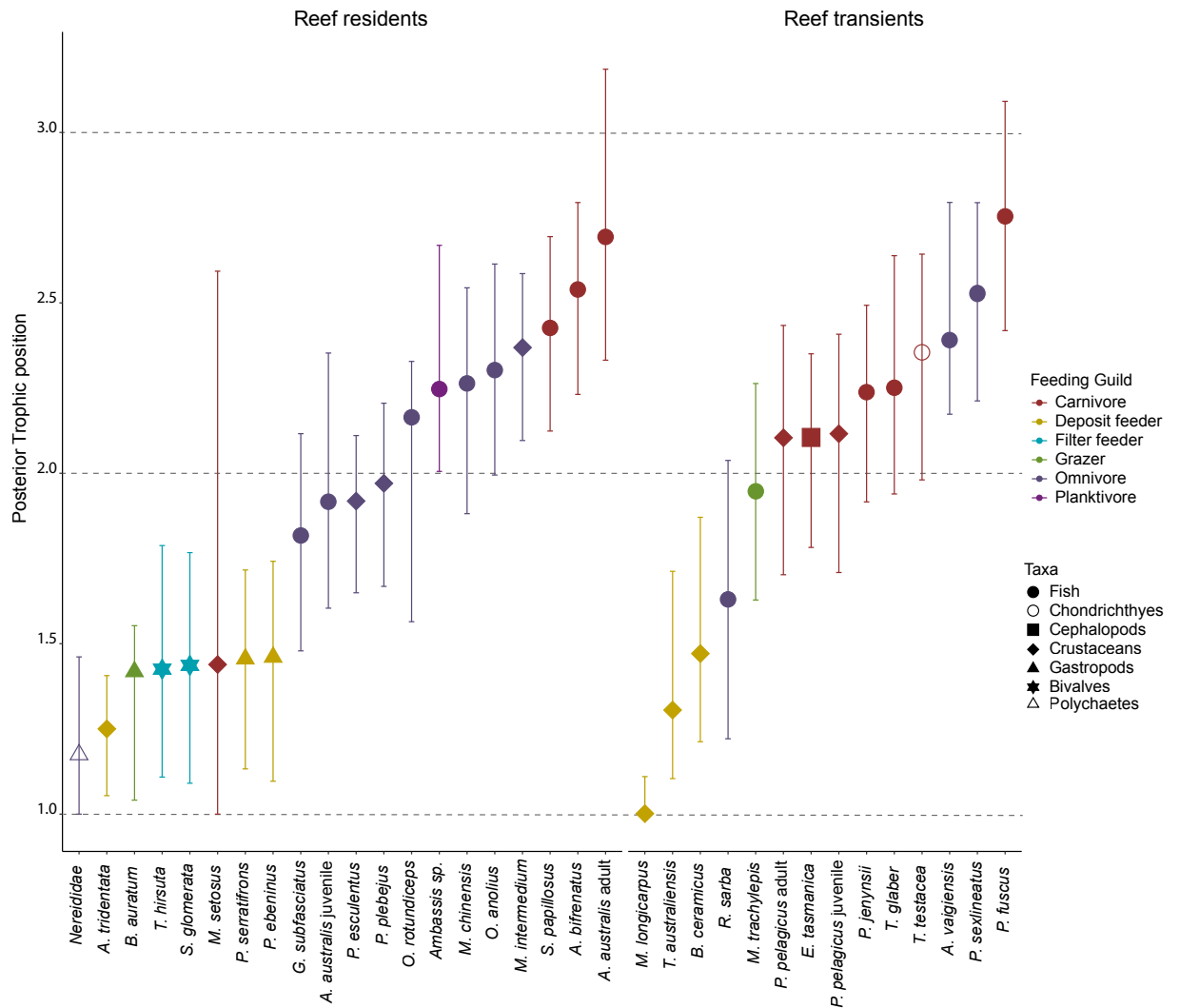


Figure 3.4: Posterior trophic positions and 95% credibility intervals for target species, classified according to their reef relationship and feeding guild.

3.4.3 Isotopic niches and niche overlap within the oyster reef seascape

The standard ellipse area (SEA_B) of the hairy mussel (*Trichomya hirsuta*) was larger than the SEA_B of the Sydney rock oyster (*Saccostrea glomerata*), with the two ellipses occupying different isotopic spaces, though with some overlap (Figure 3.5, Appendix B, Table B.5). The isotopic niche of Sydney rock oysters had a larger proportion of overlap with the niche of hairy mussel (27.9%, CI: 7.2 – 60.1%) than the overlap of the hairy mussels with the isotopic niche of the Sydney rock oyster (16.9%, CI: 3.7 – 37.9%) (Appendix B, Table B.5, Figure B.1).

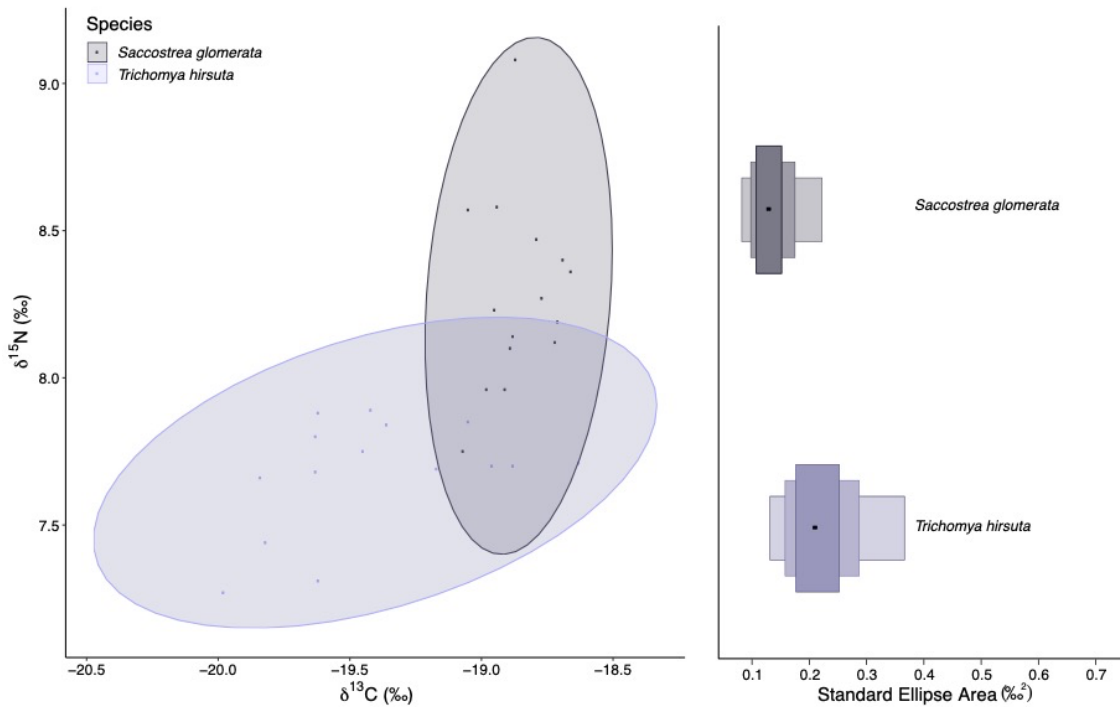


Figure 3.5: Isotopic standard ellipse areas encompassing 95% of the distribution of the reef forming species: Sydney rock oysters and hairy mussels. The plot on the left represents the mathematical ellipse areas per species, as a proxy of the isotopic niche, and the plot on the right represents the density plots of the respective Bayesian ellipse areas per species.

Among the reef resident community, the feeding guild of carnivores had the largest SEA_{BS} , followed by omnivores, deposit feeders, planktivores, filter feeders, and grazers (Figure 3.6, Appendix B, Table B.5). Among reef transients, omnivores had the largest SEA_{B} , followed by carnivores, deposit feeders and grazers (Figure 3.6, Appendix B, Table B.5). The reef resident community had a greater total convex hull area (8.2‰^2), with their correspondent ellipses ranging to a greater extent in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures than the reef transient community which had a total convex hull area of 2.3‰^2 (Figure 3.6). Among reef residents, the isotopic niche of carnivores had the largest probability of overlap with omnivores (65.1%, CI: 52.6 – 76.9%), in much lesser extent with deposit feeders (10.7%, CI: 3.3 – 22.9%), planktivores (9.5%, CI: 5.0 – 16.1%) and grazers (0.7%, CI: 0.1 – 1.6%), and no probability of overlap with filter feeders. The isotopic niche of omnivores had the largest probability of overlap with carnivores (79.9%, CI: 66.7 – 91.3%) followed by deposit feeders (28.8%, CI: 13.7 – 50.4%) and in a much lesser extent with filter feeders (0.6%, CI: 0.2 – 1.3%) and grazers (0.3%, CI: 0.1 – 0.8%). Planktivores had an isotopic niche that only overlapped with carnivores (75.9%, CI: 50.3 – 95.1%) and omnivores (69.3%, CI: 29.7 – 95.8%). Deposit feeders shared the largest probability of overlap with the isotopic niche of omnivores (56.9%, CI: 34.4 – 76.94%), followed by carnivores (39.5%, CI: 13.6 – 73.46%) and grazers (4.1%, CI: 1.5 –

8.9%) with no probability of overlap with filter feeders (Figure 3.6, Appendix B, Figure B.2).

The probability of overlap between filter feeders, reef residents and reef transients, was greater for all feeding guilds groups from the transient community, than the overlap for all groups from the resident community. Among feeding guilds, filter feeders had a larger probability of overlap with transient deposit feeders (40.9%, CI: 11.3 – 69.7%) than resident deposit feeders (2.6%, CI: 0 – 23.9%) (Appendix B, Figure B.4). Filter feeders only overlapped with transient grazers with a very low probability (0.03%, CI: 0 – 0.2%); between omnivores, they had a larger probability of overlap with transient omnivores (35.4%, CI: 2.6 – 94.5%) than with resident omnivores (26.6%, CI: 3.7 – 64.6%) and very low probability of overlap with transient carnivores (2.6%, CI: 0.1 – 0.5%) (Figure 3.7, Appendix B, Figure B.5-B.7).

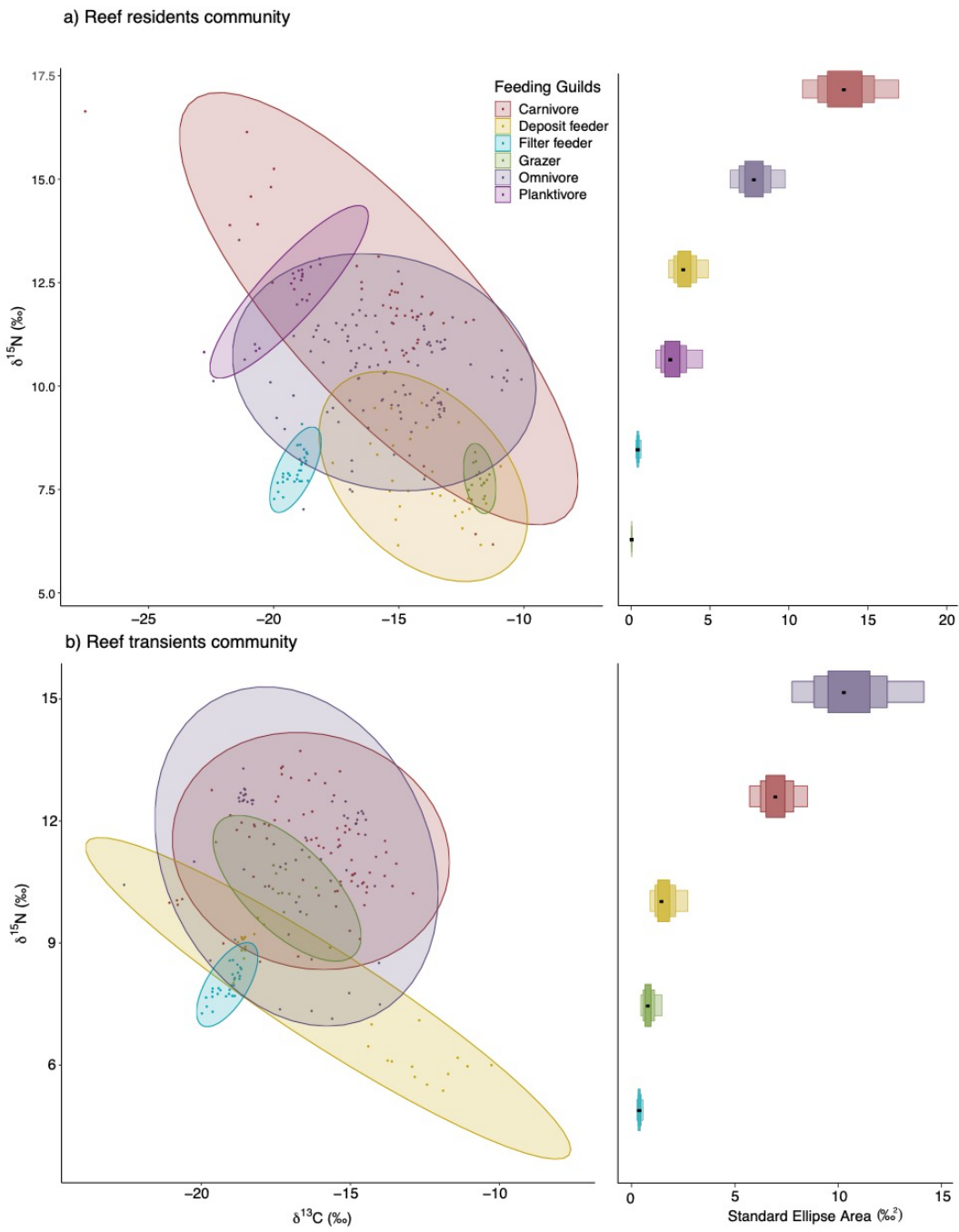


Figure 3.6: Isotopic standard ellipse areas encompassing 95% of the distribution of the reef resident species and reef transients, grouped by feeding guilds. The plot on the left represents the mathematical ellipse areas per feeding guild, as a proxy of the isotopic niche, and the plot on the right represents the density plots of the respective posterior Bayesian ellipse areas per guild.

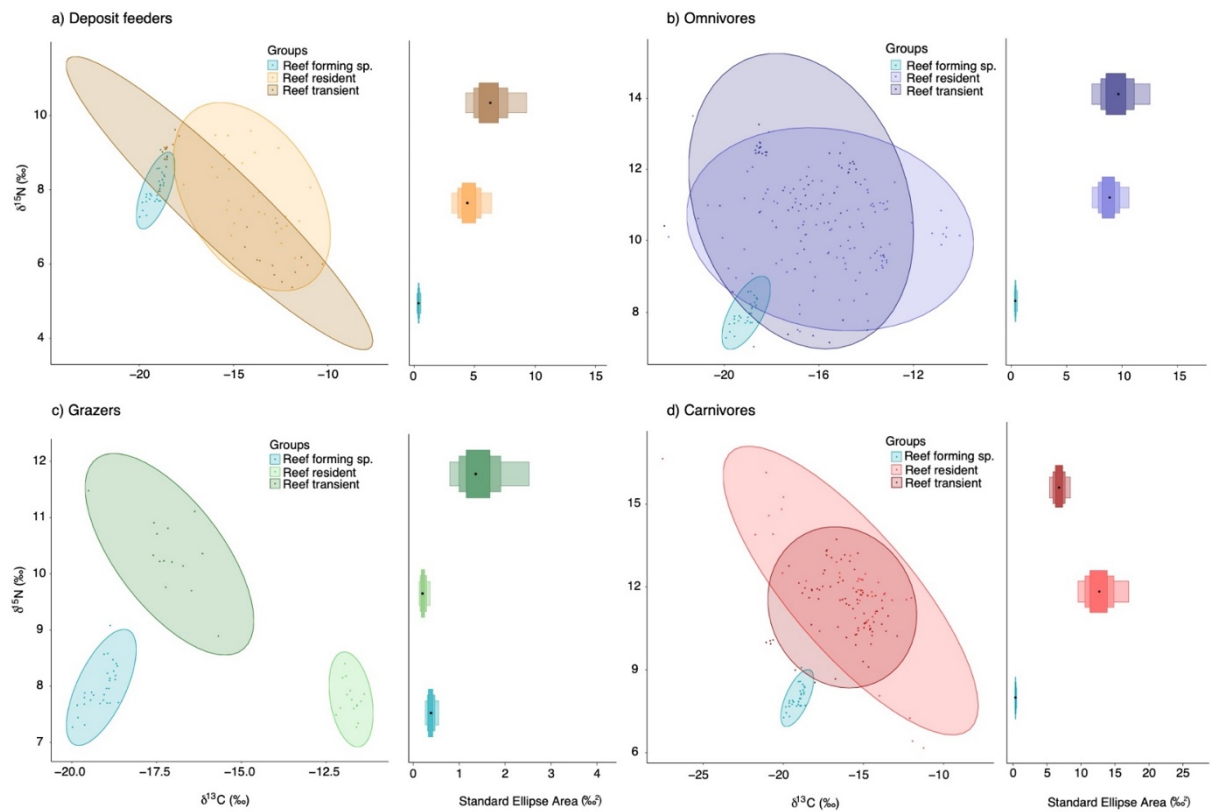


Figure 3.7: Isotopic standard ellipse areas encompassing 95% of the distribution of reef forming species as compared to a) deposit feeders, b) grazers, c) omnivores and d) carnivores, grouped by residents and transients. Density plots are shown for each group representing the respective posterior Bayesian ellipse areas.

3.5 DISCUSSION

The mechanisms by which oyster reefs support diverse and productive communities of fish and invertebrates are broadly acknowledged to span trophic and structural relationships (Grabowski 2004, Humphries et al. 2011, Quan et al. 2011). Species of invertebrates and fish that are resident or transient users of the oyster reef habitat, may have trophic linkages to oyster reefs through consumption of bivalves, benthic organic matter and/or oyster reef resident fauna. Our results confirm that in east Australian estuaries, oyster reefs contribute to the estuarine energy transfer to higher trophic levels directly, through organisms that predate on reef forming species, and indirectly, through consumption of the reef benthic organic matter and predation of the oyster reef infauna (Figure 3.8).

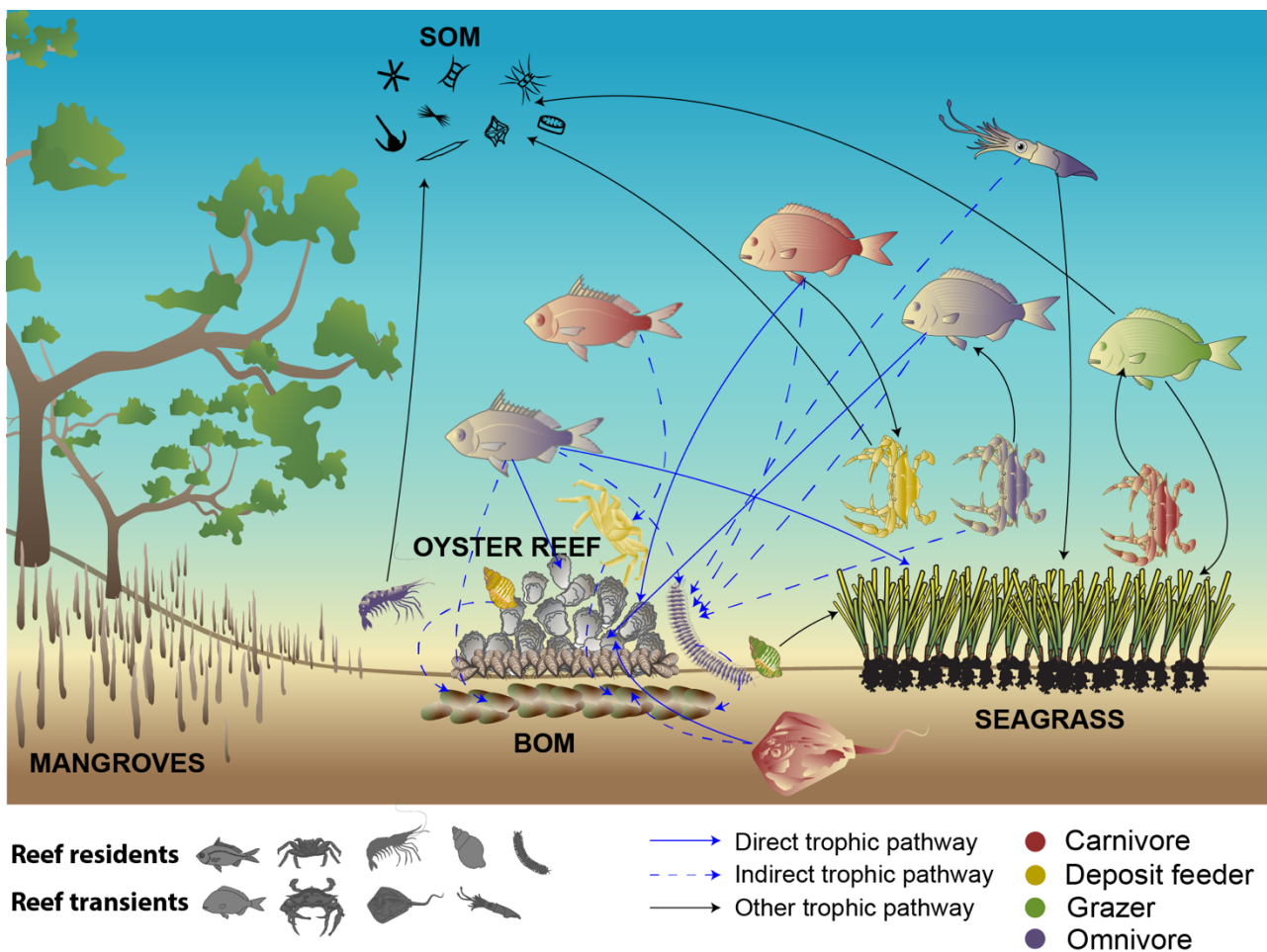


Figure 3.8: Conceptual diagram of the main trophic linkages in an east Australian oyster reef seascape. Arrows indicate trophic linkages (direct: consumption of reef forming species, indirect: consumption of reef-dwellers and other trophic pathways: consumption of non-reef related organisms) that were identified using Bayesian mixing models as having a greater than 40% resource contribution to taxa. Taxonomic groups are assigned as reef residents and reef transients (symbols) and as a carnivore, deposit feeder, grazer or omnivore (colours).

3.5.1 Oyster reef trophodynamics

A variety of species, including crabs, seahorses, mudworms, flatworms, oyster drills, fish and rays, are known predators of east Australian oysters (Thomson 1954, Nell 1993, Anderson & Connell 1999, Hadwen et al. 2007). Here, oysters and mussels and Nereididae polychaetes, which could not be isotopically separated, were an important prey group for resident and transient species (>40% contribution), including blue

swimmer crabs, toadfish, bream, oyster gobies and stingarees. Each of these predator species are known consumers of oysters in Australian waters (Thomson 1954, Nell 1993, Anderson & Connell 1999, Hadwen et al. 2007) and may, in some instances, exert top-down control on oysters that limits reef establishment and growth. For example, similar taxa appear to play an important role in limiting oyster reefs to the intertidal along sections of the Gulf Coast, USA (Johnson & Smee 2014). As oyster reef restoration efforts increase in Australia, it will be important to more fully understand the size classes of oysters these predators are capable of consuming, their consumption rates across a range of environmental conditions, and hence their capacity to limit the success of restoration efforts in the absence of mitigating measures.

The trophic role of oyster reefs extended beyond direct predation of oysters, to incorporate indirect pathways involving consumption of reef-derived organic matter resources and reef residents (Figure 3.8). Benthic organic matter (BOM) from the oyster reef was a key resource for many oyster reef residents (41 – 59% contribution), including crabs, gastropods and polychaetes, and two omnivorous fish species, as well as several species that utilised oyster reefs transiently. Previous studies highlight the importance of shellfish biodeposits to estuarine and coastal food webs. For example, in north-east Florida chlorophyll *a* concentrations were found to be three times higher in oyster reef than bare sediments, facilitating increased benthic microalgal abundances (Southwell et al. 2017). In Sweden, biodeposits from shellfish reefs supplied up to 31% of the energy requirements of the resident macroinvertebrate community, composed by similar taxa groups found on this study such as crustaceans, gastropods and polychaetes (Norling & Kautsky 2007). Along the east coast of Australia, the production and abundance of this macroinvertebrate community can be up to 13-14 times higher in oyster reefs than adjacent bare sediments (McLeod et al. 2020). Here, the macroinvertebrate communities of oyster reefs were an important prey resource for fish which in turn supported higher trophic predators such as blue swimmer crab, stingaree and flathead. Hence there is energy and biomass transfer from oyster biodeposits to higher trophic levels, via successive predation that links resident to transient species (Quan et al. 2011, Abeels et al. 2012).

For most feeding guilds, we found similar trophic positions and considerable isotopic niche overlap, indicative of shared feeding grounds, among the reef forming species, most of the reef resident species and between resident and transient species. The exception was grazers, which did not overlap in trophic niche between resident and reef groups. Reef resident grazers fed on sources more enriched in $\delta^{13}\text{C}$, close to signatures of seagrasses, macroalgae and seagrass epiphytes. Transient grazers had more depleted $\delta^{13}\text{C}$ signatures, suggesting a different source of carbon, closer to the signature of benthic and suspended organic matter and mangroves. Despite large overlap, the $\delta^{13}\text{C}$ range of the isotopic niche of reef-resident deposit feeders was more

constrained than the isotopic niche of the transients group, suggesting that, while sharing some common resources, transients were feeding on a wider variety of sources compared to residents. Omnivores and carnivores had the largest variability in $\delta^{15}\text{N}$ signatures and, hence, overlap between reef resident and transient groups. These findings are similar to those in other seascapes, such as tropical coral reefs, with a higher degree of overlap among species of different feeding guilds that potentially share benthic resources across the seascape (Zhu et al. 2019). This likely reflects their high mobility and ability to move across the estuarine seascape of oyster reefs, seagrasses, mangroves and bare sediments to forage on a wider variety of resources.

3.5.2 Implications for management

Our results, in combination with those of other studies (Quan et al. 2011, Abeels et al. 2012) demonstrate the important trophic role of oyster reefs in the estuarine seascape. This suggests that the high densities and diversities of fish observed around remnant south east Australian oyster reefs do not simply reflect the complex structure of oyster reefs attracting fish away from adjacent habitats. Oyster reefs enhance the productivity of fisheries by enhancing the resource base of a trophically connected food web. Consequently, the productivity of oyster reef ecosystems and the value to associated fisheries productivity needs to be determined.

Nevertheless, a caveat is that this study considered only a snapshot of the trophic system for one site in one estuary and for one sampling event. Resource availability may, however, vary temporally and spatially according to ontogenetic and seasonal shifts in species' habitat utilisation, variation in the productivity of the system as well as variation in the seascape mosaic and habitat connectivity (Staveley et al. 2017, Gilby et al. 2018a, Martin et al. 2018). How the trophic role of remnant oyster reefs varies across the variety of seascape, climatic and biogeographic contexts across which they are found along the south-east Australian coast, needs to be assessed. Temporally replicated studies would also enable the trophic role of oyster reefs to be integrated over time which would assist in identifying sites and settings at which oyster reef restoration might lead to greatest benefits in enhancing estuarine food webs.

A further limitation of this study was that only two tracers, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, were used to model resources, preventing discrimination between some resource groups (Phillips et al. 2014). The inclusion of a third isotopic tracer, such as sulfur, could assist in discriminating among sources that are similar on their isotopic composition (Parnell et al. 2013) and enable inclusion of a greater number of potential sources in Bayesian mixing models (Parnell et al. 2010). More detailed understanding of the pathways by which remnant oyster reefs fuel key commercial or recreational fishery species would help in the development of targeted restoration projects. Determining the

proportionate contribution of oyster biodeposits to benthic organic matter in these systems will also be key to valuing oyster reefs in terms of their fisheries productivity.

3.5.3 Conclusion

Using stable isotopes, we have shown trophic linkages between remnant oyster reefs of south eastern Australia to wide range of estuarine invertebrates and fish, including both reef residents and transients. While some taxa are connected to reefs through the direct consumption of reef-forming bivalves, others consume organic matter that accumulates in the reef interstices or the resident oyster-reef invertebrates. As a result, the role of oyster reefs in these systems extends beyond the provision of complex habitat to the enhancement of the estuarine food resource base.

3.6 ACKNOWLEDGMENTS

This project was funded by the Department of Biology from Macquarie University, the Macquarie University Research Excellence Scholarship (MQRES) and the Holsworth Wildlife Research Endowment – Equity Trustees Charitable Foundation & the Ecological Society of Australia. We thank the NSW Department of Primary Industries for their support on equipment and logistics. Thank you to Derrick Cruz for his support and assistant and to Giulia Ferretto for assisting us as a field volunteer. We acknowledge and pay our respects to the Worimi nation, Traditional Custodians of the lands on which this study has taken place and whose culture have nurtured and conserved our study estuarine habitats to date.

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Chapter 4: Oyster reefs as nursery habitat

A FORGOTTEN COMPONENT OF THE ESTUARINE SEASCAPE NURSERY

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4.1 ABSTRACT

Vegetated estuarine habitats such as seagrasses, mangroves and saltmarshes, are widely documented to serve as important nursery habitats to juvenile fish, providing them with food and refuge until they undergo ontogenetic migrations to other habitats. Although other structured biogenic habitats, such as oyster reefs, may be expected to play a similar role to submerged aquatic vegetation, their nursery role has been relatively unexplored. Historically, oyster reefs were a dominant component of estuaries in subtropical to temperate regions, but have experienced declines in excess of 90% in many estuaries since industrialisation. Quantification of the ecosystem services that they provide is important to justify their conservation and restoration. In this study, we evaluated the nursery role of intertidal remnant Sydney rock oyster, *Saccostrea glomerata*, reefs for fish in two estuaries in south-east Australia: Botany Bay and Port Stephens. We used remote underwater cameras to compare the nursery value of oyster reefs within a mosaic of interconnected habitats including seagrasses, mangroves and bare sediment. At high tide, intertidal remnant oyster reefs supported a unique juvenile fish community with greater juvenile fish observations and a higher juvenile to adult ratio for many species than adjacent habitats. Juvenile and adult fishes of recreationally and commercially important fish species used the four habitats differently, with juveniles utilising oyster reefs, seagrasses and mangroves; and adults venturing further to bare sediments. This was especially apparent in summer, when juvenile fish were present in greater numbers. Analyses of inferred behaviour showed that a similar proportion of juvenile fishes present in oyster reefs, seagrass and mangroves were feeding and resting. This study highlights that remnant oyster reefs serve as an important nursery for fish within the complex estuarine seascape.

4.2 INTRODUCTION

Estuaries are broadly recognised as important nurseries where juvenile fish and invertebrates grow and mature before moving into other habitats (Beck et al. 2001). While some of these juveniles migrate to coastal waters as adults, others complete their life cycle within estuarine and inshore coastal waters (Gillanders 2002, Gillanders et al. 2003, Abrantes et al. 2015). This function of estuaries stems in part from their high productivity, which ranks among the greatest for any ecosystem in the world (Correll 1978), the protection they offer from wave-action (Cooper 2001), the presence of structured and biogenic habitats that in some instances lowers the foraging efficiency of predators (Heck & Thoman 1981, Grabowski & Powers 2004), as well as their connectivity to marine and freshwater habitats (Gillanders 2002, Gillanders et al. 2003,

Abrantes et al. 2015). Due to their high productivity and sheltered waters, estuaries are, however, also often the foci of human populations. These human populations have placed considerable pressure on estuaries, leading to their ecological degradation (Stronge et al. 2005, Lotze et al. 2006, Wolanski et al. 2019). Measuring the nursery function of estuarine habitats for fish and invertebrates is important for both conservation planning and fisheries management (Beck et al. 2001, Nagelkerken et al. 2015, Lefcheck et al. 2019).

The concept of the estuarine nursery has evolved since its original framing by Beck et al. (2001). Early studies defined nursery habitats on the basis of them supporting a greater density, rate of growth and rate of survival of juveniles than other habitats (Heck et al. 2003, Minello et al. 2003, Sheridan and Hays 2003). Recognising that some species spend their entire life-history in the one habitat, Gillanders et al. (2003) emphasised that a habitat should only be considered a nursery if the species can then recruit into other habitats as an adult. Additionally, the early focus of the nursery concept on habitat units was criticised because it neglected to consider that even habitats that contributed relatively few individuals to adult populations could be critical in some years with low recruitment (Dahlgren et al. 2006). More recently, the nursery concept has been broadened to recognise the importance of connectivity of habitat patches within the estuarine seascape (Boström et al. 2011, Pittman 2017), and the contribution of multiple habitats to the ontogeny of many fish and invertebrates (Sheaves 2009). The concept of the “seascape nursery” defines nurseries spatially, rather than as habitat units, identifying hotspots for each life history stage and establishing migration corridors between juvenile and adult habitats (Nagelkerken et al. 2015, Sheaves et al. 2015, Litvin et al. 2018, Lefcheck et al. 2019)

Within the estuarine seascape, vegetated habitats, such as seagrasses, mangroves and saltmarshes are broadly considered as important nursery grounds (Minello et al. 2003, Igulu et al. 2014, Whitfield 2017, Le et al. 2019). These vegetated habitats have been the focus of a majority of seascape nursery studies in tropical (Bradley et al. 2019, Berkström et al. 2020) and temperate systems (Leslie et al. 2017, Perry et al. 2018). The role of shellfish reefs, by contrast, remains largely unexplored, despite indications that they may have even stronger effects on juvenile abundance, richness and survival than vegetated habitats (Beck et al. 2001, zu Ermgassen et al. 2016, Lefcheck et al. 2019). Previous studies on oyster reefs have, instead, focused on the habitat value of oyster reefs for whole communities (i.e. comprising both juveniles and adults) of invertebrates (La Peyre et al. 2019, Pfirrmann & Seitz 2019, McLeod et al. 2020) and fish (Harding & Mann 2001), and/or quantifying their fisheries productivity (Harding & Mann 2001, Peterson et al. 2003, Pierson & Eggleston 2014). The few studies on the nursery potential of oyster reefs come from the Gulf of Mexico and the South- and Mid-Atlantic coasts of the USA, resulting in large geographic gaps in our knowledge, and due to the

scarcity of remnant oyster reefs, most of them have focussed on restored oyster reefs in subtidal areas, leaving intertidal remnant oyster reefs and their nursery value largely unexplored (Beck et al. 2001, zu Ermgassen et al. 2016, Lefcheck et al. 2019).

The nursery value of oyster reefs is of particular interest given the presently degraded state of this habitat, globally (Beck et al. 2011), and the growing interest and investment in shellfish reef restoration (Laing et al. 2006, Gillies et al. 2015b, Pogoda et al. 2019). Oyster reefs were once a conspicuous component of temperate and subtropical estuaries globally, covering vast areas (Beck et al. 2011). For example, intertidal reefs of the eastern oyster (*Crassostrea virginica*) extended for kilometers along James River in Chesapeake Bay, USA (Woods et al. 2005) and reefs of Sydney rock oysters (*Saccostera glomerata*) up to ten hectares in area were recorded in New South Wales, Australia (Oyster Culture Commission 1877). Overharvest, often using destructive fishing methods such as dredging, coupled with water pollution associated with coastal development, led to significant oyster reef decline throughout much of their former range (Beck et al. 2011). In Australia, this decline extends to the important habitat-forming species, flat oysters (*Ostrea angasi*) and Sydney rock oysters (*S. glomerata*) (Gillies et al. 2018). Loss of habitat formed by these two species is estimated at over 90% since industrialisation (Gillies et al. 2020). In Australia, little is known about the role of remnant oyster reefs as habitat and supporting fisheries productivity (Gilby et al. 2018b, McLeod et al. 2020), and no studies to date have attempted to quantify their role as nursery habitats for fishes.

Our study aimed to determine the role of remnant intertidal Sydney rock oyster (*S. glomerata*) reefs as fish nurseries within estuarine seascapes along the east coast of Australia. Specifically, we tested the hypotheses that 1) remnant oyster reefs would support a distinct juvenile fish community to adjacent estuarine habitats; 2) remnant oyster reefs would support greater juvenile fish observations than unvegetated habitat, and equal to or greater values as compared to other adjacent vegetated habitats; 3) remnant oyster reefs would support a juvenile to adult ratio of fish observations that is greater than unvegetated habitat, and equal to or greater than other adjacent vegetated habitats; 4) behaviours of juvenile fishes would differ between oyster reefs and other adjacent habitats, including foraging and wandering behaviours.

4.3 METHODS

4.3.1 Study sites

Hypotheses were tested in two estuaries of New South Wales, Australia: Botany Bay and Port Stephens. Two study sites were sampled in each estuary, each containing four habitat types adjacent to one other: remnant intertidal oyster reefs, seagrasses, mangroves and bare sediment. Sites (comprising the four habitat types) ranged in area from 0.5 to 1 km² and depth from 1 to 3 meters at high tide. In Botany Bay, the study sites were situated in Quibray Bay (34° 0'58.08"S, 151°10'45.78"E) and Carters Island (34° 0'40.35"S, 151° 8'47.32"E). In Port Stephens, study sites were Corrie Island (32°40'41.26"S, 152° 7'16.09"E) and Soldiers Point (32°42'14.34"S, 152° 3'28.26"E) (Figure 4.1).

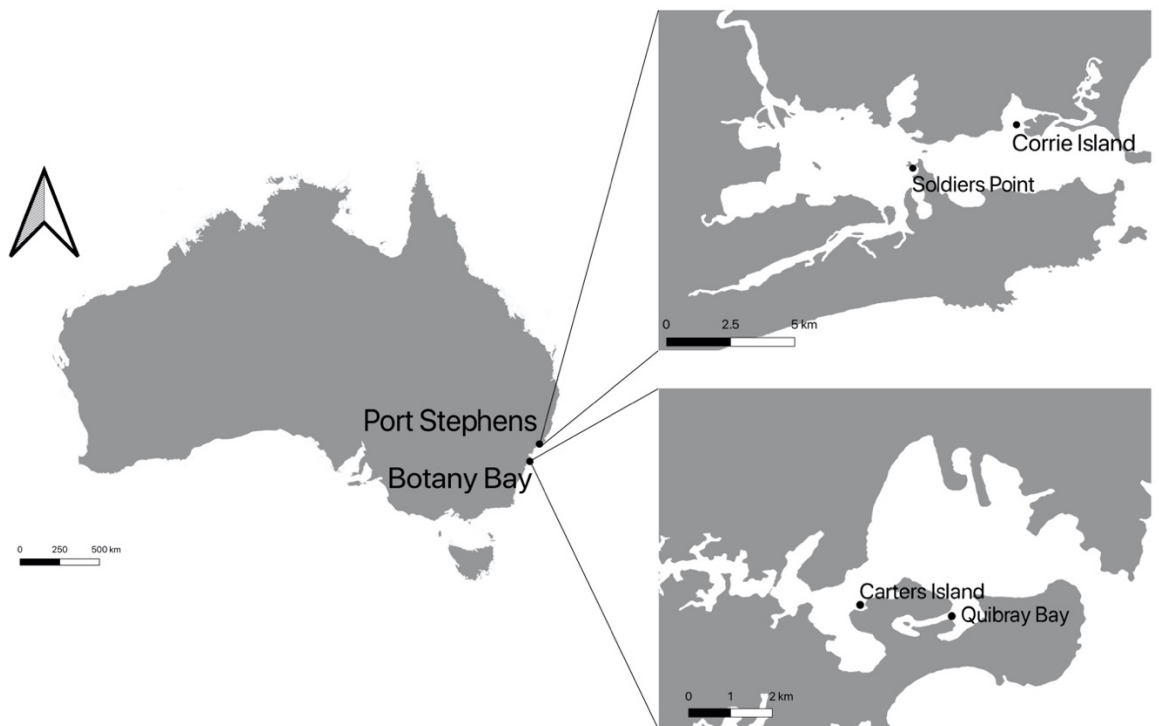


Figure 4.1: Location of the four study sites, within two estuaries of New South Wales, Australia: Botany Bay and Port Stephens.

4.3.2 Sampling

To test hypotheses about differences in juvenile fish communities, and their contributions to total fish observations, among habitat types, sampling at each of the four sites was conducted in two winters and two summers (2017-2019). Within each season of each year, each site was sampled on three replicate days. As only a single site could be sampled each day, repeated sampling of sites was temporally interspersed. On days of wind speeds of less than 10 knots, four unbaited remote underwater cameras (GoPro Hero 4, Silver Edition) were simultaneously deployed in each of the four habitats within a site to give a total of 16 underwater cameras. All sampling occurred during daylight hours within 1.5 hours of high tide. Within habitats, cameras were placed haphazardly, facing the habitat and pointing away from the sun, in order to minimise glare. Cameras were separated at least five meters and were at least 20 meters away from the next adjacent habitat. Cameras were mounted on top of a metal frame of 25 cm height, attached to a rope with a float and were left recording for 1 hour and 25 minutes. On each sampling day, visibility was measured at each site using a 1.2 m methacrylate tube with a secchi disk at its base. The tube was filled with water and the water discharged until the secchi disk could be seen, with the corresponding water depth at which the secchi disk was first visible recorded. For each sampling event, visibility was classified as: <0.8 , $0.8 - 1$, $1 - 1.1$, > 1.2 m. If visibility was less than or equal to 0.8, sampling did not proceed.

4.3.3 Video analysis

Raw videos were processed using Adobe After Effects (2020, Adobe®). Footage was merged into a single clip per camera of 75 minutes in length, with the first and last 5 minutes of video excluded due to disturbances associated with deployment and retrieval. Once a 75 min video was obtained, the video was then colour balanced. Videos were then processed in EventMeasure (SeaGIS Pty. Ltd.) software to quantify fish communities and behaviour.

For this study, fish observations were separately scored by two life history stages: juveniles and to assess juvenile to adult ratios, also adults. This differentiation was made based on morphological features such as markings and body shape, by a single trained observer, F. Martínez-Baena (Sheaves et al. 2020). In order to minimise any bias towards juveniles countings, individuals that presented mixed morphological features and body shapes were labelled as adults. Species for which juveniles were not present, or for which juveniles and adults could not readily be discriminated between were excluded from analysis.

Total observations were separately calculated for each camera for both juveniles and adults. The total number of observations was the sum of fish observations across frames for a camera. Total observations were used as an indicator of habitat use (Lanham 2019), recognising that an individual fish may be recorded on a camera multiple times. Nevertheless, to limit inflation of counts, individuals that swam in and out of the frame in a span of 20 seconds were counted only once. Further, to eliminate any bias towards species that naturally shoal (form groups naturally of individuals of the same species), we counted all individuals of the same species that appeared simultaneously in the same frame as one observation. To test hypotheses about juvenile to adult ratios, the natural logarithm of the number of observations of juveniles divided by adults was calculated.

Every observation of a juvenile was categorised according to one of four main behaviours: passing, wandering, feeding and chasing. An individual was considered "passing" when it swam through the frame, at constant speed, without interacting with the surrounding habitat. "Wandering" was where an individual swam slowly around the habitat, occasionally stopping to interact with the habitat. "Feeding" was defined as an individual feeding on prey, surface or organic matter. Lastly, "chasing" behaviour involved an individual actively chasing another individual of the same or another species across the visual frame. As chasing observations were very low, they were not statistically analysed. In frames where individuals of the same species displayed differing behaviours, one observation per behaviour and species was recorded.

4.3.4 Data analysis

To test the hypothesis that juvenile fish communities would differ among habitats, a permutational multivariate analysis of variance (PERMANOVA, (Anderson et al., 2008)), was run using PRIMER. The analysis used Bray Curtis dissimilarities calculated from the matrix of untransformed observations of juveniles by species for each camera. A "dummy variable" of 1 was added to the matrix so samples containing no fish could be included in the analysis (Clarke et al., 2006). The multivariate analysis included the factors: Habitat (4 levels, fixed: Oyster reefs, Seagrass, Mangroves and Bare), Estuary (2 levels, random: Botany Bay and Port Stephens), Site (2 levels, random: nested within each estuary), Year (2 levels, random: 1 and 2), Season (2 levels, fixed: Winter and Summer), and Day (3, random, nested within Year x Season x Site). Statistically significant interactions (at $\alpha = 0.05$) from the multivariate analysis were further examined using a *posteriori* pairwise PERMANOVA tests. In cases where the number of possible permutations of the data was less than 100, a *posteriori* tests used Monte-Carlo simulations to generate p-values (Anderson et al., 2008).

To visually examine spatio-temporal variation in the juvenile fish community with respect to the predictor variables, we used a distance-based redundancy analysis (db-RDA,

Legendre and Anderson, 1999) on the juvenile Bray Curtis dissimilarity matrix within the function "capscale" of the "vegan" package (Oksanen et al., 2019) in R (R Core Team, 2019). Permutational tests were then carried out on each axis and marginal terms to test for statistical significance. On the plot, each camera drop is a point in multidimensional space, with its location determined by the contribution of species to spatio-temporal predictors (Borcard et al., 2018). For visual clarity, vectors were only included for species that were positioned +/- 0.2 along either axis.

To assess the nursery function of remnant oyster reefs as compared to adjacent habitats, Univariate Linear Mixed Effects Models were run within the package "lme4" (Bates et al., 2015) in R (R Core Team, 2019). Separate analyses were run on each of the following metrics: 1) total number of juvenile observations, 2) juvenile fish observations for each of the four most observed species with a high recreational or commercial interest: breem (*Acanthopagrus australis*), luderick (*Girella tricuspidata*), tarwhine (*Rhabdosargus sarba*) and silverbiddy (*Gerres subfasciatus*), 3) the logratio of juvenile to adult total fish observations; 4) the logratio of juvenile to adult observations for breem, luderick, tarwhine and silverbiddy, 5) the percentage contribution of feeding, wandering and passing behaviours to total observations for juveniles. Chasing behaviour was not analysed as chasing observations were very few. For each linear mixed effects model, the same five factors included in the PERMANOVA analysis were used, but with the difference of treating Season and Site as fixed effects, as for these models, random effects require at least five "levels" to achieve a robust estimate of variance (Harrison et al., 2018). As a consequence, a random factor was included in the model with the factor Day, nested within Site, Estuary, Season and Year (24 levels) to account for small-scale spatio-temporal variation in our models. Model assumptions, including normality of data, were checked using visual inspection of the model residuals, and in all instances were met. Significance of fixed factors and interactions were tested using the Likelihood Ratio test (LRT) with the "drop1" and "anova" function on the model and the significance of the random effects was tested using the "ranova" function from the "lmerTest" package (Kuznetsova et al., 2017). Pairwise comparison tests on the significant interactions were performed using Estimated Marginal Means (EMMS) within the "emmeans" package (Lenth et al., 2020).

4.4 RESULTS

4.4.1 Species composition

A total of 37 fish species from 23 different families were observed in this study (Appendix C, Table C.1). Juveniles were present for all 37 species, with 21 species (8 unique to this habitat) recorded from the oyster reefs, 18 (10 unique) from the seagrass, 11 (2 unique) from the mangrove and 8 (3 unique) from the bare sediment (Appendix C, Table C.1). Adults were present for 31 of the 37 fish species, with 22 species (2 unique) in the oyster reef, 26 (6 unique) in seagrass, 12 (0 unique) in the mangroves and 17 (1 unique) in the bare sediment (Appendix C, Table C.1). Juveniles of four species and adults of 8 species were common to all four habitats. Out of a total of 19,887 observations, 22.4% of these were juveniles and 77.6% were adults. Yellowfin bream (*Acanthopagrus australis*) was the most observed species in oyster reefs and mangroves for both juveniles and adults, juveniles of tarwhine (*Rhabdosargus sarba*) and adults of luderick (*Girella tricuspidata*) were most observed in seagrasses and both juveniles and adults of whiting (*Sillago ciliata*) were most observed in bare sediment. Season play an important role in structuring fish communities, with four times more fish observations in Summer (16,021) than in winter (3,866). This pattern was particularly pronounced for juveniles, where over 5 times the observations were recorded for Summer (3,770) than Winter (689).

4.4.2 Juvenile fish community structure and species composition among habitat

Juvenile fish communities displayed differences among habitats that varied by site and year (sig. Year x Site(Estuary) x Habitat, Appendix C, Table C.2). In year one, all four habitats supported statistically distinct juvenile fish communities at two of the sites (Quibray Bay, Soldiers Point), while at the other two (Carters Island, Corrie Island), communities differed among oyster reefs, bare habitat and seagrass, and at Carters Island, also differed between bare habitat and mangroves. In year two, we similarly found differences among most of the habitats at each of the sites. However, at three of the sites (Soldiers Point, Carters Island, Corrie Island) bare and seagrass did not differ, at two of the sites (Quibray Bay, Soldiers Point) oyster reef and mangrove did not differ, and at one site, oyster reefs and bare (Quibray Bay) and mangroves and bare (Carters Island) did not differ.

Multivariate differences in juvenile fish communities among habitats were in part driven by differences in species composition and, in part, driven by differences in observations.

Bream (*A. australis*) were particularly important in driving habitat differences, contributing to CAP1 and CAP2 axes of the dbRDA (Figure 4.2), with luderick (*G. tricuspidata*), and the reef residents, gunther's wrasse (*Pseudolabrus guentheri*) and silverbiddy (*Gerres subfasciatus*) also contributing strongly (Figure 4.2).

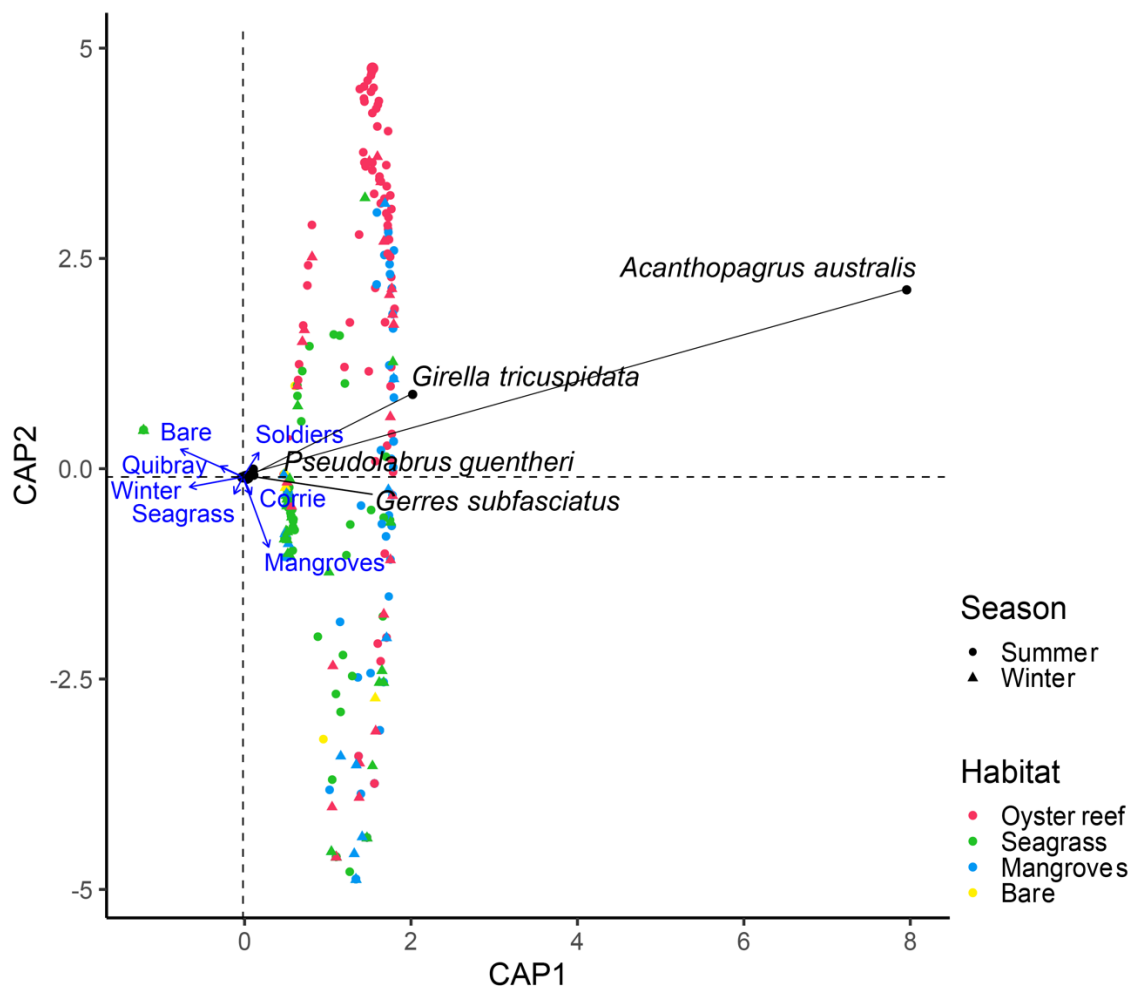


Figure 4.2: Distance-based Redundancy Analysis (dbRDA) triplot of transformed fish observations of juvenile fish communities, across four habitats, sites and seasons. Species exceeding a critical value of ± 0.2 for juveniles on both axes are indicated. Points represent individual cameras ($n = 740$).

At all sites, juvenile fish observations in summer were greatest in oyster reefs and least in bare habitats, with mangroves and seagrass displaying variable differences among sites and years (Sig. Year x Season x Site(Estuary) x Habitat; Appendix C, Table C.4, Figure 4.3). In winter, when observations were 17% of summer levels, few differences among habitats were observed (Figure 4.3, Sig. Year x Season x Site(Estuary) x Habitat; Appendix C, Table C.4.). Bream, which accounted for 67.4% of juvenile observations, displayed similar spatial and temporal patterns to total observations. Bream observations were generally (with a few exceptions) greatest in oyster reef and lowest in bare habitat in the summer, with few habitat differences in winter when juveniles of this species were rare (Figure 4.4, sig. Year x Season x Site(Estuary) x Habitat; Appendix C, Table C.6). Luderick, which accounted for 18.4% of juvenile observations, displayed a similar pattern of generally greater observations in oyster reef than the other habitats in summer, but few habitat differences in winter where juveniles were absent or rare from the habitats (Figure 4.5, sig. Year x Season x Site(Estuary) x Habitat; Appendix C, Table C.8). Tarwhine observations (accounting for 5.1% of juvenile observations) by contrast were for most time points and sites, greatest in seagrass, with observations rare or absent from the other habitats (Figure 4.6, sig. Year x Season x Site(Estuary) x Habitat; Appendix C, Table C.10). Juvenile observations for silverbiddy (accounting for 2% of juvenile observations) displayed site-specific differences among habitats (Figure 4.7, sig. Site(Estuary) x Habitat; Appendix C, Table C.13). At one of the four sites (Soldiers Point) oyster reef and mangrove had higher juvenile silverbiddy observations than the other habitats, but at all other sites, observations did not differ among habitats.

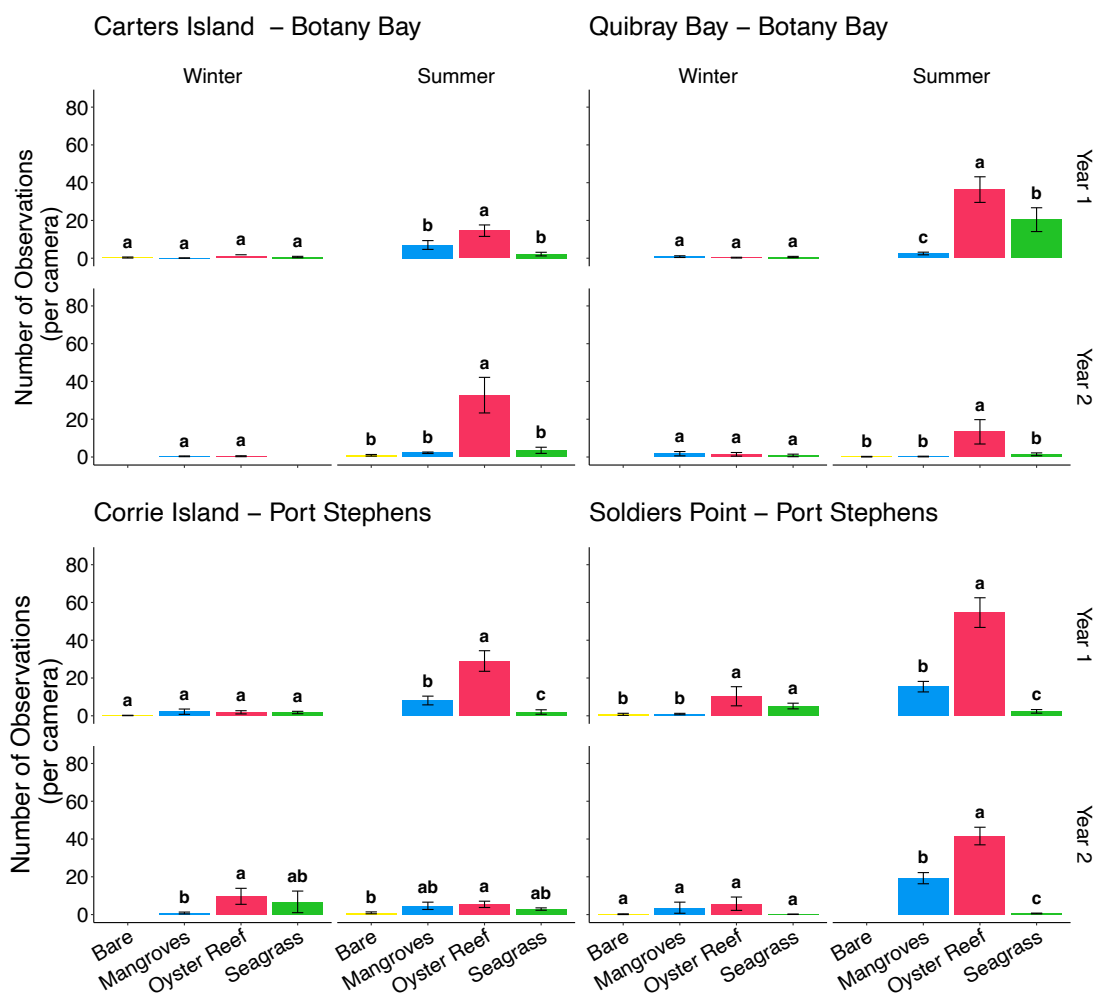


Figure 4.3: Mean ($\pm$ SE) observations of juvenile fish, per habitat, site, season and year, as documented by 75 min Remote Underwater Video deployments, $n = 64$. Letters indicate statistically significant (at $\alpha < 0.05$) pairwise comparisons between habitats within each year, site and season.

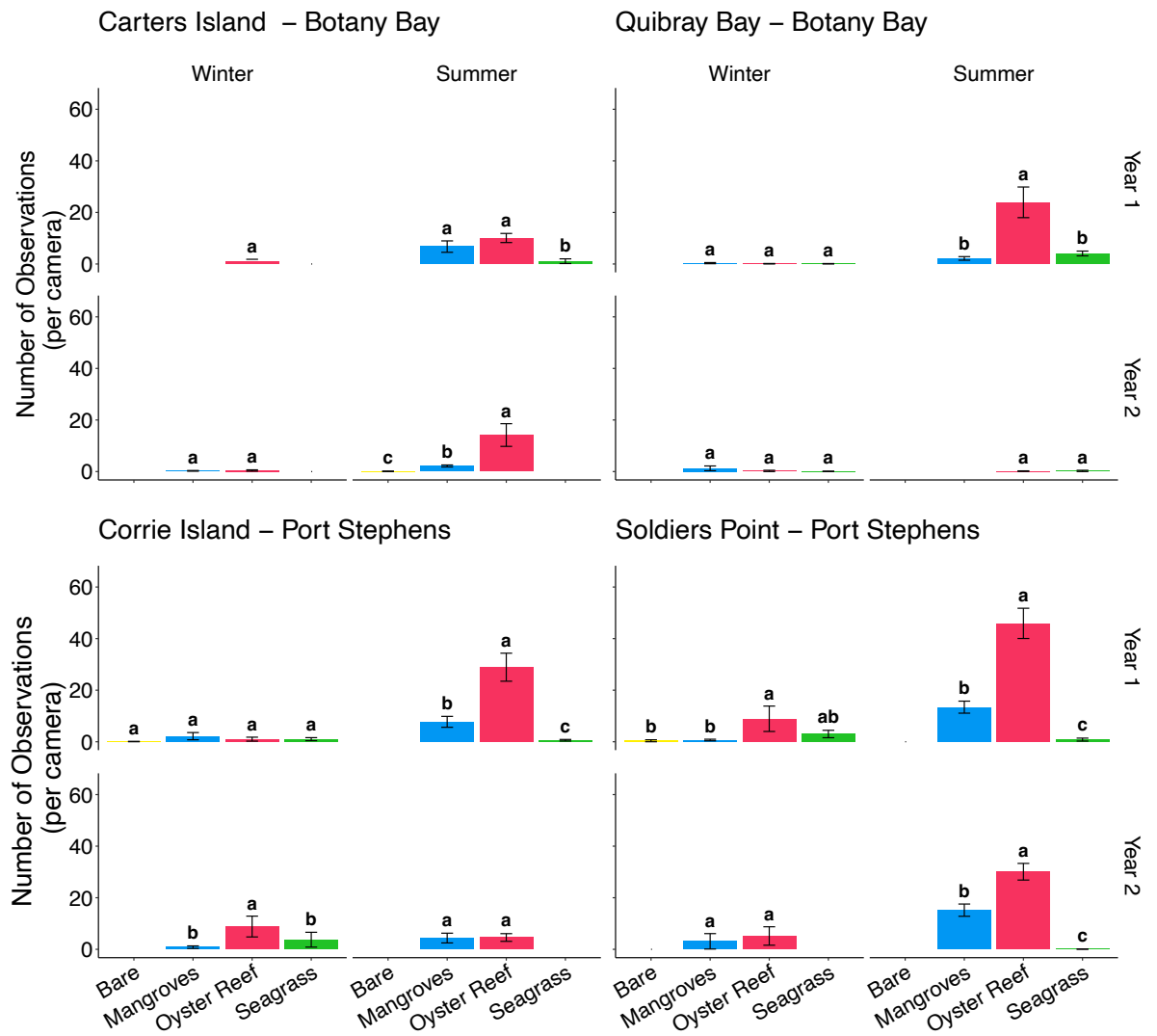


Figure 4.4: Mean ($\pm$ SE) observations of juvenile bream, per habitat, site, season and year, as documented by 75 min Remote Underwater Video deployments, $n = 64$. Letters indicate statistically significant pairwise comparisons at a < 0.05 within each year, site and season.

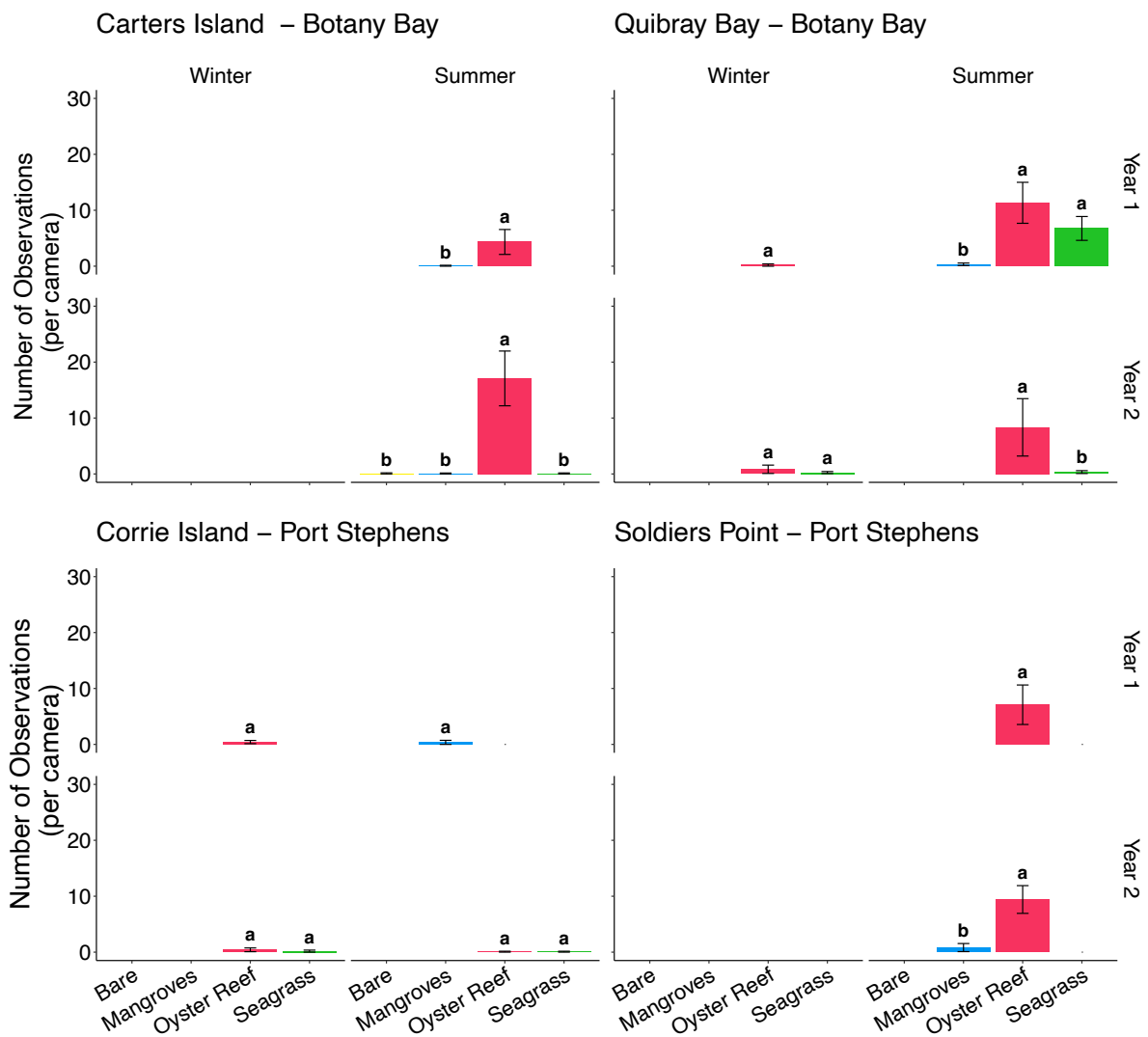


Figure 4.5: Mean ($\pm$ SE) observations of juvenile luderick, per habitat, site, season and year, as documented by 75 min Remote Underwater Video deployments, $n = 64$. Letters indicate statistically significant (at $\alpha < 0.05$) pairwise comparisons between habitats within each year, site and season.

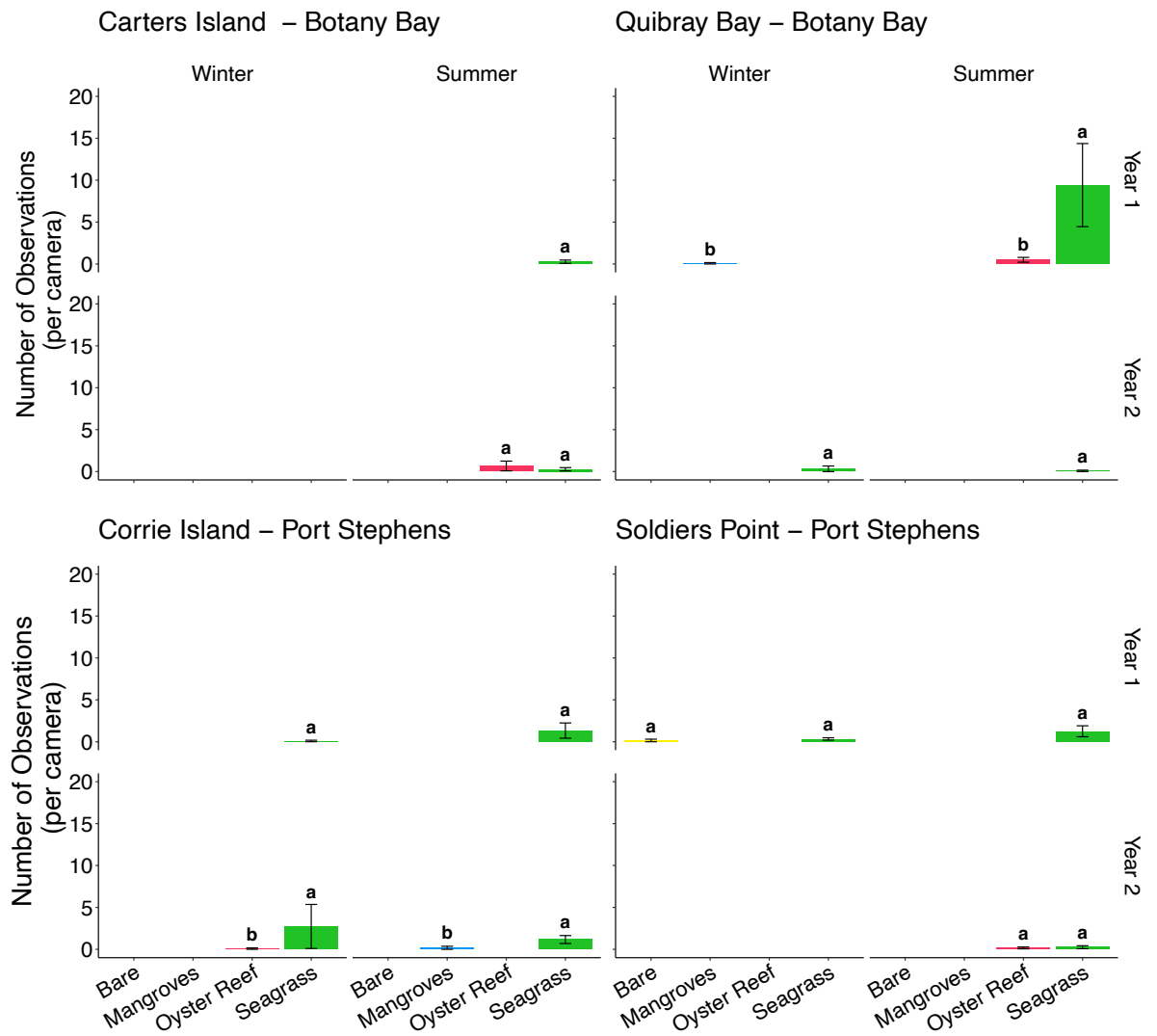


Figure 4.6: Mean ($\pm$ SE) observations of juvenile tarwhine, per habitat, site, season and year, as documented by 75 min Remote Underwater Video deployments, $n = 64$. Letters indicate statistically significant (at $\alpha < 0.05$) pairwise comparisons between habitats within each year, site and season.

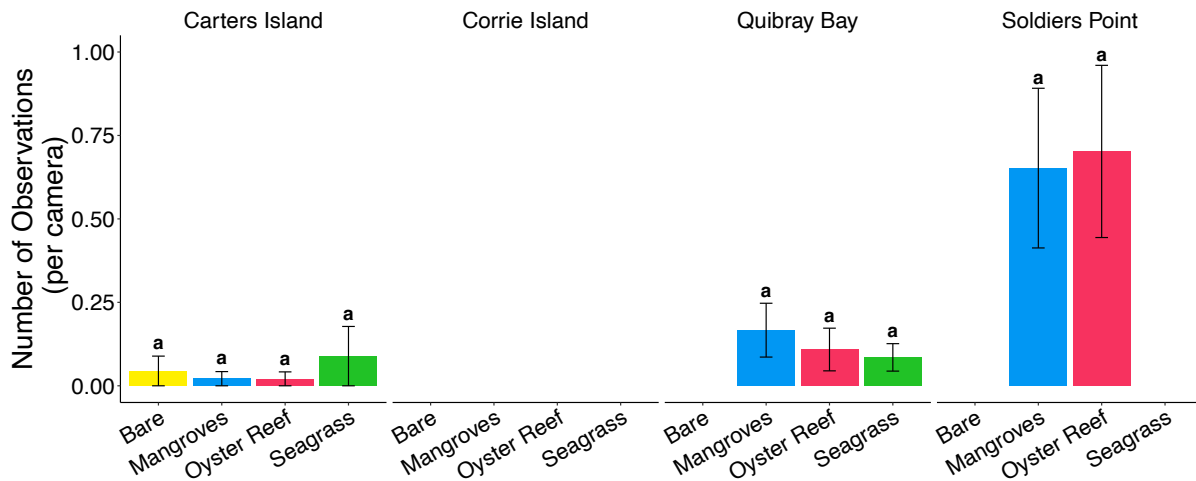


Figure 4.7: Mean ($\pm$ SE) observations of juvenile silverbiddy, per habitat and site, as documented by 75 min Remote Underwater Video deployments, $n = 16$. Letters indicate statistically significant (at $\alpha < 0.05$) pairwise comparisons between habitats within each site.

4.4.3 Ratios of juveniles to adults among habitats

Analyses of logratios of juvenile to adult observations indicated that differences among habitats in juvenile observations did not simply reflect differences in adult observations, and hence overall species fidelity for certain habitats. In summer, the logratio of juvenile to adult observations was less (less juveniles than adults) in the bare habitat than any of three structured habitats and in winter, less in the bare habitat than in seagrass in year one, and than in mangroves or oyster reefs in year two. Among the rest of the habitats, which were all structured, the logratio did not significantly differ (Figure 4.8, Appendix C, Table C.3).

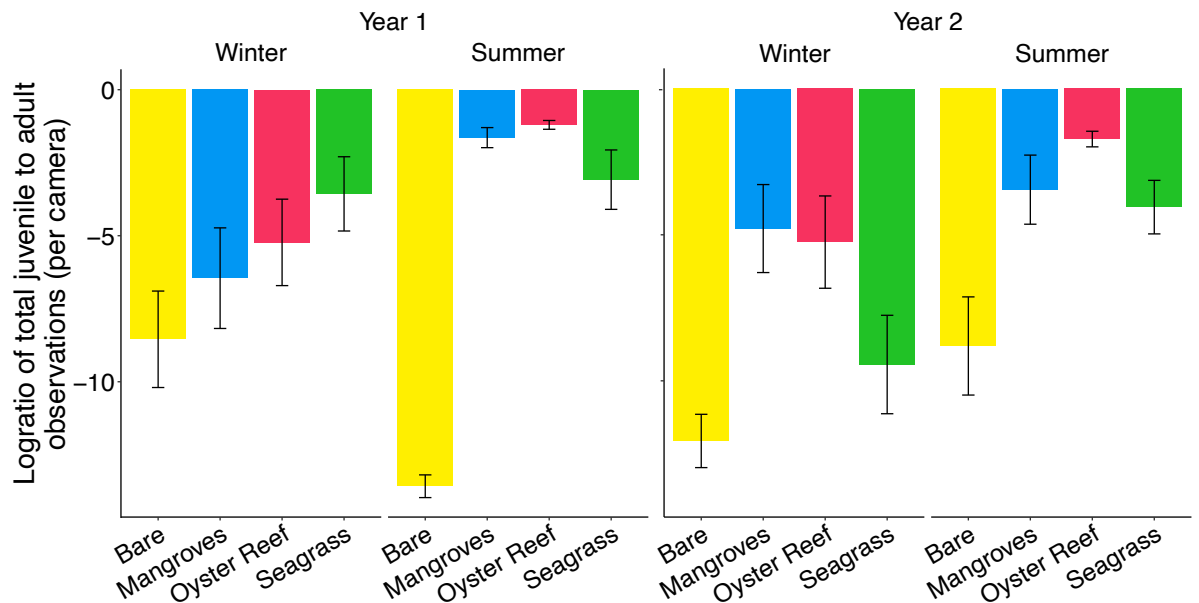


Figure 4.8: Mean ($\pm$ SE) logratio of total juvenile to adult observations by year, season and habitat as documented by 75 min Remote Underwater Video deployments, $n = 32$.

When logratios were analysed separately by species, bream displayed a greater ratio for mangroves and oyster reef, than bare sediment and seagrass in summer, but did not significantly differ among habitats in winter (sig. Season x Habitat. Appendix C, Table C.5, Figure C.1). Logratios for luderick, similarly displayed temporally but also spatially variable patterns of difference among habitats (sig. Season x Site(Estuary) x Habitat; Appendix C, Table C.7, Figure C.2). In summer, at three of the four sites differences among habitats were apparent, with oyster reef generally displaying a greater or equal ratio than the other habitats. In winter, at all but one of the four sites, the logratio did not differ among habitats. The logratio for tarwhine did not differ across habitats in Botany Bay, while in Port Stephens, it was significantly greater in seagrass than the other habitats (sig. Estuary x Habitat, Appendix C, Table C.9, Figure C.3). In Year 1, silverbiddy logratios displayed idiosyncratic differences among habitats at one of the four sites in winter, and one of the four in summer, but no differences were found in winter (sig. Year x Season x Site(Estuary) x Habitat; Appendix C, Table C.12, Figure C.4).

4.4.4 Behavioural observations among habitats

Of juveniles, 17% displayed feeding behaviour, 77% wandering behaviour and 6% passing behaviour. The percentage of juvenile fish that were feeding was similar across habitats and sites in year one, and only differed among habitats in Quibray Bay in year two, where oyster reefs had a higher relative percentage of feeding observations than other habitats (Figure 4.9, Appendix C, Table C.13). The percentage of juveniles that

were wandering was significantly lower for bare sediment than for all other habitats in each year and season, with the exception of mangroves in winter of year one and summer of year two, and seagrass in winter in year two, which did not significantly differ from bare (Figure 4.9, Appendix C, Table C.14). The percentage of juveniles that were passing displayed differences among habitats that varied by year (Figure 4.9, Appendix C, Table C.15). In year one, the percentage of observations that were passing was significantly greater for seagrass than bare habitat or oyster reef, while no differences were revealed among habitats for year two.

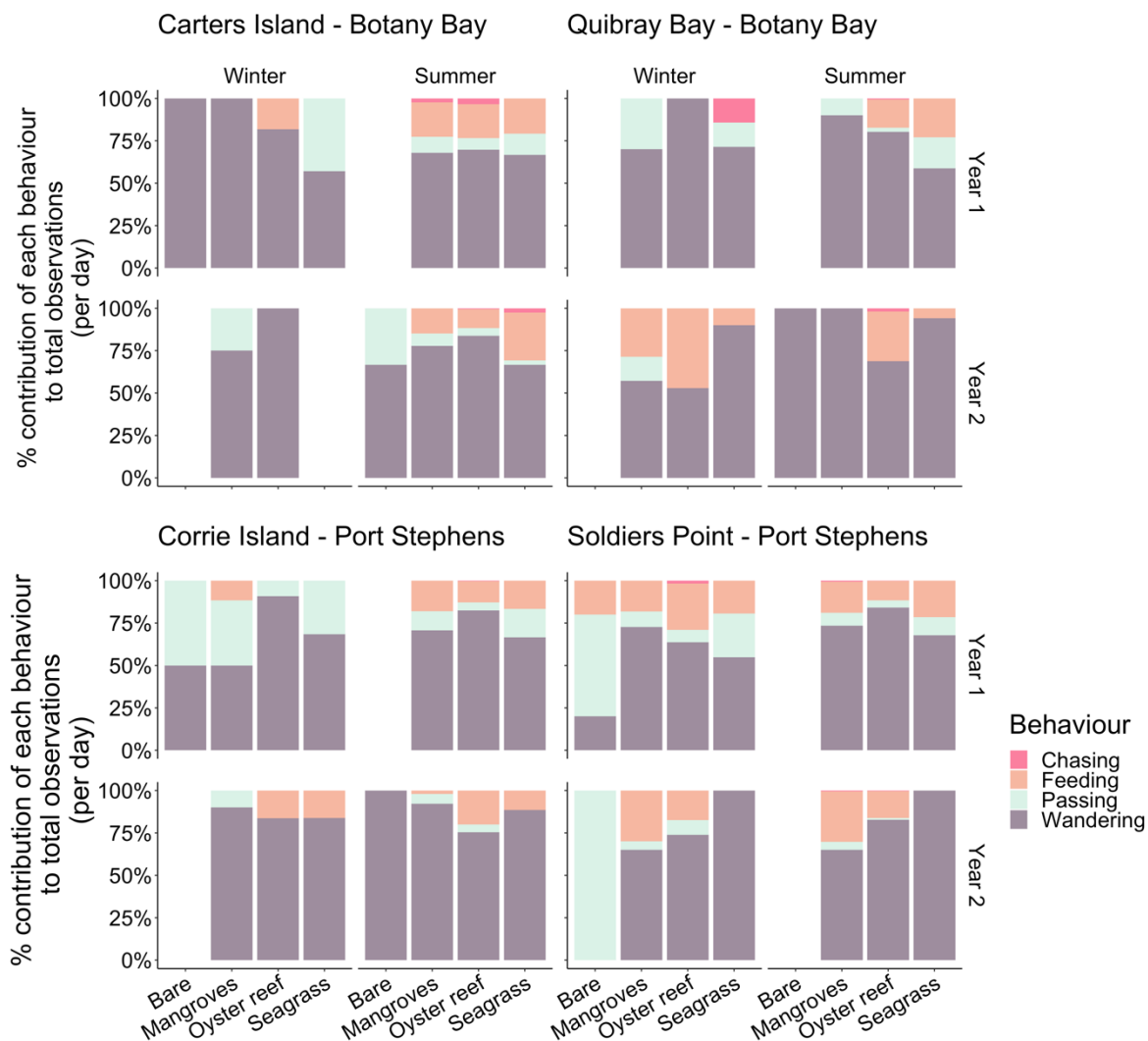


Figure 4.9: Mean percentage contribution of each behaviour to total juvenile observations that were recorded per habitat, site, season and year, as documented by 75 min Remote Underwater Video deployments, $n = 64$. Letters indicate statistically significant (at $\alpha < 0.05$) pairwise comparisons between habitats within each site, season and year.

4.5 DISCUSSION

Although oyster reefs are often inferred to have a nursery role based on the productive fisheries they support (Lehnert & Allen 2002, Tolley & Volety 2005, Gain et al. 2016, Gilby et al. 2018b), few studies have quantified this ecosystem service (zu Ermgassen et al. 2016, Lefcheck et al. 2019). Our study determined the critical role that intertidal remnant Sydney rock oyster reefs play in contributing to the seascape nursery of two temperate estuaries in south-eastern Australia: Botany Bay and Port Stephens. These remnant oyster reefs, at high tide, supported a unique juvenile fish community, with more juvenile fish and a higher juvenile to adult ratio of several species than adjacent habitats. This difference was especially prevalent in summer, when juvenile observations were highest. These results support earlier observations, predominantly from the USA, that oyster reefs are important fish nurseries (Beck et al. 2001, zu Ermgassen et al. 2016).

As expected, based on previous studies of structured estuarine habitats (Lefcheck et al. 2019), oyster reefs, seagrass and mangroves each supported greater juvenile fish observations and higher juvenile to adult ratios than unstructured bare sediments. Structured habitats can lower the foraging efficiency of some predators (Heck & Thoman 1981, Bishop & Byers 2015), protect inhabitants from stressors, such as high wave energy and currents (Fonseca & Cahalan 1992, Peterson et al. 2004), and trap organic matter and particles, that can serve as important food resources (Agawin & Duarte 2002). Yet, not only did oyster reefs support a greater ratio of juvenile to adult fish than bare sediments, but for several species they also supported higher ratios than adjacent structured habitats. The higher juvenile to adult ratio for some species in oyster reefs than other habitats suggests that oyster reefs are not only supporting species that spend their entire life-history in this habitat, but also species that move from oyster reef nurseries into other habitats as well. This suggests that oyster reefs contribute to the estuarine seascape nursery function, alongside seagrass, mangroves and bare sediment to a certain extent. Yet, when compared to mangrove and bare habitats, oyster reefs and seagrass had particularly high numbers of unique species of juvenile fish. Consequently, each habitat appeared to disproportionately benefit different species, despite some redundancy among oyster reefs, mangroves and seagrasses in their nursery function.

Most of the species observed in this study were not confined to a single habitat, but were instead present in at least two of the three structured habitats. The four species (bream, luderick, tarwhine and silverbiddy) that accounted for most of the juvenile fish observations in this study were each present in all four habitats sampled. Seascape ecology studies have determined that mobile animals move readily among habitat patches within the seascape depending on their requirements (Boström et al. 2011, Skilleter et al. 2017, Gilby et al. 2018a). Nevertheless, our comparisons of juvenile and

adult observations, through the calculation of logratios, suggested that certain habitats were contributing disproportionately as nurseries for these species. Generally, juveniles of bream, luderick and silverbiddy had higher observations in oyster reefs and mangroves than in bare and seagrass habitats, but adults were found in higher proportions in bare habitat and seagrasses (Appendix C, Tables C.6, C.8 and C.12 respectively). Similarly, whereas juvenile tarwhine had the highest observations in seagrass, adult tarwhine, though still present in seagrass, were more common in remnant oyster reefs and mangroves (Appendix C, Table C.10). Studies on the biology of these four species, have determined that each uses shallow coastal habitats for nursery, primarily recruiting to seagrasses and mangroves within estuaries, with adults migrating to deeper water or other coastal habitats (Hughes et al. 2008, Curley et al. 2013). That oyster reef, seagrass and mangroves have been identified as important nurseries for bream, luderick and silverbiddy suggests that they may be performing tidal migrations, occupying intertidal habitats such as mangroves and oyster reef at high tide, and migrating to adjacent subtidal seagrass at low tide. Bream, tarwhine, luderick and silverbiddy cumulatively account for an average, 20% of the total commercial landings by weight of the estuary general fishery of New South Wales (DPI 2003, 2020), attesting to the economic significance of the nursery role of oyster reefs, and adjacent structured habitats.

Few studies have attempted to quantify explicit habitat usage of the patches composing the seascape nursery by the juvenile community (Nagelkerken et al. 2015). Our study quantified habitat usage of the juvenile fish community by looking at four specific behaviours, feeding, wandering, passing and chasing. Our results suggested that at high tide, juvenile fish communities are using remnant oyster reefs, seagrasses and mangroves for feeding and as habitat. The much greater contribution of wandering than passing behaviour to observations suggests that these fish communities are not just passing through these habitats, but interacting with them, whether looking for food, shelter, or just a resting. Thus, oyster reefs, seagrass and mangroves are not providing only a complex structure on which juvenile fishes are aggregating, but also important foraging, resting and sheltering grounds, key contributors to the survival of these species and to the nursery function of the seascape (Nagelkerken et al. 2015, Sheaves et al. 2015).

Although, in this study, oysters consistently supported greater summer observations of fish than all other habitats across the four study sites, this study was limited to a narrow geographic area and considered only intertidal oyster reefs. Previous studies on juvenile fish elsewhere have found that the nursery function of structured habitats, including seagrass, mangroves and biogenic and rocky reef varies according to geographic location, as well as the habitats comprising the seascape (Bradley et al. 2019, Lefcheck et al. 2019). While a number of studies have found higher juvenile fish numbers in

seagrass and mangroves than coral reefs, or in temperate areas, saltmarshes and reed beds (Jaxion-Harm et al. 2012, Igulu et al. 2014, McDevitt-Irwin et al. 2016, Whitfield 2017), other studies have found that coral reefs can be as important as seagrass and mangroves (Nagelkerken et al. 2000, Dorenbosch et al. 2004, Eggleston et al. 2004, Kimirei et al. 2011). Similarly whether rocky reefs or seagrasses have the more important nursery function has been found to vary with habitat setting (Perry et al. 2018, Bradley et al. 2019). The way in which oyster reefs work with other structured estuarine habitats to contribute to the estuarine seascape may vary with the tidal elevation of oyster reefs and adjacent habitats, the tidal amplitude and habitat connectivity. Intertidal nursery habitats can only support fish at high tide, and these must migrate to alternate habitats when these are aerially exposed. Previous studies examining the effects of habitat connectivity have found that fish densities and diversity decreasing with higher spatial separation among habitats (Berkström et al. 2020).

In assessing the contribution of oyster reefs to the estuarine seascape nursery (*sensu* Nagelkerken et al. (2015), Sheaves et al. (2015)) we considered (1) juvenile observations on oyster reefs relative to structured and unstructured estuarine habitats; (2) the extent to which spatial patterns in juveniles mirrored those of adults and (3) juvenile fish behaviours on reefs. While these three aspects are key to evaluating the nursery function of habitats, tracking fish movement among habitats at various ontogenetic stages would provide a more complete vision of the nursery function of these seascapes (Nagelkerken et al. 2015, Sheaves et al. 2015). Tidal and diel migrations, site fidelity, habitat movements and habitat connectivity are all important in shaping the seascape nursery to which remnant oyster reefs contribute (Nagelkerken et al. 2015, Sheaves et al. 2015). In this study, fish were classed as juvenile or adult based on their morphology. This morphological distinction could be made for most species using footage from remote underwater cameras, and, despite certain limitations, is an approach that has previously been successfully used to quantify the nursery roles of habitats (Bradley et al. 2019, Sheaves et al. 2020). Length measurements, which can be obtained using stereo remote underwater videos, would, however, enable specific age classes to be identified. More direct measurements of fish abundance, in addition to the observations measures used here, may also help in discriminating between the productivity of oyster reefs versus the site fidelity of fish.

4.5.1 CONCLUSIONS

Our study provides compelling evidence for a nursery role for remnant oyster reefs within the mosaic of habitats that comprises the estuarine seascape (Beck et al. 2001, Whitfield 2017). It is generally accepted that vegetated habitats, such as mangroves, seagrass and saltmarshes form the core of the seascape nursery (Whitfield 2017, Lefcheck et al. 2019). Our study suggests that oyster reefs are just as important as these

vegetated habitats, providing an important nursery function at high tide. The presence of oyster reefs, mangroves and seagrasses in close proximity forms an interconnected mosaic of habitats, that is key to the survival of juvenile of many fish species. Within the habitat mosaic, fish species may migrate between habitats depending on their ontogenetic stage and tide level.

Oyster reefs in general have historically been undervalued, and consequently are globally at the brink of functional extinction (Beck et al. 2001, Beck et al. 2011, Alleway & Connell 2015, Gillies et al. 2018). Studies over the past two decades highlighting the important ecosystem services provided by oyster reefs (Coen et al. 2007, Grabowski & Peterson 2007) and their degraded ecosystem status (Beck et al. 2011, Alleway & Connell 2015, Gillies et al. 2020) have, however, led to a shift in attitude towards oyster reefs, and a surge of interest in oyster reef restoration. Our study adds to the growing literature on oyster reef ecosystem services by assessing for the first time their nursery function in south-eastern Australian estuaries. In combination with other recent studies documenting their habitat provision to invertebrates in Australia (McLeod et al. 2020) our study builds a strong ecological case for their conservation and restoration in this region.

4.6 ACKNOWLEDGMENTS

This research was funded by the Department of Biology from Macquarie University through the Macquarie University Research Excellence Scholarship (MQRES). We thank the Department of Biology from Macquarie University and the NSW Department of Primary Industries Fisheries Department and University of New South Wales for their support on equipment and logistics. Special thanks to our volunteers Steph Bagala and Justin McNab and our fieldwork manager Nick Harris. We acknowledge and pay our respect the Dharawal, Dharug, Eora and Worimi nations, Traditional Custodians of the lands on which this study has taken place and whose cultures have nurtured and conserved estuarine habitats.

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Chapter 5: De-novo reefs

FISH HABITAT PROVISION VARIES WITH FARMING METHOD

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5.1 ABSTRACT

Aquaculture industries have the capacity to produce positive ecosystem service benefits, such as habitat to wild animals, essentially serving as artificial reef infrastructure. Sydney Rock oyster cultivation is the oldest and largest aquaculture industry in south-eastern Australia. Oyster spat are grown to marketable size in rack-and-rail or on longline-and-basket configurations, which add structure to estuarine waters where culture occurs. This study assessed (1) how communities of fish utilise oyster infrastructure, as compared to adjacent natural habitats, and (2) how the fish communities associated with oyster farms vary with production method (rack-and-rail versus longline-and-baskets) and (3) whether oyster infrastructure can serve as de-facto oyster reefs in supporting similar fish communities. We used remote underwater video to survey fish communities utilizing oyster rack-and-rail, oyster longline-and-baskets, remnant oyster reefs, seagrasses, mangroves and bare sediment, during summer and winter in each of two consecutive years. The number of fish sightings and species richness were generally greater for rack- than basket- based cultivation, and higher for rack-and-rail than adjacent natural habitats. Fish communities were, in general, most similar between racks and baskets than in other habitats, and fish communities were most dissimilar between racks and bare sediments. Despite community differences, racks and baskets supported a fish community with similar number abundance and richness to remnant oyster reefs and seagrasses, respectively. Overall, this study suggests that the infrastructure associated with oyster aquaculture can provide important fish habitat, with estuarine fishes of recreational and commercial value using them extensively as foraging grounds and shelter. Use of oyster-growing infrastructure emulated use of other important biogenic habitats, such as mangroves seagrasses and remnant oyster reefs. Subsidiary ecosystem services provided by aquaculture should be considered in estuarine habitat enhancement, conservation and restoration.

Keywords: aquaculture, ecosystem services, habitat, oyster, reef, artificial structure, fish, RUV

5.2 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). Within estuarine, coastal and marine environments, aquaculture is the fastest growing and most

conspicuous agro-ecosystem and is viewed as an essential solution to feeding the world's burgeoning population, approaching 8 billion (FAO 2018). Besides food production, coastal aquaculture has the capacity to produce a range of other provisioning (e.g., production of raw materials, food, pharmaceuticals), as well as regulating (e.g., wave attenuation, carbon sequestration, water filtration), cultural (e.g., tourism, recreation, employment) and habitat and supporting services (e.g., habitat provision, genetic diversity; (Alleway et al. 2019, Gentry et al. 2019). Provision of these services is likely to depend on the biological and physico-chemical environment in which the aquaculture is occurring, farm-design, operational standards, stocking densities, stock rotation, as well as maintenance (Alleway et al. 2019; Gentry et al., 2019).

Despite the capacity of aquaculture to provide a range of positive environmental benefits, the industry often suffers from a reputation for adverse environmental impacts (Froehlich et al. 2017b). Poorly managed fish farming practices carried out in the last 20 years have resulted in organic enrichment, spread of non-native species and disease, genetic pollution and human-use conflict (Farmaki et al. 2014, He et al. 2016, Oo & Oo 2016, Wang et al. 2018). Consent requirements for aquaculture development are often focused on controlling or managing perceived negative impacts, and often do not take into account the potential positive environmental benefits that these can provide (Froehlich et al. 2017a). As aquaculture industries continue to expand in the coastal zone, home of 40% of the world's population (United Nations 2019), there is a need to actively plan aquaculture sites with the objective of enhancing their range of services (over and above food production) that benefit a range of coastal stakeholders (Froehlich et al. 2017a, Theuerkauf et al. 2019).

Habitat provision for aquatic species is among the ecosystem services provided by many aquaculture operations (Dealteris et al. 2004, Glenn 2016, Callier et al. 2017). The three-dimensional structures of pens, cages, baskets and other infrastructure provide substrate for attachment and growth of fouling organisms which, in turn, may also provide food and shelter to finfish and mobile invertebrates (Tallman & Forrester 2007, van der Schatte Olivier et al. 2020). Wild populations of mobile species 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. 2017). Consequently, aquaculture farms can support similar abundances of fish and invertebrates as natural habitats, either by way of attraction or increased production (Tallman & Forrester 2007, Glenn 2016, Mercaldo-Allen et al. 2019). 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. This is the case of wild-harvest oyster fisheries globally, on which closure of fished areas following the depletion of natural

oyster reefs was accompanied by the growth and development of oyster aquaculture industries (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 historic overharvest, have been reduced to <15% of their 1700-1800s abundance (Beck et al. 2011). 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 have been generally situated in shallow-water intertidal estuarine environments in which oyster reefs were once common. Oysters produced in hatcheries, or wild caught in estuaries, are typically grown in cages, racks, trays and baskets, to marketable size, suspended above unvegetated soft-bottom, or seagrass beds, and alongside an estuarine mosaic habitat that, depending on geographic location, may include remnant oyster reefs, seagrass beds, mangrove forests, saltmarshes and/or mud/sand flats. The infrastructure provided by oyster farms may support communities of benthic invertebrates and crypto-benthic fishes with similar, or in some instances greater, biomass, abundance and richness than adjacent habitats, including rocky reef, seagrass beds, mudflats and oyster reefs (Glenn 2016, Muething 2018, Coe 2019, Mercaldo-Allen et al. 2019). Studies to date have primarily sampled farm-associated fish using small traps placed on the sea floor, that target small fish and mobile invertebrates (Glenn 2016, Mercaldo-Allen et al. 2019). By contrast, little is known about how larger fishes utilise oyster farms (but see Muething (2018) for a study that utilised video).

Further, there are a paucity of studies considering how fish habitat provision by oyster farms varies as a function of farming methodology. Farming methods may vary in their provision of habitat to fish communities according to differences in the amount and complexity of structural habitat they introduce, their positive or negative effects on adjacent, ecologically connected habitats, and the extent to which they modify environmental 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). Such effects of farm type on the environment may, in combination with differences in their habitat structure, lead to differences in the fish communities they support. A single study compared fish communities associated with oyster farms using long-line versus on-bottom cultivation (Muething 2018), concluding that fish habitat utilisation of on-bottom cultivation was less than long-line cultivation or natural eelgrass habitats. Understanding how farming

methodology influences the provision of habitat to fish is critical in designing multi-purpose aquaculture facilities (Alleway et al. 2019).

Here, we determined the habitat value for fish communities of two different oyster farming methods: rack-and-rail and longlines-with-baskets (Figure 5.1), that are set within a mosaic of natural habitats (remnant oyster reefs, seagrasses, mangroves and bare sediment). To assess whether these farming methods can serve as de-facto habitats in terms of fish provision, 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 longlines-with-baskets would support a more abundant and species-rich fish community than the farms using rack-and-rail because they provide less impact on the seagrass habitats below. Consequently, we also expected that farms using longlines-with-baskets would support fish communities that are more similar to those of seagrass beds than other adjacent natural habitats. By contrast, we expect that farms using rack-and-rail will 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 that may attract reef residents. We further expected that feeding activity of fish would be proportionately higher on rack-and-rail 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.

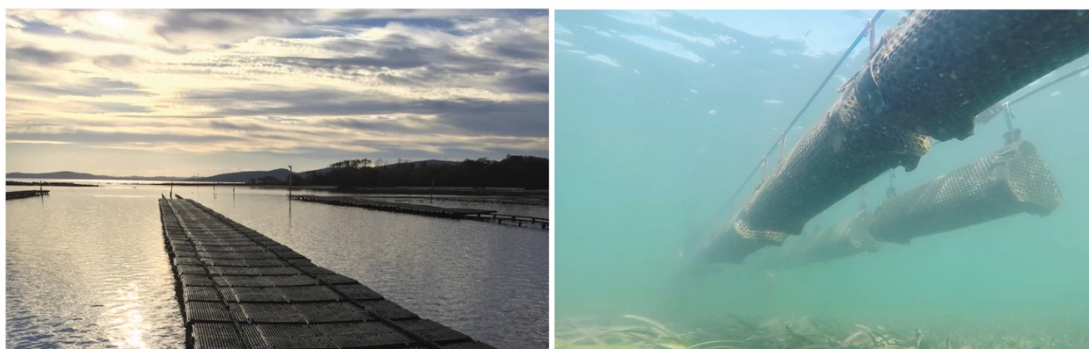


Figure 5.1: Examples of rack-and-rail infrastructure (left) and longlines-and-baskets infrastructure (right) in Port Stephens, New South Wales, Australia (source: F Martinez Baena).

5.3 METHODS

5.3.1 Study location

The study was conducted at two sites within the Port Stephens estuary in New South Wales, Australia: Corrie Island (32°40'41.26"S, 152° 7'16.09"E) and Soldiers Point (32°42'14.34"S, 152° 3'28.26"E; Figure 5.2). At each site, oyster farms utilising rack-and-rail and longlines-with-basket cultivation systems were present. Rack-and-rail (hereafter 'racks') consist of mesh-covered trays of oysters sitting on two parallel wooden rails and longline-and-basket (hereafter 'baskets') systems consist on baskets with oysters attached to horizontal longlines (Figure 5.1, (Nell 1993, 2001). Both farming methods are situated in mid- to low-intertidal areas alongside mosaic natural oyster reefs, seagrass beds, mangroves or bare sediment habitats, within an area of 0.5 to 1 km². Within each location, water-depth ranged between 1-3 m at mean high water. All sampling occurred during daylight hours within 1.5 hours of the high tide.

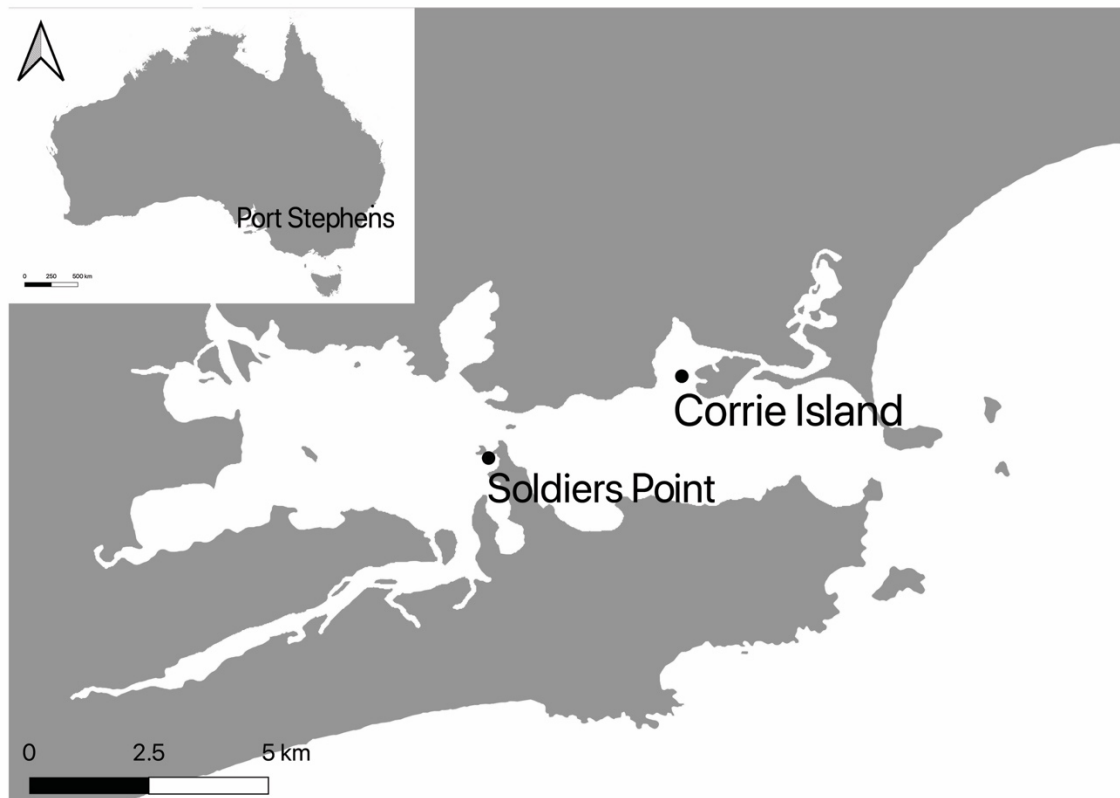


Figure 5.2: Map including sampling sites in Port Stephens estuary, New South Wales.

5.3.2 Sampling

Sampling of each site was done on three days during the winter and the summer of two 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, four unbaited remote underwater cameras (GoPro hero 4, Silver Edition) were deployed within each of the six habitats (2 farm types, 4 natural habitats) per site, to give a total of 24 simultaneously deployed cameras per site. Cameras were deployed haphazardly within each habitat, with a minimum distance of 5 meters from each other, and at least 20 meters from other habitats. Cameras faced toward the habitat they were targeting and faced away from the sun in order to eliminate glare. Each camera was mounted on a metal frame that held it 25 cm off the sediment surface. Videos were left recording for 1 hour and 25 minutes, with the first and last 5 minutes of each video excluded from analysis, in order to eliminate disturbances caused by the deployment and retrieval. This left 1 hour and 15 minutes of footage per camera deployment, for analysis. Visibility was measured at each site on each day with a turbidity tube, consisting on a 1.2-meter-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.

5.3.3 Video analysis

Raw footage from each camera deployment was compiled into a 75-minute video, and colour enhanced with Adobe After Effects and Adobe Encoder (2020, Adobe®). To quantify fish communities and behaviour, each video was then reviewed using EventMeasure software (SeaGIS Pty. Ltd.).

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 enters the frame, for a given camera, across all species. Individual fish that swam into and out of the frame multiple times within a span of 20 seconds 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 habitat use, rather than a relative measure of abundance (Lanham 2019).

To assess any differences in how fish utilised the habitats, every fish that appeared in a frame was assigned one of four 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” behaviour was 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 reported in a similar fashion as per observations, with the exception that if different individuals within a shoal exhibited different behaviours, an observation per behaviour was noted for that shoal.

5.3.4 Data analysis

Permutational multivariate analysis of variance, calculated in PRIMER (PERMANOVA, (Anderson et al. 2008)), run on Bray-Curtis dissimilarities using the matrix of observations per species, assessed differences in fish community structure among habitats. The analysis, run on untransformed data, had five 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 x Season x Site). A dummy variable of one 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 on the Vegan package in R (R Core Team, 2019). The significant factors in the previous PERMANOVA were included in the model and a permutational test assessed statistical significance of canonical axis produced by the dbRDA, and the triplot was made. For clarity, only species that were positioned +/- 0.5 along either axis were plotted.

Univariate Linear Mixed Effects Models, that utilised square root transformed data, were run within the package “lme4” (Bates et al. 2015) in R on the following metrics calculated for each camera: (1) the total number of fish observations, (2) the total species richness, (3) species-specific observations of five most abundant fish species with a commercial or recreational value that were found in the study: bream (*Acanthopagrus*

australis), luderick (*Girella tricuspidata*), silverbiddy (*Gerres subfasciatus*), whiting (*Sillago ciliata*) and mulloway (*Argyrosomus japonicus*) (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 is a behaviour that commonly occur at scales greater than the habitat. The analyses included the same five factors as the PERMANOVA, but with Year, Season and Site treated as fixed effects because Linear Mixed Effects Models require at least five "levels" for a random intercept to achieve a robust estimate of variance (Harrison et al. 2018). Day, which is nested in Site, Season and Year was considered a random factor, with all possible 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 from the "lmerTest" package. After each analysis, models were checked visually to confirm that in all instances their residuals conformed with the assumptions of normality. Pairwise comparisons examining sources of significant interactions were performed using Estimated Marginal Means (EMMs) using the "emmeans" package.

A total of 510 videos, totalling 586.5 hours of footage, could be analysed, once cameras that had failed to record, that tipped over, or had footage that was obstructed in some way were excluded. Of the analysed videos, 96 focused on the longlines and baskets, 95 on the rack-and-rail farms, 83 on the oyster reefs, 82 on the seagrass, 79 on the mangroves and 75 on the bare sediment.

5.4 RESULTS

5.4.1 Fish community structure

A total of 90 species of fish from 51 families were observed in this study (Appendix D, Table D.1). Fifty species were associated with racks, of which nine were unique to this habitat, 45 with baskets, of which three were unique, 54 with oyster reefs of which six were unique, 43 with seagrasses, of which eight were unique, 29 with mangroves, of which one was unique, and 36 with bare sediment, of which three were unique. Eleven species were observed in all six habitats.

In general, racks and baskets supported more similar fish communities than other habitat contrasts, and racks and bare sediments the most dissimilar (Appendix D, Table

D.2; Figure 5.3). 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 (Appendix D, Table D.2; Figure 5.3). 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 (Appendix D, Table D.2). In all other instances, fish communities significantly differed among habitats, within each site, season and year. The three species that contributed most differences in community structure among habitats were *Acanthopagrus australis* (yellowfin bream), *Omobranchus anolius* (oyster blenny) and *Girella tricuspidata* (luderick; Figure 5.3). Bream, oyster blenny and rotund blenny (*Omobranchus rotundiceps*) were species that characterised oyster reefs and mangroves, while luderick was associated with racks and baskets. *Microcanthus strigatus* (stripey), *Gerres subfasciatus* (silverbiddy), and *Dicotylichthis punctulatus* (three-barred porcupinefish) were associated with racks, baskets as well as oyster reefs. *Pelates sexlineatus* (trumpeter) was one of the main residents of seagrass but was also associated with oyster farms (Figure 5.3).

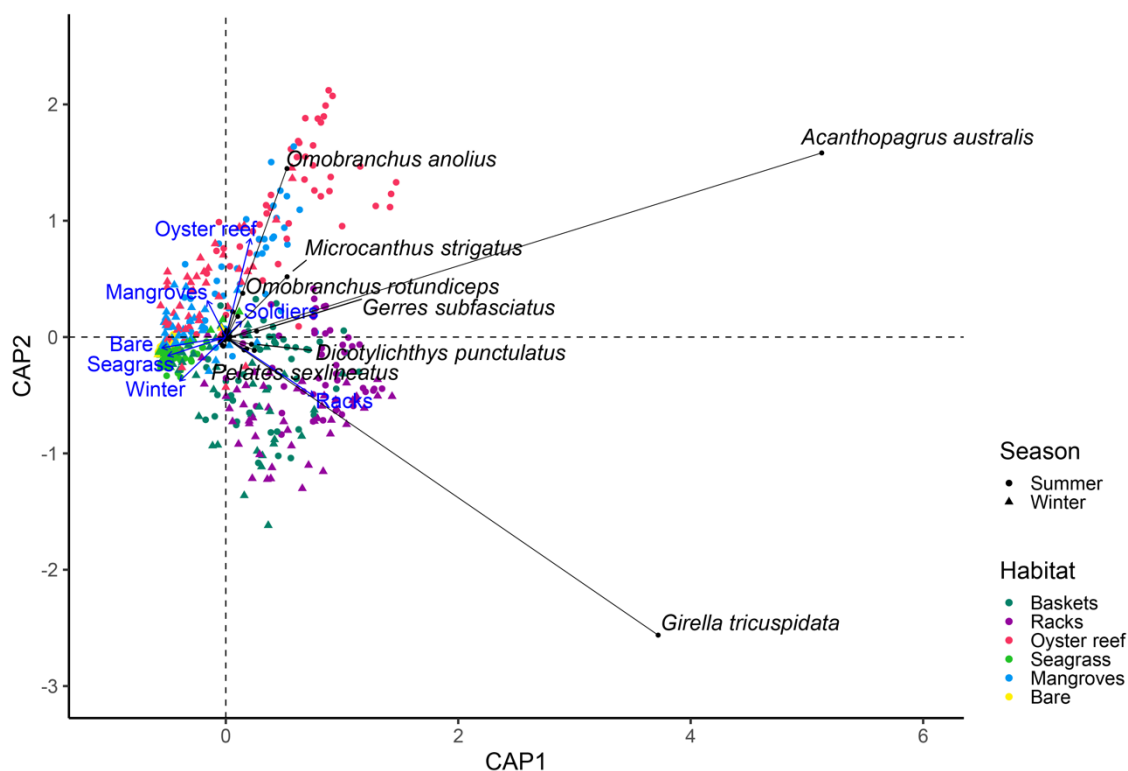


Figure 5.3: Distance-based Redundancy Analysis (dbRDA) triplot of transformed fish observations data, across four habitats, sites and seasons. Species exceeding a critical value of ± 0.5 on one of the axes are indicated. Points represent individual cameras.

The total number of fish observations were 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 (four-way interaction among Habitat, Site, Season and Year; Figure 5.4. Appendix D, Table D.3). In summer, racks and oyster reefs generally had similarly high observations, that were greater than the other natural habitats (Appendix D, Table D.3, Figure 5.4). However, at Corrie Island in the second year, reefs had fewer observations than racks. In winter, racks generally supported more observations than baskets, and than oyster reefs, which was the natural habitat with generally highest observations of this season. In general, the baskets had fewer fish observations than oyster reef, similar observations to the structured habitats of mangroves and/or seagrass, and greater observations than bare sediment (Figure 5.4).

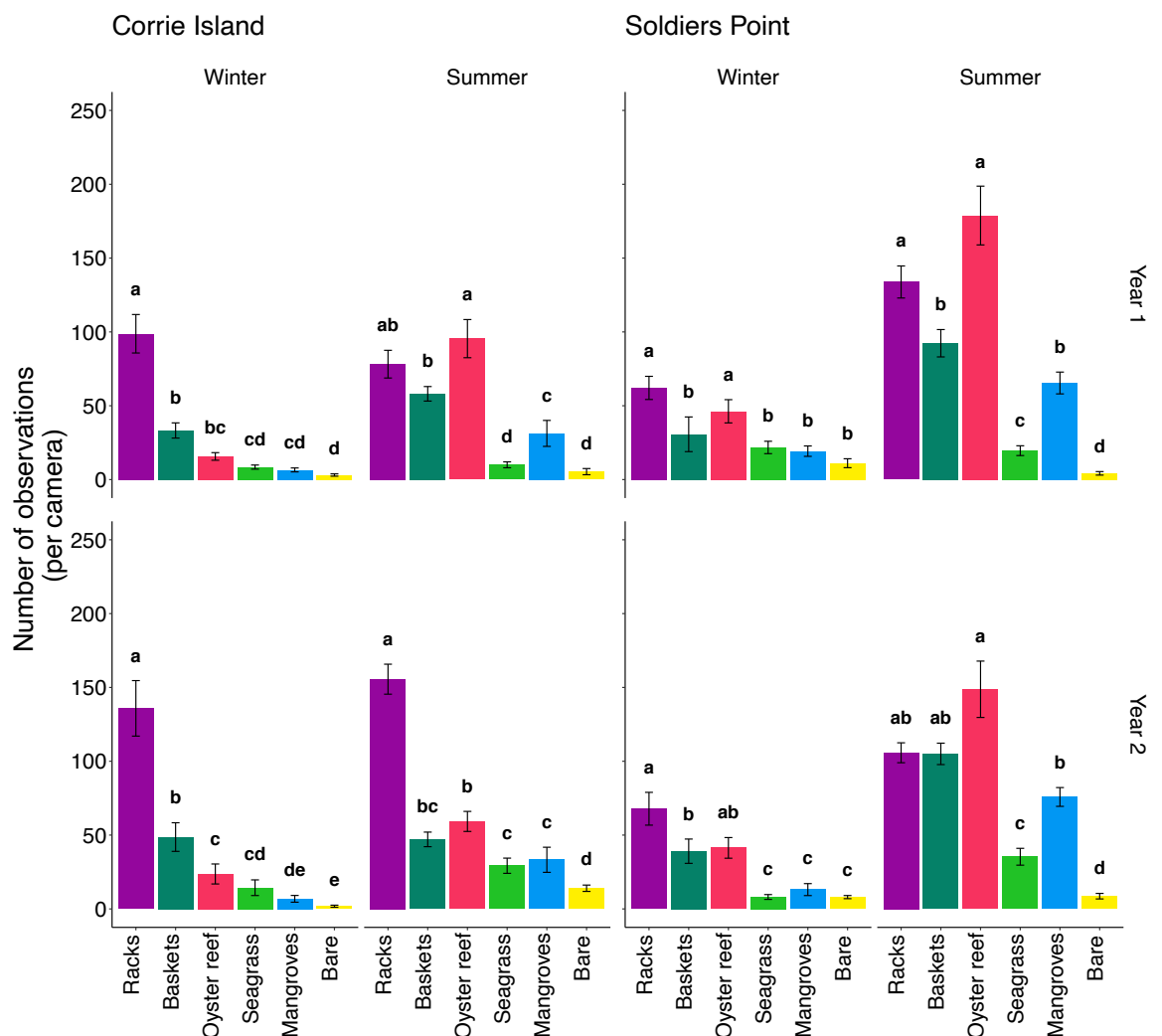


Figure 5.4: Mean ($\pm$ SE) fish observations, per habitat, site, season, and year as documented by 75 min Remote Underwater Video deployments, $n = 48$. Letters above columns denote treatments that were found to significantly differ (at $\alpha = 0.05$) within each year, site and season by Estimated Marginal Means.

Species richness generally did not differ between racks and baskets, except in summer at Corrie Island, where racks had the greater richness (three-way interaction between Habitat, Site, and Season; Figure 5.5, Appendix D, Table D.4). 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 habitats, including oyster reef. At Corrie Island, baskets had a similar species richness to oyster reefs in both summer and winter, but at Soldiers Point baskets had a smaller species richness than oyster reef in both seasons (Figure 5.5).

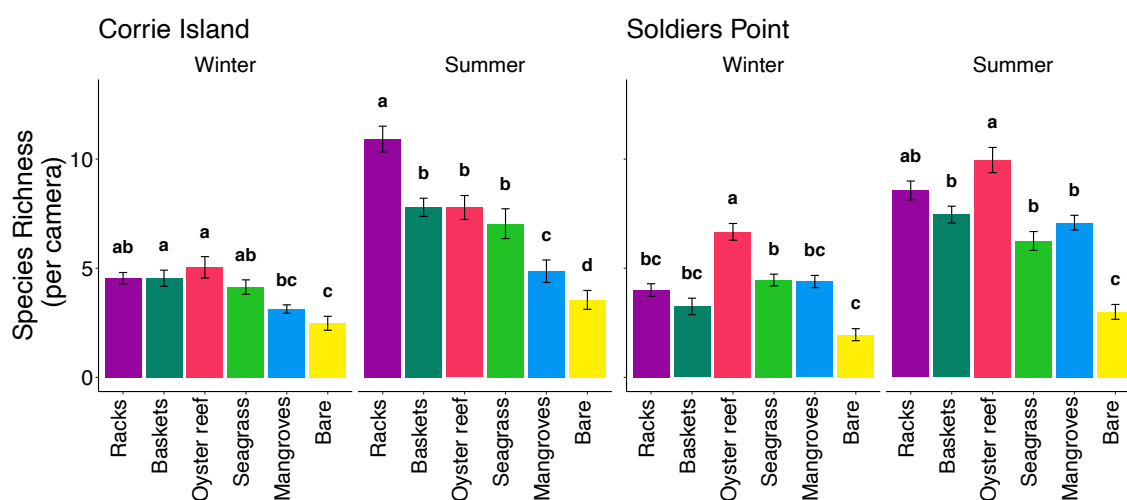


Figure 5.5: Mean ($\pm$ SE) species richness, per habitat, site and season, as documented by 75 min Remote Underwater Video deployments, $n = 24$. Letters above columns denote treatments that were found to significantly differ (at $\alpha = 0.05$) within each site and season, by Estimated Marginal Means.

5.4.2 Species-specific distributions

The commercially and recreationally important species, yellowfin bream (*A. australis*), luderick (*G. tricuspidata*), silverbiddy (*G. subfasciatus*), whiting (*S. ciliata*) and mullet (*Agyrosomus japonicus*) together accounted for 72% of the total number of observations recorded by the study. Among these, bream was the most common species with 11,576 observations, 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 (three-way interaction among Habitat, Site and Season; Figure 5.6, Appendix D, Table D). Baskets generally supported similar

numbers of bream to mangroves, and greater numbers than seagrass or bare habitats. The exception was at Corrie Island in winter when baskets displayed greater observations than seagrass, mangrove or bare habitats, and similar numbers to oyster reef (Figure 5.6).

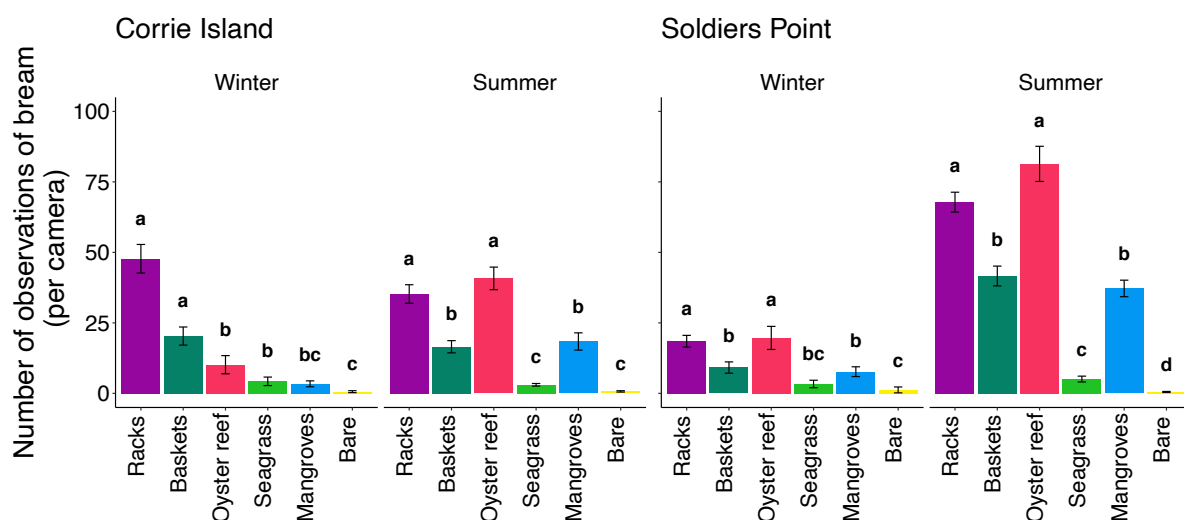


Figure 5.6: Mean ($\pm$ SE) observations of bream, as documented by 75 min Remote Underwater Video deployments, $n = 24$. Letters above columns denote treatments that were found to significantly differ (at $\alpha = 0.05$) within each site and season by Estimated Marginal Means.

Luderick accounted for 24% of total fish observations and their observations were greater for farmed than natural habitats, and between farmed habitats, for racks than baskets, although the latter difference was not always significant (four-way interaction among Habitat, Site, Season and Year; Figure 5.7, Appendix D, Table D.6).

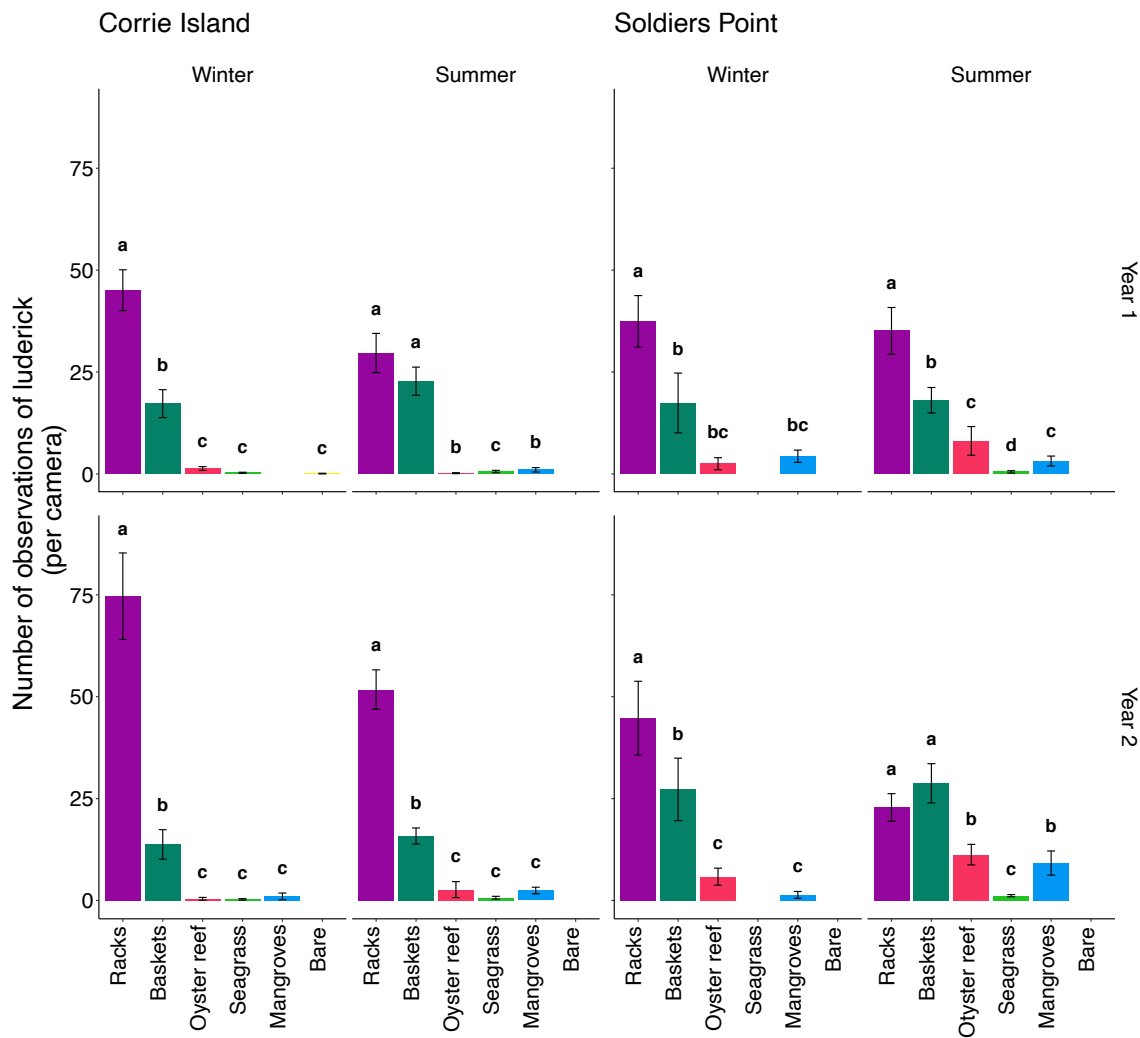


Figure 5.7: Mean ($\pm$ SE) observations of luderick as documented by 75 min Remote Underwater Video deployments, $n = 48$. Letters above columns denote treatments that were found to significantly differ (at $\alpha = 0.05$) within each year, site and season by Estimated Marginal Means.

Silverbiddy were accounted for 3% of the total fish observations. In winter, silverbiddy 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; Figure 5.8, Appendix D, Table D.7).

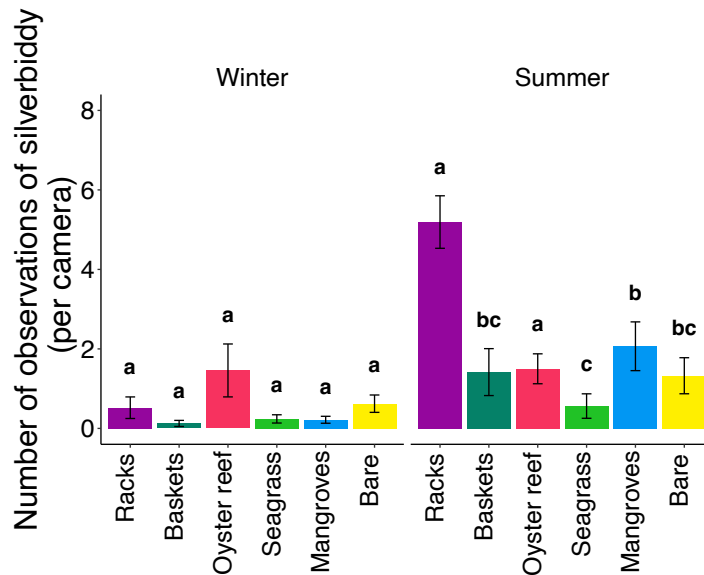


Figure 5.8: Mean ($\pm$ SE) observations of silverbiddy as documented by 75 min Remote Underwater Video deployments, $n = 12$. Letters above columns denote treatments that were found to significantly differ (at $\alpha = 0.05$) season by Estimated Marginal Means.

Whiting, which accounted for 3% of fish observations, were generally more abundant in bare sediment than any of the other habitats (Figure 5.9). Of the remaining five habitats, racks and baskets generally supported the next greatest number of whiting observations, through this varied with Season and Year (three way interaction between Habitat, Season and Year; Figure 5.9, Appendix D, Table D.8)

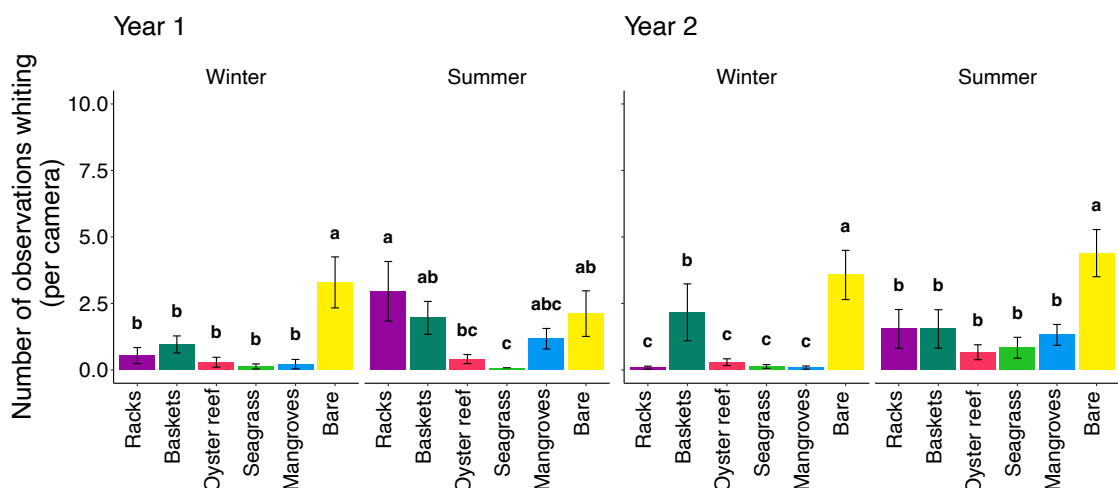


Figure 5.9: Mean ($\pm$ SE) observations of sand whiting in 75 min Remote Underwater Video deployments. Data are averaged across the two sites, as these did not significantly differ, with four cameras deployed on 3 replicate days of each site, to give $n = 24$. Letters above columns

denote treatments that were found to significantly differ (at $\alpha = 0.05$) within each year and season by Estimated Marginal Means.

Mulloway accounted for 0.74% of the total observations and displayed the greatest habitat fidelity of the five species examined (four way interaction among Habitat, Site, Season and Year; Figure 5.10, Appendix D, Table D.9). 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 year one (Figure 5.10).

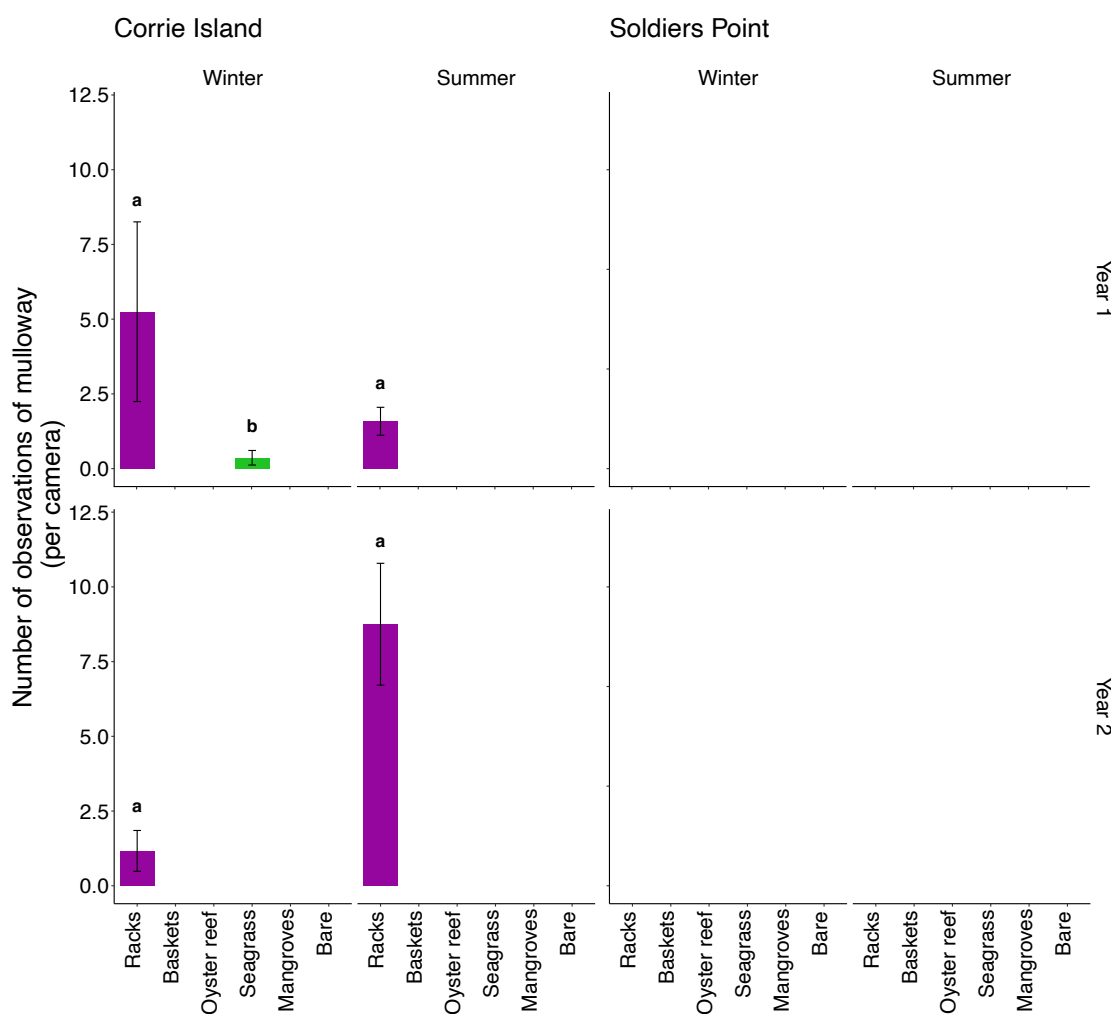


Figure 5.10: Mean ($\pm$ SE) observations of mulloway in 75 min Remote Underwater Video deployments, $n = 48$. Letters above columns denote treatments that were found to significantly differ (at $\alpha = 0.05$) within each habitat, site, season and year by Estimated Marginal Means.

5.4.3 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 by the study, 84 species exhibited wandering behaviour, 40 species exhibited feeding behaviour and 51 species exhibited passing behaviour. The percentage of fish that were 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) sediment (three-way interaction between Habitat, Season and Year; Figure 5.11, Appendix D, Table D.10). The percentage of observations attributed to feeding behaviour only differed among habitats and sites in winter (three-way interaction between Habitat, Site and Season; Figure 5.11, Appendix D, Table D.11). In winter, at Corrie Island, oyster reefs and baskets had the highest percentage of fish that were feeding, although their percentages did not differ to those of mangroves and racks. At Soldiers point, bare sediment had the greatest percentage of observations that were of feeding, though this was only significantly greater than percentages for racks and baskets, but not the other natural habitats. Passing percentages were greater for bare sediment than the other habitats in each of the sites and in both seasons (three-way interaction between Habitat, Site and Season; Figure 5.11, Appendix D, Table D.12).

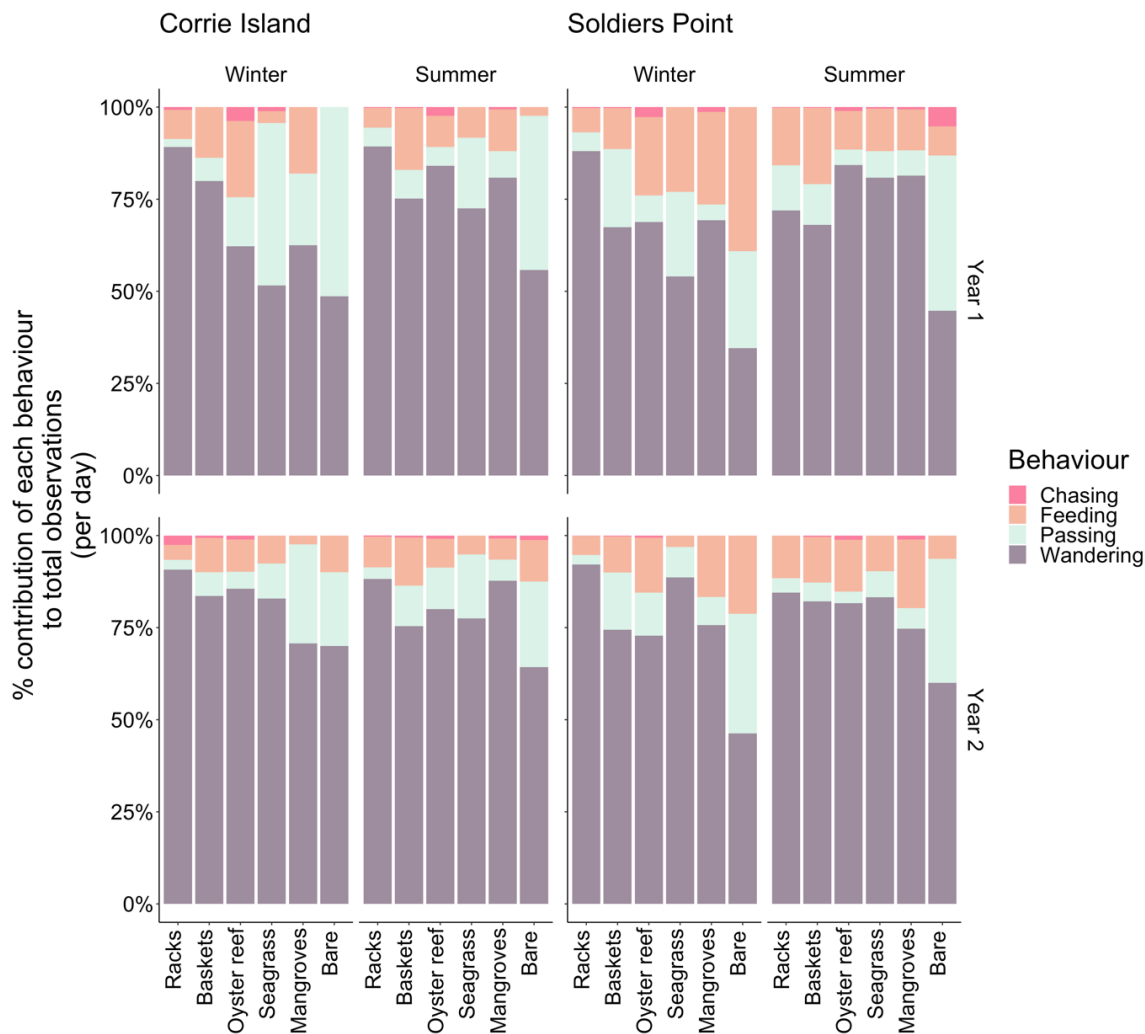


Figure 5.11: Mean percentage contribution of each behaviour to total observations recorded during 75 min Remote Underwater Video deployments for each habitat, site, season and year $n = 64$. Letters above columns denote habitats that were found to significantly differ (at $\alpha = 0.05$) within each year and season by Estimated Marginal Means.

5.5 DISCUSSION

In Australia, and globally, oyster reefs have been greatly reduced over the last two centuries, primarily due to over-harvest using destructive fishing practices (Beck et al. 2011; Gillies et al. 2018). In environments where natural ecosystems have been destroyed, damaged or degraded, aquaculture infrastructure can serve as important habitat to wild organisms. There is growing evidence that off-bottom shellfish aquaculture can provide important fish habitat (Dealteris et al. 2004, Muething 2018, Mercado-Allen 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 aquaculture. This study found

that both racks and basket oyster farms supported fish communities that were often more diverse than adjacent complex biogenic estuarine habitats. Although the two 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 than in unstructured sediments, where fish were more commonly observed just passing through the habitat without any further engagement. The similarity between racks and remnant oyster reefs in fish communities and their behaviourally-inferred engagement with the habitat 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 New South Wales, the depletion of natural oyster reefs was followed by the rise of oyster aquaculture, often in areas once supporting natural reefs (Nell 1993). 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 their primary habitat (Beck et al. 2011; Gillies et al. 2018). Oyster gobies and blennies that were found only on oyster reefs or in mangrove forests with fouling oysters, were also found around racks and baskets. While there is growing interest and investment in oyster reef restoration in Australia (Gillies et al. 2015a, McAfee et al. 2020b), it is possible that in environments unsuitable for oyster reef restoration, perhaps as a consequence of conflicting human uses of estuaries, or unstable bottom types, oyster farms may provide many of the same habitat functions. The consideration of sustainable oyster aquaculture as potential habitat analogues in restoration projects may not only contribute to the improvement of the ecosystem habitat function but to the additional benefit of oyster production and other cultural provisioning services such as increasing employment opportunities in coastal communities (Alleway et al. 2019, Gentry et al. 2019).

Yet, despite the similarities in fish communities between 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 two 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 (Dumbauld et al. 2009). Luderick feed on epiphytes of macroalgae such as *Enteromorpha* spp. and *Ulva* spp., that foul low intertidal and shallow subtidal hard substrate such as 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. Martinez Baena, pers. obs.). Additionally, mulloway and luderick which can exhibit strong site fidelity with subtidal reefs (Ferguson et al. 2013) or habitat features (Taylor et al. 2016),

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 of the two farming methods, their environmental context, as well as 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 baskets may allow colonization 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, Mercaldo-Allen et al. 2019, McLeod et al. 2020). Differences in the fish communities between the two farming methods may also relate to differences in their degree of shading and/or underlying benthic habitat. Shading can prevent survival of seagrasses on the substrate below (Thorne 1998, Madigan et al. 2000), and studies examining piers and overwater artificial structures have shown that the level of shading created by these is detrimental to certain fish communities diminishing their abundances and richnesses (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. 2003, 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 (Figure 5.14).

The underlying habitat found beneath the racks was mostly bare, bare with the presence of *Sargassum* sp., and bare with woody and shell debris product of the aquaculture infrastructure, while the underlying habitat beneath the baskets was seagrasses, bare, or bare with woody and shell debris. As predicted from differences in underlying habitat, the fish communities associated with baskets were generally more similar to those of seagrass habitats than were the communities associated with racks. This pattern was driven by similarity in the identity and richness of species present, with fish observations by contrast higher for baskets, which were of greater complexity, than seagrass. Previous studies have likewise found similar invertebrate and fish communities between seagrasses and longlines with baskets (Muething 2018, Coe 2019), although in some instances baskets supported higher abundances but lower richnesses of fish than seagrass habitats (Dealteris et al. 2004, Glenn 2016). By contrast, the fish communities of racks were more similar in composition to those of oyster reefs than seagrass. Despite mangroves also providing a great extent of hard substrate and habitat complexity and a similar shade effect to racks, our study found greater fish observations and richness in oyster farms than mangroves. Few other studies have compared

ecological communities between oyster farms and oyster reefs, and comparisons between oyster farms and mangroves remain a major research gap. Erbland and Ozbay (2008) compared macrofaunal communities between oyster cages and a restored oyster reefs, finding higher richness and abundances in oyster cages. Although not directly considering oyster reefs, Mercaldo-Allen et al. (2019) 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 feeding opportunities on invertebrates living on or below the racks and by providing structured habitat that offers refuge from predators. Further studies would be required to disentangle the mechanisms by which the two farm types support differing fish communities.

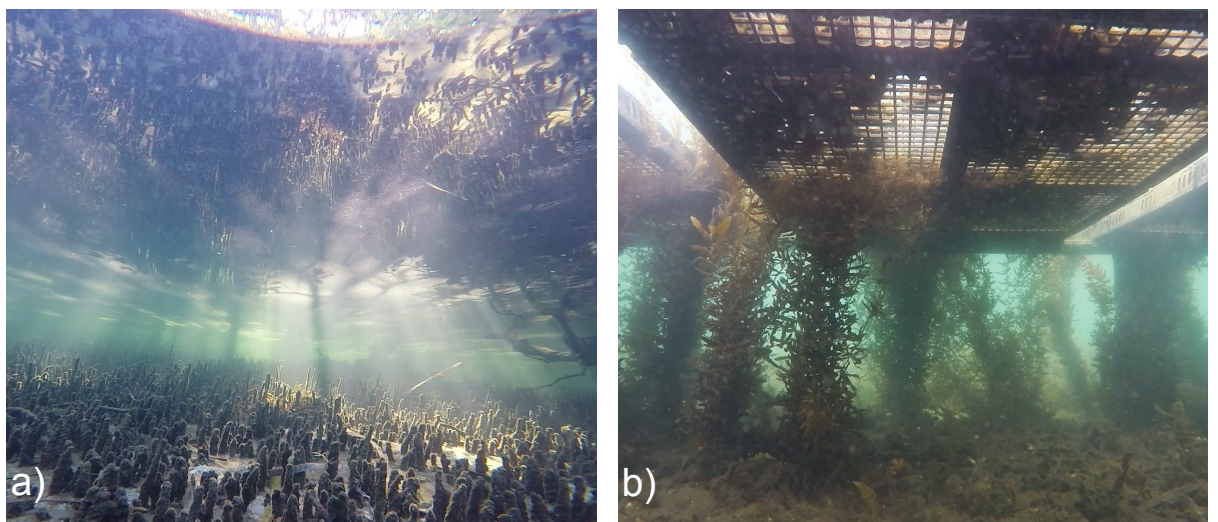


Figure 5.12: Photographs of a) mangrove forest and b) rack aquaculture system at Port Stephens. (F. Martínez-Baena)

The 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). This is the first study quantifying utilisation of oyster aquaculture infrastructure by commercially and recreationally important fish species in Australia. The important role of oyster farms in providing habitat to fish extended beyond small cryptic species to commercially and recreationally important species that used farms as sites for foraging and refuge. Bream, luderick, silverbiddy, whiting and luderick, which collectively account for 21% of the total commercial and recreational estuarine fisheries landings by weight in New South Wales (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 the case of mullet. Local recreational community groups are aware of the value of oyster aquaculture infrastructure as

hotspots for fishing valued recreational fish species (author 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. 2019). Our study contributes to a growing body of research demonstrating that aquaculture, and specifically, shellfish cultivation, can provide considerable environmental benefits (Froehlich et al. 2017a, Alleway et al. 2019, Gentry et al. 2019, van der Schatte Olivier et al. 2020). Our study supports claims that these benefits will likely depend on farming practice (Alleway et al. 2019, Gentry et al. 2019). Here, racks and baskets farms supported distinct fish communities despite being situated alongside one another. Our study was, however, limited to two 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 habitat that may be differentially modified by alternate farming practices. Building knowledge of the relationship between farm design and the provision of ecosystem services is essential for optimising positive environmental effects of aquaculture infrastructure (Gentry et al. 2019).

5.6 ACKNOWLEDGMENTS

We thank the Department of Biology from Macquarie University for their continuous support through the Macquarie University Research Excellence Scholarship (MQRES), the NSW Department of Primary Industries Fisheries Department and University of New South Wales for their support on equipment and logistics. Special acknowledgment to Wayne O'Connor, Michael Dove, Ian Lyall and Kylie Russell for their support and assistance and we would like to thank our fieldwork manager Nick Harris and volunteers Steph Bagala and Justin McNab for their continuous assistance with the fieldwork. We acknowledge and pay our respect to the Worimi nation, Traditional Custodians of the lands on which this study has taken place and whose culture have nurtured and conserved our study estuarine habitats to date.

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Chapter 6: General Discussion



6.1 STATUS OF AUSTRALIAN OYSTER REEFS

Oyster reefs were a key natural feature of the Australian seascape until the 19th century (Gillies et al. 2018). Conspicuous components of temperate and subtropical Australian estuaries, they fed first nations people and subsequent settlers. In providing a building material, oysters were also key to industrial hubs that were the foundations of modern Australia. Historic overharvest using destructive dredging practices, along with growing water pollution and disease, pushed oyster reefs to the brink of extinction, leading to their complete extirpation from many locations as well as the social memory (Alleway & Connell 2015, Gillies et al. 2018). In the absence of natural reefs suitable for wild harvest, a valuable oyster aquaculture industry grew, which today is the most important aquaculture industry in the state of New South Wales. Despite some larval supply from oyster leases, and subsequent oyster colonisation of marine urban structures, oyster reefs in Australia have remained depleted, unseen and forgotten until recent decades, when oyster reef conservation and restoration gained momentum worldwide (Beck et al. 2011, Gillies et al. 2015b, Humphries & La Peyre 2015, Graham et al. 2017, McAfee et al. 2020b).

Reviews on the status of oyster reefs in Australia point to the need to quantify the ecosystem services and ecological function of remnant oyster reefs. Indeed, this is listed as a key action, among 12, required to facilitate their restoration and conservation success (Gillies et al. 2015a). Several studies, mainly from the USA, have documented the importance of intertidal and subtidal oyster reefs as essential fish habitat (Harding & Mann 2001, Peterson et al. 2003, Tolley & Volety 2005, Stunz et al. 2010, Joyce 2011, Gain et al. 2016, Gilby et al. 2018b), nursery (Beck et al. 2001, zu Ermgassen et al. 2016, Lefcheck et al. 2019, Berkström et al. 2020) and foraging grounds (Grabowski & Powers 2004, Grabowski et al. 2008, Quan et al. 2011, Abeels et al. 2012, Hughes et al. 2012, Kimbro et al. 2014). However, no such studies exist for Australia (Gillies et al. 2020, McLeod et al. 2020). Australia-specific studies are required due to the different seascape context in which oyster reefs are found. The US studies have documented the role of intertidal oyster reefs as fish habitat compared to other adjacent structured habitats, including seagrass, saltmarshes and bare unstructured sediments (Shervette & Gelwick 2008, Gain et al. 2016), but none of them have compared these to mangroves and only few compared them to oyster aquaculture infrastructure (Glenn 2016, Muething 2018, Coe 2019, Mercaldo-Allen et al. 2019) --- also important components of the south-east Australian seascape.

This thesis filled a critical knowledge gap regarding role that remnant intertidal Sydney rock oyster reefs in temperate Australia provide as fish habitat. Specifically, it aimed to determine the role of oyster reefs in supporting fish communities in the context of the seascape habitat mosaic of seagrass beds, mangrove forests and bare sediments in

which remnant eastern Australian oyster reefs are commonly found. Additionally, this thesis assessed the extent to which the oyster farms that arose as a consequence of closure of wild oyster harvest provide similar habitat functions to fish as remnant oyster reefs. A growing body of literature points to the important role appropriately managed aquaculture operations can play in bolstering a range of provisioning, regulating, cultural and supporting ecosystem services, particularly in environments where these are no longer sustained by natural ecosystems (Alleway et al. 2019, Gentry et al. 2019, Theuerkauf et al. 2019, Gravestock et al. 2020, van der Schatte Olivier et al. 2020). Although oyster farms differ in complexity and habitat structure to wild reefs, like reefs they add hard structure to otherwise largely sedimentary environments (Dealteris et al. 2004, Tallman & Forrester 2007, Dumbauld et al. 2009, Coe 2019). Additionally, like oysters on reefs, farmed oysters produce biodeposits that can influence trophic pathways (Dumbauld et al. 2009, Ray & Fulweiler 2020).

Collectively, this thesis shows that at high tide, remnant Sydney rock oyster reefs and oyster farms support unique fish communities with, generally, a greater number of fish observations and greater species richness, as compared to adjacent habitats (Chapter 2 – 5). These fish communities, which include several recreationally and commercially fished species, utilise oyster habitat as foraging grounds, shelter and nursery. These roles of oyster reef and farms are similar and in the case of reefs, in some instance more important, as they provide habitat to higher numbers of species, of greater abundance, than adjacent structured estuarine biogenic habitats, that have high conservation status in part due to their fisheries value (Chapters 2 - 4). Many of the fish species associated with oyster reefs and farms also utilised the other biogenic habitats in the estuarine mosaic, reinforcing the importance of the seascape concept and habitat connectivity for the survival of many species (Boström et al. 2011, Pittman 2017).

6.2 ROLE OF OYSTER REEFS IN SUPPORTING FISH COMMUNITIES WITHIN THE ESTUARINE SEASCAPE

Understanding which habitats are more or less valuable for certain fish communities, and why, is critical in enabling managers to decide how to prioritise limited resources towards conservation initiatives (Levin & Stunz 2005). The habitat value of a patch is determined by its environmental attributes, as well as ecological factors such as the identity, complexity, size and ecological connectivity (Boström et al. 2011, Martinez-Ricart 2016, Pittman 2017, Ferrari et al. 2018). These factors determine the nature and quality of shelter provided, the foraging and feeding opportunities, the spawning areas

availability and the successful development of associated species through different life stages (Rice 2005). However, determining habitat value for highly mobile species is complex, as these species are generally not limited to a single habitat unit, but instead utilise a mosaic of functionally interacting habitats across which they migrate at a range of temporal and spatial scales (Sheaves 2009, Boström et al. 2011, Sheaves et al. 2015). This thesis compared fish community composition, foraging and resting behaviours, and ontogenic stage between oyster reefs and three adjacent habitats that are part of the same estuarine seascape, comparing and contrasting their habitat value to fish. The results indicate the importance of oyster reef within the estuarine seascape as foraging, resting and nursery habitat. Identifying functionally integrated seascapes is crucial to designing restoration strategies (Boström et al. 2011).

6.2.1 Foraging grounds

Studies, predominantly from the USA, have provided evidence for an important trophic role for intertidal and subtidal oyster reefs (Micheli & Peterson 1999, Grabowski 2004, Grabowski & Powers 2004, Stunz et al. 2010, Joyce 2011, Quan et al. 2011, Abeels et al. 2012, Kimbro et al. 2014). This trophic role stems from oysters providing a direct source of food for shellfish-feeding species, but also from them modifying resource availability through nutrient cycling, organic deposition and provision of hard substrate on which epibiota can grow (Dame & Libes 1993, Norling & Kautsky 2007, McAfee & Bishop 2019). Given that east Australian oyster reefs are highly oligotrophic (Scanes et al. 2007), and nutrient input has been documented to result in strong positive effects on both primary and secondary productivity (Bishop et al. 2006, York et al. 2012), it was hypothesised that oysters would also have an important trophic role in the estuaries studied here.

This thesis utilised two approaches to quantifying the trophic role of oyster reefs: direct observations of fish foraging using unbaited remote underwater cameras (Chapter 2), and stable isotope analyses (Chapter 3). Together, the two approaches suggest that oyster habitats (remnant oyster reefs and oyster aquaculture infrastructure), are important foraging grounds for fish, that are at least if not more valuable in supporting estuarine trophic pathways as adjacent mangroves, seagrasses and bare sediments (Chapters 2 – 5). First, direct observations of fish foraging in video footage indicated that the proportion of fish activity that was foraging was greater for oyster reef than unvegetated habitat and similar between oyster reef and other biogenic structured habitats, broadly regarding as important foraging areas (Whitfield 2017, Le et al. 2019). Second, the stable isotopes analyses (Chapter 3) indicated that fish and other macroinvertebrates utilising oyster reefs as primary habitat (residents), or on an occasional basis (transients), were not only consuming the bivalves forming the reef, but also the biodeposits generated on the reef, and other resident species. These trophic

links are facilitated by the benthic-pelagic coupling of oysters (Dame et al. 2001, Newell 2004), and predation (Anderson & Connell 1999, Grabowski 2004, Brown et al. 2008). As oysters filter large amounts of phytoplankton and organic matter from the pelagic system, they also release large amounts of inorganic nutrients to both the pelagic, and the sediment system, increasing benthic mineralization and sediment enrichment (Dame & Libes 1993, Dame et al. 2001). This release of nutrients feeds back to positively influence phytoplankton and microphytobenthos production (Miller et al. 1996, Prins et al. 1997, Southwell et al. 2017) and, in turn, the consumers that directly utilise these resources, or prey upon herbivores (Norling & Kautsky 2007, Quan et al. 2011, Abeels et al. 2012, McLeod et al. 2020).

While this thesis addressed the bottom-up role of oyster reefs in underpinning estuarine food webs, it did not consider the top-down role of oyster predators in limiting reef establishment and growth. Particularly when unprotected by the complex microhabitats of established reefs, juvenile oysters can be highly susceptible to a range of vertebrate and invertebrate predators (Bishop & Peterson 2006, Amaral et al. 2012, Wilkie & Bishop 2012). Consequently, post-settlement consumption of juvenile oysters by benthic predators can be an important factor limiting oyster recruitment, reef growth and development (Johnson & Smee 2014). Although controversial, it has been hypothesised that shell-boring polychaete worms, including species from the genera *Boccardia*, *Pseudopolydora*, *Dipolydora* and *Polydora*, contributed to the complete decimation of subtidal oyster reefs in Australia (Kirby 2004, Ogburn et al. 2007). Understanding not only the bottom-up role of oyster reefs in sustaining estuarine food webs, but also the top-down role of oyster consumers in constraining the development of these will be critical to the development of effective strategies for oyster reef restoration.

Furthermore, given the oligotrophic and nutrient limited status of east Australian estuarine systems (Scanes 2011) examining trophic subsidies of organic matter from oyster reefs to adjacent habitats remains a key research need. Stable isotopes analyses that not only include carbon and nitrogen, but also sulphur biotracers (Herzka 2005), would help with disentangling sources of organic matter and hence the contribution of oyster biodeposition to primary and secondary productivity in adjacent habitats in the estuarine seascape.

6.2.2 Shelter and resting grounds

Oyster habitats not only benefited fish by providing feeding grounds, but also by providing shelter and resting areas. The behavioural analyses determined that a high proportion of fish displayed indiscriminate wandering behaviour in oyster reefs and the other complex biogenic habitats examined here. By contrast, in unstructured bare sediment habitats, fish more commonly passed through at high speed, or fed (Chapters

2, 4, 5). Our scoring of wandering activity involved grouping three main activities: (1) fish slowly swimming through the habitat at very low speed, (2) fish slowly swimming, stopping to investigate a specific area, and continuing to swim slowly again, and (3) fish in a resting position not moving or looking at any specific area of the habitat. Based on these, we cannot conclude whether our wandering observations are just related to individuals looking for shelter, or a combination of individuals looking for food resources, individuals looking for shelter, and individuals resting. More detailed behavioural observations, such as those obtained from tracking, would help to disentangle these activities. Nevertheless, based on these results, it appears that habitat complexity is playing a major role in influencing fish behaviour in the estuarine seascape mosaic.

The complexity of oyster reefs may, like, that of other structured estuarine habitats, benefit small fishes by reducing competition and territorial interactions, increasing niche and space, and by reducing the foraging efficiency of top predators (Grabowski 2004, Grabowski & Powers 2004, Grabowski et al. 2008, Hill & Weissburg 2013). Habitat metrics associated with complexity include rugosity, area of hard surface, and shading. Cryptic fish species, such as gobies and blennies use oyster reefs as shelter (Harding & Mann 2000, Nevins et al. 2014, Harding et al. 2019), and were an important component of the oyster reef community here (Chapter 2). The complex three-dimensional structure that oyster reefs create, enhances microhabitat availability (McAfee & Bishop 2019). A greater range and availability of microhabitats allows for the coexistence of a greater number of species through niche partitioning (Nagelkerken et al. 2018). In providing protective microhabitats and providing shading, complexity can also decrease predator foraging efficiencies, conferring advantages to prey (Grabowski 2004, Grabowski & Kimbro 2005). A reduction in light intensities can negatively influence prey detection (Benfield & Minello 1996, Cocheret de la Morinière et al. 2003, Verweij et al. 2006). Predation rates can also diminish on complex habitats as prey organisms actively seek refuge within the complexity (Grabowski 2004, Grabowski et al. 2005, Grabowski & Kimbro 2005, Hughes & Grabowski 2006).

This study provided some insight into differential use of estuarine habitats by fish, but within these, did not consider how patch morphology and arrangement influence patterns of habitat utilisation, especially by larger fish. Further studies looking at how reef patch size, shape, heterogeneity and connectivity influences habitat use by larger fish species would help resolve shelter and resting values of this habitat.

6.2.3 Nursery grounds

The nursery value of habitats is one of the provisioning services most valued by fisheries managers, and is commonly used as strong justification for their protection and conservation (Beck et al. 2001, Lefcheck et al. 2019). While vegetative habitats such as seagrasses, mangroves and saltmarshes have long been recognised as important components of the estuarine seascape nursery, other estuarine habitats, such as oyster reefs have received little attention (Beck et al. 2001, Tse et al. 2008, Igulu et al. 2014, Whitfield 2017, Le et al. 2019, Lefcheck et al. 2019). Despite numerous reviews pointing to the urgent need to consider the nursery value of oyster reefs (Beck et al. 2001, Beck et al. 2011, Lefcheck et al. 2019), previous assessments of this service have been largely limited to the USA (Grabowski et al. 2005, Geraldi et al. 2009, zu Ermgassen et al. 2016).

This thesis provided information on the nursery role of remnant intertidal Sydney rock oyster reefs in Australia, by: (1) describing the juvenile fish community utilising remnant oyster reefs; (2) comparing this to adjacent habitats (seagrass, mangroves and bare sediments) several of which are established nursery grounds; and (3) contrasting habitat utilisation of juveniles versus adults of the same species (Chapter 4). Our results indicate that remnant oyster reefs provide habitat to a unique community of juvenile fish, that contains greater observations of juveniles than bare habitats and similar numbers to adjacent biogenic habitats with established nursery values. The high number of juveniles in oyster reefs did not simply reflect species that spend their entire life history in this habitat; juvenile to adult ratios were greater for oyster reefs than other habitats. Behavioural analyses indicated that juveniles were utilising the biogenic, structural habitats for foraging and shelter, reinforcing the important value of structured biogenic habitats such as remnant oyster reefs, mangroves and seagrasses within the seascape nursery (Nagelkerken et al. 2015, Lefcheck et al. 2019). Given that Australian oyster reefs are presently considered degraded and functionally extinct (Beck et al. 2011, Gillies et al. 2020), it is likely that higher quality, restored oyster habitat may play an even greater role in the estuarine seascape, thereby enhancing local fisheries productivity.

Many of the species for which juveniles were present in high abundance on oyster reefs, also utilised adjacent habitats as juvenile habitats. This reinforces the idea that species utilise multiple interconnected habitats as juveniles and it is their interactive rather than independent function that underpins the estuarine nursery service (Nagelkerken et al. 2015, Sheaves et al. 2015). Given that in many estuaries, seagrasses are threatened by declining water quality (Ralph et al. 2006, Evans et al. 2018), it will be especially important that remnant oyster habitats are protected and lost reefs reinstated to reinforce the estuarine seascape nursery.

While this thesis provides preliminary evidence for the nursery role of remnant oyster reefs, further studies would help to elucidate their specific role. Measurements of habitat connectivity, diel, tidal and ontogenetic migrations, and ecosystem corridors to adult populations would build greater understanding of how juveniles utilise the multiple habitats comprising the estuarine seascape mosaic collectively (Nagelkerken et al. 2015, Sheaves et al. 2015). In particular, utilisation of stereo-BRUVs would help determine the specific size classes of species utilising the various habitats and acoustic telemetry techniques could be used to establish connectivity patterns and migrations among habitats (Brownscombe et al. 2019, Piggott et al. 2020).

6.3 ROLE OF OYSTER FARMS IN SUPPORTING FISH COMMUNITIES WITHIN THE ESTUARINE SEASCAPE

Given the trajectory of rapid environmental change, the maintenance of a present ecological state, or return to a past one, is not always feasible (McDonald et al. 2016, Bulleri et al. 2020). This is particularly the case in estuaries, which are hotspots for human settlements (Mayer-Pinto et al. 2017, Strain et al. 2018b, O'Shaughnessy et al. 2019), and are experiencing extremely rapid rates of warming and acidification (Scanes et al. 2020). There is growing recognition that in such circumstances, artificial structures might serve as important habitats, that in excluding damaging activities such as trawling can also act as *de novo* marine protected areas (Ashley et al. 2014, Thurstan et al. 2018, Nugraha et al. 2019). Consequently, there has been growing effort in quantifying their ecosystem services as compared to natural habitats (Mayer-Pinto et al. 2018), and eco-engineering these so that they provide not only their primary function, but also improved ecological functions and services (Strain et al. 2018b, Airolidi et al. 2020).

As part of this new wave of thinking, there is growing interest in the ecosystem services provide by aquaculture and how farming practices might maximise these (Alleway et al. 2019, Brugère et al. 2019, Gentry et al. 2019, van der Schatte Olivier et al. 2020). Since the depletion of oyster reefs in the 19th century, oyster aquaculture infrastructure has expanded into areas once occupied by reefs. Today, oyster farms constitute an important habitat component of the south-east Australian estuarine seascape (Nell 1993, 2001, DPI 2017). Consequently, effective management of estuarine seascapes requires not only knowledge of the ecological role of remnant oyster reefs but also oyster aquaculture infrastructure.

This thesis examined fish utilisation of two oyster farm types -- rack-and-rail and longline-and-basket as compared to adjacent patches of remnant oyster reef, bare sediment, seagrass and mangrove. It found that rack-and-rail farms provided habitat to a generally richer fish community, including higher numbers of fish observations, than longlines-with-baskets. Nevertheless, the two oyster farming methods generally had more similar fish communities to one another than to natural habitats. Of natural habitats, the fish community observed on racks was most similar to that of remnant oyster reefs, and the community of longlines-with-baskets was most similar to that of seagrass beds. These results add to the growing evidence and recognition of the benefits of sustainable oyster aquaculture methods and point to the need to consider such artificial habitats in developing estuarine-wide conservation and restoration plans.

Although isotope analyses were not conducted for oyster farms, analysis of video footage indicated that the mechanisms by which oyster infrastructure facilitated fish communities, like wild reefs, spanned trophic, shelter, and nursery roles. Oyster farms supported seasonally high numbers of not only adult, but also juvenile fish – suggestive of a nursery role. Fish were observed foraging on epibiota on oyster bags and racks, and on the organic-rich sediments below oyster farms. A high proportion of fish were also found wandering in this habitat. The cages, trays and baskets where oysters grow and the infrastructure that supports these create a multilayered refuge for large and small fish (Dealteris et al. 2004, Glenn 2016, Muething 2018, Mercaldo-Allen et al. 2019).

The similar fish communities supported by oyster reefs and rack-and-rail oyster farms suggests that particularly in environments where oyster reefs can no longer be sustained, oyster farms may serve as important habitat surrogates. Further investigation of how fish habitat provision by oyster aquaculture infrastructure varies depending on the seascape context and environmental conditions is required to assess the range of circumstances under which oyster infrastructure serves as valuable fish habitat. In particular, so as to fully understand the capacity of oyster reefs to serve as surrogate habitats, there is need to assess the functional role of oyster farms in degraded estuaries where oyster reefs are locally extinct.

6.4 APPLICATION OF RESULTS TO MANAGEMENT

As oyster reef restoration gains momentum in Australia, it is important to prioritise those management actions that will optimise the ecosystem service and economic outcomes of restoration activities (Gilby et al. 2019a). A key management action is to strategically

determine best restoration placements in the estuarine seascape (Stewart-Sinclair et al. 2020). For this, it is necessary to integrate a seascape ecology approach in oyster reef restoration projects by identifying best habitat mosaic arrangements on which the ecosystem services of the restored habitat will yield greatest benefits (Gilby et al. 2019a). The results from this thesis have highlighted the importance of the overall seascape, with its interconnected habitats being equally important in some instances, to the estuarine fish community associated with remnant oyster reef. Specifically it has found that several recreationally and commercially exploited species, utilise a combination of oyster reefs, adjacent structured, and unstructured habitats for foraging, nursery and/or refuge.

In New South Wales fishing is an extremely valuable source of revenue, employment, food and leisure. Recreational fishing generates AUD \$3.4 billion and 14,000 fulltime jobs and commercial fishing, AUD \$370 million and 3,500 fulltime jobs annually (DPI 2003, 2020). Locating restoration areas adjacent to other structured habitats, such as mangroves and seagrasses will enhance habitat provision of several key species, such as bream, luderick, whiting, mullet and silverbiddy, which collectively account for > 21% of the total commercial and recreational estuarine fisheries landings by weight in New South Wales (DPI 2003, 2020). Showcasing the importance of oyster reefs to fishing industries will be critical in building a business case for oyster reef restoration in Australia (Gillies et al. 2018). Additionally, given the importance of oyster reefs to these industries, integrating them as stakeholders will be crucial for ensuring investment in and stewardship of restoration projects.

Recent studies have highlighted the benefits of multi-species restoration, both in terms of the successful reinstatement of key habitat-forming species and also in maximising the provision of associated ecosystem services (McAfee et al. 2020a, Reeves et al. 2020). For example, restoring shellfish reefs and seagrass beds simultaneously can enhance the performance of seagrass restoration, both as a consequence of oyster reefs dampening hydrodynamic energy (Sharma et al. 2016) and also reducing turbidity and hence light penetration through benthic-pelagic coupling (Porter et al. 2010, Gaudron et al. 2016, Ray & Fulweiler 2020). As another example, multi-habitat restoration of oyster reefs and mangroves accelerates the ecological succession of these degraded habitats and their communities (Milbrandt et al. 2015). While small-scale pilots have demonstrated the benefits of multispecies restoration with oysters and kelp in South Australia (McAfee et al. 2020a), large-scale multi-habitat restoration projects that include oyster reefs have not yet been attempted in Australia. With restoration attempts also growing for mangrove and seagrass habitat (Worthington & Spalding 2018, Stewart-Sinclair et al. 2020, Tan et al. 2020), there is a need to unify efforts and establish multi-habitat restoration hotspots that not only benefit the establishment of the habitat-forming species targeted by the restoration, but also enhance the ecosystem services

cumulatively provided by the multiple habitats. In order to guide best-practice restoration, further studies are needed that assess how patch identity, size and arrangement in estuarine and coastal seascapes influence their cumulative multifunctionality.

The results of this thesis also highlight the importance of considering oyster aquaculture in seascape scale ecosystem service assessments and restoration planning. Oyster aquaculture is the largest industry in the state of New South Wales, covering an area of 4,300 hectare (DPI 2017) and globally, shellfish demand is expected to increase in the upcoming decades (Pauly & Zeller 2017). This thesis focused on how farming infrastructure can create habitat for fish. In addition, oyster farming may also benefit oyster reef restoration efforts by (1) providing a source of larvae in estuaries with otherwise very low or non-existent natural oyster populations; and (2) providing the hatchery infrastructure and genetic resources required for seeding restoration projects in areas with very limited natural recruitment (Froehlich et al. 2017a). This thesis has shown how the location of and cultivation method of oyster farms can influence provision of habitat to fish, but how such factors influence multifunctionality remains a research gap. Such knowledge would facilitate appropriate inclusion of oyster farms in conservation planning.

6.5 CONCLUSIONS

Using a seascape ecology approach (Boström et al. 2011, Pittman et al. 2011) this thesis has provided the first assessment of the role of intertidal Sydney rock oyster reef and oyster farming infrastructure in providing fish habitat as compared to adjacent biogenic and nonbiogenic habitats. It has documented both unique and overlapping roles of oyster reef and farming infrastructure in providing refuge, feeding and nursery services to a range of fish species, including those of recreational and commercial fishing value.

As fish communities are highly mobile, and these remnant oyster reefs are located intertidally, this thesis has only provided a snapshot of the ecological functioning of the seascape where these remnant oyster reefs are located. For this reason, further research and monitoring of fish habitat provisioning services is needed across the tidal cycle (Gilby et al. 2018b, Gilby et al. 2019a, Gilby et al. 2019b). Further research must focus on the spatial arrangement and size of reef patches within remnant reefs, spatial habitat configuration within different seascapes and habitat types, habitat connectivity patterns, and diel, tidal and ontogenetic community migrations.

The study will serve as an important baseline against which to assess the efficacy of restoration efforts, and will be useful in guiding estuarine planning and rehabilitation efforts. As recreational fishing is a key driver of investment in marine habitat restoration in south-eastern Australia, documentation of the fisheries benefits of oyster reef restoration will also assist in building a business case for restoration.

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Appendix A:

CHAPTER 2 SUPPLEMENTARY MATERIAL

A.1 FIGURES

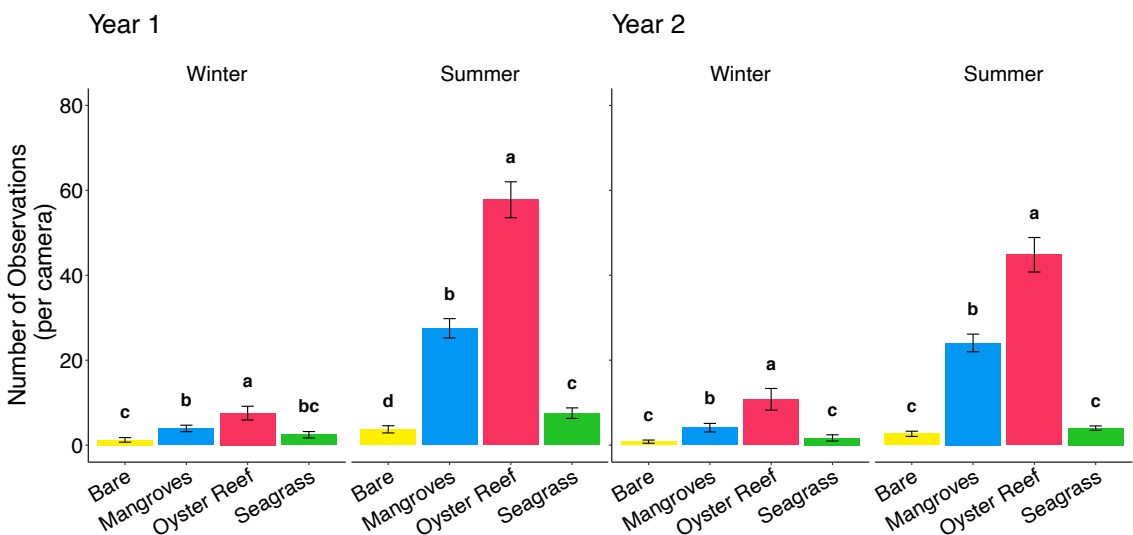


Figure A.1 Mean ($\pm$ SE) breem observations, per habitat, season and year, as documented by 75 min Remote Underwater Video deployments, $n = 16$ (when cameras are pooled for each Habitat $\times$ Season $\times$ Year combination). Different letters above columns denote treatments that were found to significantly differ at $\alpha = 0.05$, by season, using estimated marginal means pairwise comparisons.

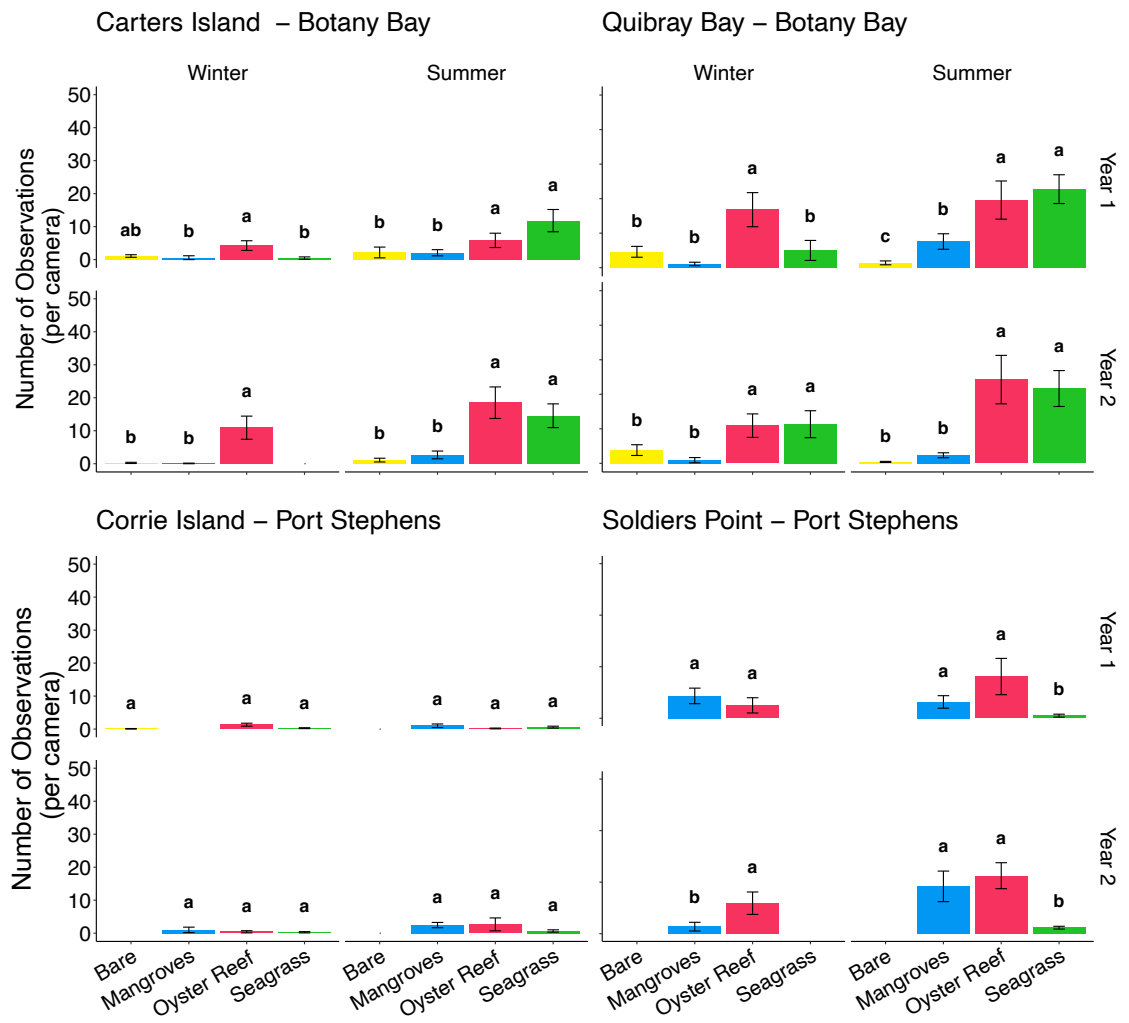


Figure A.2: Mean ($\pm$ SE) luderick observations, per habitat, site and season, as documented by 75 min Remote Underwater Video deployments, $n = 64$ (when cameras are pooled for each Habitat $\times$ Site $\times$ Season $\times$ Year combination). Different letters above columns denote treatments that were found to significantly differ at $\alpha = 0.05$, by season, using estimated marginal means pairwise comparisons.

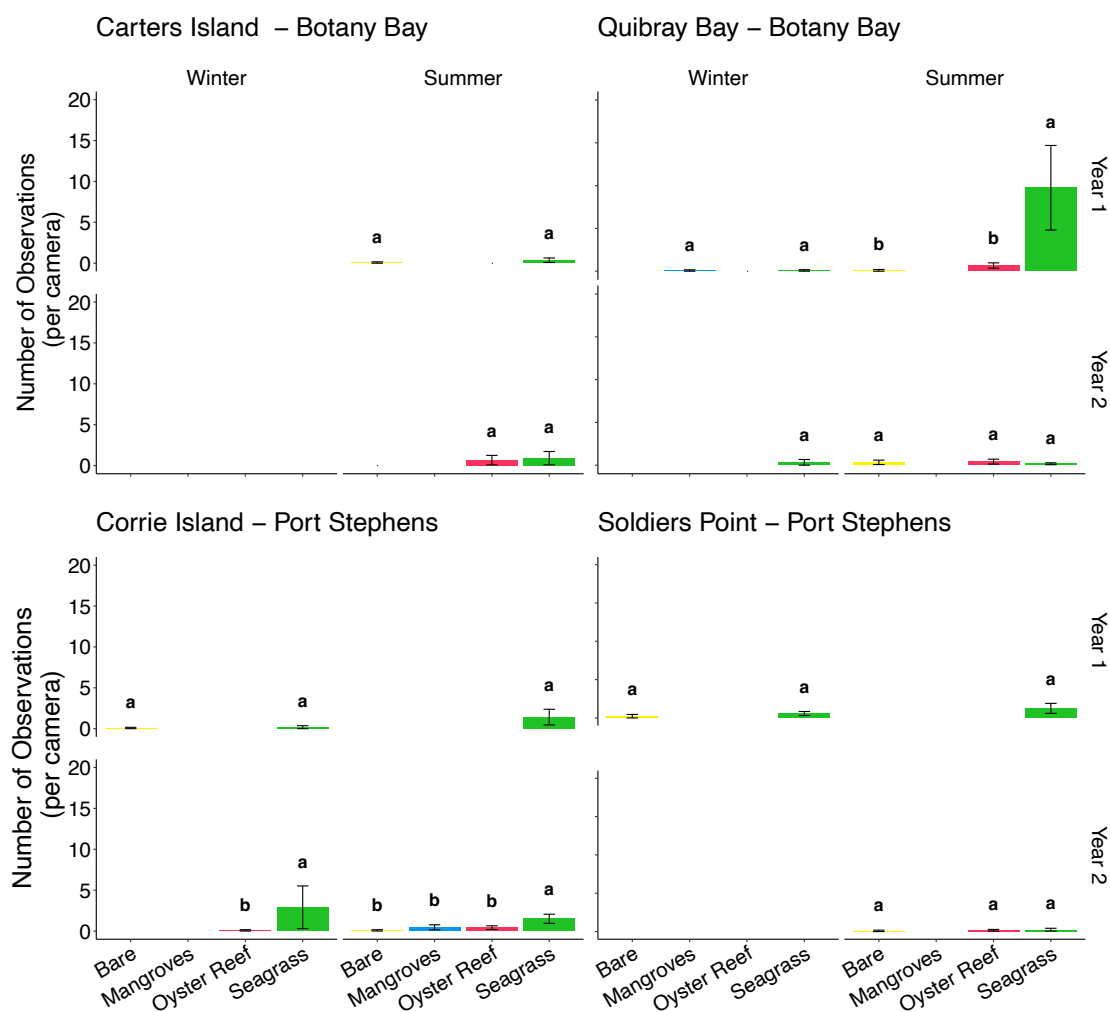


Figure A.3: Mean ($\pm$ SE) tarwhine observations, per habitat, site, season, and year, as documented by 75 min Remote Underwater Video deployments, $n = 64$ (when cameras are pooled for each Habitat $\times$ Site $\times$ Season $\times$ Year combination). Different letters above columns denote treatments that were found to significantly differ at $\alpha = 0.05$, by season, using estimated marginal means pairwise comparisons.

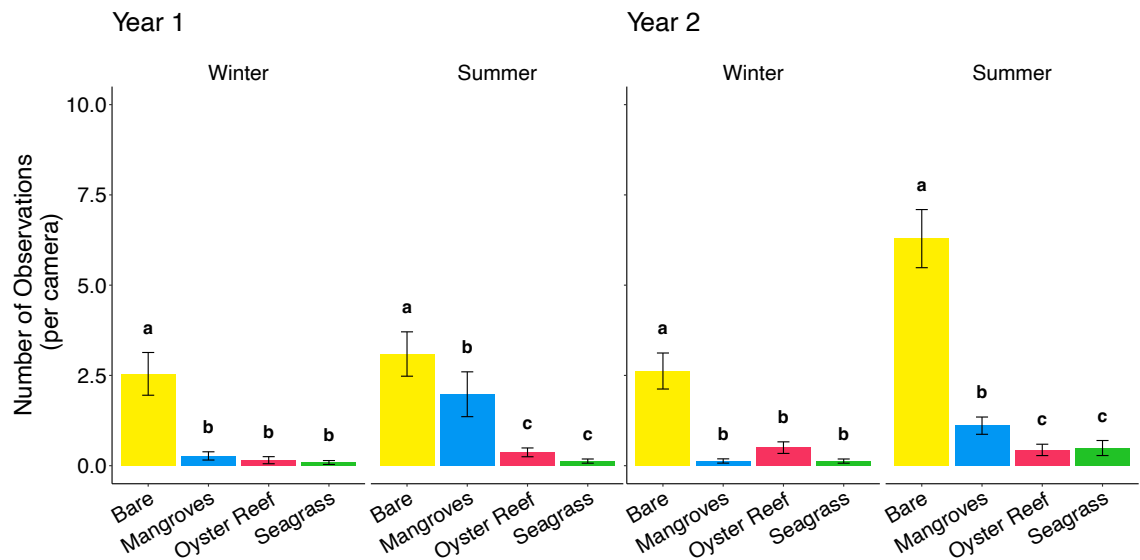


Figure A.4: Mean ($\pm$ SE) sand whiting observations, per habitat, season and year, as documented by 75 min Remote Underwater Video deployments, $n = 16$ (when cameras are pooled for each Habitat $\times$ Season $\times$ Year combination). Different letters above columns denote treatments that were found to significantly differ at $\alpha = 0.05$, by season, using estimated marginal means pairwise comparisons.

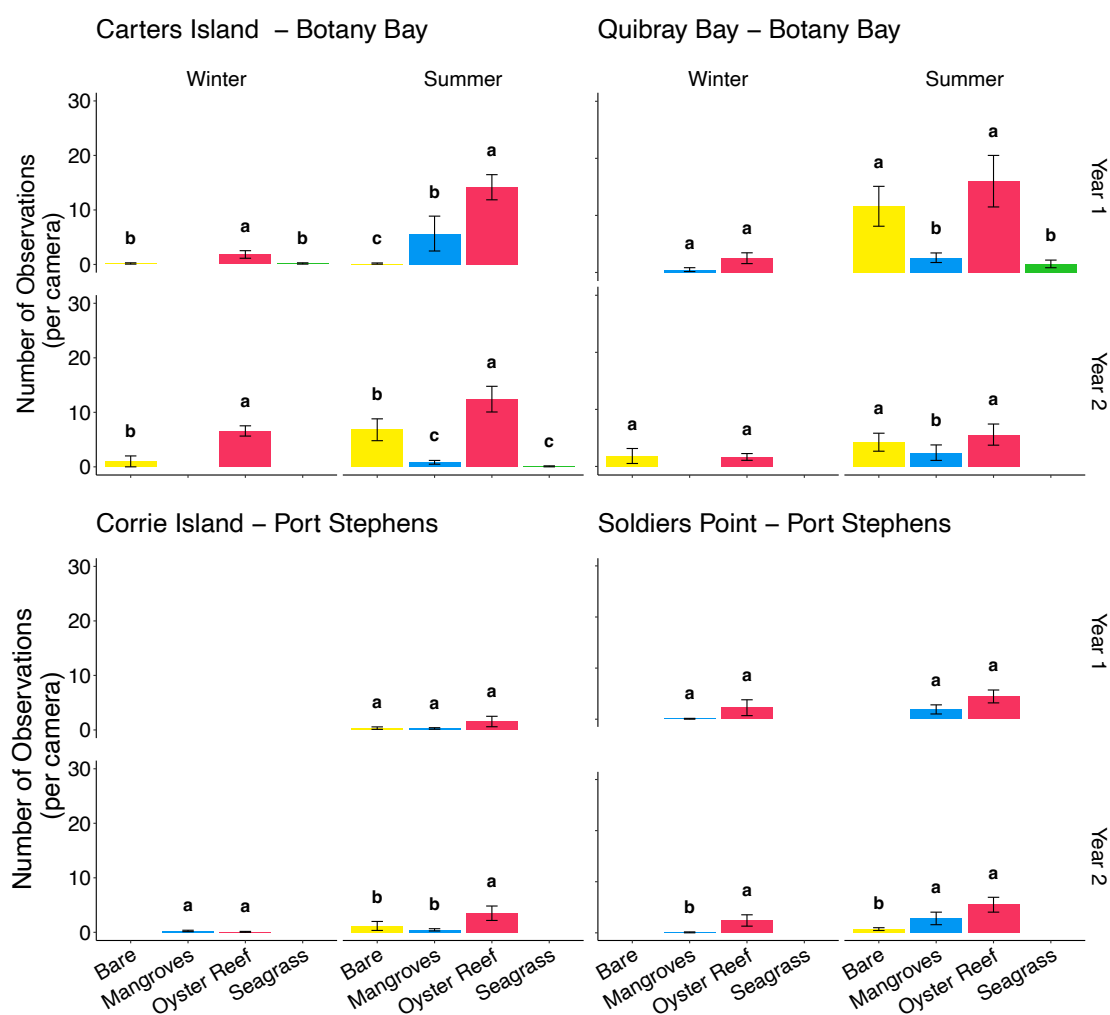


Figure A.5: Mean ($\pm$ SE) mullet observations, per habitat, site and season, as documented by 75 min Remote Underwater Video deployments $n = 64$ (when cameras are pooled for each Habitat $\times$ Site $\times$ Season $\times$ Year combination). Different letters above columns denote treatments that were found to significantly differ at $\alpha = 0.05$, by season, using estimated marginal means pairwise comparisons.

A.2 TABLES

Table A.1: List of fish identified during the study. The total number of observations, across all cameras, and the mean and standard error (SE) observation per camera per habitat are shown.

Family	Species	Total number of Observations	Oyster reef N = 66		Seagrass N = 60		Mangroves N = 40		Bare N = 43	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Apogonidae	<i>Silphamia cephalotes</i>	94	0.00	0.00	47.00	2.00	0.00	0.00	0.00	0.00
Arripidae	<i>Arripis trutta</i>	6	1.00	0.00	1.50	0.50	0.00	0.00	1.00	0.00
Belonidae	<i>Strongylura leiura</i>	32	24.00	0.00	0.00	0.00	3.00	2.00	2.00	0.00
Belonidae	<i>Tylosurus gavioloides</i>	29	8.50	6.50	2.50	1.50	3.00	0.00	2.00	0.00
Blennidae	<i>Aspidontus dussumieri</i>	4	3.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Blennidae	<i>Omobranchus anolius</i>	3510	625.00	77.72	0.00	0.00	252.25	59.46	1.00	0.00
Blennidae	<i>Omobranchus rotundiceps</i>	650	151.50	74.76	0.00	0.00	11.00	5.60	0.00	0.00
Blennidae	<i>Parablennius intermedius</i>	3	1.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00
Blennidae	<i>Petroscirtes breviceps</i>	1	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Blennidae	<i>Petroscirtes lupus</i>	18	1.00	0.00	4.25	1.31	0.00	0.00	0.00	0.00
Carangidae	<i>Pseudocaranx georgianus</i>	84	11.00	6.00	22.00	3.00	0.00	0.00	18.00	0.00
Carangidae	<i>Seriola lalandi</i>	3	0.00	0.00	1.50	0.50	0.00	0.00	0.00	0.00
Carangidae	<i>Trachurus novaezelandiae</i>	1	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Chaetodontidae	<i>Chaetodon flavirostris</i>	1	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cheilodactylidae	<i>Cheilodactylus vestitus</i>	1	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Clupeidae	<i>Herklotichthys castelnaui</i>	100	1.00	0.00	24.50	13.63	0.00	0.00	0.00	0.00
Clupeidae	<i>Hyperlophus vittatus</i>	1	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dasyatidae	<i>Hemitrygon fluviorum</i>	44	2.50	0.50	11.50	8.50	1.00	0.00	5.00	1.53
Dasyatidae	<i>Neotrygon australiae</i>	6	1.00	0.00	2.00	0.00	1.00	0.00	2.00	0.00
Dinolestidae	<i>Dinolestes lewini</i>	7	1.00	0.00	2.00	1.00	0.00	0.00	0.00	0.00
Diodontidae	<i>Dicotylichthys punctulatus</i>	108	11.33	6.33	12.75	1.80	4.33	1.86	3.33	1.45

			Oyster reef N = 66		Seagrass N = 60		Mangroves N = 40		Bare N = 43	
Family	Species	Total number of Observations	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Echeneidae	<i>Echeneis naucrates</i>	1	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elopidae	<i>Elops hawaiiensis</i>	3	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00
Enoplosidae	<i>Enoplosus armatus</i>	2	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Fistulariidae	<i>Fistularia petimba</i>	1	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Gerreidae	<i>Gerres subfasciatus</i>	768	41.25	22.83	37.00	18.89	39.25	21.46	74.50	20.06
Girellidae	<i>Girella elevata</i>	2	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Girellidae	<i>Girella tricuspidata</i>	3367	419.75	160.52	265.00	166.12	116.00	36.27	54.67	31.78
Gobiidae	<i>Acanthogobius flavimanus</i>	2	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00
Gobiidae	<i>Amblygobius phalaena</i>	3	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gobiidae	<i>Arenigobius bifrenatus</i>	107	16.25	6.07	0.00	0.00	10.50	3.33	0.00	0.00
Gobiidae	<i>Bathygobius krefftii</i>	24	6.50	5.50	0.00	0.00	5.50	3.50	0.00	0.00
Gobiidae	<i>Callogobius mucosus</i>	3	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gobiidae	<i>Cryptocentroides gobioides</i>	607	84.50	15.65	0.00	0.00	67.25	15.91	0.00	0.00
Gobiidae	<i>Favonigobius exquisitus</i>	85	16.50	7.64	0.00	0.00	4.00	0.41	3.00	0.00
Gobiidae	<i>Favonigobius lentiginosus</i>	326	26.75	5.06	0.00	0.00	20.25	5.82	34.50	10.78
Gobiidae	<i>Redigobius macrostoma</i>	397	94.00	86.38	11.00	0.00	5.00	3.00	0.00	0.00
Hemiramphidae	<i>Hyporhamphus australis</i>	11	0.00	0.00	1.00	0.00	0.00	0.00	4.50	3.50
Hemiramphidae	<i>Hyporhamphus regularis</i>	4	0.00	0.00	3.00	0.00	1.00	0.00	0.00	0.00
Hypnidae	<i>Hypnos monopterygius</i>	1	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Kyphosidae	<i>Kyphosus sydneyanus</i>	2	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Labridae	<i>Achoerodus viridis</i>	3	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00
Labridae	<i>Neoodax balteatus</i>	25	0.00	0.00	25.00	0.00	0.00	0.00	0.00	0.00
Labridae	<i>Ophthalmolepsis lineolata</i>	2	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00

Family	Species	Total number of Observations	Oyster reef N = 66		Seagrass N = 60		Mangroves N = 40		Bare N = 43	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Labridae	<i>Pictilabrus laticlavus</i>	4	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Labridae	<i>Pseudolabrus guentheri</i>	367	183.00	171.00	1.00	0.00	0.00	0.00	0.00	0.00
Monacanthidae	<i>Acanthaluteres spilomelanurus</i>	210	0.00	0.00	52.50	18.31	0.00	0.00	0.00	0.00
Monacanthidae	<i>Acanthaluteres vittiger</i>	21	0.00	0.00	5.25	2.17	0.00	0.00	0.00	0.00
Monacanthidae	<i>Brachaluteres jacksonianus</i>	7	0.00	0.00	1.50	0.29	1.00	0.00	0.00	0.00
Monacanthidae	<i>Meuschenia freycineti</i>	16	0.00	0.00	8.00	1.00	0.00	0.00	0.00	0.00
Monacanthidae	<i>Meuschenia trachylepis</i>	436	0.00	0.00	108.75	31.40	0.00	0.00	1.00	0.00
Monacanthidae	<i>Meuschenia venusta</i>	11	0.00	0.00	2.75	0.85	0.00	0.00	0.00	0.00
Monacanthidae	<i>Monacanthus chinensis</i>	77	9.67	4.91	10.00	3.94	0.00	0.00	4.00	2.00
Monacanthidae	<i>Scobinichthys granulatus</i>	11	1.00	0.00	3.33	0.88	0.00	0.00	0.00	0.00
Monodactylidae	<i>Monodactylus argenteus</i>	11	0.00	0.00	5.50	3.50	0.00	0.00	0.00	0.00
Mugilidae	<i>Liza argentea</i>	426	52.25	23.55	2.00	0.00	34.25	14.10	25.33	18.11
Mugilidae	<i>Mugil cephalus</i>	955	166.50	60.39	8.50	7.50	15.25	6.70	70.33	37.12
Mugilidae	<i>Myxus elongatus</i>	27	6.67	2.96	0.00	0.00	2.50	0.50	2.00	0.00
Mugilidae	<i>Paramugil georgii</i>	78	20.00	9.29	0.00	0.00	4.00	1.00	5.00	2.00
Mullidae	<i>Parupeneus spilurus</i>	13	4.00	0.00	9.00	0.00	0.00	0.00	0.00	0.00
Mullidae	<i>Upeneichthys lineatus</i>	2	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Myliobatidae	<i>Myliobatis tenuicaudatus</i>	6	4.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00
Paralichthyidae	<i>Pseudorhombus arsius</i>	6	1.00	0.00	0.00	0.00	2.00	0.00	3.00	0.00
Paralichthyidae	<i>Pseudorhombus jenynsii</i>	4	1.50	0.50	0.00	0.00	0.00	0.00	1.00	0.00
Platycephalidae	<i>Platycephalus fuscus</i>	19	1.67	0.67	1.33	0.33	0.00	0.00	2.50	0.87
Plotosidae	<i>Cnidogobius macrocephalus</i>	5	1.00	0.00	1.33	0.33	0.00	0.00	0.00	0.00
Plotosidae	<i>Plotosus lineatus</i>	1	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Pomacentridae	<i>Abudefduf sexfasciatus</i>	1	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00

			Oyster reef N = 66		Seagrass N = 60		Mangroves N = 40		Bare N = 43	
Family	Species	Total number of Observations	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Pomacentridae	<i>Parma microlepis</i>	1	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pomatomidae	<i>Pomatomus saltatrix</i>	38	2.50	0.50	15.00	4.00	2.00	0.00	1.00	0.00
Rhinobatidae	<i>Aptychotrema rostrata</i>	1	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Scatophagidae	<i>Selenotoca multifasciata</i>	2	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Sciaenidae	<i>Argyrosomus japonicus</i>	4	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00
Scorpididae	<i>Atypichthys strigatus</i>	1	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Scorpididae	<i>Microcanthus strigatus</i>	1041	249.50	79.71	2.00	0.00	41.00	0.00	0.00	0.00
Sillaginidae	<i>Sillago ciliata</i>	922	17.25	4.94	9.75	3.77	40.75	17.38	162.75	33.13
Sillaginidae	<i>Sillago maculata</i>	7	2.00	0.00	0.00	0.00	2.00	0.00	1.50	0.50
Soleidae	<i>Aseraggodes lenisquamis</i>	1	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Sparidae	<i>Acanthopagrus australis</i>	9560	1418.75	330.69	183.25	37.04	694.50	120.07	93.50	36.55
Sparidae	<i>Rhabdosargus sarba</i>	279	7.25	2.29	58.00	25.00	3.00	2.00	3.00	0.91
Sphyraenidae	<i>Sphyraena obtusata</i>	201	1.00	0.00	49.75	15.04	0.00	0.00	0.00	0.00
Syngnathidae	<i>Stigmatopora nigra</i>	12	0.00	0.00	6.00	5.00	0.00	0.00	0.00	0.00
Syngnathidae	<i>Urocampus carinirostris</i>	1	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Terapontidae	<i>Pelates sexlineatus</i>	781	23.67	16.18	175.00	71.04	2.00	0.00	4.00	2.00
Tetraodontidae	<i>Marilyna pleurosticta</i>	2	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Tetraodontidae	<i>Reicheltia halsteadii</i>	1	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Tetraodontidae	<i>Tetractenos glaber</i>	81	4.00	2.00	7.00	2.45	7.50	2.36	5.00	2.00
Tetraodontidae	<i>Tetractenos hamiltoni</i>	31	1.00	0.00	2.00	0.58	9.00	5.00	3.00	0.00
Tetraodontidae	<i>Tetractenos squamicauda</i>	2	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tetraodontidae	<i>Torquigener pleurogramma</i>	6	1.00	0.00	0.00	0.00	1.50	0.50	1.00	0.00
Tetrarogidae	<i>Centropogon australis</i>	48	12.00	5.76	0.00	0.00	0.00	0.00	0.00	0.00

			Oyster reef N = 66		Seagrass N = 60		Mangroves N = 40		Bare N = 43	
Family	Species	Total number of Observations	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Tripterygiidae	<i>Enneapterygius atrogulare</i>	22	21.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Tripterygiidae	<i>Lepidoblennius haplodactylus</i>	10	5.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00
Trygonorrhinidae	<i>Trygonorrhina fasciata</i>	56	4.00	1.47	6.00	2.80	2.00	0.00	3.50	1.55
Urolophidae	<i>Trygonoptera testacea</i>	125	4.33	1.20	17.00	12.01	3.00	1.00	13.75	5.11
Urolophidae	<i>Urolophus kapalensis</i>	2	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00

Table A.2: List of fish identified during the study. The total number of observations per habitat (n) across all cameras, and the percentage of the number of observed behaviours across all cameras per habitat is shown.

	Oyster reefs					Seagrass					Mangroves					Bare				
	% of number of observed behaviours					% of number of observed behaviours					% of number of observed behaviours					% of number of observed behaviours				
Species	n	Chasing	Feeding	Passing	Wandering	n	Chasing	Feeding	Passing	Wandering	n	Chasing	Feeding	Passing	Wandering	n	Chasing	Feeding	Passing	Wandering
<i>Siphamia cephalotes</i>	0	0	0	0	0	94	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Arripis trutta</i>	1	0	0	100	0	3	0	0	100	0	0	0	0	0	0	2	0	0	100	0
<i>Strongylura leiura</i>	24	0	0	0	100	0	0	0	0	0	6	0	0	0	100	2	0	0	50.00	50.00
<i>Tylosurus gavioides</i>	17	0	0	5.88	94.12	5	0	0	0	100	3	0	0	0	100	4	0	0	50.00	50.00
<i>Aspidontus dussumieri</i>	3	0	0	0	100	0	0	0	0	0	0	0	0	0	0	1	0	0	100	0
<i>Omobranchus anolius</i>	2500	5.40	11.96	0.04	82.60	0	0	0	0	0	1009	3.07	9.42	0.10	87.41	1	0	0	0	100
<i>Omobranchus rotundiceps</i>	606	4.13	20.46	0.17	75.25	0	0	0	0	0	44	2.27	9.09	0	88.64	0	0	0	0	0

<i>Parablennius intermedius</i>	3	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Petroscirtes breviceps</i>	0	0	0	0	100	1	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Petroscirtes lupus</i>	1	0	0	0	0	17	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Pseudocaranx georgianus</i>	22	0	18.18	54.55	27.27	44	0	15.91	52.27	31.82	0	0	0	0	0	18	0	16.67	38.89	44.44
<i>Seriola lalandi</i>	0	0	0	0	0	3	0	0	33.33	66.67	0	0	0	0	0	0	0	0	0	0
<i>Trachurus novaezelandiae</i>	0	0	0	0	0	1	0	0	100	0	0	0	0	0	0	0	0	0	0	0
<i>Chaetodon flavirostris</i>	1	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheilodactylus vestitus</i>	1	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Herklotichthys castelnaui</i>	2	0	0	0	100	98	0	0	30.61	69.39	0	0	0	0	0	0	0	0	0	0
<i>Hyperlophus vittatus</i>	1	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hemitrygon fluviorum</i>	5	0	0	40.00	60.00	23	0	0	56.52	43.48	1	0	0	100	0	15	0	13.33	46.67	40.00
<i>Neotrygon australiae</i>	1	0	0	100	0	2	0	0	0	100	1	0	0	100	0	2	0	0	50.00	50.00

<i>Dinolestes lewini</i>	1	0	0	0	100	6	0	0	50.00	50.00	0	0	0	0	0	0	0	0	0	0
<i>Dicotylichthys punctulatus</i>	34	0	5.88	2.94	91.18	51	0	0	9.80	90.20	13	0	0	0	100	10	0	0	40.00	60.00
<i>Echeneis naucrates</i>	1	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Elops hawaiiensis</i>	0	0	0	0	0	3	0	0	66.67	33.33	0	0	0	0	0	0	0	0	0	0
<i>Enoplosus armatus</i>	0	0	0	0	0	2	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Fistularia petimba</i>	0	0	0	0	0	1	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Gerres subfasciatus</i>	165	2.42	35.76	12.73	49.09	148	2.70	8.78	38.51	50.00	157	1.27	52.87	14.65	31.21	298	1.34	35.57	28.52	34.56
<i>Girella elevata</i>	2	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Girella tricuspidata</i>	1679	2.62	15.92	9.54	71.91	1060	1.51	11.32	30.28	56.89	464	0.43	22.20	15.52	61.85	164	0	17.07	57.32	25.61
<i>Acanthogobius flavimanus</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	0	100	0	0	0	0	0
<i>Amblygobius phalaena</i>	3	0	33.33	0	66.67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Arenigobius bifrenatus</i>	65	0	29.23	0	70.77	0	0	0	0	0	42	0	14.29	0	85.71	0	0	0	0	0

<i>Bathygobius krefftii</i>	13	0	0	0	100	0	0	0	0	0	11	0	27.27	0	72.73	0	0	0	0	0
<i>Callogobius mucosus</i>	3	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cryptocentroides gobioides</i>	338	4.14	6.80	0	89.05	0	0	0	0	0	269	1.86	13.75	0.74	83.64	0	0	0	0	0
<i>Favonigobius exquisitus</i>	66	3.03	3.03	0	93.94	0	0	0	0	0	16	0	18.75	0	81.25	3	0	0	0	100
<i>Favonigobius lentiginosus</i>	107	0	8.41	0	91.59	0	0	0	0	0	81	0	16.05	1.23	82.72	138	0.72	1.45	0.00	97.83
<i>Redigobius macrostoma</i>	376	0	0.27	0.27	99.47	11	0	0	0	100	10	0	0	0	100	0	0	0	0	0
<i>Hyporhamphus australis</i>	0	0	0	0	0	2	0	0	50.00	50.00	0	0	0	0	0	9	0	0	100	0
<i>Hyporhamphus regularis</i>	0	0	0	0	0	3	0	0	33.33	66.67	1	0	0	0	100	0	0	0	0	0
<i>Hypnos monopterygius</i>	0	0	0	0	0	1	0	0	100	0	0	0	0	0	0	0	0	0	0	0
<i>Kyphosus sydneyanus</i>	2	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Achoerodus viridis</i>	0	0	0	0	0	3	0	33.33	0	66.67	0	0	0	0	0	0	0	0	0	0

<i>Neoodax balteatus</i>	0	0	0	0	0	25	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Ophthalmolepsis lineolata</i>	0	0	0	0	0	2	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Pictilabrus laticlavus</i>	4	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudolabrus guentheri</i>	366	0.27	12.84	0.27	86.61	1	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Acanthaluteres spilomelanurus</i>	0	0	0	0	0	210	0.48	15.24	2.38	81.90	0	0	0	0	0	0	0	0	0	0
<i>Acanthaluteres vittiger</i>	0	0	0	0	0	21	0	19.05	0	80.95	0	0	0	0	0	0	0	0	0	0
<i>Brachaluteres jacksonianus</i>	0	0	0	0	0	6	0	16.67	0	83.33	1	0	0	100	0	0	0	0	0	0
<i>Meuschenia freycineti</i>	0	0	0	0	0	16	0	37.50	0	62.50	0	0	0	0	0	0	0	0	0	0
<i>Meuschenia trachylepis</i>	0	0	0	0	0	435	0	24.83	2.76	72.41	0	0	0	0	0	1	0	0	0	100
<i>Meuschenia venusta</i>	0	0	0	0	0	11	0	27.27	0	72.73	0	0	0	0	0	0	0	0	0	0
<i>Monacanthus chinensis</i>	29	0	58.62	0	41.38	40	0	10.00	12.50	77.50	0	0	0	0	0	8	0	25.00	25.00	50.00

<i>Scobinichthys granulatus</i>	1	0	0	0	100	10	0	10.00	0	90.00	0	0	0	0	0	0	0	0	0	
<i>Monodactylus argenteus</i>	0	0	0	0	0	11	0	0	45.45	54.55	0	0	0	0	0	0	0	0	0	
<i>Liza argentea</i>	209	0	6.22	36.84	56.94	4	0	0	100	0	137	0	5.84	60.58	33.58	76	0	10.53	84.21	5.26
<i>Mugil cephalus</i>	666	0.15	14.71	23.12	62.01	17	0	0	76.47	23.53	61	0	26.23	27.87	45.90	211	0	18.96	60.66	20.38
<i>Myxus elongatus</i>	20	0	20.00	30.00	50.00	0	0	0	0	0	5	0	0	60.00	40.00	2	0	0	100	0
<i>Paramugil georgii</i>	60	0	21.67	45.00	33.33	0	0	0	0	0	8	0	50.00	37.50	12.50	10	0	10.00	90.00	0
<i>Parupeneus spilurus</i>	4	0	25.00	0	75.00	9	0	11.11	0	88.89	0	0	0	0	0	0	0	0	0	0
<i>Upeneichthys lineatus</i>	0	0	0	0	0	2	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Myliobatis tenuicaudatus</i>	4	0	0	50.00	50.00	1	0	0	100	0	0	0	0	0	0	1	0	0	0	100
<i>Pseudorhombus arsius</i>	1	0	0	0	100	0	0	0	0	0	2	0	0	0	100	3	0	0	0	100
<i>Pseudorhombus jenynsii</i>	3	0	0	0	100	0	0	0	0	0	0	0	0	0	0	1	0	0	0	100
<i>Platycephalus fuscus</i>	5	0	0	60.00	40.00	4	0	0	75.00	25.00	0	0	0	0	0	10	0	0	40.00	60.00

<i>Cnidoglanis macrocephalous</i>	1	0	0	0	100	4	0	0	25.00	75.00	0	0	0	0	0	0	0	0	0	0
<i>Plotosus lineatus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	100	0	0	0	0	0	0
<i>Abudefduf sexfasciatus</i>	0	0	0	0	0	1	0	0	0	100	0	0	0	0	0	0	0	0	0	0
<i>Parma microlepis</i>	1	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pomatomus saltatrix</i>	5	0	0	100	0	30	0	0	56.67	43.33	2	0	0	100	0	1	0	0	100	0
<i>Aptychotrema rostrata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	100
<i>Selenotoca multifasciata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	100	0
<i>Argyrosomus japonicus</i>	0	0	0	0	0	4	0	0	75.00	25.00	0	0	0	0	0	0	0	0	0	0
<i>Atypichthys strigatus</i>	0	0	0	0	0	1	0	0	100	0	0	0	0	0	0	0	0	0	0	0
<i>Microcanthus strigatus</i>	998	0.10	6.41	0.30	93.19	2	0	0	0	100	41	2.44	0	0	97.56	0	0	0	0	0
<i>Sillago ciliata</i>	69	1.45	1.45	39.13	57.97	39	0	0	58.97	41.03	163	0.61	13.50	23.31	62.58	651	1.54	17.05	29.80	51.61
<i>Sillago maculata</i>	2	0	0	50.00	50.00	0	0	0	0	0	2	0	0	50.00	50.00	3	0	0	66.67	33.33

<i>Aseraggodes lenisquamis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	100	0
<i>Acanthopagrus australis</i>	5675	0.16	9.45	6.05	84.34	733	0	2.73	28.65	68.62	2778	0.11	11.09	9.18	79.63	374	0	5.35	50.80	43.85
<i>Rhabdosargus sarba</i>	29	0	0	10.34	89.66	232	0	26.29	10.34	63.36	6	0	33.33	16.67	50.00	12	0	0	66.67	33.33
<i>Sphyraena obtusata</i>	2	0	0	0	100	199	0	0	20.60	79.40	0	0	0	0	0	0	0	0	0	0
<i>Stigmatopora nigra</i>	0	0	0	0	0	12	0	41.67	0	58.33	0	0	0	0	0	0	0	0	0	0
<i>Urocampus carinirostris</i>	0	0	0	0	0	1	0	100	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pelates sexlineatus</i>	71	1.41	16.90	7.04	74.65	700	0.29	13.14	4.43	82.14	2	0	0	0	100	8	0	12.50	37.50	50.00
<i>Marilyna pleurosticta</i>	1	0	0	0	100	0	0	0	0	0	0	0	0	0	0	1	0	0	0	100
<i>Reicheltia halsteadi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	100
<i>Tetractenos glaber</i>	8	12.5 0	0	25.00	62.50	28	0	3.57	7.14	89.29	30	0	20.00	10.00	70.00	15	0	13.33	0	86.67
<i>Tetractenos hamiltoni</i>	1	0	0	0	100	6	0	0	0	100	18	0	0	11.11	88.89	6	0	0	16.67	83.33

<i>Tetractenos squamicauda</i>	2	0	0	50.00	50.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Torquigener pleurogramma</i>	1	0	0	100	0	0	0	0	0	0	3	0	0	0	100	2	0	0	0	100
<i>Centropogon australis</i>	48	0	6.25	0	93.75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Enneapterygius atrogulare</i>	21	0	0	4.76	95.24	0	0	0	0	0	1	0	0	0	100	0	0	0	0	0
<i>Lepidoblennius haplodactylus</i>	10	0	50.00	0	50.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trygonorrhina fasciata</i>	16	0	0	12.50	87.50	24	0	0	58.33	41.67	2	0	0	0	100	14	0	7.14	42.86	50.00
<i>Trygonoptera testacea</i>	13	0	0	53.85	46.15	51	0	3.92	70.59	25.49	6	0	33.33	50.00	16.67	55	0	7.27	18.18	74.55
<i>Urolophus kapalensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	100

Table A.3: a) Five-factor mixed-model PERMANOVAs testing for differences in the observations data for each fish species observed among habitats (fish community per habitat), across sites and sampling times and (b) a posteriori pairwise PERMANOVAs examining significant differences between habitats, within sites and seasons. Analyses used Bray Curtis dissimilarities calculated using fish observations (by species). Boldface indicates significance at $P < 0.05$.

(a)

Source	df	MS	Pseudo-F	P(perm)
Year	1	9479.9	2.100	0.487
Season	1	1.8508E+05	4.632	0.181
Estuary	1	50033	11.085	0.325
Habitat	3	1.4762E+05	5.179	0.002
Site(Estuary)	2	29758	7.155	0.096
Year:Habitat	3	3983.6	1.072	0.451
Season:Habitat	3	41694	3.569	0.006
Estuary:Habitat	3	25235	6.792	0.002
Site(Estuary):Habitat	6	11506	3.013	0.001
Year:Season:Habitat	3	4588.1	1.555	0.223
Year:Estuary:Habitat	3	3715.1	1.222	0.177
SeasonxEstuary:Habitat	3	7920.4	2.686	0.044
Year:Site(Estuary):Habitat	6	3818.3	1.256	0.084
Season:Site(Estuary):Habitat	6	8219.1	2.115	0.011
Year:Season:Estuary:Habitat	3	2949	0.970	0.522
Day(Year:Season:Site(Estuary))	32	3468.7	2.639	0.001
Year:Season:Site(Estuary):Habitat	6	3886.7	1.278	0.073
Day(Year:Season:Site(Estuary)):Habitat	95	3047.6	2.319	0.001
Residuals	549	1314		
Total	739			

df – degrees of freedom; SS – sum of squares; Pseudo-F – F value by permutation, P-values based on 999 permutations.

(b)

Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.76	0.692	3.15	0.015	2.19	0.056	2.91	0.035
Bare – Oyster Reef	1.80	0.136	2.58	0.021	2.68	0.032	4.76	0.001
Bare – Seagrass	1.46	0.180	1.64	0.117	1.97	0.063	2.92	0.025
Mangroves – Oyster Reef	2.68	0.019	2.35	0.03	4.41	0.009	2.81	0.014
Mangroves – Seagrass	1.02	0.454	2.30	0.02	3.03	0.017	2.45	0.046
Oyster reef – Seagrass	2.20	0.056	1.56	0.114	4.09	0.005	3.32	0.012

Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	2.40	0.023	3.12	0.016	2.89	0.02	4.96	0.001
Bare – Oyster Reef	3.05	0.004	5.67	0.002	2.85	0.039	5.22	0.003
Bare – Seagrass	3.41	0.006	3.12	0.014	2.43	0.026	3.43	0.002
Mangroves – Oyster Reef	1.84	0.081	1.64	0.114	2.71	0.034	5.34	0.007
Mangroves – Seagrass	2.71	0.018	3.00	0.007	3.3	0.013	4.56	0.006
Oyster reef – Seagrass	3.42	0.004	3.30	0.004	3.14	0.013	4.85	0.004

Table A.4: Summary of Linear Mixed Effects Models of total fish observations per video showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		34.77	<0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	0.02	0.01	0.927
Season	1	760.09	315.90	<0.001
Estuary	1	56.88	23.64	<0.001
Site(Estuary)	2	77.27	32.11	<0.001
Habitat	3	789.03	327.92	<0.001
Year:Habitat	3	1.70	0.71	0.547
Season:Habitat	3	179.04	74.41	<0.001
Estuary:Habitat	3	46.80	19.44	<0.001
Site(Estuary):Habitat	6	20.37	8.46	<0.001
Year:Season:Habitat	3	12.58	5.23	0.001
Year:Estuary:Habitat	3	6.17	2.56	0.054
Season:Estuary:Habitat	3	24.80	10.31	<0.001
Year:Site(Estuary):Habitat	6	2.57	1.07	0.379
Season:Site(Estuary):Habitat	6	14.59	6.06	<0.001
Year:Season:Estuary:Habitat	3	4.62	1.92	0.125
Year:Season:Site(Estuary):Habitat	6	10.84	4.51	<0.001

(b)

Year 1								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.63	0.923	0.81	0.850	-4.03	<0.001	-3.37	0.004
Bare – Oyster Reef	-1.40	0.498	-2.74	0.032	-8.17	<0.001	-11.32	<0.001
Bare – Seagrass	-0.04	1.000	0.65	0.916	-2.14	0.142	-5.30	<0.001
Mangroves – Oyster Reef	-2.08	0.161	-3.66	0.001	-4.14	<0.001	-7.93	<0.001
Mangroves – Seagrass	-0.67	0.908	-0.15	0.999	1.80	0.276	-1.84	0.255
Oyster reef – Seagrass	1.36	0.524	3.45	0.003	5.85	<0.001	6.32	<0.001

Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.95	0.778	-2.22	0.119	-5.92	<0.001	-8.74	<0.001
Bare – Oyster Reef	-3.51	0.002	-5.91	<0.001	-12.58	<0.001	-16.01	<0.001
Bare – Seagrass	-1.84	0.257	-2.64	0.042	-2.79	0.028	-3.32	0.005
Mangroves – Oyster Reef	-2.56	0.052	-3.62	0.002	-6.52	<0.001	-8.01	<0.001
Mangroves – Seagrass	-0.91	0.799	-0.42	0.975	3.20	0.008	5.85	<0.001
Oyster reef – Seagrass	1.59	0.384	3.20	0.008	9.85	<0.001	13.73	<0.001

Year 2								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.77	0.289	0.57	0.942	-0.96	0.771	-2.83	0.024
Bare – Oyster Reef	-6.41	<0.001	-1.67	0.343	-6.77	<0.001	-12.56	<0.001
Bare – Seagrass	-0.60	0.933	-1.38	0.515	-1.38	0.511	-1.95	0.210
Mangroves – Oyster Reef	-4.49	<0.001	-2.23	0.115	-6.10	<0.001	-9.72	<0.001
Mangroves – Seagrass	1.19	0.635	-1.94	0.211	-0.46	0.968	0.89	0.811
Oyster reef – Seagrass	5.81	<0.001	0.29	0.991	5.50	<0.001	10.61	<0.001

Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-2.28	0.104	-0.62	0.926	-2.62	0.044	-8.75	<0.001
Bare – Oyster Reef	-5.28	<0.001	-5.36	<0.001	-6.23	<0.001	-14.09	<0.001
Bare – Seagrass	-3.72	0.001	0.06	0.999	-2.49	0.063	-4.50	<0.001
Mangroves – Oyster Reef	-3.07	0.012	-4.86	<0.001	-3.47	0.003	-5.14	<0.001
Mangroves – Seagrass	-1.52	0.422	0.71	0.892	0.19	0.997	4.45	<0.001
Oyster reef – Seagrass	1.47	0.456	5.70	<0.001	3.74	0.001	9.82	<0.001

Table A.5: Summary of Linear Mixed Effects Models of species richness per video showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df	LRT	Pr(>Chisq)
Day:Site:Season:Year	1	9.29	0.002
Fixed effects	df	MS	F value
Year	1	0.83	3.87
Season	1	67.69	315.17
Estuary	1	1.84	8.59
Site(Estuary)	2	4.35	20.27
Habitat	3	30.89	143.84
Year:Habitat	3	0.26	1.21
Season:Habitat	3	1.64	7.62
Estuary:Habitat	3	1.44	6.72
Site(Estuary):Habitat	6	1.28	5.95
Year:Season:Habitat	3	0.89	4.16
Year:Estuary:Habitat	3	0.70	3.24
Season:Estuary:Habitat	3	0.67	3.14
Year:Site(Estuary):Habitat	6	0.35	1.65
Season:Site(Estuary):Habitat	6	0.41	1.93
Year:Season:Estuary:Habitat	3	0.15	0.69
Year:Season:Site(Estuary):Habitat	6	0.71	3.30

(b)

Year 1								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	1.69	0.328	0.37	0.982	-1.87	0.240	-1.73	0.307
Bare – Oyster Reef	-1.43	0.478	-1.92	0.221	-5.73	<0.001	-3.74	0.001
Bare – Seagrass	0.46	0.967	-0.36	0.984	-4.45	<0.001	-5.15	<0.001
Mangroves – Oyster Reef	-3.20	0.008	-2.37	0.084	-3.85	<0.001	-2.01	0.185
Mangroves – Seagrass	-1.22	0.614	-0.76	0.870	-2.62	0.044	-3.45	0.003
Oyster reef – Seagrass	1.91	0.226	1.60	0.381	1.14	0.663	-1.48	0.449
Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.63	0.923	-3.67	0.001	-4.60	<0.001	-5.65	<0.001
Bare – Oyster Reef	-4.07	<0.001	-6.38	<0.001	-7.83	<0.001	-7.86	<0.001
Bare – Seagrass	-2.09	0.158	-4.45	<0.001	-5.86	<0.001	-4.32	<0.001
Mangroves – Oyster Reef	-4.70	<0.001	-2.65	0.040	-3.16	0.009	-2.49	0.061

Mangroves – Seagrass	-2.70	0.036	-0.77	0.869	-1.12	0.678	1.44	0.476
Oyster reef – Seagrass	1.89	0.234	1.89	0.234	2.10	0.153	3.90	<0.001

Year 2								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-4.17	<0.001	-0.03	1.000	-1.17	0.646	-2.81	0.026
Bare – Oyster Reef	-7.43	<0.001	-1.71	0.320	-5.46	<0.001	-5.79	<0.001
Bare – Seagrass	-1.03	0.732	-3.40	0.004	-2.24	0.114	-3.00	0.015
Mangroves – Oyster Reef	-3.09	0.011	-1.68	0.337	-4.51	<0.001	-2.98	0.016
Mangroves – Seagrass	3.16	0.009	-3.37	0.004	-1.14	0.662	-0.19	0.997
Oyster reef – Seagrass	6.39	<0.001	-1.70	0.326	3.26	0.006	2.78	0.028

Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-2.50	0.061	-4.09	<0.001	-2.61	0.045	-4.07	<0.001
Bare – Oyster Reef	-3.32	0.005	-6.85	<0.001	-5.45	<0.001	-6.53	<0.001
Bare – Seagrass	-3.22	0.007	-3.85	<0.001	-6.26	<0.001	-3.54	0.002
Mangroves – Oyster Reef	-0.84	0.835	-2.74	0.032	-2.71	0.035	-2.36	0.086
Mangroves – Seagrass	-0.79	0.856	0.34	0.987	-3.51	0.003	0.62	0.924
Oyster reef – Seagrass	0.02	1.000	3.14	0.009	-0.82	0.846	3.05	0.013

Table A.6: Summary of Linear Mixed Effects Models of adult stage observations per video showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		33.25	<0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	1.35	0.71	0.407
Season	1	621.42	324.57	<0.001
Estuary	1	33.35	17.42	<0.001
Site(Estuary)	2	69.22	36.15	<0.001
Habitat	3	565.59	295.41	<0.001
Year:Habitat	3	1.43	0.74	0.526
Season:Habitat	3	111.99	58.49	<0.001
Estuary:Habitat	3	29.47	15.39	<0.001
Site(Estuary):Habitat	6	13.94	7.28	<0.001
Year:Season:Habitat	3	6.30	3.29	0.020
Year:Estuary:Habitat	3	2.30	1.20	0.308
Season:Estuary:Habitat	3	16.75	8.75	<0.001
Year:Site(Estuary):Habitat	6	0.78	0.40	0.875
Season:Site(Estuary):Habitat	6	12.57	6.56	<0.001
Year:Season:Estuary:Habitat	3	3.08	1.61	0.187

Year:Season:Site(Estuary):Habitat 6 11.24 5.87 <0.001

(b)

Year 1								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.61	0.927	1.07	0.709	-3.81	<0.001	-3.36	0.004
Bare – Oyster Reef	-1.96	0.205	-3.01	0.014	-7.87	<0.001	-10.35	<0.001
Bare – Seagrass	0.07	0.999	0.82	0.845	-1.97	0.201	-4.15	<0.001
Mangroves – Oyster Reef	-2.63	0.043	-4.20	<0.001	-4.07	<0.001	-6.96	<0.001
Mangroves – Seagrass	-0.55	0.947	-0.24	0.995	1.75	0.298	-0.69	0.900
Oyster reef – Seagrass	2.02	0.180	3.90	<0.001	5.73	<0.001	6.51	<0.001
Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.19	0.997	-2.48	0.063	-5.01	<0.001	-8.21	<0.001
Bare – Oyster Reef	-3.42	0.004	-5.53	<0.001	-11.33	<0.001	-14.40	<0.001
Bare – Seagrass	-1.11	0.681	-1.82	0.263	-2.63	0.043	-3.27	<0.001
Mangroves – Oyster Reef	-3.24	0.007	-2.99	0.015	-6.19	<0.001	-6.85	<0.001
Mangroves – Seagrass	-0.93	0.787	0.65	0.916	2.44	0.071	5.33	<0.001
Oyster reef – Seagrass	2.23	0.115	3.64	0.002	8.76	<0.001	12.05	<0.001
Year 2								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.40	0.501	0.82	0.846	-0.91	0.799	-3.42	0.004
Bare – Oyster Reef	-6.64	<0.001	-1.78	0.281	-4.90	<0.001	-13.39	<0.001
Bare – Seagrass	-0.06	0.999	-1.53	0.417	-1.25	0.596	-2.09	0.158
Mangroves – Oyster Reef	-5.09	<0.001	-2.60	0.046	-4.19	<0.001	-9.98	<0.001
Mangroves – Seagrass	1.34	0.540	-2.35	0.087	-0.37	0.982	1.33	0.544
Oyster reef – Seagrass	6.58	<0.001	0.25	0.994	3.72	0.001	11.31	<0.001
Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.74	0.304	-0.38	0.981	-2.67	0.038	-7.84	<0.001
Bare – Oyster Reef	-3.75	0.001	-5.43	<0.001	-6.64	<0.001	-12.62	<0.001
Bare – Seagrass	-2.03	0.177	0.08	0.999	-2.52	0.058	-4.97	<0.001
Mangroves – Oyster Reef	-2.05	0.169	-5.17	<0.001	-3.81	<0.001	-4.60	<0.001
Mangroves – Seagrass	-0.34	0.986	0.48	0.963	0.22	0.996	3.06	0.012
Oyster reef – Seagrass	1.67	0.342	5.78	<0.001	4.12	<0.001	7.83	<0.001

Table A.7: Summary of Linear Mixed Effects Models of juveniles stage observations per video showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		12.2	<0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	15.42	10.51	0.003
Season	1	211.30	144.12	<0.001
Estuary	1	26.77	18.26	<0.001
Site(Estuary)	2	8.49	5.79	0.007
Habitat	3	226.09	154.21	<0.001
Year:Habitat	3	5.11	3.48	0.015
Season:Habitat	3	115.65	78.88	<0.001
Estuary:Habitat	3	19.91	13.58	<0.001
Site(Estuary):Habitat	6	11.50	7.84	<0.001
Year:Season:Habitat	3	9.03	6.15	<0.001
Year:Estuary:Habitat	3	5.86	3.99	0.008
Season:Estuary:Habitat	3	9.50	6.48	<0.001
Year:Site(Estuary):Habitat	6	6.24	4.25	<0.001
Season:Site(Estuary):Habitat	6	10.66	7.27	<0.001
Year:Season:Estuary:Habitat	3	1.85	1.26	0.286
Year:Season:Site(Estuary):Habitat	6	6.18	4.22	<0.001

(b)

Year 1								
Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.42	0.975	-0.94	0.785	-4.45	<0.001	-2.97	0.016
Bare – Oyster Reef	-0.18	0.998	-0.45	0.970	-7.16	<0.001	-10.74	<0.001
Bare – Seagrass	-0.45	0.969	-0.69	0.901	-2.10	0.155	-7.68	<0.001
Mangroves – Oyster Reef	-0.62	0.923	0.47	0.965	-2.71	0.035	-7.84	<0.001
Mangroves – Seagrass	-0.88	0.814	0.24	0.995	2.25	0.110	-4.73	<0.001
Oyster reef – Seagrass	-0.28	0.992	-0.23	0.996	4.90	<0.001	3.21	0.008
Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.93	0.786	-0.29	0.991	-5.41	<0.001	-6.95	<0.001
Bare – Oyster Reef	-1.35	0.534	-3.42	0.004	-10.02	<0.001	-13.13	<0.001
Bare – Seagrass	-1.58	0.389	-3.21	0.008	-1.75	0.296	-2.04	0.176
Mangroves – Oyster Reef	-0.41	0.977	-3.07	0.012	-4.52	<0.001	-6.80	<0.001
Mangroves – Seagrass	-0.67	0.909	-2.86	0.022	3.69	0.001	5.30	<0.001
Oyster reef – Seagrass	-0.27	0.993	0.21	0.997	8.30	<0.001	11.99	<0.001

Year 2								
Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.74	0.882	-1.31	0.554	-1.79	0.281	-0.15	0.999
Bare – Oyster Reef	-0.80	0.854	-1.08	0.704	-8.56	<0.001	-4.82	<0.001
Bare – Seagrass	-0.03	1.000	-0.67	0.908	-1.41	0.493	-1.28	0.575
Mangroves – Oyster Reef	-0.05	1.000	0.24	0.995	-7.11	<0.001	-4.66	<0.001
Mangroves – Seagrass	0.70	0.895	0.64	0.920	0.35	0.985	-1.13	0.673
Oyster reef – Seagrass	0.77	0.868	0.41	0.977	7.31	<0.001	3.54	0.002

Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.16	0.653	-1.83	0.259	-2.07	0.162	-8.19	<0.001
Bare – Oyster Reef	-3.96	<0.001	-2.29	0.102	-3.02	0.014	-12.45	<0.001
Bare – Seagrass	-2.02	0.181	-0.05	1.000	-1.96	0.205	-0.97	0.767
Mangroves – Oyster Reef	-2.87	0.022	-0.43	0.973	-0.87	0.818	-4.08	<0.001
Mangroves – Seagrass	-0.91	0.800	1.87	0.242	0.16	0.998	7.40	<0.001
Oyster reef – Seagrass	1.90	0.230	2.35	0.087	1.06	0.713	11.74	<0.001

Table A.8: Summary of Linear Mixed Effects Models of breem observations showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Season and Site. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		19.24	<0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	9.57	6.76	0.014
Season	1	69.07	48.79	<0.001
Estuary	1	3.01	2.13	0.154
Site(Estuary)	2	5.52	3.90	0.030
Habitat	3	54.96	38.83	<0.001
Year:Habitat	3	1.04	0.73	0.532
Season:Habitat	3	31.17	22.02	<0.001
Estuary:Habitat	3	9.12	6.44	<0.001
Site(Estuary):Habitat	6	3.26	2.31	0.032
Year:Season:Habitat	3	3.81	2.69	0.045
Year:Estuary:Habitat	3	0.26	0.18	0.907
Season:Estuary:Habitat	3	3.54	2.50	0.053
Year:Site(Estuary):Habitat	6	1.21	0.85	0.529
Season:Site(Estuary):Habitat	6	1.26	0.89	0.501
Year:Season:Estuary:Habitat	3	2.01	1.42	0.234
Year:Season:Site(Estuary):Habitat	6	1.45	1.02	0.407

(b)

	Year 1				Year 2			
	Winter		Summer		Winter		Summer	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-3.55	0.002	-14.59	<0.001	-4.40	<0.001	-14.41	<0.001
Bare – Oyster Reef	-6.31	<0.001	-24.09	<0.001	-8.27	<0.001	-21.27	<0.001
Bare – Seagrass	-1.71	0.319	-4.00	<0.001	-1.35	0.530	-2.41	0.075
Mangroves – Oyster Reef	-2.83	0.025	-9.64	<0.001	-3.84	<0.001	-6.71	<0.001
Mangroves – Seagrass	1.81	0.272	10.90	<0.001	3.10	0.011	12.19	<0.001
Oyster reef – Seagrass	4.57	<0.001	20.64	<0.001	6.99	<0.001	19.08	<0.001

Table A.9: Summary of Linear Mixed Effects Models of Iuderic observations showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		9.66	0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	1.01	0.75	0.392
Season	1	0.98	0.73	0.399
Estuary	1	2.09	1.55	0.221
Site(Estuary)	2	3.94	2.94	0.067
Habitat	3	0.71	0.53	0.669
Year:Habitat	3	6.25	4.66	0.003
Season:Habitat	3	4.31	3.21	0.022
Estuary:Habitat	3	2.86	2.13	0.095
Site(Estuary):Habitat	6	2.59	1.93	0.074
Year:Season:Habitat	3	1.78	1.33	0.264
Year:Estuary:Habitat	3	0.50	0.37	0.772
Season:Estuary:Habitat	3	3.09	2.30	0.076
Year:Site(Estuary):Habitat	6	3.52	2.63	0.015
Season:Site(Estuary):Habitat	6	2.99	2.23	0.038
Year:Season:Estuary:Habitat	3	2.61	1.94	0.121
Year:Season:Site(Estuary):Habitat	6	2.90	2.16	0.045

(b)

Year 1								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	1.20	0.624	2.11	0.150	-0.33	0.987	-2.84	0.024
Bare – Oyster Reef	-1.83	0.258	-3.30	0.005	-2.58	0.049	-5.92	<0.001
Bare – Seagrass	0.94	0.782	0.20	0.997	-4.60	<0.001	-7.11	<0.001
Mangroves – Oyster Reef	-3.11	0.011	-5.55	<0.001	-2.25	0.112	-3.07	0.012
Mangroves – Seagrass	-0.24	0.995	-1.96	0.203	-4.28	<0.001	-4.30	<0.001
Oyster reef – Seagrass	2.80	0.027	3.57	0.002	-2.10	0.161	-1.26	0.590

Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.32	0.988	-3.53	0.002	-1.65	0.349	-2.37	0.084
Bare – Oyster Reef	-1.64	0.356	-1.86	0.246	-0.47	0.966	-3.80	<0.001
Bare – Seagrass	-0.30	0.990	0.04	1.000	-1.18	0.641	-0.61	0.929
Mangroves – Oyster Reef	-1.96	0.203	1.63	0.360	1.16	0.652	-1.59	0.385
Mangroves – Seagrass	-0.62	0.926	3.50	0.003	0.50	0.959	1.90	0.229
Oyster reef – Seagrass	1.30	0.562	1.87	0.242	-0.68	0.904	3.45	0.003

Year 2								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.06	0.999	2.42	0.075	-0.85	0.830	-1.62	0.365
Bare – Oyster Reef	-5.56	<0.001	-2.72	0.035	-6.22	<0.001	-8.53	<0.001
Bare – Seagrass	0.39	0.979	-3.17	0.009	-5.10	<0.001	-8.35	<0.001
Mangroves – Oyster Reef	-5.49	<0.001	-5.14	<0.001	-5.64	<0.001	-6.90	<0.001
Mangroves – Seagrass	0.32	0.988	-5.59	<0.001	-4.46	<0.001	-6.72	<0.001
Oyster reef – Seagrass	5.95	<0.001	-0.45	0.969	1.05	0.720	0.17	0.998

Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.00	0.749	-1.37	0.521	-2.51	0.059	-5.34	<0.001
Bare – Oyster Reef	-0.52	0.953	-4.28	<0.001	-2.07	0.164	-6.37	<0.001
Bare – Seagrass	-0.60	0.930	-0.08	0.999	-1.04	0.723	-1.80	0.275
Mangroves – Oyster Reef	0.49	0.962	-2.96	0.016	0.48	0.962	-0.91	0.801
Mangroves – Seagrass	0.38	0.981	1.35	0.532	1.49	0.445	3.66	0.001
Oyster reef – Seagrass	-0.09	0.999	4.41	<0.001	1.03	0.734	4.67	<0.001

Table A.10: Summary of Linear Mixed Effects Models of tarwhine observations showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year,. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		41.35	<0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	0.50	2.11	0.156
Season	1	0.67	2.84	0.102
Estuary	1	0.05	0.20	0.660
Site(Estuary)	2	0.58	2.43	0.105
Habitat	3	2.57	10.83	<0.001
Year:Habitat	3	0.90	3.81	0.010
Season:Habitat	3	2.09	8.79	<0.001
Estuary:Habitat	3	0.65	2.75	0.042
Site(Estuary):Habitat	6	1.40	5.88	<0.001
Year:Season:Habitat	3	1.30	5.47	0.001
Year:Estuary:Habitat	3	0.45	1.89	0.130
Season:Estuary:Habitat	3	0.13	0.57	0.637
Year:Site(Estuary):Habitat	6	1.32	5.55	<0.001
Season:Site(Estuary):Habitat	6	1.19	4.99	<0.001
Year:Season:Estuary:Habitat	3	0.13	0.56	0.638
Year:Season:Site(Estuary):Habitat	6	0.92	3.87	<0.001

(b)

Year 1								
Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.26	0.994	-0.38	0.981	0.21	0.997	-1.35	0.529
Bare – Oyster Reef	-0.28	0.992	-0.01	1.000	0.53	0.953	-1.53	0.420
Bare – Seagrass	-0.17	0.998	-0.21	0.997	-0.44	0.972	-10.06	<0.001
Mangroves – Oyster Reef	-0.56	0.944	0.38	0.981	0.32	0.989	-0.13	0.999
Mangroves – Seagrass	-0.43	0.973	0.17	0.998	-0.64	0.920	-8.74	<0.001
Oyster reef – Seagrass	0.11	0.999	-0.21	0.997	-0.95	0.778	-8.95	<0.001
Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.77	0.868	1.11	0.680	-0.85	0.830	0.25	0.995
Bare – Oyster Reef	0.38	0.981	1.26	0.586	-0.21	0.997	0.02	1.000
Bare – Seagrass	-0.01	1.000	-1.62	0.369	-3.08	0.011	-3.20	0.008
Mangroves – Oyster Reef	-0.39	0.989	0.15	0.999	0.63	0.923	-0.24	0.995

Mangroves – Seagrass	-0.75	0.876	-2.68	0.038	-2.16	0.135	-3.72	0.001
Oyster reef – Seagrass	-0.37	0.982	-2.83	0.025	-2.80	0.027	-3.40	0.004

Year 2								
Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.33	0.988	0.11	0.999	-0.29	0.991	1.19	0.639
Bare – Oyster Reef	-0.43	0.973	0.07	0.999	-1.49	0.443	-0.48	0.963
Bare – Seagrass	-0.08	0.999	-0.73	0.886	-1.53	0.419	0.12	0.999
Mangroves – Oyster Reef	-0.09	0.999	-0.04	1.000	-1.26	0.589	-1.66	0.344
Mangroves – Seagrass	0.25	0.995	-0.84	0.834	-1.30	0.560	-1.06	0.712
Oyster reef – Seagrass	0.35	0.985	-0.80	0.855	-0.07	0.999	0.600	0.932

Port Stephens								
Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.28	0.992	-0.16	0.997	-1.10	0.689	0.45	0.970
Bare – Oyster Reef	-0.44	0.971	-0.53	0.953	-1.44	0.476	-0.24	0.995
Bare – Seagrass	-3.96	<0.001	-0.06	0.999	-4.23	<0.001	-0.39	0.980
Mangroves – Oyster Reef	-0.17	0.998	-0.38	0.982	-0.30	0.990	-0.70	0.896
Mangroves – Seagrass	-3.78	0.001	0.10	0.999	-3.03	0.013	-0.85	0.833
Oyster reef – Seagrass	-3.61	0.002	0.48	0.963	-2.79	0.027	-0.15	0.999

Table A.11: Summary of Linear Mixed Effects Models of sand whiting observations showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		14.41	<0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	0.89	2.07	0.159
Season	1	0.23	0.54	0.467
Estuary	1	0.14	0.32	0.575
Site(Estuary)	2	1.14	2.66	0.085
Habitat	3	2.36	5.50	<0.001
Year:Habitat	3	2.91	6.77	<0.001
Season:Habitat	3	1.84	4.28	0.005
Estuary:Habitat	3	0.42	0.97	0.405
Site(Estuary):Habitat	6	1.26	2.94	0.007
Year:Season:Habitat	3	2.60	6.05	<0.001
Year:Estuary:Habitat	3	0.05	0.12	0.949
Season:Estuary:Habitat	3	0.21	0.50	0.686
Year:Site(Estuary):Habitat	6	0.46	1.07	0.381

Season:Site(Estuary):Habitat	6	0.35	0.81	0.561
Year:Season:Estuary:Habitat	3	0.36	0.84	0.474
Year:Season:Site(Estuary):Habitat	6	0.35	0.81	0.560

(b)

	Year 1				Year 2			
	Winter		Summer		Winter		Summer	
	t	p	t	p	t	p	t	p
Bare – Mangroves	6.81	<0.001	2.87	0.022	7.62	<0.001	10.81	<0.001
Bare – Oyster Reef	7.16	<0.001	7.24	<0.001	6.10	<0.001	14.09	<0.001
Bare – Seagrass	7.34	<0.001	8.48	<0.001	7.78	<0.001	14.33	<0.001
Mangroves – Oyster Reef	0.44	0.972	4.44	<0.001	-1.64	0.356	3.18	0.008
Mangroves – Seagrass	0.65	0.916	5.70	<0.001	0.12	0.999	3.47	0.003
Oyster reef – Seagrass	0.21	0.997	1.23	0.605	1.78	0.285	0.32	0.989

Table A.12: Summary of Linear Mixed Effects Models of mullet observations per video showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year,. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		29.29	<0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	0.02	0.02	0.872
Season	1	7.28	11.42	<0.001
Estuary	1	0.35	0.55	0.465
Site(Estuary)	2	1.71	2.69	0.083
Habitat	3	6.60	10.36	<0.001
Year:Habitat	3	1.33	2.08	0.100
Season:Habitat	3	3.27	5.13	0.001
Estuary:Habitat	3	0.96	1.51	0.211
Site(Estuary):Habitat	6	1.85	2.90	0.008
Year:Season:Habitat	3	1.07	1.68	0.169
Year:Estuary:Habitat	3	1.65	2.59	0.052
Season:Estuary:Habitat	3	2.51	3.94	0.008
Year:Site(Estuary):Habitat	6	1.69	2.65	0.014
Season:Site(Estuary):Habitat	6	4.07	6.38	<0.001
Year:Season:Estuary:Habitat	3	2.75	4.32	0.005
Year:Season:Site(Estuary):Habitat	6	3.60	5.65	<0.001

(b)

Habitat Contrasts	Year 1
	Botany Bay

	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.70	0.897	-0.88	0.814	-3.74	0.001	5.25	<0.001
Bare – Oyster Reef	-2.71	0.035	-3.24	0.007	-10.42	<0.001	-2.08	0.160
Bare – Seagrass	-0.09	0.999	0.10	0.999	0.75	0.878	6.30	<0.001
Mangroves – Oyster Reef	-3.49	0.003	-2.49	0.062	-6.68	<0.001	-7.59	<0.001
Mangroves – Seagrass	-0.79	0.858	1.02	0.740	4.40	<0.001	0.90	0.805
Oyster reef – Seagrass	2.62	0.045	3.42	0.004	10.93	<0.001	8.80	<0.001

Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.21	0.997	0.01	1.000	-0.62	0.925	-2.72	0.033
Bare – Oyster Reef	-0.02	1.000	-2.22	0.118	-1.43	0.480	-4.80	<0.001
Bare – Seagrass	0.14	0.999	0.10	0.999	0.33	0.987	0.10	0.999
Mangroves – Oyster Reef	-0.24	0.995	-2.19	0.127	-0.79	0.858	-2.29	0.102
Mangroves – Seagrass	-0.07	0.999	0.08	0.999	0.95	0.780	3.05	0.013
Oyster reef – Seagrass	-0.16	0.998	2.28	0.105	1.75	0.297	5.26	<0.001

Habitat Contrasts	Year 2 Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.62	0.925	2.17	0.131	4.45	<0.001	2.34	0.089
Bare – Oyster Reef	-7.02	<0.001	-0.71	0.893	-3.28	0.005	-1.37	0.521
Bare – Seagrass	0.84	0.837	2.17	0.131	6.02	<0.001	4.99	<0.001
Mangroves – Oyster Reef	-7.48	<0.001	-2.88	0.021	-8.12	<0.001	-3.71	0.001
Mangroves – Seagrass	0.19	0.997	0.01	1.000	1.74	0.304	2.64	0.042
Oyster reef – Seagrass	7.86	<0.001	2.88	0.021	9.67	<0.001	6.35	<0.001

Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.89	0.809	-0.34	0.986	0.13	0.999	-2.05	0.172
Bare – Oyster Reef	-0.24	0.995	-3.05	0.013	-3.41	0.004	-4.50	<0.001
Bare – Seagrass	-0.22	0.996	0.01	1.000	1.21	0.621	1.75	0.296
Mangroves – Oyster Reef	0.66	0.911	-2.77	0.030	-3.47	0.003	-2.40	0.078
Mangroves – Seagrass	0.66	0.911	0.36	0.984	1.05	0.721	3.85	<0.001
Oyster reef – Seagrass	0.01	1.000	3.20	0.008	4.62	<0.001	6.40	<0.001

Table A.13: Summary of Linear Mixed Effects Models of the relative percentages of feeding observations per day showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method). Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.75	0.386
Fixed effects	df	MS	F value	Pr(>F)
Year	1	1.04	0.46	0.500
Season	1	3.28	1.46	0.235
Estuary	1	16.52	7.34	0.011
Site(Estuary)	2	6.40	2.84	0.072
Habitat	3	2.92	1.30	0.279
Year:Habitat	3	1.12	0.50	0.683
Season:Habitat	3	2.40	1.06	0.366
Estuary:Habitat	3	0.82	0.36	0.778
Site(Estuary):Habitat	6	4.54	2.02	0.070
Year:Season:Habitat	3	3.45	1.53	0.210
Year:Estuary:Habitat	3	2.29	1.02	0.388
Season:Estuary:Habitat	3	1.78	0.79	0.500
Year:Site(Estuary):Habitat	6	3.79	1.68	0.133
Season:Site(Estuary):Habitat	6	3.02	1.34	0.245
Year:Season:Estuary:Habitat	3	3.79	1.68	0.175
Year:Season:Site(Estuary):Habitat	6	2.08	0.92	0.481

Table A.14: Summary of Linear Mixed Effects Models of the relative percentages of wandering observations by day showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		1.14	0.286
Fixed effects	df	MS	F value	Pr(>F)
Year	1	10.93	9.89	0.003
Season	1	2.25	2.04	0.163
Estuary	1	0.70	0.63	0.431
Site(Estuary)	2	0.58	0.52	0.596
Habitat	3	6.61	5.98	<0.001
Year:Habitat	3	0.87	0.79	0.501
Season:Habitat	3	8.47	7.66	<0.001
Estuary:Habitat	3	1.83	1.65	0.182
Site(Estuary):Habitat	6	0.67	0.61	0.723
Year:Season:Habitat	3	9.45	8.54	<0.001
Year:Estuary:Habitat	3	2.40	2.17	0.096
Season:Estuary:Habitat	3	1.51	1.36	0.257
Year:Site(Estuary):Habitat	6	0.63	0.57	0.751

Season:Site(Estuary):Habitat	6	0.97	0.87	0.516
Year:Season:Estuary:Habitat	3	1.90	1.72	0.167
Year:Season:Site(Estuary):Habitat	6	0.92	0.83	0.546

(b)

	Year 1				Year 2			
	Winter		Summer		Winter		Summer	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-4.06	<0.001	-6.18	<0.001	-5.50	<0.001	-2.86	0.026
Bare – Oyster Reef	-3.10	0.013	-7.41	<0.001	-7.49	<0.001	-3.08	0.014
Bare – Seagrass	-1.64	0.359	-5.98	<0.001	-6.46	<0.001	-2.07	0.172
Mangroves – Oyster Reef	0.959	0.773	-0.98	0.757	-1.98	0.201	-0.22	0.996
Mangroves – Seagrass	2.41	0.081	0.397	0.979	-0.96	0.773	0.79	0.858
Oyster reef – Seagrass	1.45	0.468	1.43	0.483	1.03	0.735	1.01	0.743

Table A.15: Summary of Linear Mixed Effects Models of the relative percentages of passing observations by day showing (a) main effects and interactions of random factor effect in the ANOVA for random effects, and among fixed effects in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		3.41	0.065
Fixed effects	df	MS	F value	Pr(>F)
Year	1	7.23	4.27	0.047
Season	1	1.20	0.70	0.406
Estuary	1	12.10	7.14	0.011
Site(Estuary)	2	2.96	1.75	0.189
Habitat	3	16.88	9.97	<0.001
Year:Habitat	3	4.76	2.81	0.043
Season:Habitat	3	15.06	8.89	<0.001
Estuary:Habitat	3	0.95	0.56	0.641
Site(Estuary):Habitat	6	1.56	0.92	0.483
Year:Season:Habitat	3	15.34	9.06	<0.001
Year:Estuary:Habitat	3	0.69	0.41	0.747
Season:Estuary:Habitat	3	1.69	0.99	0.398
Year:Site(Estuary):Habitat	6	1.38	0.82	0.558
Season:Site(Estuary):Habitat	6	1.06	0.63	0.708
Year:Season:Estuary:Habitat	3	2.72	1.61	0.193
Year:Season:Site(Estuary):Habitat	6	1.59	0.94	0.471

(b)

	Year 1				Year 2			
	Winter		Summer		Winter		Summer	
	t	p	t	p	t	p	t	p
Bare – Mangroves	4.60	<0.001	6.60	<0.001	4.70	<0.001	3.37	0.005
Bare – Oyster Reef	3.34	0.006	8.74	<0.001	7.39	<0.001	4.42	<0.001
Bare – Seagrass	0.47	0.966	5.10	<0.001	6.24	<0.001	1.82	0.268
Mangroves – Oyster Reef	-1.26	0.593	1.84	0.259	2.68	0.042	1.05	0.722
Mangroves – Seagrass	-4.13	<0.001	-1.67	0.343	1.53	0.423	-1.55	0.413
Oyster reef – Seagrass	-2.87	0.025	-3.64	0.002	-1.15	0.659	-2.59	0.052

Appendix B:

CHAPTER 3 SUPPLEMENTARY MATERIAL

B.1 FIGURES

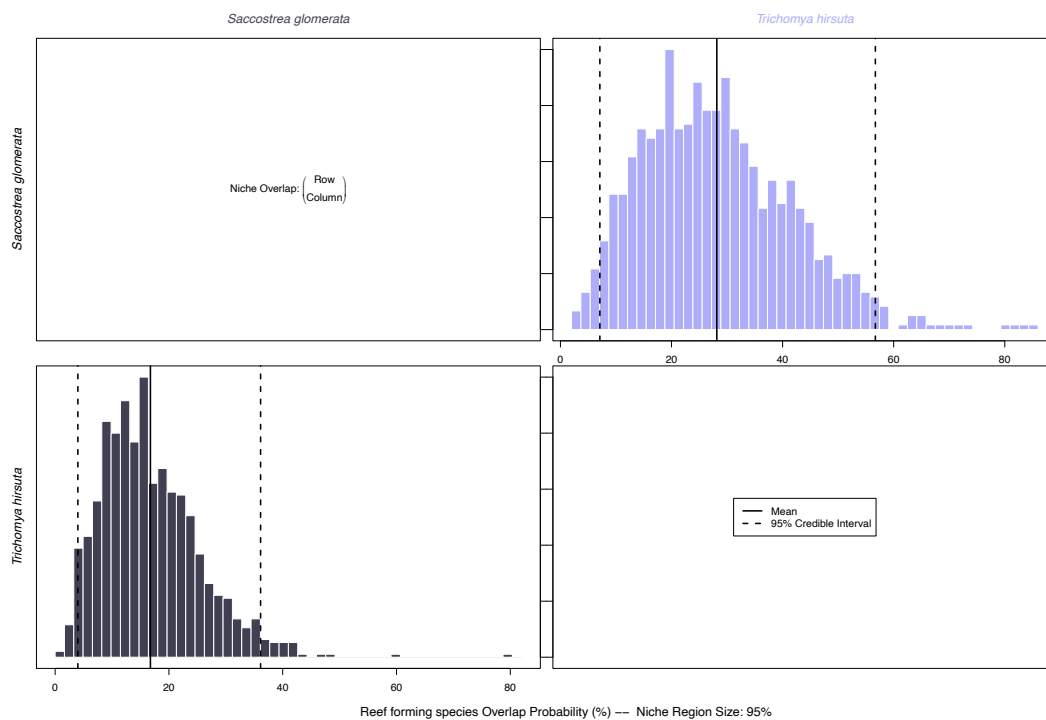


Figure B.1: Distribution of estimated probability of niche overlap between reef forming species, indicating mean and 95% credibility intervals.

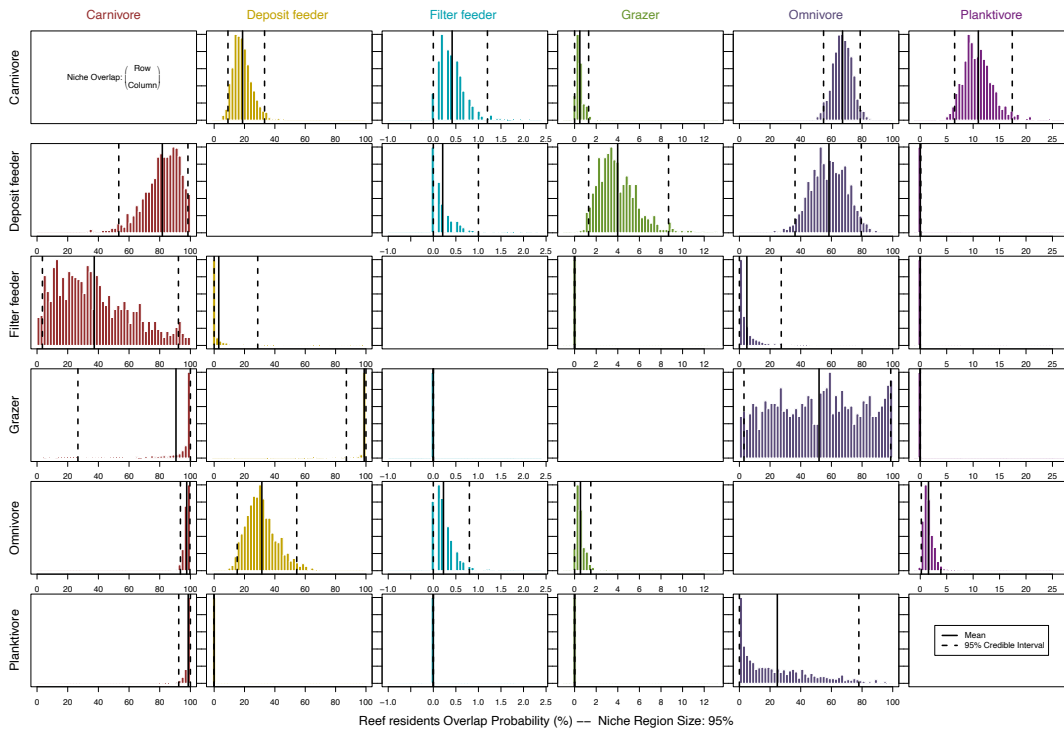


Figure B.2: Distribution of estimated probability of niche overlap between reef residents community grouped by feeding guild, indicating mean and 95% credibility intervals.

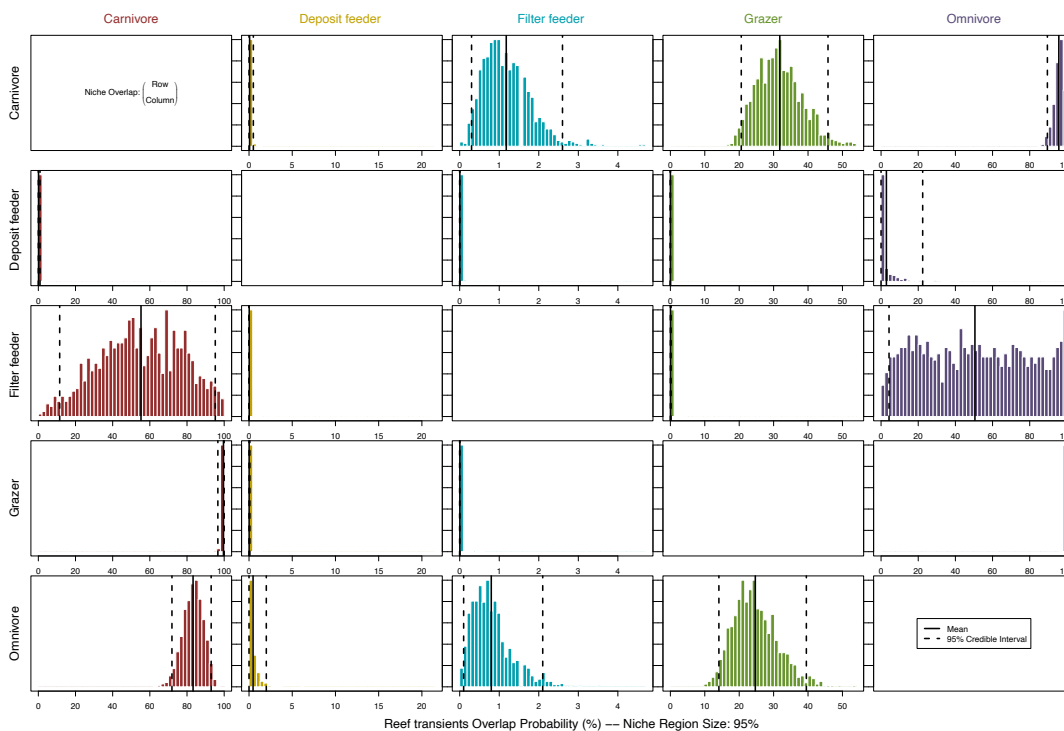


Figure B.3: Distribution of estimated probability of niche overlap between reef transients community grouped by feeding guild, indicating mean and 95% credibility intervals.

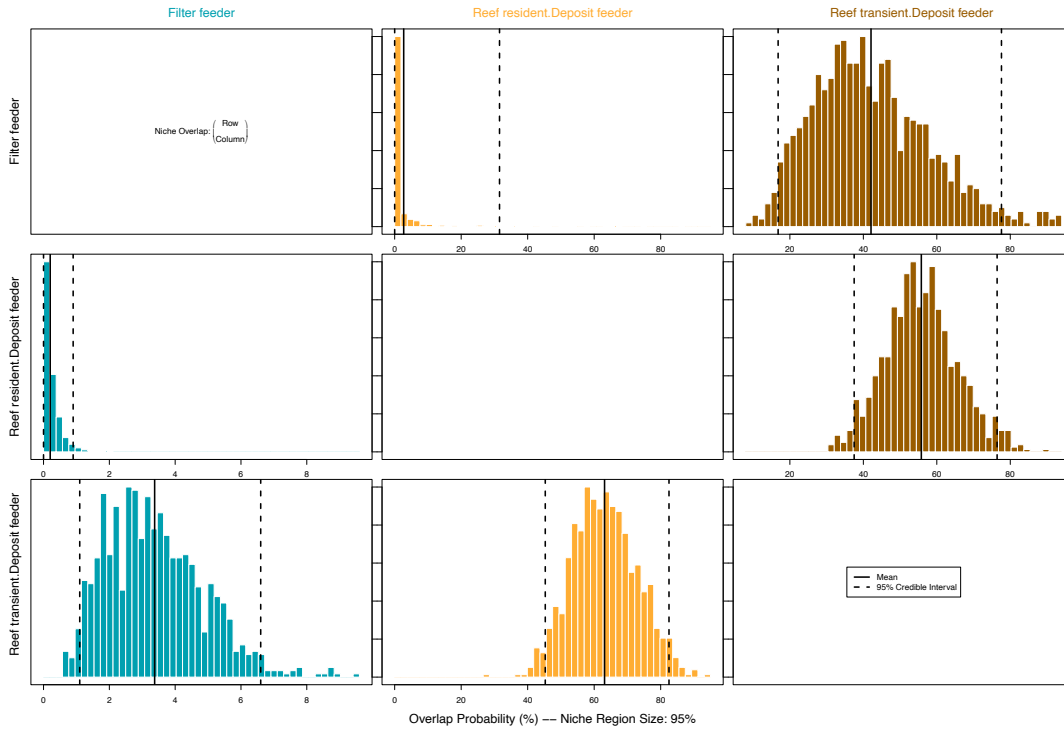


Figure B.4: Distribution of estimated probability of niche overlap between residents and transients deposit feeders group and filter feeders (reef forming species), indicating mean and 95% credibility intervals.

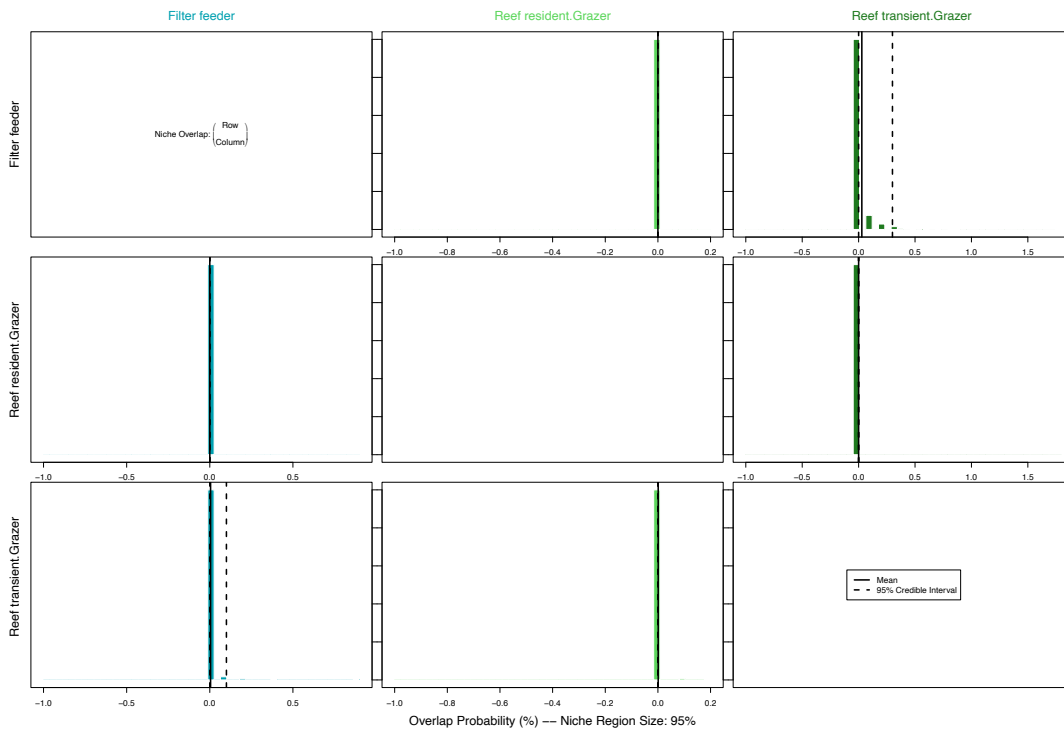


Figure B.5: Distribution of estimated probability of niche overlap between residents and transients grazers group and filter feeders (reef forming species), indicating mean and 95% credibility intervals.

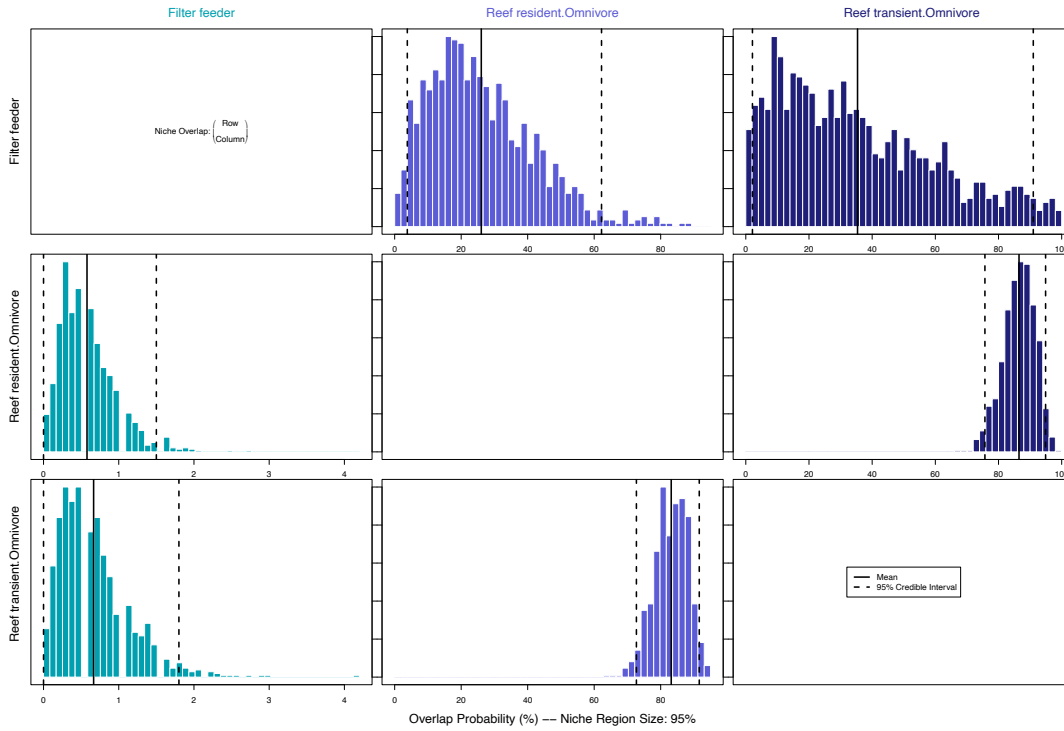


Figure B.6: Distribution of estimated probability of niche overlap between residents and transients omnivores group and filter feeders (reef forming species), indicating mean and 95% credibility intervals.

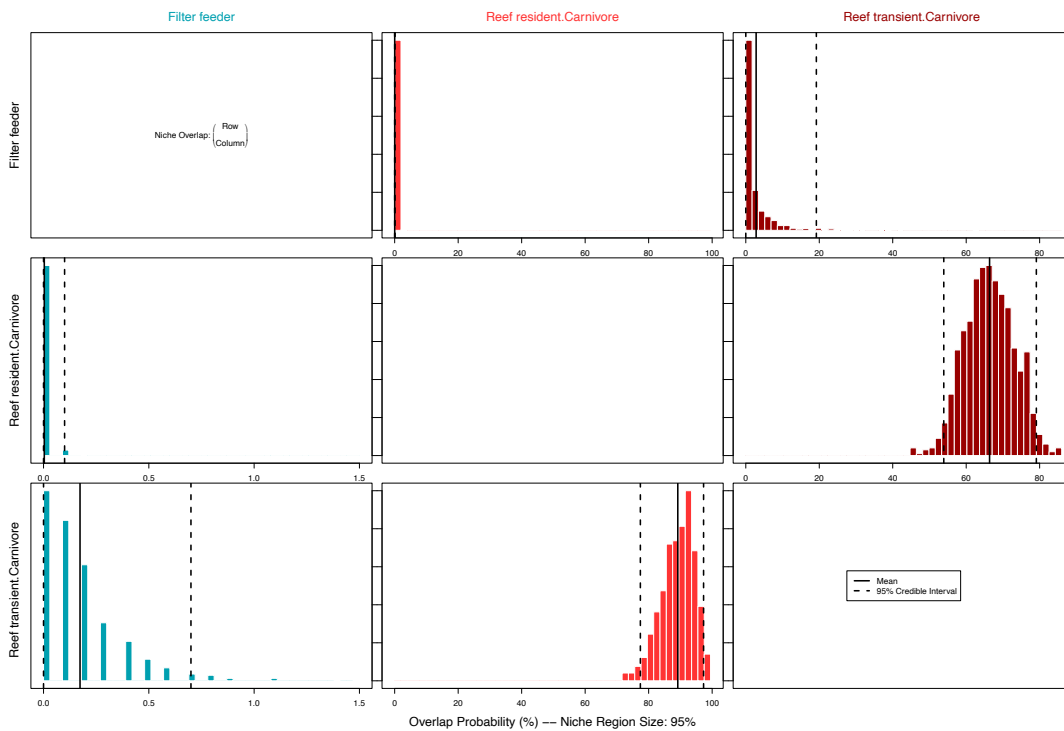


Figure B.7: Distribution of estimated probability of niche overlap between residents and transients carnivores group and filter feeders (reef forming species), indicating mean and 95% credibility intervals

B.2 TABLES

Table B.1: List of sampled species with scientific name, feeding guild, reef relationship, sample size (n), mean $\delta^{13}\text{C} \pm \text{sd}$, mean $\delta^{15}\text{N} \pm \text{sd}$, and posterior trophic position with 95% confidence intervals.

<i>Species</i>	<i>Feeding guild</i>	<i>Reef relationship</i>	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	<i>Trophic position</i>
<i>SOM-Sargassum</i>	Organic matter-Primary producers	Organic matter-Primary producers	15	-17.80 ± 1.84	8.15 ± 0.46	-
<i>Mangroves</i>	Primary producers	Primary producers	12	-27.05 ± 1.78	5.46 ± 0.61	-
<i>Seagrass-Epiphytes-Homorsira</i>	Primary producers	Primary producers	40	-11.37 ± 2.13	6.45 ± 0.73	-
<i>BOM</i>	Organic matter/detritus	Organic matter/detritus	18	-20.98 ± 2.08	4.66 ± 0.88	-
<i>Trichomya hirsuta</i>	Filter feeder	Reef resident	15	-19.40 ± 0.39	7.68 ± 0.19	1.43 (1.13 - 1.81)
<i>Saccostrea glomerata</i>	Filter feeder	Reef resident	15	-18.86 ± 0.13	8.28 ± 0.32	1.44 (1.11 - 1.8)
<i>Bembicium auratum</i>	Grazer	Reef resident	15	-11.77 ± 0.24	7.76 ± 0.31	1.42 (1.03 - 1.55)
<i>Pyrazus ebeninus</i>	Deposit feeder	Reef resident	7	-15.55 ± 1.22	8.18 ± 0.74	1.46 (1.1 - 1.74)
<i>Nereididae</i>	Omnivore	Reef resident	5	-17.27 ± 0.86	7.62 ± 0.46	1.17 (1.01 - 1.52)
<i>Pilumnopus serratifrons</i>	Deposit feeder	Reef resident	14	-14.27 ± 1.30	8.02 ± 1.19	1.46 (1.13 - 1.71)
<i>Australoplax tridentata</i>	Deposit feeder	Reef resident	9	-12.46 ± 0.84	7.21 ± 0.42	1.25 (1.05 - 1.4)
<i>Macrobrachium intermedium</i>	Omnivore	Reef resident	15	-13.80 ± 0.48	11.10 ± 0.32	2.37 (2.02 - 2.55)
<i>Penaeus plebejus</i>	Omnivore	Reef resident	9	-14.14 ± 1.01	9.76 ± 0.46	1.97 (1.6 - 2.17)
<i>Penaeus esculentus</i>	Omnivore	Reef resident	14	-13.95 ± 0.71	9.56 ± 0.26	1.92 (1.55 - 2.08)
<i>Macrophthalmus setosus</i>	Carnivore	Reef resident	5	-12.87 ± 1.60	7.95 ± 2.31	1.44 (1.04 - 3.08)
<i>Omobranchus rotundiceps</i>	Omnivore	Reef resident	8	-10.93 ± 0.59	10.29 ± 0.29	2.17 (1.56 - 2.32)
<i>Omobranchus anolius</i>	Omnivore	Reef resident	7	-17.04 ± 0.65	11.60 ± 0.15	2.30 (2 - 2.62)
<i>Arenigobius bifrenatus</i>	Carnivore	Reef resident	15	-14.87 ± 0.66	11.81 ± 0.59	2.54 (2.2 - 2.77)
<i>Mugillidae</i>	Omnivore	Reef resident	7	-16.15 ± 2.64	9.71 ± 1.91	1.82 (1.21 - 2.48)

<i>Monacanthus chinensis</i>	Omnivore	Reef resident	6	-16.32 ± 1.57	11.17 ± 0.31	2.26 (1.87 - 2.53)
<i>Girella tricuspidata</i>	Omnivore	Reef resident	13	-16.10 ± 1.63	10.99 ± 0.73	2.23 (1.86 - 2.5)
<i>Scorpaena papillosus</i>	Carnivore	Reef resident	10	-13.86 ± 1.12	11.33 ± 0.54	2.43 (2.06 - 2.65)
<i>Gerres subfasciatus</i>	Omnivore	Reef resident	15	-16.99 ± 1.48	9.83 ± 0.72	1.82 (1.48 - 2.11)
<i>Acanthopagrus australis</i> - juvenile	Omnivore	Reef resident	15	-18.60 ± 1.93	10.87 ± 1.21	1.92 (1.62 - 2.37)
<i>Acanthopagrus australis</i> - adult	Carnivore	Reef resident	15	-19.01 ± 3.38	13.59 ± 1.57	2.69 (2.35 - 3.21)
<i>Ambassis</i> sp.	Planktivore	Reef resident	15	-19.38 ± 1.16	12.28 ± 0.76	2.25 (2.03 - 2.7)
<i>Mictyris longicarpus</i>	Deposit feeder	Reef transient	13	-12.56 ± 1.26	6.10 ± 0.51	1.00 (1 - 1.13)
<i>Trypaea australiensis</i>	Deposit feeder	Reef transient	10	-18.63 ± 0.13	8.85 ± 0.33	1.30 (1.12 - 1.73)
<i>Biffarius ceramicus</i>	Deposit feeder	Reef transient	5	-18.29 ± 0.32	9.25 ± 0.31	1.47 (1.22 - 1.88)
<i>Portunus pelagicus</i> - juvenile	Omnivore	Reef transient	5	-14.48 ± 0.94	10.34 ± 0.44	2.12 (1.69 - 2.39)
<i>Portunus pelagicus</i> - adult	Carnivore	Reef transient	9	-16.01 ± 1.30	10.53 ± 0.95	2.10 (1.69 - 2.43)
<i>Euprymna tasmanica</i>	Carnivore	Reef transient	15	-15.16 ± 1.37	10.34 ± 0.72	2.10 (1.74 - 2.33)
<i>Tetractenos glaber</i>	Carnivore	Reef transient	15	-17.67 ± 0.93	11.71 ± 0.93	2.25 (1.95 - 2.65)
<i>Pseudorhombus jenynsii</i>	Carnivore	Reef transient	10	-15.20 ± 0.76	10.79 ± 0.54	2.24 (1.87 - 2.46)
<i>Meuschenia trachylepis</i>	Grazer	Reef transient	14	-17.12 ± 0.90	10.35 ± 0.65	1.95 (1.62 - 2.26)
<i>Rhabdosargus sarba</i>	Omnivore	Reef transient	15	-17.37 ± 2.18	9.34 ± 1.66	1.63 (1.22 - 2.04)
<i>Pelates sexlineatus</i>	Omnivore	Reef transient	15	-15.00 ± 0.59	11.77 ± 0.75	2.53 (2.18 - 2.77)
<i>Atherinomorus vaigiensis</i>	Omnivore	Reef transient	15	-18.53 ± 0.15	12.63 ± 0.21	2.39 (2.2 - 2.83)
<i>Sillago</i> sp.	Carnivore	Reef transient	13	-17.73 ± 2.47	11.19 ± 1.36	2.09 (1.73 - 2.55)
<i>Trygonoptera testacea</i>	Carnivore	Reef transient	8	-15.74 ± 1.48	11.36 ± 0.57	2.36 (1.97 - 2.63)
<i>Platycephalus fuscus</i>	Carnivore	Reef transient	9	-16.78 ± 1.29	13.11 ± 0.33	2.75 (2.42 - 3.09)

Table B.2: Estimated marginal means results for the Analysis of variance (ANOVA) of the isotopic signatures, which was used to group sources together. Bold shows non-significant differences (at $\alpha = 0.05$).

Contrast	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
	t ratio	p.value	t ratio	p.value
<i>Avicennia marina</i> leaves – <i>Avicennia marina</i> pneumatophores	-3.1	0.5235	1.38	1.0000
Epiphytes - <i>Homorsira banksii</i>	1.18	1.0000	-1.94	0.9992
Epiphytes - <i>Posidonia australis</i>	-5.9	<.0001	-0.09	1.0000
<i>Homorsira banksii</i> - <i>Posidonia australis</i>	-7.07	<.0001	1.855	0.9997
<i>Posidonia australis</i> – <i>Zostera sp.</i>	0.79	1.0000	-4.19	0.0255
<i>Sargassum sp.</i> - SOM	3.61	0.1687	-0.67	1.0000
BOM mangroves - BOM oyster reef	-3.04	0.5786	-2.9	0.6949
Bivalves - Neredidae	-1.99	0.3467	0.544	0.9943
Crustaceans - Gastropods	-1.21	0.8328	2.33	0.1827
Fish - Cephalopods	2.91	0.0434	-2.29	0.2003

Table B.3: Trophic discrimination factors (mean and sd) per taxa and references.

Taxa	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	References
Fish	1.42 ± 1.32	3.64 ± 1.05	Selleslagh et al., 2014
			Costalago et al., 2012
			Matley et al., 2015
			Escalas et al., 2015
			Landry et al., 2018
			Lamontagne et al., 2016
			Carrozzo et al., 2014
General crustaceans	3.23 ± 2.67	3.25 ± 1.97	McKenzie et al. 2019
			Herbon and Nordhaus 2013
			Bui and Lee 2014
			Alderson et al., 2013
			Rosewarne et al., 2016
			Al-wazzan et al., 2019
			Bojorquez- Mascareño & Soto-Jimenez 2016
Blue swimmer crabs	3.23 ± 2.67	1.37 ± 0.82	Carrozzo et al., 2014
Bivalves	1.37 ± 1.52	2.64 ± 1.25	Kwan et al., 2018
			Lopez-van Oosterom et al. 2016
			Alomar et al., 2015 & McCutchan et al., 2003
			Bloomberg et al., 2017
			Emmery et al., 2011
			Page & Lastra 2003
Invertebrates - Deposit feeders	5.3 ± 0.8	4.2 ± 0.7	Wooi Teoh et al., 2018
Invertebrates - Grazers	1.3 ± 0.8	2.2 ± 0.8	Lopez-van Oosterom et al. 2016
Cephalopods	1.1 ± 0.77	3.27 ± 0.54	Hobson and Cherel 2006
			Kwan et al., 2018
			Kang et al., 2015
Chondrichthyes	1.3 ± 0.5	2.29 ± 0.50	Albo-Puigserver et al., 2015
			Escalas et al., 2015

Table B.4: Mean proportion and standard deviation of contribution to diet of each species as predicted by Bayesian mixing models. BN: Bivalves-Nereididae, BOM: Benthic Organic Matter, SOM-S: Suspended Organic Matter and Sargassum, HES: Homorsira – Epiphytes – Seagrass, CG: Crustaceans-Gastropods, FC: Fish-Cephalopods. Values in bold are significant contributors.

Species	BN	BOM	Mangroves	SOM-S	HES	Invertebrates	CG	FC
<i>Nereididae</i>	-	0.419 (0.185)	0.275 (0.128)	0.131 (0.102)	0.175 (0.093)	-	-	-
<i>B. auratum</i>	-	0.176 (0.049)	0.023 (0.021)	-	0.801 (0.037)	-	-	-
<i>P. ebeninus</i>	-	0.505 (0.213)	0.262 (0.141)	0.101 (0.087)	0.131 (0.088)	-	-	-
<i>A. tridentata</i>	-	0.441 (0.063)	-	0.069 (0.054)	0.490 (0.059)	-	-	-
<i>P. serratifrons</i>	-	0.591 (0.070)	-	0.089 (0.086)	0.319 (0.062)	-	-	-
<i>P. esculentus</i>	-	0.182 (0.039)	-	0.635 (0.058)	0.183 (0.056)	-	-	-
<i>P. plebejus</i>	-	0.131 (0.047)	-	0.752 (0.068)	0.118 (0.062)	-	-	-
<i>A. bifrenatus</i>	0.335 (0.126)	0.087 (0.061)	-	-	-	-	0.471 (0.061)	0.107 (0.066)
<i>S. papillosus</i>	0.075 (0.071)	0.170 (0.051)	-	-	-	-	0.755 (0.057)	-
<i>A. australis</i> juvenile	0.431 (0.169)	0.115 (0.086)	0.230 (0.093)	-	0.090 (0.065)	0.134 (0.097)	-	-
<i>G. subfasciatus</i>	0.217 (0.083)	0.527 (0.060)	-	-	0.146 (0.052)	0.110 (0.071)	-	-
<i>G. tricuspidata</i>	0.506 (0.153)	0.175 (0.077)	-	-	0.112 (0.067)	0.207 (0.124)	-	-
<i>M. chinensis</i>	0.636 (0.150)	0.123 (0.078)	-	-	0.097 (0.073)	0.143 (0.107)	-	-
<i>Mugillidae</i>	0.222 (0.149)	0.415 (0.136)	-	-	0.363 (0.106)	-	-	-
<i>O. anolius</i>	0.801 (0.088)	0.080 (0.043)	-	-	0.043 (0.029)	0.076 (0.064)	-	-
<i>O. rotundiceps</i>	0.089 (0.054)	0.092 (0.042)	-	-	0.739 (0.071)	0.080 (0.065)	-	-
<i>B. ceramicus</i>	-	0.119 (0.066)	0.351 (0.053)	0.530 (0.044)	-	-	-	-
<i>T. australiensis</i>	-	0.192 (0.080)	0.366 (0.057)	0.442 (0.044)	-	-	-	-
<i>P. pelagicus</i> juvenile	0.468 (0.200)	0.098 (0.086)	-	-	-	-	0.076 (0.081)	0.358 (0.135)
<i>P. pelagicus</i> adult	0.395 (0.191)	0.139 (0.097)	-	-	-	-	0.059 (0.056)	0.407 (0.124)
<i>E. tasmanica</i>	0.404 (0.120)	0.163 (0.077)	-	-	0.273 (0.088)	-	0.16 (0.116)	-
<i>P. jenynsii</i>	0.123 (0.088)	0.317 (0.053)	-	-	-	-	0.559 (0.060)	-
<i>T. glaber</i>	0.750 (0.295)	0.083 (0.137)	-	-	-	-	0.044 (0.027)	0.123 (0.153)
<i>M. trachylepis</i>	-	0.188 (0.112)	0.170 (0.091)	0.425 (0.104)	0.217 (0.092)	-	-	-

<i>P. sexlineatus</i>	0.489 (0.104)	0.054 (0.048)	-	-	0.143 (0.075)	0.314 (0.131)	-	-
<i>R. sarba</i>	0.206 (0.131)	0.324 (0.159)	0.190 (0.116)	-	0.279 (0.104)	-	-	-
<i>S. maculata</i>	0.652 (0.100)	-	-	-	-	-	0.169 (0.105)	0.178 (0.085)
<i>T. testacea</i>	0.509 (0.113)	-	-	-	-	-	0.202 (0.116)	0.289 (0.096)

Table B.5: SEA_B ($\%o^2$) Modes and 95% credibility intervals for reef forming species, reef residents and reef transients grouped by feeding guild, and Total Convex Hull areas of the reef residents community and reef transients community.

SEA_B ($\%o^2$)		
Reef forming species		
<i>Saccostrea glomerata</i>	0.12 (0.07 – 0.21)	
<i>Trichomya hirsuta</i>	0.21 (0.12 – 0.36)	
	Reef resident groups	Reef transient groups
Filter feeders	0.38 (0.26 – 0.55)	
Grazers	0.21 (0.12 – 0.37)	1.76 (1.00 – 3.16)
Deposit feeders	4.45 (3.09 – 6.48)	1.38 (0.78 – 2.43)
Planktivores	1.54 (0.90 – 2.63)	-
Omnivores	8.76 (7.26 – 10.52)	10.18 (7.67 – 14.27)
Carnivores	12.45 (9.33 – 16.88)	7.62 (6.23 – 9.29)

Appendix C:

CHAPTER 4 SUPPLEMENTARY MATERIAL

C.1 FIGURES

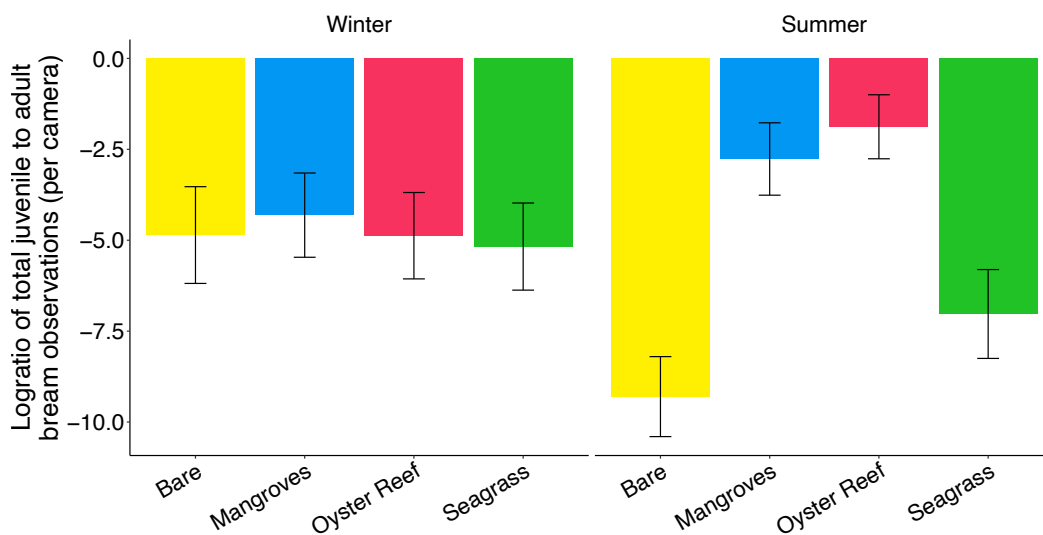


Figure C.1: Mean ($\pm$ SE) logratio of total juvenile to adult observations of breem by season and habitat as documented by 75 min Remote Underwater Video deployments, $n = 8$.

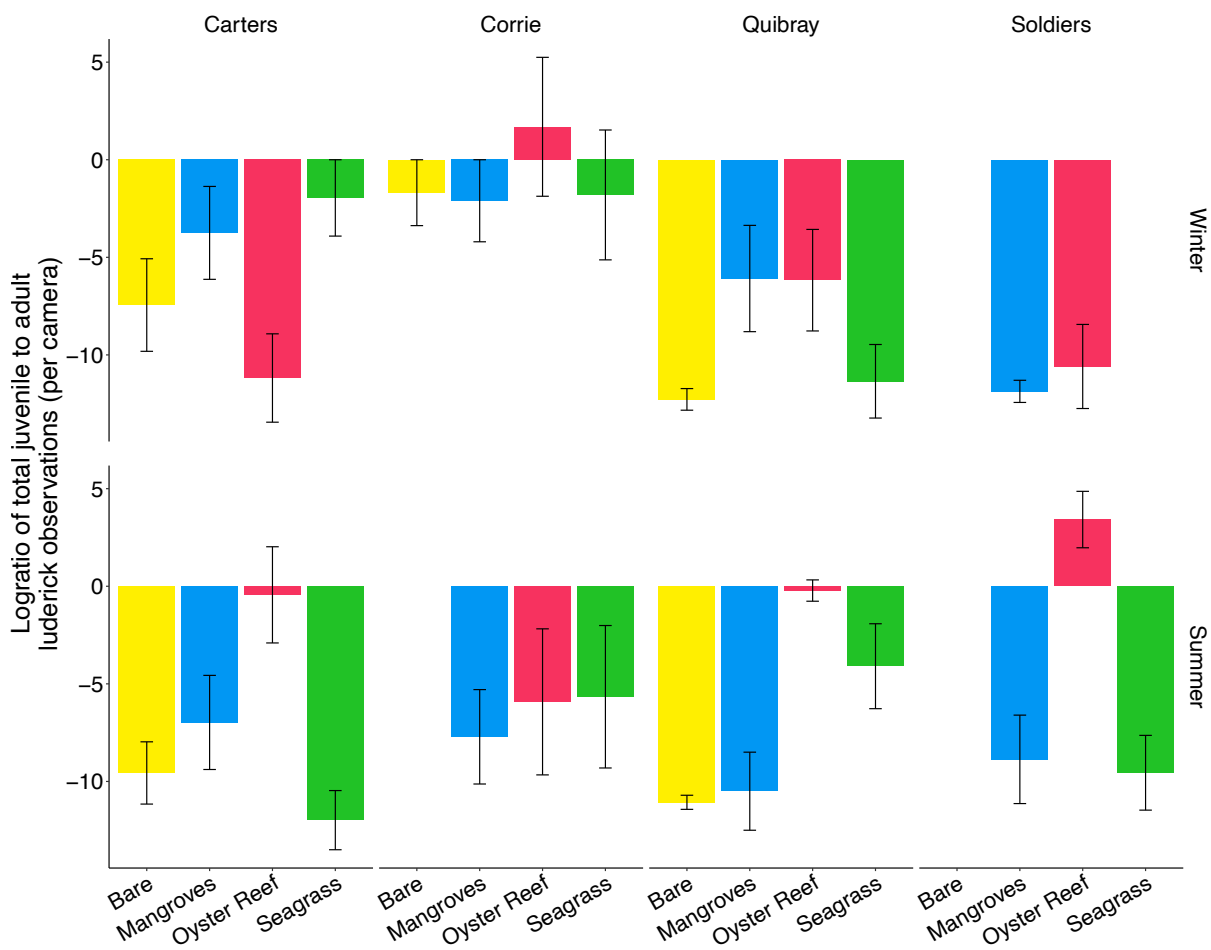


Figure C.2: Mean ($\pm$ SE) logratio of total juvenile to adult observations of luderick by season, site and habitat as documented by 75 min Remote Underwater Video deployments, $n = 32$.

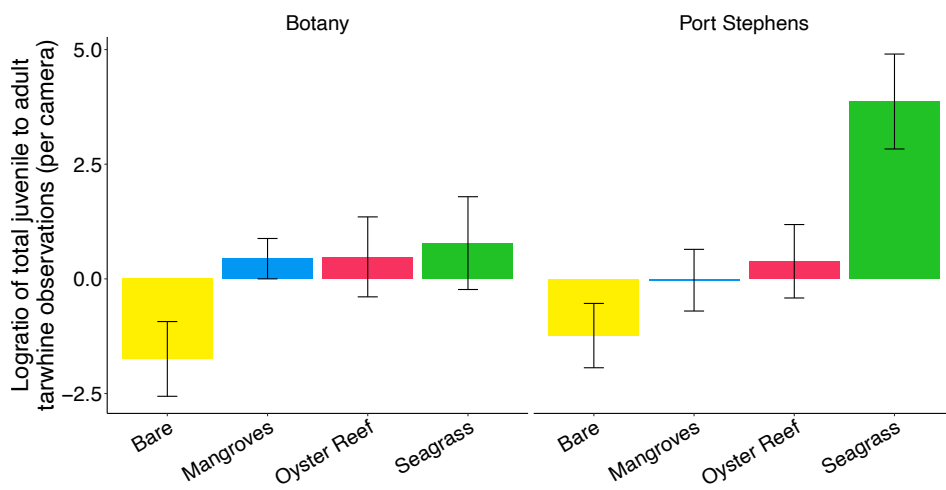


Figure C.3: Mean ($\pm$ SE) of logratio of total juvenile to adult observations of tarwhine by estuary and habitat as documented by 75 min Remote Underwater Video deployments, $n = 8$.

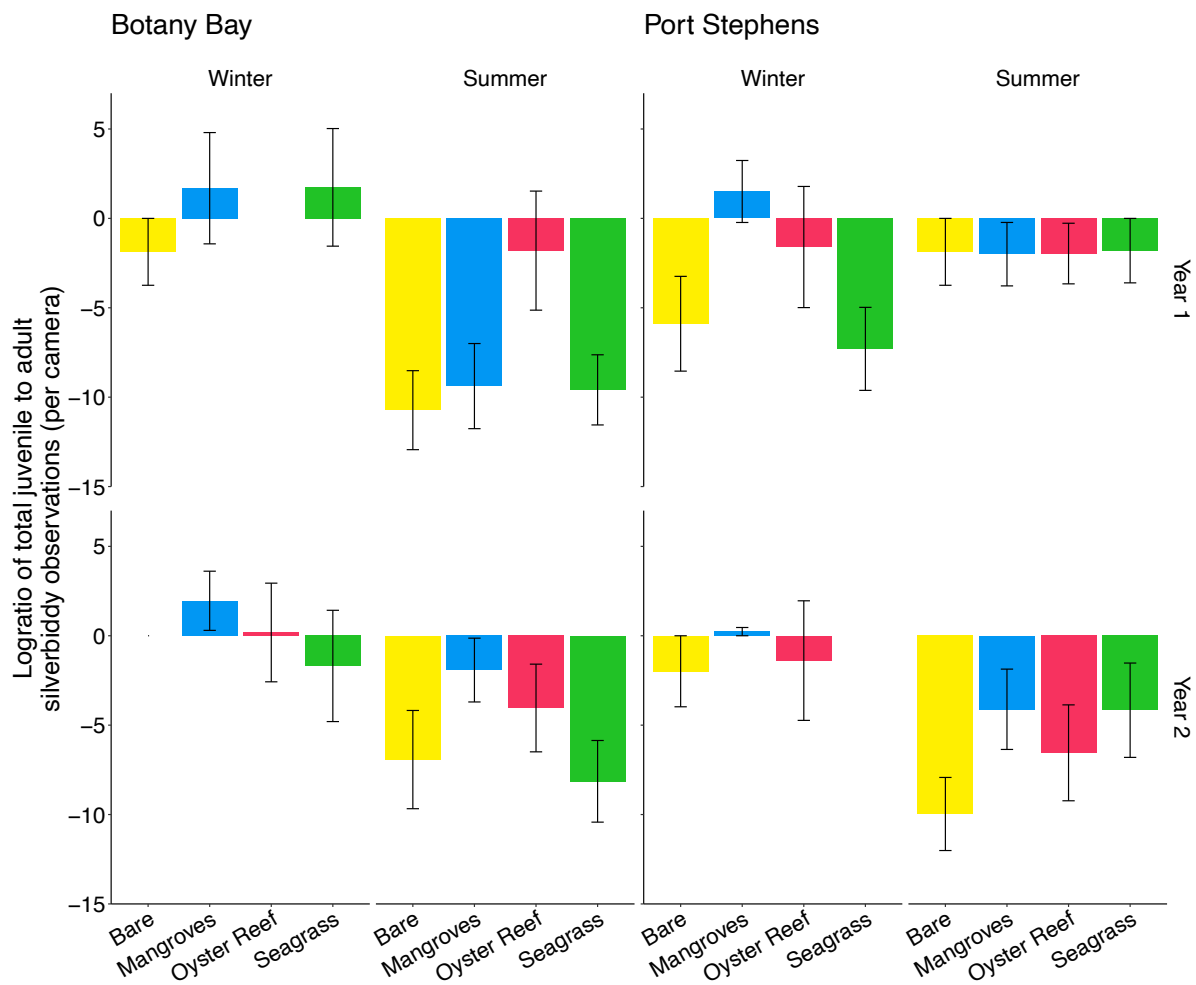


Figure C.4: Mean ($\pm$ SE) logratio of total juvenile to adult observations of silverbiddy by estuary, year, season and habitat as documented by 75 min Remote Underwater Video deployments, $n = 32$.

C.2 TABLES

Table C.1: Summary table of juvenile and adult fish species identified during the study. The total number of observations (Total n), across all cameras, and the mean and standard error (SE) observation per camera per habitat are shown.

		Juveniles										Adults									
		Oyster reef N= 66		Seagrass N= 60		Mangroves N= 40		Bare N= 43				Oyster reef N= 66		Seagrass N= 60		Mangroves N= 40		Bare N= 43			
Family	Species	Total n	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Total n	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Apogonidae	<i>Siphamia cephalotes</i>	1	0	0	1	0	0	0	0	0	93	0	0	46.5	2.5	0	0	0	0	0	0
Chaetodontidae	<i>Chaetodon flavirostris</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheilodactylidae	<i>Cheilodactylus vestitus</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clupeidae	<i>Herklotichthys castelnaui</i>	6	0	0	6	0	0	0	0	0	94	1	0	23	14.02	0	0	0	0	0	0
Dinolestidae	<i>Dinolestes lewini</i>	6	1	0	2.5	1.5	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Gerreidae	<i>Gerres subfasciatus</i>	88	13	10.07	4	0	13	8.74	2	0	680	31.5	15.76	35	18.28	29.5	14.8	74	19.8		
Girellidae	<i>Girella elevata</i>	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Girellidae	<i>Girella tricuspidata</i>	819	176.8	57.15	30.7	28.7	4.75	1.49	1	0	2546	243	116.6	242	146.5	111.3	35	54.3	31.8		
Kyphosidae	<i>Kyphosus sydneyanus</i>	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Labridae	<i>Achoerodus viridis</i>	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Labridae	<i>Pseudolabrus guentheri</i>	58	58	0	0	0	0	0	0	0	309	154	142	1	0	0	0	0	0	0	0
Monacanthidae	<i>Acanthaluteres spilomelanurus</i>	17	0	0	5.67	1.45	0	0	0	0	193	0	0	48.25	17.39	0	0	0	0	0	0

Monacanthidae	<i>Meuschenia freycineti</i>	1	0	0	1	0	0	0	0	0	15	0	0	7.5	0.5	0	0	0	0
Monacanthidae	<i>Meuschenia trachylepis</i>	18	0	0	4.5	2.22	0	0	0	0	418	0	0	104.3	31.85	0	0	1	0
Monacanthidae	<i>Monacanthus chinensis</i>	23	14	0	3	1.15	0	0	0	0	54	5	2.65	7.75	3.28	0	0	4	2
Monacanthidae	<i>Scobinichthys granulatus</i>	5	0	0	5	0	0	0	0	0	6	1	0	2.5	0.5	0	0	0	0
Monodactylidae	<i>Monodactylus argenteus</i>	1	0	0	1	0	0	0	0	0	10	0	0	5	3	0	0	0	0
Mugilidae	<i>Liza argentea</i>	2	0	0	0	0	2	0	0	0	424	52.3	23.55	2	0	33.75	14.3	25.3	18.1
Mugilidae	<i>Mugil cephalus</i>	21	0	0	0	0	21	0	0	0	934	167	60.39	8.5	7.5	10	4.56	70.3	37.1
Mullidae	<i>Parupeneus spilurus</i>	5	0	0	5	0	0	0	0	0	8	4	0	4	0	0	0	0	0
Mullidae	<i>Upeneichthys lineatus</i>	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Paralichthyidae	<i>Pseudorhombus arsius</i>	3	1	0	0	0	2	0	0	0	3	0	0	0	0	0	0	3	0
Platycephalidae	<i>Platycephalus fuscus</i>	1	0	0	0	0	0	0	1	0	18	1.67	0.67	1.33	0.33	0	0	2.25	0.75
Pomacentridae	<i>Parma microlepis</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pomatomidae	<i>Pomatomus saltatrix</i>	4	2	0	0	0	2	0	0	0	34	3	0	15	4	0	0	1	0
Scorpididae	<i>Microcanthus strigatus</i>	10	5	1	0	0	0	0	0	0	1031	247	80.32	2	0	41	0	0	0
Sillaginidae	<i>Sillago ciliata</i>	44	2	0	0	0	6.33	4.84	5.75	1.9	878	16.8	4.59	9.75	3.77	36	16.4	157	34.8
Sillaginidae	<i>Sillago maculata</i>	4	2	0	0	0	2	0	0	0	3	0	0	0	0	0	0	1.5	0.5
Sparidae	<i>Acanthopagrus australis</i>	2999	531.5	173.8	43	10.6	174	70.2	2.33	1.3	6558	887	185.5	140.3	29.8	521	81.5	91.8	37.3
Sparidae	<i>Rhabdosargus sarba</i>	229	4.25	1.65	51.8	24.9	1.5	0.5	2	0	50	6	1	6.25	1.18	3	0	2.5	0.87
Sphyrinaeidae	<i>Sphyræna obtusata</i>	21	1	0	5	1.41	0	0	0	0	180	1	0	44.75	14.2	0	0	0	0

Terapontidae	<i>Pelates sexlineatus</i>	44	7.5	0.5	7.25	4.61	0	0	0	0	737	18.7	14.31	167.8	67.9	2	0	4	2
Tetraodontidae	<i>Tetractenos glaber</i>	3	0	0	0	0	0	0	3	0	78	4	2	7	2.45	7.5	2.36	4	1
Tetraodontidae	<i>Tetractenos hamiltoni</i>	1	0	0	0	0	0	0	1	0	30	1	0	2	0.58	9	5	2.5	0.5
Tetraodontidae	<i>Tetractenos squamicauda</i>	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Tetraodontidae	<i>Torquigener pleurogramma</i>	1	0	0	0	0	1	0	0	0	5	1	0	0	0	1	0	1	0
Tetrarogidae	<i>Centropogon australis</i>	12	6	2	0	0	0	0	0	0	36	9	4.78	0	0	0	0	0	0

Table C.2: Five-factor mixed-model PERMANOVAs testing for differences of the observations of juveniles of each species observed per habitat (fish community of each habitat), across sites and sampling times, (b) a posteriori pairwise PERMANOVAs examining significant differences between habitats, within sites and years of the juveniles fish community. Analyses used Bray Curtis dissimilarities calculated using fish observations (by species). Boldface indicates significance at $P < 0.05$.

(a)

Source	df	Juveniles				
		SS	MS	Pseudo-F	P(perm)	perms
Year	1	12285	12285	12.734	0.348	8
Season	1	86984	86984	10.115	0.168	684
Estuary	1	17792	17792	4.234	0.096	911
Habitat	3	1.6767E+05	55890	5.7844	0.009	999
Site(Estuary)	2	8287.2	4143.6	1.0845	0.429	821
Year:Season	1	4733.6	4733.6	0.75547	0.594	344
Year:Estuary	1	964.75	964.75	0.25273	0.794	902
Year:Habitat	3	7580.4	2526.8	2.3575	0.091	998
Season:Estuary	1	4485.1	4485.1	0.90005	0.559	999
Season:Habitat	3	69466	23155	2.3612	0.100	999
Estuary:Habitat	3	21962	7320.7	2.2378	0.057	998
Year:Site(Estuary)	2	7641.7	3820.9	2.4531	0.029	999
Season:Site(Estuary)	2	8447.9	4224	0.85201	0.572	998
Site(Estuary):Habitat	6	19522	3253.7	1.3922	0.234	998
Year:Season:Estuary	1	6265.7	6265.7	1.2651	0.388	996
Year:Season:Habitat	3	10465	3488.4	2.4642	0.089	997
Year:Estuary:Habitat	3	3215.5	1071.8	0.45984	0.886	999
Season:Estuary:Habitat	3	20754	6917.9	1.6219	0.164	999
Year:Season:Site(Estuary)	2	9915.3	4957.6	3.1829	0.010	999
YearxSite(Estuary):Habitat	6	14023	2337.1	1.6337	0.023	997
SeasonxSite(Estuary):Habitat	6	25234	4205.7	1.9299	0.110	997
Year:Season:Estuary:Habitat	3	4246.8	1415.6	0.65125	0.726	997
Day(Year:Season:Site(Estuary))	32	51319	1603.7	1.7654	0.001	997
Year:Season:Site(Estuary):Habitat	6	13075	2179.2	1.5233	0.058	997
Day(Year:Season:Site(Estuary)):Habitat	92	1.3466E+05	1463.7	1.6113	0.001	996
Res	490	4.4512E+05	908.41			
Total	677	1.2692E+06				

(b)

Habitat Contrasts	Year 1							
	Botany Bay				Port Stephens			
	Carters Island		Quibray Bay		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	3.89	0.001	3.58	0.005	2.09	0.062	4.98	0.001
Bare – Oyster Reef	4.40	0.001	5.53	0.001	3.20	0.003	4.21	0.001
Bare – Seagrass	1.31	0.152	4.25	0.001	1.61	0.116	1.90	0.038
Mangroves – Oyster Reef	1.40	0.174	2.96	0.001	1.26	0.248	2.00	0.031
Mangroves – Seagrass	1.36	0.161	2.29	0.011	1.49	0.137	1.72	0.042
Oyster reef – Seagrass	2.49	0.005	1.72	0.033	2.82	0.005	2.39	0.007

Habitat Contrasts	Year 2							
	Botany Bay				Port Stephens			
	Carters Island		Quibray Bay		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	2.15	0.049	1.31	0.219	2.94	0.008	5.10	0.001
Bare – Oyster Reef	2.14	0.030	3.21	0.003	3.55	0.004	8.61	0.001
Bare – Seagrass	0.69	0.801	1.82	0.060	1.54	0.084	1.08	0.352
Mangroves – Oyster Reef	2.18	0.017	3.04	0.002	1.71	0.107	1.83	0.052
Mangroves – Seagrass	2.19	0.005	0.95	0.466	2.04	0.017	4.80	0.001
Oyster reef – Seagrass	2.01	0.012	1.60	0.087	2.00	0.029	7.74	0.001

Table C.3: Summary of Linear Mixed Effects Models of the logratio of total fish observations for adults and juveniles per day showing (a) main effects and interactions of random effects in the ANOVA for random effects and interactions among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Estuary and Year. Significant effects ($P < 0.05$) are in bold. Intercepts are: Habitat – Bare; Season – Summer; Site – Carters Island, Estuary – Botany, Year 1 and their respective interactions.

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.81	0.369
Fixed effects	df	MS	F value	Pr(>F)
Year	1	23.37	1.31	0.262
Season	1	170.24	9.54	0.004
Estuary	1	57.42	3.22	0.083
Site(Estuary)	2	0.21	0.01	0.988
Habitat	3	569.3	31.91	<0.001
Year:Habitat	3	38.58	2.16	0.098
Season:Habitat	3	41.73	2.34	0.078
Estuary:Habitat	3	12.33	0.691	0.559
Site(Estuary):Habitat	6	14.56	0.81	0.560
Year:Season:Habitat	3	85.78	4.81	0.003
Year:Estuary:Habitat	3	6.00	0.34	0.799
Season:Estuary:Habitat	3	11.91	0.67	0.574
Year:Site(Estuary):Habitat	6	9.89	0.55	0.765
Season:Site(Estuary):Habitat	6	20.11	1.13	0.353
Year:Season:Estuary:Habitat	3	8.84	0.49	0.686

Year:Season:Site:Habitat	6	11.27	0.63	0.704
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(b)

	Year 1				Year 2			
	Winter		Summer		Winter		Summer	
	t ratio	p	t ratio	p	t ratio	p	t ratio	p
Bare – Mangroves	-1.39	0.508	-6.60	<0.001	-4.49	<0.001	-3.20	0.010
Bare – Oyster Reef	-2.33	0.098	-7.17	<0.001	-4.06	<0.001	-4.27	<0.001
Bare – Seagrass	-2.91	0.023	-5.88	<0.001	-1.60	0.381	-2.65	0.045
Mangroves – Oyster Reef	-0.94	0.783	-0.35	0.985	0.46	0.966	-1.07	0.710
Mangroves – Seagrass	-1.51	0.433	0.93	0.788	3.08	0.014	0.55	0.947
Oyster reef – Seagrass	-0.57	0.939	1.33	0.546	2.62	0.049	1.61	0.375

Table C.4: Summary of Linear Mixed Effects Models showing of total fish observations for juveniles per video (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		12.2	<0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	15.79	9.97	0.003
Season	1	190.84	120.54	<0.001
Estuary	1	24.60	15.54	<0.001
Site(Estuary)	2	7.05	4.45	0.002
Habitat	3	198.85	125.59	<0.001
Year:Habitat	3	3.54	2.23	0.083
Season:Habitat	3	96.52	60.96	<0.001
Estuary:Habitat	3	17.99	11.36	<0.001
Site(Estuary):Habitat	6	9.06	5.72	<0.001
Year:Season:Habitat	3	8.23	5.19	0.001
Year:Estuary:Habitat	3	5.69	3.59	0.013
Season:Estuary:Habitat	3	8.03	5.07	0.002
Year:Site(Estuary):Habitat	6	6.09	3.84	<0.001
Season:Site(Estuary):Habitat	6	11.21	7.08	<0.001
Year:Season:Estuary:Habitat	3	1.47	0.93	0.425
Year:Season:Site(Estuary):Habitat	6	5.99	3.78	0.001

(b)

Year 1								
Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.35	0.986	-1.21	0.755	-4.28	<0.001	-2.85	0.023
Bare – Oyster Reef	-0.18	0.997	-0.99	0.978	-6.89	<0.001	-10.33	<0.001
Bare – Seagrass	-0.64	0.841	-0.61	0.909	-2.02	0.182	-7.39	<0.001
Mangroves – Oyster Reef	-0.54	0.999	0.23	0.930	-2.61	0.046	-7.55	<0.001
Mangroves – Seagrass	-0.99	0.913	0.62	0.987	2.17	0.133	-4.55	<0.001
Oyster reef – Seagrass	-0.47	0.930	0.39	0.992	4.72	<0.001	3.08	0.011

Port Stephens								
Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.19	0.631	-0.19	0.997	-3.32	0.005	-6.25	<0.001
Bare – Oyster Reef	-1.50	0.440	-3.15	0.009	-6.45	<0.001	-11.80	<0.001
Bare – Seagrass	-1.41	0.491	-2.95	0.017	-0.83	0.841	-1.87	0.241
Mangroves – Oyster Reef	-0.21	0.996	-2.96	0.017	-4.35	<0.001	-6.55	<0.001
Mangroves – Seagrass	0.10	0.999	-2.75	0.030	3.55	0.002	5.10	<0.001
Oyster reef – Seagrass	0.12	0.999	0.20	0.997	7.99	<0.001	11.53	<0.001

Year 2								
Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.62	0.926	-1.21	0.620	-1.72	0.316	-0.15	0.998
Bare – Oyster Reef	-0.57	0.941	-0.99	0.756	-8.24	<0.001	-4.63	<0.001
Bare – Seagrass	-0.04	1.000	-0.61	0.930	-1.48	0.451	-1.23	0.606
Mangroves – Oyster Reef	0.10	0.999	0.23	0.996	-6.84	<0.001	-4.49	<0.001
Mangroves – Seagrass	0.66	0.913	0.62	0.926	0.17	0.998	-1.08	0.669
Oyster reef – Seagrass	0.60	0.931	0.39	0.979	6.69	<0.001	3.40	0.004

Port Stephens								
Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.45	0.467	-2.03	0.178	-2.00	0.190	-7.71	<0.001
Bare – Oyster Reef	-3.77	0.001	-2.19	0.125	-2.90	0.019	-11.69	<0.001
Bare – Seagrass	-1.98	0.196	-0.04	1.000	-1.88	0.236	-0.92	0.794
Mangroves – Oyster Reef	-2.91	0.019	-0.01	1.000	-0.83	0.834	-3.92	<0.001
Mangroves – Seagrass	-0.66	0.913	2.07	0.163	0.15	0.998	7.12	<0.001
Oyster reef – Seagrass	2.28	0.102	2.26	0.108	1.02	0.737	11.30	<0.001

Table C.5: Summary of Linear Mixed Effects Models of the logratio of breem observations for adults and juveniles per day showing (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat and Season. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.11	0.739
Fixed effects	df	MS	F value	Pr(>F)
Year	1	109.71	3.85	0.059
Season	1	2.27	0.08	0.779
Estuary	1	27.85	0.98	0.331
Site(Estuary)	2	71.32	2.50	0.098
Habitat	3	190.91	6.70	<0.001
Year:Habitat	3	17.90	0.63	0.598
Season:Habitat	3	115.33	4.05	0.009
Estuary:Habitat	3	76.70	2.69	0.051
Site(Estuary):Habitat	6	28.13	0.99	0.438
Year:Season:Habitat	3	20.05	0.70	0.552
Year:Estuary:Habitat	3	4.48	0.16	0.925
Season:Estuary:Habitat	3	26.58	0.93	0.428
Year:Site(Estuary):Habitat	6	12.77	0.45	0.844
Season:Site(Estuary):Habitat	6	10.33	0.36	0.901
Year:Season:Estuary:Habitat	3	41.81	1.47	0.228
Year:Season:Site:Habitat	6	8.41	0.29	0.938

(b)

Habitat Contrasts	Winter		Summer	
	t	p	t	p
Bare – Mangroves	-0.79	0.857	-4.28	<0.001
Bare – Oyster Reef	-0.48	0.963	-4.90	<0.001
Bare – Seagrass	-0.30	0.990	-1.62	0.374
Mangroves – Oyster Reef	0.32	0.988	-0.56	0.943
Mangroves – Seagrass	0.50	0.958	2.73	0.037
Oyster reef – Seagrass	0.18	0.998	3.34	0.006

Table C.6: Summary of Linear Mixed Effects Models of juvenile breem observations per video showing (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		8.67	0.003
Source	df	MS	F value	Pr(>F)
Year	1	23.45	22.60	<0.001
Season	1	125.90	121.32	<0.001
Estuary	1	27.60	26.59	<0.001
Site(Estuary)	2	6.44	6.21	0.005
Habitat	3	161.12	155.26	<0.001
Year:Habitat	3	5.77	5.56	<0.001
Season:Habitat	3	75.62	72.87	<0.001
Estuary:Habitat	3	15.26	14.71	<0.001
Site(Estuary):Habitat	6	6.80	6.55	<0.001
Year:Season:Habitat	3	11.08	10.68	<0.001
Year:Estuary:Habitat	3	2.36	2.28	0.079
Season:Estuary:Habitat	3	6.44	6.21	<0.001
Year:Site(Estuary):Habitat	6	3.88	3.4	0.001
Season:Site(Estuary):Habitat	6	6.63	6.38	<0.001
Year:Season:Estuary:Habitat	3	1.09	1.05	0.368
Year:Season:Site:Habitat	6	5.00	4.82	<0.001

(b)

Year 1								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.06	0.999	-0.59	0.934	-5.22	<0.001	-2.81	0.026
Bare – Oyster Reef	-0.88	0.815	-0.21	0.996	-7.19	<0.001	-10.12	<0.001
Bare – Seagrass	-0.13	0.999	-0.11	0.999	-0.81	0.848	-4.10	<0.001
Mangroves – Oyster Reef	-0.96	0.771	0.39	0.979	-1.98	0.198	-7.40	<0.001
Mangroves – Seagrass	-0.19	0.997	0.50	0.959	4.29	<0.001	-1.24	0.598
Oyster reef – Seagrass	0.72	0.887	0.11	0.999	6.22	<0.001	6.32	<0.001

Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.70	0.324	-0.47	0.964	-3.99	<0.001	-7.17	<0.001
Bare – Oyster Reef	-0.92	0.792	-3.91	<0.001	-7.91	<0.001	-13.41	<0.001
Bare – Seagrass	-0.85	0.829	-2.30	0.098	-0.37	0.983	-0.94	0.783
Mangroves – Oyster Reef	0.83	0.842	-3.43	0.004	-5.45	<0.001	-7.36	<0.001
Mangroves – Seagrass	0.94	0.784	-1.83	0.260	5.14	<0.001	7.26	<0.001
Oyster reef – Seagrass	0.09	0.999	1.60	0.377	10.70	<0.001	14.46	<0.001

Year 2								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.68	0.903	-1.12	0.679	-3.12	0.010	0.02	1.000
Bare – Oyster Reef	-0.69	0.898	-0.29	0.991	-7.15	<0.001	-0.55	0.947
Bare – Seagrass	-0.05	1.000	-0.13	0.999	0.35	0.985	-0.44	0.972
Mangroves – Oyster Reef	0.02	1.000	0.85	0.832	-4.24	<0.001	0.56	0.942
Mangroves – Seagrass	0.73	0.887	1.01	0.743	3.48	0.003	-0.45	0.969
Oyster reef – Seagrass	0.75	0.878	0.17	0.998	7.52	<0.001	0.11	0.999

Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.67	0.339	-1.57	0.394	-3.54	0.002	-8.46	<0.001
Bare – Oyster Reef	-4.22	<0.001	-2.49	0.063	-4.03	<0.001	-12.29	<0.001
Bare – Seagrass	-1.94	0.211	0.01	1.000	-0.10	0.999	-0.12	0.999
Mangroves – Oyster Reef	-3.20	0.008	-0.76	0.872	-0.40	0.978	-3.75	0.001
Mangroves – Seagrass	-0.33	0.988	1.65	0.351	3.43	0.003	8.73	<0.001
Oyster reef – Seagrass	2.90	0.020	2.62	0.044	3.93	<0.001	12.78	<0.001

Table C.7: Summary of Linear Mixed Effects Models of the logratio of luderick observations for adults and juveniles per day showing (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat and Site and Habitat and Season. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.59	0.441
Fixed effects	df	MS	F value	Pr(>F)
Year	1	2.55	0.09	0.763
Season	1	0.03	0.01	0.972
Estuary	1	95.72	3.48	0.072
Site(Estuary)	2	35.36	1.29	0.291
Habitat	3	101.07	3.67	0.015
Year:Habitat	3	3.33	0.12	0.947
Season:Habitat	3	221.53	8.06	<0.001
Estuary:Habitat	3	206.96	7.53	<0.001
Site(Estuary):Habitat	6	38.54	1.40	0.222
Year:Season:Habitat	3	19.89	0.72	0.540
Year:Estuary:Habitat	3	16.48	0.59	0.617
Season:Estuary:Habitat	3	12.64	0.46	0.711
Year:Site(Estuary):Habitat	6	46.83	1.70	0.129
Season:Site(Estuary):Habitat	6	182.32	6.63	<0.001
Year:Season:Estuary:Habitat	3	7.66	0.28	0.841
Year:Season:Site:Habitat	6	6.03	0.22	0.969

(b)

Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.78	0.291	-2.06	0.174	-0.85	0.828	-0.30	0.990
Bare – Oyster Reef	0.51	0.955	-2.05	0.178	-3.01	0.017	-3.58	0.003
Bare – Seagrass	-2.33	0.098	-0.32	0.988	0.81	0.847	-2.30	0.105
Mangroves – Oyster Reef	2.44	0.076	0.01	1.000	-2.16	0.142	-3.06	0.015
Mangroves – Seagrass	-0.59	0.934	1.74	0.310	1.67	0.346	-1.86	0.254
Oyster reef – Seagrass	-3.03	0.016	1.73	0.316	3.83	0.001	1.28	0.578

Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.04	1.000	3.98	<0.001	2.38	0.088	2.93	0.022
Bare – Oyster Reef	-1.17	0.646	3.50	0.004	1.82	0.268	-1.13	0.673
Bare – Seagrass	-0.05	0.999	0.01	1.000	1.74	0.307	3.15	0.011
Mangroves – Oyster Reef	-1.29	0.572	-0.48	0.963	-0.59	0.934	-4.06	<0.001
Mangroves – Seagrass	-0.09	0.999	-3.98	<0.001	-0.68	0.905	0.23	0.996
Oyster reef – Seagrass	1.19	0.634	-3.50	0.004	-0.09	0.999	4.28	<0.001

Table C.8: Summary of Linear Mixed Effects Models of juvenile luderick observations per video showing (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		8.63	0.003
Fixed effects	df	MS	F value	Pr(>F)
Year	1	0.14	0.23	0.633
Season	1	30.49	51.78	<0.001
Estuary	1	0.40	0.69	0.412
Site(Estuary)	2	0.68	1.15	0.325
Habitat	3	29.62	50.31	<0.001
Year:Habitat	3	1.94	3.30	0.020
Season:Habitat	3	19.79	33.61	<0.001
Estuary:Habitat	3	0.07	0.13	0.944
Site(Estuary):Habitat	6	3.26	5.53	<0.001
Year:Season:Habitat	3	2.11	3.59	0.013
Year:Estuary:Habitat	3	0.47	0.79	0.496
Season:Estuary:Habitat	3	0.04	0.06	0.979
Year:Site(Estuary):Habitat	6	1.29	2.20	0.041
Season:Site(Estuary):Habitat	6	4.95	8.41	<0.001
Year:Season:Estuary:Habitat	3	0.84	1.42	0.234
Year:Season:Site:Habitat	6	1.59	2.71	0.013

(b)

Year 1								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.12	0.995	0.02	1.000	-0.40	0.978	0.02	0.750
Bare – Oyster Reef	-0.21	0.996	-0.40	0.979	-3.86	<0.001	-5.41	<0.001
Bare – Seagrass	-0.14	0.999	0.15	0.998	0.25	0.994	-0.85	<0.001
Mangroves – Oyster Reef	-0.34	0.987	-0.43	0.973	-3.46	0.003	-5.44	<0.001
Mangroves – Seagrass	-0.26	0.976	0.13	0.999	0.65	0.917	-0.87	<0.001
Oyster reef – Seagrass	0.05	0.999	0.56	0.944	4.03	<0.001	4.57	0.465

Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.23	0.996	0.25	0.994	-0.64	0.917	0.02	1.000
Bare – Oyster Reef	-1.00	0.751	0.35	0.986	0.04	1.000	-4.47	<0.001
Bare – Seagrass	0.14	0.999	0.08	0.999	-0.13	0.999	-0.03	1.000
Mangroves – Oyster Reef	-1.16	0.654	0.09	0.999	0.95	0.775	-5.21	<0.001
Mangroves – Seagrass	-0.10	0.999	-0.18	0.998	0.73	0.884	-0.06	0.999
Oyster reef – Seagrass	1.16	0.652	-0.27	0.993	-0.24	0.995	5.15	<0.001

Year 2								
Botany Bay								
Habitat Contrasts	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.18	0.997	0.06	0.999	-0.23	0.995	0.02	1.000
Bare – Oyster Reef	-0.22	0.996	-1.00	0.747	-10.11	<0.001	-5.41	<0.001
Bare – Seagrass	-0.06	0.999	-0.57	0.942	0.18	0.998	-0.85	0.832
Mangroves – Oyster Reef	-0.04	1.000	-1.09	0.696	-10.36	<0.001	-5.44	<0.001
Mangroves – Seagrass	0.14	0.999	-0.64	0.918	0.42	0.976	-0.87	0.820
Oyster reef – Seagrass	0.18	0.997	0.45	0.970	10.29	<0.001	4.57	<0.001

Port Stephens								
Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.24	0.995	-0.04	1.000	-0.03	1.000	-1.00	0.7481
Bare – Oyster Reef	-0.77	0.869	-0.34	0.987	-0.43	0.974	-7.88	<0.001
Bare – Seagrass	-0.55	0.945	-0.04	1.000	-0.40	0.978	0.11	0.999
Mangroves – Oyster Reef	-0.66	0.913	-0.29	0.991	-0.38	0.981	-7.03	<0.001
Mangroves – Seagrass	-0.39	0.979	-0.01	1.000	-0.36	0.984	1.16	0.652
Oyster reef – Seagrass	0.27	0.993	0.31	0.989	0.02	1.000	8.38	<0.001

Table C.9: Summary of Linear Mixed Effects Models of the logratio of tarwhine observations for adults and juveniles per day showing (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat and Estuary. Significant effects ($P < 0.05$) are in bold

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.13	0.722
Fixed effects	df	MS	F value	Pr(>F)
Year	1	7.36	0.49	0.490
Season	1	0.01	0.01	0.998
Estuary	1	48.60	3.22	0.082
Site(Estuary)	2	28.26	1.87	0.169
Habitat	3	112.59	7.46	<0.001
Year:Habitat	3	0.78	0.05	0.984
Season:Habitat	3	12.22	0.81	0.453
Estuary:Habitat	3	56.51	3.74	0.013
Site(Estuary):Habitat	6	19.03	1.26	0.283
Year:Season:Habitat	3	6.54	0.43	0.729
Year:Estuary:Habitat	3	9.07	0.60	0.616
Season:Estuary:Habitat	3	12.40	0.82	0.484
Year:Site(Estuary):Habitat	6	19.33	1.28	0.273
Season:Site(Estuary):Habitat	6	12.87	0.85	0.532
Year:Season:Estuary:Habitat	3	6.13	0.40	0.748
Year:Season:Site:Habitat	6	14.42	0.95	0.459

(b)

Habitat Contrasts	Botany Bay		Port Stephens	
	t ratio	p	t ratio	p
Bare – Mangroves	-1.88	0.243	-1.06	0.714
Bare – Oyster Reef	-1.95	0.214	-1.42	0.492
Bare – Seagrass	-2.22	0.126	-4.43	<0.001
Mangroves – Oyster Reef	-0.04	1.000	-0.37	0.983
Mangroves – Seagrass	-0.30	0.990	-3.47	0.004
Oyster reef – Seagrass	-0.27	0.993	-3.11	0.013

Table C.10: Summary of Linear Mixed Effects Models of juvenile tarwhine observations per video showing (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		40.54	<0.001
Fixed effects	df	MS	F value	Pr(>F)
Year	1	0.82	3.71	0.063
Season	1	2.59	11.68	0.001
Estuary	1	0.01	0.05	0.815
Site(Estuary)	2	0.04	0.21	0.812
Habitat	3	4.48	20.18	<0.001
Year:Habitat	3	0.68	3.07	0.027
Season:Habitat	3	1.56	7.04	<0.001
Estuary:Habitat	3	0.33	1.48	0.220
Site(Estuary):Habitat	6	0.66	2.97	0.007
Year:Season:Habitat	3	1.18	5.34	0.001
Year:Estuary:Habitat	3	0.19	0.88	0.451
Season:Estuary:Habitat	3	0.03	0.17	0.914
Year:Site(Estuary):Habitat	6	0.79	3.58	0.001
Season:Site(Estuary):Habitat	6	0.45	2.03	0.059
Year:Season:Estuary:Habitat	3	0.08	0.34	0.793
Year:Season:Site:Habitat	6	0.62	2.81	0.010

(b)

Year 1								
Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.20	0.997	-0.48	0.963	-0.22	0.996	-1.73	0.311
Bare – Oyster Reef	-0.34	0.986	-0.01	1.000	0.11	0.999	-1.47	0.458
Bare – Seagrass	-0.23	0.955	0.18	0.997	-0.74	0.882	-10.21	<0.001
Mangroves – Oyster Reef	-0.56	0.944	0.48	0.962	0.33	0.987	0.32	0.988
Mangroves – Seagrass	-0.44	0.972	0.69	0.901	-0.52	0.954	-8.50	<0.001
Oyster reef – Seagrass	0.09	0.999	0.20	0.997	-0.84	0.833	-9.18	<0.001
Port Stephens								
Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	0.33	0.987	1.03	0.734	-0.77	0.869	0.24	0.999
Bare – Oyster Reef	-0.11	0.999	1.18	0.642	-0.30	0.990	0.03	1.000
Bare – Seagrass	-0.18	0.997	-0.99	0.752	-2.30	0.099	-3.05	0.013
Mangroves – Oyster Reef	-0.42	0.974	0.15	0.998	0.65	0.916	-0.25	0.995
Mangroves – Seagrass	-0.51	0.957	-2.02	0.181	-2.16	0.134	-3.84	<0.001
Oyster reef – Seagrass	-0.08	0.999	-2.17	0.132	-2.83	0.025	-3.51	0.003
Year 2								
Habitat Contrasts	Botany Bay							
	Winter				Summer			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.29	0.991	0.07	0.999	-0.31	0.989	0.04	1.000
Bare – Oyster Reef	-0.35	0.985	0.03	1.000	-1.55	0.405	-0.32	0.989
Bare – Seagrass	-0.09	0.999	-0.77	0.867	-0.86	0.826	-0.63	0.923
Mangroves – Oyster Reef	-0.06	0.999	-0.04	1.000	-1.30	0.562	-0.36	0.984
Mangroves – Seagrass	0.23	0.996	-0.86	0.822	-0.58	0.938	-0.67	0.909
Oyster reef – Seagrass	0.29	0.991	-0.82	0.843	0.66	0.912	-0.31	0.989
Habitat Contrasts	Port Stephens							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.700	0.897	-0.07	0.999	-0.68	0.905	0.01	1.000
Bare – Oyster Reef	-0.66	0.911	-0.54	0.948	-0.26	0.994	-0.72	0.889
Bare – Seagrass	-2.87	0.022	-0.07	0.999	-3.75	0.001	-0.87	0.822
Mangroves – Oyster Reef	0.05	1.000	-0.45	0.968	0.42	0.975	-0.74	0.881
Mangroves – Seagrass	-2.77	0.029	0.01	1.000	-2.98	0.016	-0.89	0.810
Oyster reef – Seagrass	-2.76	0.030	0.50	0.959	-3.48	0.003	-0.15	0.999

Table C.11: Summary of Linear Mixed Effects Models of the logratio of silverbiddy observations for adults and juveniles per day showing (a) main effects and interactions of the random effect in the ANOVA for random effects and interactions among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Estuary, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.49	0.486
Fixed effects	df	MS	F value	Pr(>F)
Year	1	2.36	0.08	0.772
Season	1	782.3	28.27	<0.001
Estuary	1	6.57	0.24	0.629
Site(Estuary)	2	12.20	0.44	0.647
Habitat	3	115.10	4.16	0.008
Year:Habitat	3	19.05	0.69	0.561
Season:Habitat	3	19.83	0.71	0.544
Estuary:Habitat	3	74.04	2.67	0.051
Site(Estuary):Habitat	6	81.47	2.94	0.011
Year:Season:Habitat	3	37.50	1.35	0.261
Year:Estuary:Habitat	3	22.00	0.79	0.499
Season:Estuary:Habitat	3	55.94	2.02	0.116
Year:Site(Estuary):Habitat	6	4.88	0.27	0.983
Season:Site(Estuary):Habitat	6	73.02	2.64	0.021
Year:Season:Estuary:Habitat	3	77.58	2.80	0.044
Year:Season:Site:Habitat	6	53.14	1.92	0.085

(b)

Habitat Contrasts	Year 1							
	Winter				Summer			
	Botany Bay		Port Stephens		Botany Bay		Port Stephens	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-1.17	0.646	-2.45	0.075	-0.23	0.995	-0.26	0.994
Bare – Oyster Reef	-0.62	0.927	-1.42	0.487	-2.94	0.021	-0.27	0.993
Bare – Seagrass	-1.17	0.646	0.45	0.969	-0.37	0.982	-0.32	0.989
Mangroves – Oyster Reef	0.55	0.945	1.02	0.736	-2.53	0.622	-0.01	1.000
Mangroves – Seagrass	0.01	1.000	2.90	0.024	-0.12	0.999	-0.06	0.999
Oyster reef – Seagrass	-0.55	0.945	1.88	0.246	2.56	0.057	-0.05	0.999

Habitat Contrasts	Year 2							
	Winter				Summer			
	Botany Bay		Port Stephens		Botany Bay		Port Stephens	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.63	0.921	-0.67	0.907	-1.65	0.357	-1.94	0.217
Bare – Oyster Reef	-0.07	0.999	-0.17	0.998	-0.95	0.778	-1.14	0.664
Bare – Seagrass	0.51	0.957	-0.60	0.931	0.42	0.976	-1.93	0.224
Mangroves – Oyster Reef	0.60	0.932	0.533	0.951	0.69	0.897	0.80	0.853
Mangroves – Seagrass	1.21	0.619	0.076	0.999	2.06	0.172	0.17	1.000
Oyster reef – Seagrass	0.62	0.927	-0.46	0.968	1.37	0.524	-0.78	0.861

Table C.12: Summary of Linear Mixed Effects Models of juvenile silverbiddy observations per video showing (a) main effects and interactions of the random effect in the ANOVA for random effects and interactions among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat and Site and Habitat and Estuary. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		5.23	0.022
Fixed effects	df	MS	F value	Pr(>F)
Year	1	0.18	1.55	0.220
Season	1	0.86	7.30	0.010
Estuary	1	0.29	2.44	0.126
Site(Estuary)	2	0.67	5.70	0.007
Habitat	3	0.68	5.76	<0.001
Year:Habitat	3	0.12	1.05	0.371
Season:Habitat	3	0.07	0.55	0.643
Estuary:Habitat	3	0.72	6.12	<0.001
Site(Estuary):Habitat	6	0.45	3.80	<0.001
Year:Season:Habitat	3	0.07	0.60	0.613
Year:Estuary:Habitat	3	0.11	0.94	0.419
Season:Estuary:Habitat	3	0.14	1.16	0.325
Year:Site(Estuary):Habitat	6	0.09	0.75	0.604
Season:Site(Estuary):Habitat	6	0.07	0.57	0.757
Year:Season:Estuary:Habitat	3	0.11	0.91	0.433
Year:Season:Site:Habitat	6	0.05	0.41	0.871

(b)

Habitat Contrasts	Sites							
	Carters Island		Quibray Bay		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-0.36	0.984	-1.66	0.346	-0.24	0.995	-4.53	<0.001
Bare – Oyster Reef	-0.31	0.989	-1.08	0.705	-0.08	0.999	-4.64	<0.001
Bare – Seagrass	-0.04	1.000	-0.88	0.814	-0.29	0.992	0.17	0.998
Mangroves – Oyster Reef	0.06	0.999	0.60	0.931	0.19	0.998	-0.02	1.000
Mangroves – Seagrass	0.33	0.987	0.80	0.854	-0.04	1.000	4.99	<0.001
Oyster reef – Seagrass	0.28	0.992	0.19	0.997	-0.24	0.995	5.13	<0.001

Table C.13: Summary of Linear Mixed Effects Models of the relative percentage of feeding observations for juveniles per day showing (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Site and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.96	0.326
Fixed effects	df	MS	F value	Pr(>F)
Year	1	0.01	0.50	0.481
Season	1	0.09	3.45	0.072
Estuary	1	0.01	0.55	0.464
Site(Estuary)	2	0.06	2.14	0.133
Habitat	3	0.03	1.27	0.290
Year:Habitat	3	0.04	1.55	0.207
Season:Habitat	3	0.05	1.93	0.129
Estuary:Habitat	3	0.02	0.72	0.544
Site(Estuary):Habitat	6	0.05	1.67	0.136
Year:Season:Habitat	3	0.01	0.58	0.627
Year:Estuary:Habitat	3	0.05	1.74	0.163
Season:Estuary:Habitat	3	0.02	0.79	0.503
Year:Site(Estuary):Habitat	6	0.07	2.53	0.026
Season:Site(Estuary):Habitat	6	0.01	0.19	0.977
Year:Season:Estuary:Habitat	3	0.01	0.47	0.700
Year:Season:Site:Habitat	6	0.01	0.05	0.999

(b)

Habitat Contrasts	Botany Bay							
	Year 1				Year 2			
	Carters Island		Quibray Bay		Carters Island		Quibray Bay	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-2.10	0.160	-0.05	1.000	-1.54	0.417	-0.97	0.767
Bare – Oyster Reef	-2.98	0.019	-2.14	0.148	-1.63	0.366	-3.85	0.001
Bare – Seagrass	-2.59	0.054	-1.89	0.236	-1.58	0.393	-1.12	0.678
Mangroves – Oyster Reef	-0.88	0.815	-2.58	0.214	-0.09	0.999	-2.88	0.025
Mangroves – Seagrass	-0.48	0.962	-1.38	0.317	-0.04	1.000	-0.15	0.999
Oyster reef – Seagrass	0.39	0.979	1.19	0.995	0.05	1.000	2.73	0.037

Habitat Contrasts	Port Stephens							
	Year 1				Year 2			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-2.38	0.087	-1.74	0.308	-0.59	0.934	-3.81	0.001
Bare – Oyster Reef	-1.40	0.500	-2.31	0.102	-3.00	0.018	-4.14	<0.001
Bare – Seagrass	-0.61	0.928	-1.67	0.345	-1.88	0.241	0.00	1.000
Mangroves – Oyster Reef	1.05	0.721	-0.57	0.939	-2.58	0.055	-0.33	0.987
Mangroves – Seagrass	1.89	0.237	0.07	0.999	-1.38	0.512	3.81	0.001
Oyster reef – Seagrass	0.85	0.832	0.64	0.917	1.19	0.633	4.14	<0.001

Table C.14: Summary of Linear Mixed Effects Models on the percentage of fish wandering observations for juveniles per day showing (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat, Season and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		1.90	0.168
Fixed effects	df	MS	F value	Pr(>F)
Year	1	0.07	0.61	0.442
Season	1	0.05	0.43	0.516
Estuary	1	0.11	0.92	0.345
Site(Estuary)	2	0.13	1.13	0.336
Habitat	3	0.58	4.95	0.003
Year:Habitat	3	0.07	0.57	0.633
Season:Habitat	3	0.54	4.62	0.004
Estuary:Habitat	3	0.03	0.26	0.855
Site(Estuary):Habitat	6	0.07	0.56	0.758
Year:Season:Habitat	3	0.55	4.70	0.004
Year:Estuary:Habitat	3	0.08	0.73	0.533
Season:Estuary:Habitat	3	0.09	0.72	0.540
Year:Site(Estuary):Habitat	6	0.08	0.72	0.633
Season:Site(Estuary):Habitat	6	0.09	0.76	0.602
Year:Season:Estuary:Habitat	3	0.08	0.68	0.564
Year:Season:Site:Habitat	6	0.09	0.80	0.570

(b)

Habitat Contrasts	Year 1				Year 2			
	Winter		Summer		Winter		Summer	
	t	p	t	p	t	p	t	p
Bare – Mangroves	-2.14	0.147	-5.85	<0.001	-4.63	<0.001	-2.48	0.069
Bare – Oyster Reef	-2.90	0.023	-6.17	<0.001	-4.61	<0.001	-2.88	0.025
Bare – Seagrass	-2.91	0.021	-4.68	<0.001	-2.23	0.123	-2.79	0.032
Mangroves – Oyster Reef	-0.76	0.871	-0.13	0.999	0.02	1.000	-0.40	0.979
Mangroves – Seagrass	-0.81	0.850	1.35	0.534	2.56	0.057	-0.31	0.988
Oyster reef – Seagrass	-0.05	1.000	1.53	0.422	2.54	0.061	0.09	0.999

Table C.15: Summary of Linear Mixed Effects Models on the percentage of passing observations for juveniles per day showing (a) main effects and interactions of the random effect in the ANOVA for random effects, and among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors examining effects of Habitat and Year. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		1.12	0.289
Source	df	MS	F value	Pr(>F)
Year	1	0.73	14.74	<0.001
Season	1	0.01	0.01	0.988
Estuary	1	0.07	1.54	0.224
Site(Estuary)	2	0.05	1.10	0.344
Habitat	3	0.23	4.59	0.004
Year:Habitat	3	0.19	3.89	0.011
Season:Habitat	3	0.08	1.58	0.199
Estuary:Habitat	3	0.01	0.31	0.819
Site(Estuary):Habitat	6	0.01	0.27	0.951
Year:Season:Habitat	3	0.04	0.86	0.464
Year:Estuary:Habitat	3	0.01	0.15	0.926
Season:Estuary:Habitat	3	0.01	0.16	0.922
Year:Site(Estuary):Habitat	6	0.01	0.15	0.987
Season:Site(Estuary):Habitat	6	0.03	0.71	0.644
Year:Season:Estuary:Habitat	3	0.02	0.35	0.785
Year:Season:Site:Habitat	6	0.03	0.54	0.777

(b)

Habitat Contrasts	Year 1		Year 2	
	t	p	t	p
Bare – Mangroves	-1.62	0.369	-1.07	0.709
Bare – Oyster Reef	-1.07	0.711	-0.01	1.000
Bare – Seagrass	-3.50	0.004	0.85	0.829
Mangroves – Oyster Reef	0.58	0.936	1.09	0.697
Mangroves – Seagrass	-1.85	0.256	1.98	0.201
Oyster reef – Seagrass	-2.48	0.070	0.89	0.807

Appendix D:

CHAPTER 5 SUPPLEMENTARY MATERIAL

D.1 TABLES

Table D.1: List of fish identified during the study. The total number of observations, across all cameras, and the mean and standard error (SE) observation per camera per habitat are shown.

Family	Species	Total number of Observations	Baskets N=96		Racks N=95		Oyster reef N=83		Seagrass N=82		Mangroves N=79		Bare N=75	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Apogonidae	<i>Siphamia cephalotes</i>	59	10.0	0.0	0.0	0.0	0.0	0.0	49.0	0.0	0.0	0.0	0.0	0.0
Arripidae	<i>Arripis trutta</i>	2	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0
Belonidae	<i>Strongylura leiura</i>	32	0.0	0.0	0.0	0.0	24.0	0.0	0.0	0.0	3.0	2.0	2.0	0.0
Belonidae	<i>Tylosurus gavioides</i>	21	0.0	0.0	0.0	0.0	15.0	0.0	1.0	0.0	3.0	0.0	2.0	0.0
Blennidae	<i>Omobranchus anolius</i>	1906	31.5	12.5	36.0	12.0	626.5	163.5	0.0	0.0	258.5	72.5	1.0	0.0

Blennidae	<i>Omobranchus rotundiceps</i>	393	3.0	2.0	5.0	0.0	183.0	144.0	0.0	0.0	8.0	1.0	0.0	0.0
Blennidae	<i>Parablennius intermedius</i>	8	2.0	0.0	5.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Blennidae	<i>Petroscirtes breviceps</i>	1	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Blennidae	<i>Petroscirtes lupus</i>	22	5.5	2.5	0.0	0.0	1.0	0.0	5.0	3.0	0.0	0.0	0.0	0.0
Brachaeluridae	<i>Brachaelurus waddi</i>	4	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetodontidae	<i>Chaetodon auriga</i>	3	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cheilodactylidae	<i>Cheilodactylus vestitus</i>	8	5.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clupeidae	<i>Herklotichthys castelnaui</i>	60	25.0	0.0	11.0	0.0	1.0	0.0	11.5	4.5	0.0	0.0	0.0	0.0
Clupeidae	<i>Hyperlophus vittatus</i>	1	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dasyatidae	<i>Hemitrygon fluviorum</i>	49	2.5	0.5	2.0	0.0	2.5	0.5	11.5	8.5	1.0	0.0	6.5	0.5
Dasyatidae	<i>Neotrygon australiae</i>	10	3.0	0.0	1.0	0.0	1.0	0.0	2.0	0.0	1.0	0.0	2.0	0.0
Dinolestidae	<i>Dinolestes lewini</i>	2	0.0	0.0	0.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Diodontidae	<i>Dicotylichthys punctulatus</i>	350	58.0	0.0	88.0	40.0	14.5	9.5	11.5	3.5	3.0	0.0	3.0	0.0
Echeneidae	<i>Echeneis naucrates</i>	1	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Elopidae	<i>Elops hawaiiensis</i>	3	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0
Ephippidae	<i>Platax teira</i>	2	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fistulariidae	<i>Fistularia petimba</i>	1	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Gerreidae	<i>Gerres subfasciatus</i>	704	37.0	33.0	134.5	4.5	69.5	38.5	19.0	14.0	51.5	44.5	40.5	9.5
Girellidae	<i>Girella tricuspidata</i>	6671	966.5	131.5	2030.0	384.0	190.0	135.0	20.5	0.5	128.0	78.0	1.0	0.0
Gobiidae	<i>Acanthogobius flavimanus</i>	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0
Gobiidae	<i>Arenigobius bifrenatus</i>	82	0.0	0.0	0.0	0.0	26.0	5.0	0.0	0.0	15.0	1.0	0.0	0.0
Gobiidae	<i>Bathygobius krefftii</i>	10	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	9.0	0.0	0.0	0.0
Gobiidae	<i>Cryptocentroides gobioides</i>	294	1.0	0.0	2.0	0.0	66.0	28.0	0.0	0.0	79.5	30.5	0.0	0.0
Gobiidae	<i>Favonigobius exquisitus</i>	60	4.0	3.0	21.0	0.0	10.5	2.5	0.0	0.0	3.5	0.5	3.0	0.0
Gobiidae	<i>Favonigobius lentiginosus</i>	160	9.0	0.0	9.5	7.5	19.5	3.5	0.0	0.0	12.5	1.5	34.0	21.0

Gobiidae	<i>Redigobius macrostoma</i>	9	0.0	0.0	1.0	0.0	4.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemiramphidae	<i>Hyporhamphus australis</i>	2	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0
Hemiramphidae	<i>Hyporhamphus regularis</i>	3	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0
Hypnidae	<i>Hypnos monopterygius</i>	7	0.0	0.0	7.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosidae	<i>Kyphosus sydneyanus</i>	2	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kyphosidae	<i>Scorpiis lineolata</i>	1	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Labridae	<i>Achoerodus viridis</i>	4	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Labridae	<i>Neodax balteatus</i>	1	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Labridae	<i>Pictilabrus laticlavus</i>	1	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Labridae	<i>Pseudolabrus guentheri</i>	231	3.0	0.0	107.5	80.5	12.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Monacanthidae	<i>Acanthaluteres spilomelanurus</i>	127	5.0	3.0	0.0	0.0	0.0	0.0	58.5	11.5	0.0	0.0	0.0	0.0
Monacanthidae	<i>Acanthaluteres vittiger</i>	15	1.0	0.0	0.0	0.0	0.0	0.0	7.0	4.0	0.0	0.0	0.0	0.0
Monacanthidae	<i>Brachaluteres jacksonianus</i>	7	4.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Monacanthidae	<i>Meuschenia trachylepis</i>	394	14.5	13.5	50.5	41.5	0.0	0.0	131.5	69.5	0.0	0.0	1.0	0.0
Monacanthidae	<i>Meuschenia venusta</i>	6	0.0	0.0	0.0	0.0	0.0	0.0	3.0	2.0	0.0	0.0	0.0	0.0
Monacanthidae	<i>Monacanthus chinensis</i>	73	6.0	4.0	15.5	1.5	9.5	8.5	4.5	1.5	0.0	0.0	2.0	0.0
Monacanthidae	<i>Scobinichthys granulatus</i>	5	1.0	0.0	1.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0
Monodactylidae	<i>Monodactylus argenteus</i>	8	6.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0
Mugilidae	<i>Liza argentea</i>	81	0.0	0.0	18.0	0.0	11.5	2.5	0.0	0.0	13.5	6.5	13.0	0.0
Mugilidae	<i>Mugil cephalus</i>	241	19.0	0.0	25.0	0.0	82.0	70.0	0.0	0.0	16.0	14.0	1.0	0.0
Mugilidae	<i>Myxus elongatus</i>	16	0.0	0.0	0.0	0.0	4.5	3.5	0.0	0.0	2.5	0.5	2.0	0.0
Mugilidae	<i>Paramugil georgii</i>	50	2.0	0.0	0.0	0.0	17.5	15.5	0.0	0.0	3.0	0.0	5.0	2.0
Mullidae	<i>Parupeneus spilurus</i>	6	2.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Myliobatidae	<i>Myliobatis tenuicaudatus</i>	7	0.0	0.0	1.0	0.0	4.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0
Orectolobidae	<i>Orectolobus halei</i>	6	0.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orectolobidae	<i>Orectolobus maculatus</i>	1	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paralichthyidae	<i>Pseudorhombus arsius</i>	1	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Paralichthyidae	<i>Pseudorhombus jenynsii</i>	4	0.0	0.0	0.0	0.0	1.5	0.5	0.0	0.0	0.0	0.0	1.0	0.0
Pempheridae	<i>Pempheris multiradiata</i>	5	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Platycephalidae	<i>Platycephalus fuscus</i>	19	1.0	0.0	3.5	2.5	2.0	1.0	1.0	0.0	0.0	0.0	2.5	1.5
Plotosidae	<i>Cnidoglanis macrocephalous</i>	16	0.0	0.0	6.0	5.0	1.0	0.0	1.5	0.5	0.0	0.0	0.0	0.0
Pomacentridae	<i>Abudefduf sexfasciatus</i>	1	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Pomatomidae	<i>Pomatomus saltatrix</i>	56	1.0	0.0	20.0	16.0	3.0	0.0	11.0	0.0	0.0	0.0	0.0	0.0
Rhinobatidae	<i>Aptychotrema rostrata</i>	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Scatophagidae	<i>Selenotoca multifasciata</i>	9	2.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Sciaenidae	<i>Argyrosomus japonicus</i>	205	0.0	0.0	201.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0
Scorpididae	<i>Microcanthus strigatus</i>	970	87.5	47.5	99.0	92.0	278.0	122.0	0.0	0.0	41.0	0.0	0.0	0.0
Sillaginidae	<i>Sillago ciliata</i>	699	79.5	73.5	60.0	30.0	19.5	8.5	13.5	7.5	31.5	23.5	145.5	61.5
Sillaginidae	<i>Sillago maculata</i>	24	0.0	0.0	21.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Soleidae	<i>Aseraggodes lenisquamis</i>	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Sparidae	<i>Acanthopagrus australis</i>	11579	1052.0	167.0	1998.0	6.0	1764.5	579.5	184.5	17.5	758.0	275.0	32.5	4.5
Sparidae	<i>Rhabdosargus sarba</i>	158	11.5	0.5	11.0	1.0	4.0	2.0	47.0	22.0	5.0	0.0	3.0	1.0
Sphyracidae	<i>Sphyracna obtusata</i>	217	23.0	18.0	10.0	8.0	1.0	0.0	75.0	3.0	0.0	0.0	0.0	0.0
Syngnathidae	<i>Stigmatopora nigra</i>	1	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Terapontidae	<i>Pelates sexlineatus</i>	1163	254.5	222.5	84.5	64.5	35.0	20.0	203.5	126.5	2.0	0.0	6.0	0.0
Tetraodontidae	<i>Contusus brevicaudus</i>	1	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tetraodontidae	<i>Marilyna pleurosticta</i>	2	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Tetraodontidae	<i>Reicheltia halsteadii</i>	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Tetraodontidae	<i>Tetractenos glaber</i>	72	9.5	8.5	8.0	4.0	6.0	0.0	8.0	5.0	6.0	2.0	3.0	0.0
Tetraodontidae	<i>Tetractenos hamiltoni</i>	31	4.5	3.5	0.0	0.0	0.0	0.0	2.5	0.5	14.0	0.0	3.0	0.0
Tetraodontidae	<i>Tetractenos squamicauda</i>	2	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tetraodontidae	<i>Torquigener pleurogramma</i>	3	1.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tetraodontidae	<i>Torquigener squamicauda</i>	7	7.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Tetrarogidae	<i>Centropogon australis</i>	45	2.0	0.0	1.0	0.0	21.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tripterygiidae	<i>Lepidoblennius haplodactylus</i>	10	0.0	0.0	0.0	0.0	5.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trygonorrhinidae	<i>Trygonorrhina fasciata</i>	46	4.0	0.0	20.0	0.0	5.5	2.5	3.0	2.0	0.0	0.0	2.5	0.5	
Urolophidae	<i>Trygonoptera testacea</i>	47	20.0	0.0	1.0	0.0	6.0	0.0	4.0	0.0	0.0	0.0	7.5	6.5	

Table D.2: (a) Five-factor mixed-model PERMANOVAs testing for differences in the observations data of each fish species observed per habitat (fish community structure), and across sites, between years and seasons and among days. A posteriori pairwise PERMANOVAs examined significant differences (b) between habitats, within sites and seasons, and (c) between habitats, within sites and years. Analyses used Bray Curtis similarities calculated using fish observations (by species). Boldface indicates significance at $\alpha = 0.05$. For similarity, boldface indicates most and least similar comparisons.

(a)

Source	df	MS	Pseudo-F	P(perm)
Year	1	3884	1.05	0.509
Season	1	64145	2.52	0.215
Site	1	21309	5.75	0.508
Habitat	5	1.1E+05	7.48	0.001
Year:Habitat	5	3637	0.98	0.525
Season:Habitat	5	14705	1.40	0.141
Site:Habitat	5	12758	3.45	0.001
Year:Season:Habitat	5	4043	1.34	0.231
Year:Site:Habitat	5	3693	1.43	0.035
Season:Site:Habitat	5	8651	2.87	0.007
Day(Year:Season:Site)	16	3339	2.89	0.001
Year:Season:Site:Habitat	5	3016	1.16	0.184
Day(Year:Season:Site):Habitat	80	2600	2.25	0.001
Residuals	410	1156		

df – degrees of freedom; SS – sum of squares; Pseudo-F – F value by permutation, P-values based on 999 permutations.

(b)

Habitat Contrasts	Winter					
	Corrie Island			Soldiers Point		
	Similarities	t	p (MC)	Similarities	t	p (MC)
Bare – Baskets	11.31	3.88	0.010	11.09	2.79	0.02
Bare – Mangroves	28.91	2.89	0.013	15.52	3.40	0.016
Bare – Racks	3.55	3.07	0.013	8.88	6.27	0.002
Bare – Reef	17.72	6.30	0.003	7.72	6.61	0.003
Bare – Seagrass	22.72	3.45	0.002	14.73	3.38	0.012
Baskets – Mangroves	18.84	3.32	0.015	25.10	1.12	0.394
Baskets – Reef	25.10	5.14	0.002	23.21	2.10	0.035
Baskets – Racks	44.48	2.61	0.047	39.29	1.80	0.102
Baskets – Seagrass	17.80	4.25	0.005	19.56	1.26	0.297
Mangroves – Reef	31.06	1.74	0.092	34.70	1.64	0.125
Mangroves – Racks	9.24	5.70	0.001	26.39	3.30	0.017
Mangroves – Seagrass	26.06	2.60	0.006	17.50	3.00	0.010
Reef – Racks	16.10	4.06	0.011	32.28	4.73	0.005
Reef – Seagrass	20.31	3.43	0.001	12.06	3.30	0.007
Racks – Seagrass	10.01	5.41	0.002	11.78	3.42	0.010

Habitat Contrasts	Summer					
	Corrie Island			Soldiers Point		
	Similarities	t	p (MC)	Similarities	t	p (MC)
Bare – Baskets	11.82	2.97	0.020	3.10	4.81	0.002
Bare – Mangroves	12.30	3.47	0.005	9.12	4.96	0.004
Bare – Racks	7.12	3.26	0.017	2.97	5.22	0.003

Bare – Reef	5.55	3.02	0.035	5.41	4.48	0.003
Bare – Seagrass	15.02	2.89	0.016	9.70	3.43	0.009
Baskets – Mangroves	34.01	3.68	0.009	44.78	4.28	0.009
Baskets – Reef	33.39	3.90	0.010	42.21	4.12	0.013
Baskets – Racks	46.46	1.50	0.194	59.08	2.20	0.062
Baskets – Seagrass	18.26	2.93	0.016	25.84	3.02	0.014
Mangroves – Reef	41.29	2.71	0.031	49.35	5.34	0.005
Mangroves – Racks	26.93	3.21	0.010	48.99	3.64	0.016
Mangroves – Seagrass	20.34	3.30	0.005	13.91	4.56	0.002
Reef – Racks	36.45	1.78	0.134	53.84	3.54	0.014
Reef – Seagrass	11.70	3.15	0.014	9.07	4.85	0.002
Racks – Seagrass	11.36	3.16	0.008	15.96	4.34	0.006

(c)

Habitat Contrasts	Year 1					
	Corrie Island			Soldiers Point		
	Similarities	t ratio	p (MC)	Similarities	t ratio	p (MC)
Bare – Baskets	11.00	3.98	0.001	10.37	2.86	0.001
Bare – Mangroves	20.93	2.70	0.001	13.28	3.98	0.001
Bare – Racks	12.38	3.49	0.001	6.50	4.50	0.001
Bare – Reef	5.12	4.29	0.001	8.49	4.90	0.001
Bare – Seagrass	23.33	2.20	0.005	13.14	3.42	0.001
Baskets – Mangroves	23.89	4.04	0.001	27.14	2.50	0.003
Baskets – Reef	25.25	3.31	0.001	23.89	2.45	0.001
Baskets – Racks	50.48	2.18	0.010	37.97	1.87	0.024
Baskets – Seagrass	15.33	4.41	0.001	20.57	2.26	0.008
Mangroves – Reef	31.41	1.81	0.016	37.67	1.98	0.012
Mangroves – Racks	19.59	3.59	0.002	33.39	3.43	0.001
Mangroves – Seagrass	24.70	2.41	0.003	18.48	3.66	0.001
Reef – Racks	24.36	3.49	0.001	32.46	3.46	0.001
Reef – Seagrass	15.95	3.29	0.001	12.57	4.29	0.001
Racks – Seagrass	11.13	4.62	0.001	14.64	4.49	0.001

Habitat Contrasts	Year 2					
	Corrie Island			Soldiers Point		
	Similarities	t	p (MC)	Similarities	t	p (MC)
Bare – Baskets	10.50	4.56	0.006	5.55	7.33	0.001
Bare – Mangroves	17.53	2.85	0.001	14.14	5.64	0.001
Bare – Racks	10.53	3.42	0.007	6.12	7.36	0.001
Bare – Reef	3.21	5.60	0.003	4.96	8.05	0.001
Bare – Seagrass	13.66	2.51	0.016	11.83	5.73	0.001
Baskets – Mangroves	28.62	3.27	0.014	27.30	3.44	0.001
Baskets – Reef	33.77	2.88	0.008	31.15	4.01	0.001
Baskets – Racks	38.18	4.71	0.005	47.90	1.95	0.022
Baskets – Seagrass	19.97	3.37	0.003	17.85	4.27	0.001
Mangroves – Reef	30.65	1.62	0.111	34.33	2.23	0.003
Mangroves – Racks	16.02	5.02	0.004	31.00	3.38	0.001
Mangroves – Seagrass	19.97	2.25	0.016	12.70	4.59	0.001
Reef – Racks	26.67	3.71	0.004	38.13	3.25	0.001
Reef – Seagrass	16.31	3.01	0.009	9.67	4.88	0.001
Racks – Seagrass	9.52	4.52	0.001	13.21	5.25	0.001

Table D.3: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Models of total fish observations: (a) interactions among fixed and random terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors . Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		40.27	<0.001
Source	df	MS	F value	Pr(>F)
Year	1	2.57	0.99	0.332
Season	1	183.82	71.43	<0.001
Site	1	24.54	9.54	0.007
Habitat	5	706.38	274.50	<0.001
Year:Habitat	5	9.99	3.88	0.001
Season:Habitat	5	71.12	27.63	<0.001
Site:Habitat	5	52.14	20.26	<0.001
Year:Season:Habitat	5	15.69	6.10	<0.001
Year:Site:Habitat	5	11.89	4.62	<0.001
Season:Site:Habitat	5	23.32	9.06	<0.001
Year:Season:Site:Habitat	5	6.34	2.46	0.032

(b)

Habitat Contrasts	Year 1							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Baskets	-6.06	<0.001	-1.62	0.584	-7.63	<0.001	-10.73	<0.001
Bare – Mangroves	-1.27	0.799	-1.71	0.526	-4.30	<0.001	-8.45	<0.001
Bare – Racks	-12.24	<0.001	-6.89	<0.001	-9.33	<0.001	-13.23	<0.001
Bare – Reef	-3.39	0.010	-5.21	<0.001	-10.09	<0.001	-15.46	<0.001
Bare – Seagrass	-1.81	0.457	-2.11	0.282	-1.54	0.640	-3.21	0.017
Baskets – Mangroves	4.65	<0.001	-0.09	1.000	3.57	0.005	2.46	0.138
Baskets – Racks	-6.18	<0.001	-5.27	<0.001	-1.90	0.402	-2.91	0.043
Baskets – Reef	2.67	0.083	-3.58	0.005	-2.87	0.049	-5.32	<0.001
Baskets – Seagrass	4.11	<0.001	-0.49	0.996	6.82	<0.001	8.12	<0.001
Mangroves – Racks	-10.69	<0.001	-5.18	<0.001	-5.42	<0.001	-5.32	<0.001
Mangroves – Reef	-2.04	0.320	-3.50	0.006	-6.31	<0.001	-7.72	<0.001
Mangroves – Seagrass	-0.53	0.995	-0.40	0.998	3.10	0.002	5.66	<0.001
Racks – Reef	8.85	<0.001	1.68	0.543	-1.01	0.914	-2.35	0.176
Racks – Seagrass	10.15	<0.001	4.78	<0.001	8.73	<0.001	10.85	<0.001
Reef – Seagrass	1.50	0.663	3.09	0.025	9.54	<0.001	13.26	<0.001

Habitat Contrasts	Year 2							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t ratio	p	t ratio	p	t ratio	p	t ratio	p
Bare – Baskets	-8.23	<0.001	-4.54	<0.001	-5.01	<0.001	-11.23	<0.001
Bare – Mangroves	-2.07	0.306	-0.66	0.986	-2.54	0.113	-8.48	<0.001
Bare – Racks	-14.94	<0.001	-7.65	<0.001	-13.68	<0.001	-11.37	<0.001
Bare – Reef	-4.87	<0.001	-5.26	<0.001	-6.02	<0.001	-13.65	<0.001
Bare – Seagrass	-3.39	0.010	-0.02	1.000	-2.41	0.156	-4.37	<0.001
Baskets – Mangroves	6.47	<0.001	3.97	0.001	2.35	0.177	2.56	0.109
Baskets – Racks	-7.04	<0.001	-3.26	0.015	-8.67	<0.001	-0.14	1.000

Baskets – Reef	3.53	0.006	-0.75	0.975	-1.02	0.912	-2.47	0.133
Baskets – Seagrass	4.90	<0.001	4.75	<0.001	2.60	0.099	7.02	<0.001
Mangroves – Racks	-13.51	<0.001	-7.16	<0.001	-10.83	<0.001	-2.70	0.077
Mangroves – Reef	-2.94	0.040	-4.71	<0.001	-3.34	0.011	-4.98	<0.001
Mangroves – Seagrass	-1.43	0.710	0.67	0.985	0.19	1.000	4.30	<0.001
Racks – Reef	10.57	<0.001	2.51	0.123	7.66	<0.001	-2.33	0.183
Racks – Seagrass	11.78	<0.001	8.01	<0.001	11.28	<0.001	7.16	<0.001
Reef – Seagrass	1.44	0.700	5.50	<0.001	3.62	0.004	9.49	<0.001

Table D.4: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Models of species richness: (a) interactions among fixed and random terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		5.12	0.023
Source	df	MS	F value	Pr(>F)
Year	1	0.88	5.56	0.032
Season	1	19.97	125.64	<0.001
Site	1	0.09	0.54	0.469
Habitat	5	9.62	60.51	<0.001
Season:Site	1	0.15	0.96	0.338
Season:Habitat	5	1.84	11.57	<0.001
Site:Habitat	5	2.06	12.94	<0.001
Season:Site:Habitat	5	0.41	2.59	0.024
Year:Season:Site:Habitat	4	0.20	1.25	0.285

(b)

Habitat Contrasts	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t ratio	p	t ratio	p	t ratio	p	t ratio	p
Bare – Baskets	-4.64	<0.001	-2.42	0.151	-9.09	<0.001	-5.18	<0.001
Bare – Mangroves	-1.62	0.583	-5.80	<0.001	-3.53	0.006	-4.71	<0.001
Bare – Racks	-4.17	<0.001	-4.53	<0.001	-13.93	<0.001	-6.61	<0.001
Bare – Reef	-5.40	<0.001	-10.25	<0.001	-8.28	<0.001	-7.57	<0.001
Bare – Seagrass	-3.79	0.002	-6.21	<0.001	-7.31	<0.001	-4.11	<0.001
Baskets – Mangroves	3.03	0.030	-3.48	0.007	5.64	<0.001	-0.08	1.000
Baskets – Racks	0.48	0.997	-2.16	0.259	-5.08	<0.001	-1.89	0.409
Baskets – Reef	-0.78	0.971	-8.01	<0.001	0.77	0.973	-3.19	0.019
Baskets – Seagrass	0.77	0.973	-3.87	0.002	1.87	0.420	0.71	0.981
Mangroves – Racks	-2.56	0.110	1.34	0.761	-10.61	<0.001	-1.36	0.750
Mangroves – Reef	-3.80	0.002	-4.45	<0.001	-4.83	<0.001	-2.77	0.065
Mangroves – Seagrass	-2.21	0.235	-0.36	0.100	-3.81	0.002	0.71	0.981
Racks – Reef	-1.26	0.807	-5.85	<0.001	5.79	<0.001	-1.70	0.532
Racks – Seagrass	0.30	0.100	-1.72	0.522	6.95	<0.001	2.19	0.244
Reef – Seagrass	1.53	0.647	4.14	<0.001	1.09	0.887	3.55	0.006

Table D.5: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Models of total bream observations showing: (a) interactions among fixed terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		24.17	<0.001
Source	df	MS	F value	Pr(>F)
Year	1	0.10	0.05	0.810
Season	1	18.12	10.65	0.005
Site	1	9.16	5.38	0.034
Habitat	5	31.25	18.36	<0.001
Year:Habitat	5	3.91	2.30	0.044
Season:Habitat	5	26.27	15.44	<0.001
Site:Habitat	5	2.63	1.55	0.173
Year:Season:Habitat	5	12.05	7.09	<0.001
Year:Site:Habitat	5	1.98	1.16	0.326
Season:Site:Habitat	5	36.98	4.35	<0.001
Year:Season:Site:Habitat	5	2.69	1.58	0.164

(b)

Habitat Contrasts	Corrie Island				Soldiers Point			
	Winter		Summer		Winter		Summer	
	t	p	t	p	t	p	t	p
Bare – Baskets	-9.72	<0.001	-8.75	<0.001	-5.10	<0.001	-15.18	<0.001
Bare – Mangroves	-2.66	0.086	-8.82	<0.001	-5.14	<0.001	-13.90	<0.001
Bare – Racks	-16.35	<0.001	-13.72	<0.001	-9.77	<0.001	-19.66	<0.001
Bare – Reef	-5.19	<0.001	-14.36	<0.001	-9.55	<0.001	-21.16	<0.001
Bare – Seagrass	-2.94	0.040	-2.84	0.053	-2.32	0.187	-3.63	0.004
Baskets – Mangroves	7.04	<0.001	-0.26	0.999	-0.10	1.000	1.18	0.845
Baskets – Racks	-6.70	<0.001	-5.28	<0.001	-4.79	<0.001	-4.87	<0.001
Baskets – Reef	4.58	<0.001	-6.03	<0.001	-4.56	<0.001	-6.45	<0.001
Baskets – Seagrass	6.64	<0.001	6.27	<0.001	2.84	0.052	12.15	<0.001
Mangroves – Racks	-13.66	<0.001	-4.90	<0.001	-4.64	<0.001	-5.99	<0.001
Mangroves – Reef	-2.51	0.124	-5.65	<0.001	-4.41	<0.001	-7.54	<0.001
Mangroves – Seagrass	-0.32	0.999	6.39	<0.001	2.91	0.044	10.83	<0.001
Racks – Reef	11.28	<0.001	-0.81	0.965	0.22	0.999	-1.55	0.628
Racks – Seagrass	13.19	<0.001	11.55	<0.001	7.63	<0.001	16.89	<0.001
Reef – Seagrass	2.16	0.2596	12.23	<0.001	7.41	<0.001	18.46	<0.001

Table D.6: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Models of Iudrick observations showing: (a) interactions among fixed and random terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factor. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		28.04	<0.001
Source	df	MS	F value	Pr(>F)
Year	1	3.88	2.57	0.128
Season	1	0.01	0.01	0.973
Site	1	0.01	0.01	0.974
Habitat	5	39.66	26.28	<0.001
Year:Habitat	5	2.41	1.59	0.159
Season:Habitat	5	1.79	1.19	0.313
Site:Habitat	5	7.31	4.84	<0.001
Year:Season:Habitat	5	2.76	1.83	0.105
Year:Site:Habitat	5	11.91	7.89	<0.001
Season:Site:Habitat	5	3.93	2.60	0.024
Year:Season:Site:Habitat	5	3.53	2.34	0.040

(b)

Habitat Contrasts	Year 1							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Baskets	-7.64	<0.001	-4.92	<0.001	-8.34	<0.001	-7.58	<0.001
Bare – Mangroves	0.26	0.999	-3.25	0.015	-1.41	0.722	-2.23	0.225
Bare – Racks	-12.82	<0.001	-11.26	<0.001	-9.63	<0.001	-10.37	<0.001
Bare – Reef	-1.55	0.634	-1.71	0.522	-0.40	0.998	-3.54	0.006
Bare – Seagrass	-0.30	0.999	0.05	1.000	-1.00	0.917	-0.57	0.993
Baskets – Mangroves	7.73	<0.001	1.66	0.559	7.56	<0.001	5.77	<0.001
Baskets – Racks	-5.18	<0.001	-6.35	<0.001	-1.44	0.699	-3.17	0.020
Baskets – Reef	6.10	<0.001	3.20	0.018	8.67	<0.001	4.19	<0.001
Baskets – Seagrass	7.17	<0.001	4.96	<0.001	8.22	<0.001	7.56	<0.001
Mangroves – Racks	-12.80	<0.001	-8.01	<0.001	-8.97	<0.001	-8.81	<0.001
Mangroves – Reef	-1.77	0.483	1.54	0.638	1.09	0.884	-1.46	0.693
Mangroves – Seagrass	-0.55	0.993	3.30	0.013	0.47	0.997	1.79	0.473
Racks – Reef	11.27	<0.001	9.55	<0.001	10.09	<0.001	7.19	<0.001
Racks – Seagrass	12.23	<0.001	11.31	<0.001	9.66	<0.001	10.56	<0.001
Reef – Seagrass	1.21	0.832	1.76	0.491	-0.64	0.987	3.20	0.018
Habitat Contrasts	Year 2							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Baskets	-6.37	<0.001	-8.76	<0.001	-8.07	<0.001	-10.25	<0.001
Bare – Mangroves	-0.90	0.947	-1.37	0.746	-2.39	0.163	-5.03	<0.001
Bare – Racks	-16.18	<0.001	-12.10	<0.001	-14.57	<0.001	-9.41	<0.001
Bare – Reef	-0.45	0.998	-4.13	<0.001	-1.95	0.372	-6.01	<0.001

Bare – Seagrass	-0.46	0.997	-0.19	1.000	-0.98	0.923	-1.70	0.532
Baskets – Mangroves	5.60	<0.001	7.56	<0.001	5.50	<0.001	5.10	<0.001
Baskets – Racks	-10.03	<0.001	-3.51	0.006	-6.50	<0.001	0.861	0.955
Baskets – Reef	6.06	<0.001	4.86	<0.001	6.12	<0.001	4.34	<0.001
Baskets – Seagrass	5.90	<0.001	9.00	<0.001	7.09	<0.001	8.75	<0.001
Mangroves – Racks	-15.64	<0.001	-10.99	<0.001	-11.86	<0.001	-4.26	<0.001
Mangroves – Reef	0.46	0.997	-2.81	0.058	0.48	0.997	-0.85	0.955
Mangroves – Seagrass	0.43	0.998	1.24	0.819	1.42	0.712	3.45	0.008
Racks – Reef	16.10	<0.001	8.36	<0.001	12.62	<0.001	3.48	0.007
Racks – Seagrass	15.71	<0.001	12.50	<0.001	13.59	<0.001	7.89	<0.001
Reef – Seagrass	-0.02	1.000	4.14	<0.001	0.97	0.928	4.41	<0.001

Table D.7: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Model of silverbiddy observations showing: (a) interactions among fixed and random terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factor. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.01	0.945
Source	df	MS	F value	Pr(>F)
Year	1	1.81	3.06	0.099
Season	1	3.27	5.53	0.031
Site	1	8.59	14.52	0.001
Habitat	5	2.92	4.93	<0.001
Year:Habitat	5	0.96	1.62	0.152
Season:Habitat	5	2.96	5.00	<0.001
Site:Habitat	5	0.98	1.66	0.142
Year:Season:Habitat	5	0.75	1.27	0.274
Year:Site:Habitat	5	1.19	2.01	0.076
Season:Site:Habitat	5	0.59	1.00	0.415
Year:Season:Site:Habitat	5	0.96	1.62	0.152

(b)

Habitat Contrasts	Winter		Summer	
	t	p	t	p
Bare – Baskets	1.99	0.347	-0.49	0.996
Bare – Mangroves	1.23	0.820	-1.67	0.554
Bare – Racks	1.27	0.799	-9.79	<0.001
Bare – Reef	-0.80	0.967	-1.03	0.905
Bare – Seagrass	1.08	0.888	1.89	0.410
Baskets – Mangroves	-0.75	0.975	-1.25	0.812
Baskets – Racks	-0.75	0.978	-9.82	<0.001
Baskets – Reef	-2.84	0.052	-0.58	0.992
Baskets – Seagrass	-0.90	0.945	2.51	0.123
Mangroves – Racks	0.03	1.000	-8.41	<0.001
Mangroves – Reef	-2.06	0.310	0.66	0.985
Mangroves – Seagrass	-0.15	1.000	3.72	0.003
Racks – Reef	-2.11	0.283	9.13	<0.001

Racks – Seagrass	-0.18	1.000	12.31	<0.001
Reef – Seagrass	1.91	0.398	3.06	0.028

Table D.8: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Model of whiting observations showing: (a) interactions among fixed and random terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factor. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		9.61	0.001
Source	df	MS	F value	Pr(>F)
Year	1	0.35	0.67	0.433
Season	1	0.46	0.88	0.362
Site	1	1.57	3.02	0.101
Habitat	5	1.36	2.61	0.024
Year:Habitat	5	1.15	2.22	0.051
Season:Habitat	5	1.66	3.20	0.007
Site:Habitat	5	4.04	7.77	<0.001
Year:Season:Habitat	5	1.25	2.41	0.035
Year:Site:Habitat	5	1.15	2.22	0.051
Season:Site:Habitat	5	0.99	1.91	0.091
Year:Season:Site:Habitat	5	1.04	2.02	0.075

(b)

Habitat Contrasts	Year 1				Year 2			
	Winter		Summer		Winter		Summer	
	t	p	t	p	t	p	t	p
Bare – Baskets	3.99	0.001	0.11	1.000	2.17	<0.001	5.12	<0.001
Bare – Mangroves	6.00	<0.001	1.26	0.806	6.02	<0.001	4.62	<0.001
Bare – Racks	5.54	<0.001	-0.83	0.962	6.43	<0.001	4.71	<0.001
Bare – Reef	5.66	<0.001	2.73	0.071	5.31	<0.001	6.53	<0.001
Bare – Seagrass	5.94	<0.001	3.88	0.002	5.85	<0.001	6.65	<0.001
Baskets – Mangroves	2.05	0.315	1.27	0.802	4.00	0.001	-0.39	0.999
Baskets – Racks	1.55	0.633	-1.03	0.909	4.41	<0.001	-0.42	0.998
Baskets – Reef	1.67	0.552	2.88	0.048	3.26	0.015	1.43	0.708
Baskets – Seagrass	1.99	0.348	4.15	<0.001	3.84	0.002	1.55	0.630
Mangroves – Racks	-0.52	0.995	-2.27	0.208	0.36	0.999	-0.02	1.000
Mangroves – Reef	-0.40	0.999	1.61	0.594	-0.78	0.970	1.79	0.473
Mangroves – Seagrass	-0.06	1.000	2.83	0.054	-0.16	1.000	1.91	0.397
Racks – Reef	0.12	1.000	3.85	0.002	-1.16	0.857	1.85	0.436
Racks – Seagrass	0.46	0.997	5.13	<0.001	-0.52	0.995	1.97	0.361
Reef – Seagrass	0.34	0.999	1.18	0.847	0.62	0.990	0.122	1.000

Table D.9: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Models of mullock observations showing: (a) interactions among fixed and random terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factor. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		18.97	<0.001
Source	df	MS	F value	Pr(>F)
Year	1	0.02	0.13	0.717
Season	1	0.08	0.45	0.512
Site	1	0.06	0.35	0.561
Habitat	5	0.14	0.77	0.570
Year:Habitat	5	0.48	2.67	0.021
Season:Habitat	5	0.61	3.34	0.005
Site:Habitat	5	0.21	1.19	0.313
Year:Season:Habitat	5	1.50	8.30	<0.001
Year:Site:Habitat	5	0.18	0.98	0.430
Season:Site:Habitat	5	0.54	2.97	0.012
Year:Season:Site:Habitat	5	1.17	6.48	<0.001

(b)

Habitat Contrasts	Year 1							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Baskets	0.05	0.999	1.28	0.794	-0.39	0.999	-0.04	0.999
Bare – Mangroves	0.23	0.999	0.46	0.997	-0.90	0.945	0.28	0.998
Bare – Racks	-6.39	<0.001	0.98	0.924	-5.80	<0.001	0.14	0.999
Bare – Reef	-0.05	0.999	0.62	0.989	-0.25	0.999	0.13	0.999
Bare – Seagrass	-1.32	0.774	0.14	0.999	-0.67	0.985	0.18	0.999
Baskets – Mangroves	0.18	1.000	-0.82	0.963	-0.58	0.992	0.35	0.993
Baskets – Racks	-6.44	<0.001	-0.30	0.999	-6.06	<0.001	0.19	0.999
Baskets – Reef	-0.09	0.999	-0.66	0.986	0.15	0.999	0.18	0.999
Baskets – Seagrass	-1.37	0.746	-1.14	0.861	-0.32	0.999	0.24	0.999
Mangroves – Racks	-6.47	<0.001	0.52	0.995	-5.34	<0.001	-0.15	0.999
Mangroves – Reef	-0.27	0.999	0.17	0.999	0.72	0.979	-0.16	0.999
Mangroves – Seagrass	-1.51	0.654	-0.32	0.999	0.27	0.999	-0.11	0.999
Racks – Reef	6.34	<0.001	-0.35	0.999	6.07	<0.001	-0.01	0.999
Racks – Seagrass	4.97	<0.001	-0.84	0.960	5.74	<0.001	0.04	0.999
Reef – Seagrass	-1.27	0.798	-0.49	0.997	-0.46	0.997	0.05	0.999
Habitat Contrasts	Year 2							
	Winter				Summer			
	Corrie Island		Soldiers Point		Corrie Island		Soldiers Point	
	t	p	t	p	t	p	t	p
Bare – Baskets	-0.14	0.999	-0.15	0.999	-0.93	0.938	-0.83	0.962
Bare – Mangroves	-0.29	0.997	-0.18	0.999	-0.02	1.000	0.01	0.999
Bare – Racks	-2.67	0.083	0.01	0.999	-15.94	<0.001	-1.14	0.864
Bare – Reef	-0.01	0.999	-0.60	0.991	-0.29	0.999	0.16	0.999

Bare – Seagrass	-0.47	0.997	-0.07	0.999	-0.24	0.999	0.18	0.999
Baskets – Mangroves	-0.15	1.000	-0.03	0.999	0.89	0.948	0.83	0.961
Baskets – Racks	-2.59	0.101	0.17	0.999	-15.00	<0.001	-0.32	0.995
Baskets – Reef	0.13	1.000	-0.47	0.997	0.64	0.988	1.01	0.915
Baskets – Seagrass	-0.34	0.999	0.08	0.999	0.69	0.983	1.04	0.905
Mangroves – Racks	-2.44	0.145	0.19	0.999	-15.56	<0.001	-1.15	0.861
Mangroves – Reef	0.29	0.999	-0.43	0.998	-0.27	0.999	0.15	0.999
Mangroves – Seagrass	-0.19	1.000	0.11	0.999	-0.22	0.999	0.18	0.999
Racks – Reef	2.72	0.072	-0.64	0.988	15.65	<0.001	1.33	0.768
Racks – Seagrass	2.19	0.242	-0.08	0.999	15.69	<0.001	1.36	0.751
Reef – Seagrass	-0.47	0.997	0.55	0.994	0.05	0.999	0.03	0.999

Table D.10: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Model of the relative percentage of wandering observations showing: (a) interactions among fixed and random terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.79	0.374
Source	df	MS	F value	Pr(>F)
Year	1	0.08	10.74	0.004
Season	1	0.03	3.89	0.066
Site	1	0.01	0.17	0.683
Habitat	5	0.21	27.19	<0.001
Year:Habitat	5	0.01	2.09	0.075
Season:Habitat	5	0.01	1.54	0.186
Site:Habitat	5	0.01	0.73	0.599
Year:Season:Habitat	5	0.02	2.35	0.048
Year:Site:Habitat	5	0.01	0.52	0.756
Season:Site:Habitat	5	0.01	0.67	0.646
Year:Season:Site:Habitat	5	0.01	1.10	0.366

(b)

Habitat Contrasts	Year 1				Year 2			
	Winter		Summer		Winter		Summer	
	t ratio	p	t ratio	p	t ratio	p	t ratio	p
Bare – Baskets	-4.91	<0.001	-5.34	<0.001	-4.66	<0.001	-1.95	0.381
Bare – Mangroves	-3.95	0.002	-5.97	<0.001	-2.98	0.043	-1.90	0.412
Bare – Racks	-6.69	<0.001	-6.29	<0.001	-5.82	<0.001	-2.74	0.078
Bare – Reef	-3.92	0.002	-6.56	<0.001	-4.31	<0.001	-2.06	0.320
Bare – Seagrass	-2.50	0.137	-5.81	<0.001	-5.21	<0.001	-2.11	0.293
Baskets – Mangroves	0.96	0.930	-0.63	0.988	1.68	0.548	0.05	1.000
Baskets – Racks	-1.78	0.485	-0.95	0.932	-1.16	0.852	-0.79	0.968
Baskets – Reef	0.99	0.919	-1.22	0.825	0.35	0.999	-0.11	1.000
Baskets – Seagrass	2.41	0.164	-0.47	0.997	-0.55	0.994	-0.16	1.000
Mangroves – Racks	-2.73	0.079	-0.32	0.999	-2.84	0.060	-0.84	0.958
Mangroves – Reef	0.03	1.000	-0.59	0.992	-1.33	0.766	-0.16	1.000
Mangroves – Seagrass	1.46	0.692	0.17	1.000	-2.23	0.236	-0.21	0.999

Racks – Reef	2.77	0.073	-0.27	0.999	1.51	0.656	-0.86	0.983
Racks – Seagrass	4.19	0.001	0.48	0.997	0.61	0.989	0.63	0.988
Reef – Seagrass	1.42	0.713	0.75	0.974	-0.89	0.946	-0.05	1.000

Table D.11: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Models of the relative percentage of feeding observations: (a) interactions among fixed and random terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterthwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.01	0.998
Source	df	MS	F value	Pr(>F)
Year	1	0.08	5.58	0.020
Season	1	0.01	0.46	0.498
Site	1	0.42	26.54	<0.001
Habitat	5	0.07	4.55	<0.001
Year:Habitat	5	0.02	1.15	0.339
Season:Habitat	5	0.02	1.46	0.209
Site:Habitat	5	0.04	0.29	0.587
Year:Season:Habitat	5	0.02	1.21	0.311
Year:Site:Habitat	5	0.05	2.99	0.015
Season:Site:Habitat	5	0.05	3.13	0.011
Year:Season:Site:Habitat	5	0.01	0.97	0.439

(b)

Habitat Contrasts	Corrie Island				Soldiers Point			
	Winter		Summer		Winter		Summer	
	t	p	t	p	t	p	t	p
Bare – Baskets	-3.66	0.006	-2.06	0.317	3.06	0.035	-2.29	0.210
Bare – Mangroves	-2.38	0.177	-1.67	0.553	1.10	0.879	-2.07	0.311
Bare – Racks	-2.34	0.189	-0.84	0.959	3.25	0.020	-1.80	0.470
Bare – Reef	-3.88	0.003	-1.21	0.828	0.90	0.945	-1.65	0.564
Bare – Seagrass	-0.58	0.992	0.23	0.999	2.63	0.100	-0.88	0.949
Baskets – Mangroves	1.28	0.794	0.39	0.998	-1.95	0.377	0.22	0.999
Baskets – Racks	1.31	0.775	1.22	0.823	0.19	1.000	0.49	0.996
Baskets – Reef	-0.23	0.999	0.85	0.957	-2.16	0.269	0.63	0.988
Baskets – Seagrass	3.08	0.033	2.29	0.209	-0.42	0.998	1.41	0.722
Mangroves – Racks	0.03	1.000	0.84	0.959	2.15	0.274	0.27	0.999
Mangroves – Reef	-1.51	0.660	0.46	0.997	-0.20	1.000	0.42	0.998
Mangroves – Seagrass	1.80	0.472	1.90	0.408	1.54	0.643	1.19	0.839
Racks – Reef	-1.54	0.638	-0.38	0.999	-2.35	0.187	0.15	1.000
Racks – Seagrass	1.76	0.494	1.07	0.893	-0.61	0.989	0.92	0.940
Reef – Seagrass	3.31	0.017	1.44	0.700	1.74	0.512	0.77	0.971

Table D.12: Summary of analyses testing for sources of spatio-temporal variability using Linear Mixed Effects Models of the relative percentages of passing behaviour: (a) interactions among fixed and random terms in the Linear Mixed Effects Model type III ANOVA (utilising Satterhwaite's degrees of freedom method) and (b) pairwise comparison tests on the Estimated Marginal Means (EMM) of the significant factors. Significant effects ($P < 0.05$) are in bold.

(a)

Random effects	df		LRT	Pr(>Chisq)
Day:Site:Season:Year	1		0.44	0.504
Source	df	MS	F value	Pr(>F)
Year	1	0.03	1.90	0.187
Season	1	0.05	3.32	0.087
Site	1	0.09	6.10	0.025
Habitat	5	0.45	30.25	<0.001
Year:Habitat	5	0.03	2.31	0.051
Season:Habitat	5	0.03	2.29	0.053
Site:Habitat	5	0.04	2.65	0.028
Year:Season:Habitat	5	0.04	2.98	0.016
Year:Site:Habitat	5	0.02	1.73	0.136
Season:Site:Habitat	5	0.05	3.58	0.005
Year:Season:Site:Habitat	5	0.01	0.69	0.635

(b)

Habitat Contrasts	Corrie Island				Soldiers Point			
	Winter		Summer		Winter		Summer	
	t	p	t	p	t	p	t	p
Bare – Baskets	6.73	<0.001	3.39	0.013	0.82	0.962	4.95	<0.001
Bare – Mangroves	3.42	0.012	3.82	0.003	2.65	0.098	5.15	<0.001
Bare – Racks	8.15	<0.001	4.99	<0.001	4.90	<0.001	4.93	<0.001
Bare – Reef	5.35	<0.001	3.72	0.005	2.61	0.107	6.15	<0.001
Bare – Seagrass	3.38	0.013	1.59	0.603	1.39	0.735	5.07	<0.001
Baskets – Mangroves	-3.30	0.017	0.43	0.998	1.82	0.456	0.19	1.000
Baskets – Racks	1.42	0.712	1.61	0.596	4.08	0.001	-0.03	1.000
Baskets – Reef	-1.38	0.740	0.33	0.999	1.78	0.481	1.19	0.839
Baskets – Seagrass	-3.35	0.015	-1.80	0.478	0.56	0.993	0.11	1.000
Mangroves – Racks	4.73	<0.001	1.17	0.848	2.25	0.224	-0.22	0.999
Mangroves – Reef	1.92	0.393	-0.10	1.000	-0.04	1.000	0.99	0.917
Mangroves – Seagrass	-0.05	1.000	-2.22	0.238	-1.26	0.805	-0.08	1.000
Racks – Reef	-2.80	0.067	-1.28	0.796	-2.30	0.208	1.22	0.825
Racks – Seagrass	-4.78	<0.001	-3.40	0.013	-3.52	0.009	0.14	1.000
Reef – Seagrass	-1.97	0.366	-2.12	0.288	-1.22	0.825	-1.08	0.888