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Understanding fish movements and connectivity across temperate seascapes: Implications for marine conservation

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BMarScAdv (Hons)

Supervisors:

Andrew Davis, Nathan Knott, Matthew Rees & Matt Taylor

This thesis is presented as part of the requirement for the conferral of the degree:

DOCTOR OF PHILOSOPHY

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University of Wollongong

School of Earth Atmospheric and Life Sciences

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Abstract

Developing an ecological understanding on the linkages between patch types in coastal seascapes is a key goal in seascape ecology. Many reef-associated fish worldwide have complex life-histories, using vegetated nursery habitats as juveniles before undergoing ontogenetic habitat shifts to reefs. Currently, there is limited quantitative information on the spatiotemporal scales that fish connect patch types through ontogeny, particularly in temperate seascapes. Better quantifying this connectivity is essential to improving our understanding on the processes structuring fish populations, identifying critical habitats, and designing management strategies. In this thesis, I investigate the movement of reef-associated fish at both juvenile and adult life-stages to better quantify seascape connectivity and its importance for marine management and conservation.

First, I use baited remote underwater videos deployed across > 400 km of coastline to determine the scale of connectivity between estuarine nurseries and coastal reefs for a key targeted fish *Chrysophrys auratus* (pink snapper). The species were inferred to undertake ontogenetic habitat shifts to nearby coastal reefs, with smaller (~ 260 mm) and more abundant *C. auratus* observed on reefs within 8.5 km of estuaries. Interestingly, the effect of marine reserves on *C. auratus* across the study area was not influenced by estuarine proximity. Next, I sought to directly quantify the movement of juvenile *Girella tricuspidata* (luderick) and *Acanthopagrus australis* (yellowfin bream) within seagrass nursery areas and their dispersal to adult rocky reef habitats using acoustic telemetry. Before doing this, however, I needed to determine how acoustic tracking might be affected by fish moving through seagrass as this had not been previously investigated. The detection range of acoustic transmitters suitable for tracking juvenile fish (V7 tags) was ~85 m when above seagrass and decreased to 40 m when transmitters were ensconced in seagrass fronds. This information was then used to interpret and analyse the movement patterns of the tagged juvenile fish. Both species exhibited site-attachment to seagrass for up to ~400 days but also moved across large (~ 2km) expanses of seagrass meadows and to adjacent patches. Many fish were detected moving to reefs close (over 100’s m to km’s) to seagrass, but these were not permanent ontogenetic habitat shifts and instead appeared to be regular excursions to reefs. The small-scale movements of juvenile fish meant they were rarely detected crossing the boundaries of an existing marine reserve. Finally, I tracked adult *G. tricuspidata* on reefs along the open coast to assess whether the species showed generalities in their movements between different seascapes. Adult fish were highly resident to reefs for up to 589 days with only limited movements to other adjacent patches ~1 km away and they were more likely to be absent during periods of large swells. These findings were like those previously reported for *G. tricuspidata* tracked on reefs in a protected coastal embayment but differed from riverine estuaries where the species is highly mobile.

Using both inferential and direct methods, I demonstrate that juvenile and adult fish link patch types over small spatial scales (100’s m to km’s) in temperate seascapes. A key finding was that juvenile fish connect multiple patch types during their routine movements and perform ontogenetic habitat shifts in greater numbers to nearby reefs than those far away. This has implications for identifying critical fish habitats such as nursery areas, which I contend should be perceived as interconnected patch types forming a habitat mosaic (i.e. “seascape nurseries”). Furthermore, these findings highlight that the global loss of aquatic vegetation may disrupt important linkages between populations. The site-attachment and small-scale connectivity observed for reef-associated fishes can help guide the design of Marine Protected Areas and coastal restoration efforts. In conclusion, I improve current understanding on the movement and connectivity of reef-associated fishes in temperate seascapes, and this information can be integrated into actions for biodiversity conservation, remediation and ecosystem-based fisheries management.

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Firstly, I would like to extend my thanks and appreciation to my supervisors Prof. Andy Davis, Dr. Nathan Knott, Dr. Matthew Rees and Dr. Matt Taylor. I am lucky to have you as my supervisors and will always be grateful for your guidance and continual support throughout my PhD candidature. Under your supervision, I have not only become a more confident and independent researcher, but I have also grown as a person. Without your commitment to my development, I would not be placed where I am to pursue a career in marine science.

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List of Publications included as part of this thesis

This thesis has been prepared in journal article compilation style format.

Publication	Chapter	Status	Journal
Swadling, D.S., Knott, N.A., Taylor, M.D., Coleman, M.A., Davis, A.R. & Rees, M.J. (2022). Seascape connectivity of temperate fishes between estuarine nursery areas and open coastal reefs. ***Journal of Applied Ecology***. https://doi.org/10.1111/1365-2664.14157	2	Published	Journal of Applied Ecology
Swadling, D.S., Knott, N.A., Rees, M.J., Pederson, H., Adams, K.R., Taylor, M.D. & Davis, A.R. (2020). Seagrass canopies and the performance of acoustic telemetry: implications for the interpretation of fish movements. ***Animal Biotelemetry***, 8(1), 8. https://doi.org/10.1186/s40317-020-00197-w	3	Published	Animal Biotelemetry
Swadling, D.S., Knott, N.A., Rees, M.J., Taylor, M.D. & Davis, A.R. (in prep). Consequences of juvenile fish movement and seascape connectivity: Does the concept of nursery habitats need a rethink?	4	In prep	Ecological Applications
Swadling, D.S., Knott, N.A., Taylor, M.D., Rees, M.J. & Davis, A.R. (in prep). Assessing generality in movement patterns for a targeted fish: home range and residency of Luderick (*Girella tricuspidata*) on open coastal reefs.	5	In prep	Fisheries Research

Additional Publications and Presentations

In addition to the manuscripts listed above, I have published a research article in *Landscape Ecology* using data from my honours project and co-authored 2 journal articles during my candidature. I have also presented data from my thesis at one international and three national conferences. Please see below for details.

Published papers

Swadling, D.S., Knott, N.A., Rees, M.J. and Davis, A.R. (2019) Temperate zone coastal seascapes: seascape patterning and adjacent seagrass habitat shape the distribution of rocky reef fish assemblages. *Landscape Ecology*, 34, 2337–2352.

Day, J., Knott, N.A., **Swadling, D.S.,** Ayre, D.A. (2021). Dietary analysis and mesocosm feeding trials confirm the eastern rock lobster (*Sagmariasus verreauxi*) as a generalist predator that can avoid ingesting urchin spines during feeding. *Marine and Freshwater Research*, 72, 1220-1232.

Rees, M.J., Knott, N.A., Hing, M.L., Hammond, M., Williams, J., Neilson, J., **Swadling, D.S.** & Jordan, A. (2021). Habitat and humans predict the distribution of juvenile and adult snapper (Sparidae: *Chrysophrys auratus*) along Australia's most populated coastline. *Estuarine, Coastal and Shelf Science*, 257, 107397.

Conference presentations

Swadling, D. S., Davis, A. R., Taylor, M. D., Rees, M. J. and Knott, N. A. “Seascape Effects on Temperate Reef Fish: Implications for Marine Conservation”, Australian Society for Fish Biology annual conference 2018, Melbourne, Australia.

Swadling, D. S., Davis, A. R., Taylor, M. D., Rees, M. J., Adams, K. R., Pederson, H. and Knott, N. A. “Fish movements, seagrass canopies and the performance of acoustic telemetry”, International Conference on Fish Telemetry 2019, Arendal, Norway.

Swadling, D. S., Davis, A. R., Taylor, M. D., Rees, M. J. and Knott, N. A., "Using acoustic tracking to improve marine reserve design: quantifying the movements of juvenile luderick (*Girella tricuspidata*)", Australian Society for Fish Biology 2019, Canberra, Australia.

Swadling, D. S. "Seascape Effects on Temperate Reef Fish: Implications for Marine Conservation". Science Week Talks Jervis Bay Maritime Museum – Invited speaker.

Swadling, D. S., Davis, A. R., Taylor, M. D., Rees, M. J. and Knott, N. A., "Fish and chips: tracking the movements of juvenile fish in a temperate marine park", Ecological Society of Australia anniversary conference 2020 (online).

Certification

I, Daniel Scott Swadling, declare that this thesis submitted in fulfilment of the requirements for the conferral of the degree Doctor of Philosophy, from the University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. This document has not been submitted for qualification at any other academic institution.

Daniel Swadling

11th October 2021

Statement of Candidate Statement

As the primary supervisor, I, Professor Andy Davis declare that the greater part of the work in each article is attributed to the candidate, Daniel Scott Swadling. In each of the papers that constitute this thesis, Daniel led conceptual development, study design and was primarily responsible for the data collection, data analysis and data interpretation. The first draft of each manuscript was written by the candidate who was then responsible for responding to the editing suggestions of his coauthors. The co-authors were responsible for assisting with the study design, data collection, interpreting data and editing manuscripts where necessary.

Daniel Scott Swadling
PhD Candidate
Date: 11th October 2021

Professor Andy Davis
Principal supervisor
Date: 11th October 2021

Table of Contents

Abstract ii

Acknowledgements iv

List of Publications included as part of this thesis vi

Additional Publications and Presentations vii

Certification viii

Statement of Candidate Statement ix

List of Tables xiii

List of Figures xiv

List of Plates xvii

List of Appendices xvii

Chapter 1: General Introduction 1

- **1.1 Seascape ecology** 1
- **1.2 Connectivity; a central tenet of seascape ecology** 5
- **1.3 Acoustic telemetry** 9
- **1.4 Acoustic telemetry and fish movements within seascapes** 12
- **1.5 Implications for marine management** 17
- **1.6 Thesis aims and structure** 19
- **1.7 References** 22

Chapter 2: Seascape connectivity of temperate fishes between estuarine nursery areas and open coastal reefs 44

- **2.1 Introduction** 45
- **2.2 Methods** 48
  - *2.2.1 Fish assemblage sampling and video analysis* 50
  - *2.2.2 Quantifying spatial metrics* 51
  - *2.2.3 Statistical analyses* 51
- **2.3 Results** 53
- **2.4 Discussion** 60
- **2.5 References** 65

Chapter 3: Seagrass canopies and the performance of acoustic telemetry: Implications for the interpretation of fish movements 73

- **3.1 Background** 74
- **3.2 Results** 77

3.3 Discussion 81

3.3.1 Conclusion 85

3.4 Methods 86

3.4.1 Study area 86

3.4.2 Experimental design 88

3.4.3 Statistical analyses 90

3.4.4 Abbreviations 92

3.5 References 93

Chapter 4: Consequences of juvenile fish movement and seascape connectivity: Does the nursery-role concept need a rethink? 99

4.1 Introduction 100

4.2 Methods 104

4.2.1 Study Site 104

4.2.2 Fish collection and acoustic tagging 105

4.2.3 Acoustic monitoring array 108

4.2.4 Data processing 108

4.2.5 Home-range estimation 109

4.2.6 Network analysis 110

4.2.7 Modelling patterns of space use and connectivity 111

4.3 Results 112

4.3.1 General findings 112

4.3.2 Species home ranges 115

4.3.3 Species networks: Habitat use and connectivity 116

4.3.4 MPA use 123

4.4 Discussion 123

4.5 References 131

Chapter 5: Assessing generality in movement patterns for a targeted fish: home range and residency of Luderick (*Girella tricuspidata*) on open coastal reefs 146

5.1 Introduction 147

5.2 Materials and methods 149

5.2.1 Study site 149

5.2.2 Fish collection and tagging 152

5.2.3 Data analysis 153

5.3 Results 155

5.3.1 General detection patterns 155
5.3.2 Residency and Site fidelity 157
5.3.3 Space-use 160
5.3.4 Environmental variables and diel patterns 160
5.4 Discussion 164
5.4.1 Generalities in luderick movement 164
5.4.2 Relationships between movement and environmental conditions 165
5.4.3 Technical considerations 167
5.4.4 Management Implications 168
5.5 References 170
Chapter 6: General Discussion **177**
6.1 Seascape connectivity of temperate fishes 178
6.2 Applying acoustic telemetry to quantify seascape connectivity 182
6.3 Implications of connectivity for marine management and conservation 184
6.4 Future Directions 188
6.5 Concluding remarks 192
6.6 References 193
Appendix 1 **208**
Appendix 2 **216**
Appendix 3 **269**

List of Tables

Table 2.1 Best generalised additive mixed models (GAMMs) predicting the abundance and length of the study species. All models within ±2 AICc values are presented in Table A1.1. * denotes an interaction between variables. 54

Table 3.1 The minimum and maximum values of environmental conditions........ 90

Table 4.1 Summary data for the 53 tagged individuals. Values for fork length, number of detections and days at liberty represent the means ± standard deviation and in parentheses are the minimum and maximum values observed. 107

Table 4.2 Model candidates within ±2 AICc for explaining the movement patterns of tagged fish. The Akaike information criterion corrected for small sample sizes (AICc), difference between the lowest Akaike information criterion corrected for small sample sizes (ΔAICc), variance explained (R^2) and effective degrees of freedom (EDF) are reported for model comparison. Models in bold represent the most parsimonious models. 115

Table 5.1 Summary data for the 10 tagged luderick (*Girella tricuspidata*) monitored in the Bendalong array including the movements between reefs, residency to the array and the activity spaces for each fish. I_R – array: residency index to the array, MLD: Minimum linear distance between release point and the farthest receiver an individual was detected, 95% and 50% UD: utilisation distributions (UDs) using Brownian bridge movement models. 156

Table 5.2 Top three candidate models based on AICc for the Generalized Linear Mixed Models (GLMMs) exploring relationships between the daily presence/absence of fish, weekly number of stations visited and minimum linear dispersal. * denotes model with a zero-inflated negative binomial distribution. R^2m represents the marginal R^2 and R^2c is the conditional R^2. All models include fish ID as a random effect. 163

List of Figures

Figure 1.1 The growth of publications in the field of seascape ecology over the past 20 years. Columns represents the number of publications on seascape ecology each year. Publication data was gathered from Web of Science using the search term 'Seascape Ecology' and "Marine Landscape Ecology" accessed on the 05-02-2022. 4
Figure 1.2 A conceptual framework for the movement pathway selected by an organism and the influence of seascape structure adapted from Nathan et al. (2008) and Pittman (2018). Relationships between components and their effects on one another are represented by arrows. Definitions: Navigation process is the navigational ability of the organism at its current location; Locomotion process is the speed and direction of movements produced; Movement process refers to the capacity of an individual to move at its current location, internal state and navigational ability.. 8
Figure 2.1 Locations of the 629 stereo-BRUV deployments across the Batemans bioregion in South-Eastern Australia. The locations of the two Marine Parks (MPA) and their no-take marine reserves (NTMR) are included.. 49
Figure 2.2 Relative importance scores from the full-subsets analyses exploring the effect of predictor variables on the abundance and length of the study species. The X labels illustrates variables selected in the most parsimonious model(s)... 55
Figure 2.3 Relationships between explanatory variables and the abundance of a) *Chrysophrys auratus*, b) *Nemadactylus douglasii*, and c) *Pseudocaranx georgianus*. Fitted GAMM prediction curves (solid line) are included, and ribbons and error bars represent ± standard error. Grey bars = areas where fishing is permitted and red bars = 'no-take' marine reserves. Distance to estuary is measured in metres. 57
Figure 2.4 Relationships between explanatory variables and the fork length (mm) of a) *Chrysophrys auratus*, b) *Nemadactylus douglasii*, and c) *Pseudocaranx georgianus*. Fitted GAMM prediction curves (solid line) are included, and ribbons and error bars represent ± standard error. Grey bars = areas where fishing is permitted and red bars = 'no-take' marine reserves. Distance to estuary is measured in metres. 59
Figure 2.5 Length distributions for the fork lengths (mm) at reefs close and distant from estuaries for a) *Chrysophrys auratus*, b) *Nemadactylus douglasii*, and c) *Pseudocaranx georgianus*. The dashed red line highlights the approximate body length when the species reaches maturity. The *P* values are the result of a Kolmogoroc-Smirnov two-sample test. 60
Figure 3.1 Distributions of the mean daily a) positional accuracy (m), b) precision and c) system efficiency (%) for the transmitters above and within seagrass (x-axis). Data points represents the raw values, violin plots illustrate the probability density and the black line is the mean. 77
Figure 3.2 Modelled detection probability for each deployment period at varying distances between transmitters and receivers. Black dots represent transmitters above seagrass and grey triangles illustrate transmitters within seagrass. Solid lines illustrate the prediction of the model and dashed lines define the standard error. The horizontal dashed line indicates the working detection range (i.e. 50% probability of detecting a transmitter) of acoustic receivers............... 78
Figure 3.3 Relationships for the model of environmental variables found to predict the detection probability of the internal VR2Tx transmitters from a GAMM. Solid lines illustrate the

prediction of the model, and the dashed areas define the 95% confidence intervals around the fitted values. The horizontal dashed line in the distance to receiver plot represents the working detection range (i.e. 50% of transmissions received). 80

Figure 3.4 Noise (mV) at 69 kHz calculated at all three VR2Tx receivers for each hour of the day. Solid dots represent the mean hourly value and error bars are ± standard deviation. Shading indicates nocturnal hours between 19:30 - 06:00. 81

Figure 3.5 Map of the location of Jervis Bay, NSW, Australia showing the major habitats and the positions of the VPS, additional receivers and transmitters.. 87

Figure 3.6 Schematic of a VR2W acoustic receiver station (left) and two transmitters (V7-4x) suspended either above (145cm) and within (15cm) the seagrass. 89

Figure 4.1 Map of Jervis Bay Marine Park (insert shows location on NSW coastline) and the dominant patch types. Receiver stations within the array are depicted and coloured based on whether they are in seagrass “nursery” patches (dark green), reef patches (russet) or part of the acoustic gate at the bays entrance (yellow). The general location of fish capture/release (see Table A2.1) are represented by yellow arrows. No-take marine reserves (NTMR) are illustrated by areas of red cross hatching. Please note that Wollamia and Myola are both located within Currambene Creek. 106

Figure 4.2 Detection history over the study period for tagged a) luderick and b) yellowfin bream at receivers in seagrass “nurseries” (green dots), rocky reefs (brown dots) or the acoustic gate (yellow dots). Tag deployment is represented by the black dots, with shape referring to release locations; black squares = Hare Bay, black circles = Currambene Creek, black triangles = Moona Moona Creek, black diamonds = Carama Inlet. Crosses indicate the anticipated date on which battery failure occurred. Fish with no detections are not included. 113

Figure 4.3 Predictions from the best fitting generalised additive mixed model for a) the extent area home-range (i.e. 95% BBMM), b) the number of days detected within the array, c) the number of edges within a network, and d) the number of nodes visited within a network. The solid lines are fitted prediction curves and ribbons and error bars represent ± standard error. .. 114

Figure 4.4. Comparison of core (50% BBMM) and extent (95% BBMM) home ranges for luderick tagged at different sites within Jervis Bay Marine Park. Points represent the mean values and bars are ± standard deviation. Maps illustrate spatial representations of the 50% (filled dark polygons) and 95% utilisation distributions (filled light polygons) using Brownian bridge movement models for a representative individual tagged at each different site. Dashed areas illustrate no-take marine reserves. Habitats (e.g. seagrass and reef) are depicted as seen in Figure 4.1……………………………………………………………………………………118

Figure 4.5. Comparison of core (50% BBMM) and extent (95% BBMM) home ranges for yellowfin bream tagged at different sites within Jervis Bay Marine Park. Points represent the mean values and bars are ± standard deviation. Maps illustrate spatial representations of the 50% (filled dark polygons) and 95% utilisation distributions (filled light polygons) using Brownian bridge movement models for a representative individual tagged at each different site. Dashed areas illustrate no-take marine reserves. Habitats (e.g. seagrass and reef) are depicted as seen in Figure 4.1……………………………………………………………………………………119

Figure 4.6 Species habitat networks for luderick and yellowfin bream tagged in either Hare Bay or creeks. In b), the left network represents luderick released in Moona Moona Creek and the right are luderick from Currambene Creek. The size of the grey nodes is representative of the number of detections recorded for an individual fish whilst habitat node size is proportionate to the frequency a patch type was used by fish. Edge size is scaled by the number of detections an individual was recorded in a patch type…………………………………………………………...120

Figure 4.7 Individual movement networks showing connectivity and space use in JBMP for a representative fish from a) luderick released in Hare Bay, b) luderick released in Currambene Creek, c) luderick released in Moona Moona Creek, d) yellowfin bream released in Hare Bay and e) yellowfin bream released in Carama Inlet. The colour of nodes illustrates the proportion of detections at a given receiver and edge colour shows the number of movements (i.e. connectivity) between receivers. Empty black circles show the non-visited receivers. The red 'x's are the release location of fish and black crosses on receivers represent core-use receivers…122

Figure 5.1 Map of the study area (Bendalong region, NSW, Australia) showing the configuration of the acoustic receivers (black dots) deployed over the 18-month study period. Circles surrounding each receiver illustrate a 300 m detection area. Areas of rocky reef (brown) and unconsolidated soft-sediment (light grey) patch types are depicted. 151

Figure 5.2 Timing and location of detections for the 10 tagged luderick (*Girella tricuspidata*). Black diamonds denote the date fish were tagged (August and September 2018) and the final download of the acoustic receivers (March 2020). Please see Figure 5.1 for the spatial location of each station. 158

Figure 5.3 Residency index by station for 8 luderick (*Girella tricuspidata*) passively tracked in the Bendalong receiver array. The size of the filled circles and numbers illustrate the I_R values at each station. Reef patches are coloured in brown. Empty circles depict the location of acoustic receiver stations and CS* represents where each fish was captured and released. 159

Figure 5.4 Spatial representation of the 50% and 95% utilisation distributions (UD) for 8 luderick (*Girella tricuspidata*) calculated using Brownian bridge movement models. ○ 95% UD (extent of home range); ○ 50% UD (core home range); + Centres of activity (COA) estimates, CS* capture site, ● station locations. 162

Figure 5.5 The mean number of detections for each hour of the day for 8 tagged luderick (*Girella tricuspidata*) within the Bendalong array. Solid dots represent the mean hourly value and error bars are ± standard deviation. Shading illustrates nocturnal hours between 18:00 and 06:00. 164

List of Plates

Plate 2.1 Graphical abstract for Chapter 2. 44
Plate 3.1 Graphical abstract for chapter 3. 73
Plate 4.1 School of luderick (*Girella tricuspidata*) and yellowfin bream (*Acanthopagrus australis*) on a reef adjacent to seagrass in the Hare Bay sanctuary zone in Jervis Bay Marine Park, Australia...99
Plate 5.1 Commuting to our study site on the south side of Bendalong Point for a day of fish tagging...146

List of Appendices

Appendix 1 – Supplementary material of relevance to Chapter 2

Appendix 2 – Supplementary material of relevance to Chapter 4

Appendix 3 – Supplementary material of relevance to Chapter 5

Chapter 1: General Introduction

Seascape ecology is a burgeoning field that investigates the causes and ecological consequences of spatial heterogeneity in the marine environment (Grober-Dunsmore et al. 2009; Boström et al. 2011, Pittman 2018). The field has transformed scientific understanding on fish-habitat relationships by examining patterns and processes across multiple spatiotemporal scales (Boström et al. 2011, Pittman 2018). A key concept in seascape ecology is that patches are not isolated from one another and are connected by the movement of organisms (Pittman & McAlpine 2003, Grober-Dunsmore et al. 2009, Pittman 2018). This connectivity is thought to be a key mechanism that integrates seascape structure and ecological functions, due to its influence on species distributions, reproduction, fitness and resource availability (Sheaves 2009, Boström et al. 2011, Pittman 2018). Recent technological advances in remote sensing and sampling techniques have led to a proliferation of studies explicitly quantifying connectivity patterns across seascapes. For instance, acoustic telemetry is providing an opportunity to explore fish movements, habitat use, and connectivity (Donaldson et al. 2014; Finn et al. 2014, Hussey et al. 2015, Taylor et al. 2017). However, few studies tracking fish with acoustic telemetry have tested hypotheses applying a seascape framework, despite this information having significant implications for ecosystem-based fisheries management. In this chapter, I provide a brief overview of seascape ecology and seascape connectivity, highlight the need to quantify fish movements across the seascape and its importance for the management of coastal fisheries.

1.1 Seascape ecology

There has been a long-standing appreciation for the effects of environmental heterogeneity over various scales on patterns of biodiversity and ecological processes (Humboldt 1807, Jaccard 1912, Troll 1939, Andrewartha and Birch 1954). Seascape ecology is a relatively novel, multidisciplinary field combining spatial analyses and ecology to examine the causes and ecological consequences of heterogeneity within seascapes (Boström et al. 2011, Pittman 2018). A seascape can be defined as a heterogeneous marine environment, often perceived as a mosaic of nearshore patch types (but can include the pelagic environment) that exhibits some form of patterning or gradient across various spatial and temporal scales (Boström et al. 2011). The traditional view of seascapes has been as 2-D planar surfaces consisting of patches, however new technologies (e.g. Lidar) have allowed them to also be represented in 3-D, such as digital terrain models (Wedding et al. 2011, Pittman 2018, Lepczyk et al. 2021). Seascape ecology (Ray 1991) adopts many of the concepts and techniques developed in its terrestrial counterpart, landscape ecology, which was developed through the mid 1900's and has roots in several scientific theories - the most influential and well known being the theory of island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Levins 1969, Wiens 1997). Although landscape ecology is a well-established and recognised field (Forman and Godron 1986, Turner 2005), its application in the marine environment has largely been hindered by difficulties in obtaining detailed habitat and biological data over sufficiently broad scales (10's to 100 kms) (Grober-Dunsmore et al. 2009, Boström et al. 2011, Wedding et al. 2011, Pittman et al. 2021). Recent advances in remote sensing and sampling techniques means that complex, broad-scale hypotheses related to seascape structure can now be tested, and the number of studies in seascape ecology has been growing exponentially (Fig. 1.1).

Glossary of Seascape Ecology terms	
Heterogeneity	The uneven spatiotemporal distribution of objects in the environment
Seascape structure	The composition (e.g. abundance and diversity of patch types) and spatial arrangement of patch types within the seascape
Patch type	A discrete area of space with similar substratum and abiotic conditions that differs from its surroundings
Edge environment	The boundary or ecotone of one or more patch types
Habitat context	The position of a focal patch relative to surrounding habitats
Seascape connectivity	The arrangement of patch types altering their physical linkages (e.g. patch isolation)
Mosaic	An area of multiple patches of various composition
Spatial pattern metrics	A range of metrics used to quantify different spatial characteristics of seascape structure, such as patch area, fragmentation, isolation, shape and terrain surface morphology.

Historically, the influence of seascape structure on fish assemblages has been investigated across multiple spatial scales. Early literature of fish-habitat relationships predominantly focussed on how features within discrete patch types, such as structural complexity or edge environments, affect species distributions (Bell and Galzin 1984, Sale and Douglas 1984, Bell and Westoby 1986, Chittaro 2002, Jelbart et al. 2006). Both observational and controlled experiments were used in early seascape research to determine the importance of a patches size, physical structure, context and isolation for fish recruitment and abundance, and assess whether marine reserves should be designed as single large areas or several small areas (i.e. SLOSS debate; Molles 1978, Schroeder 1987, McNeill and Fairweather 1993). The importance of connectivity was also highlighted through observations of fish movements between tropical patch types (Ogden and Zieman 1977, Gladfelter et al. 1980, Parrish 1989), however few studies were able to explicitly quantify connectivity and explore its effect on assemblages across broad spatial scales in marine systems due to technological limitations. With the development of accurate and affordable remote sensing techniques (e.g. aerial and satellite imagery, Lidar), research over the past two decades has made significant progress in testing hypotheses relating to seascape structure and have identified that connectivity plays an integral role in driving patterns of biodiversity and associated ecological processes in a range of marine systems (Grober-Dunsmore et al. 2007, Pittman et al. 2007, Gullström et al. 2008, Hitt et al. 2011, Berkström et al. 2012, Olds et al. 2012b, Pittman et al. 2014, Martin et al. 2015, Staveley et al. 2016, Nagelkerken et al. 2017, Gilby et al. 2018b, Perry et al. 2018, Rees et al. 2018, Bradley et al. 2019, Swadling et al. 2019; Berkström et al. 2020).

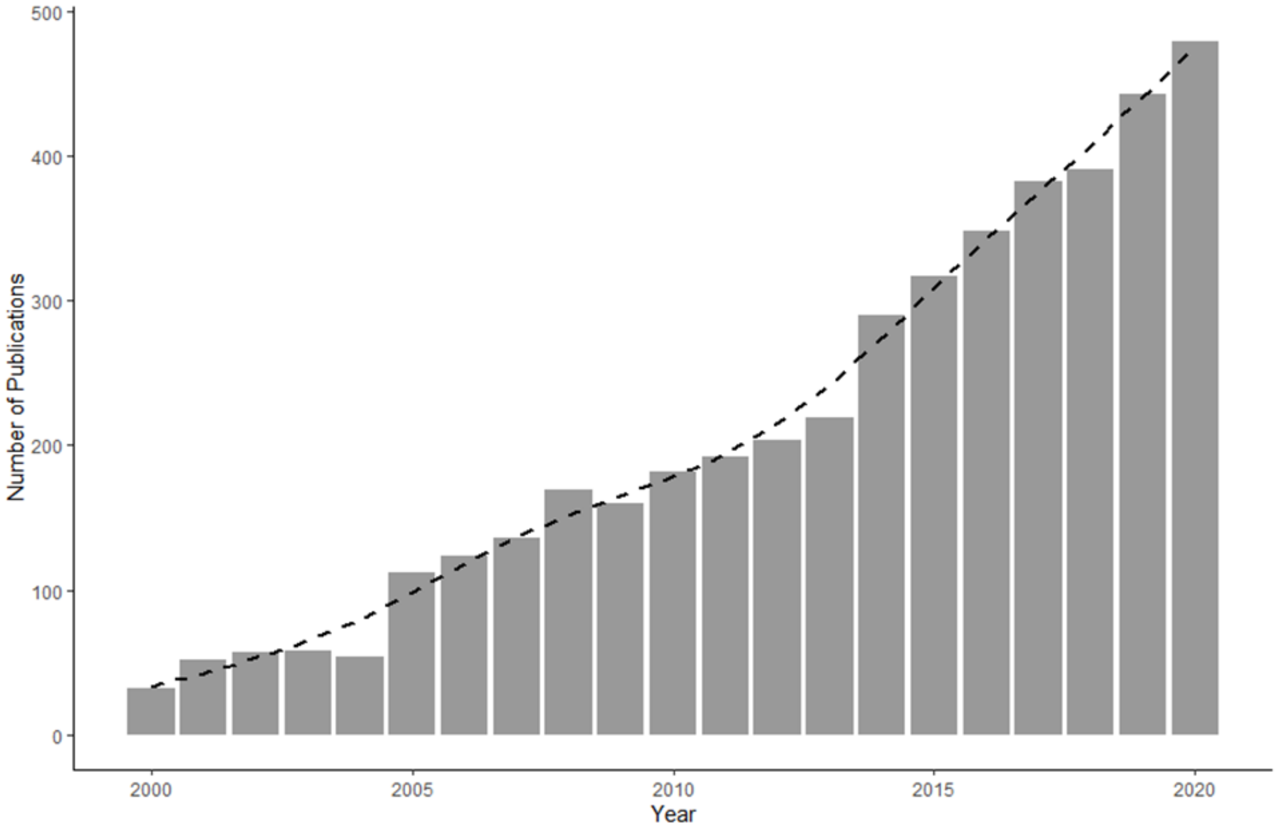


Figure 1.1 The growth of publications in the field of seascape ecology over the past 20 years. Columns represents the number of publications on seascape ecology each year. Publication data was gathered from Web of Science using the search term 'Seascape Ecology' and "Marine Landscape Ecology" accessed on the 05-02-2022.

1.2 Connectivity; a central tenet of seascape ecology

Connectivity is an important concept in seascape ecology from both a fundamental and applied perspective. While connectivity has a diverse context within ecology (Calabrese and Fagan 2004, Sheaves 2009), it can be broadly defined as the movement of organisms, materials and energy across seascapes. In animal ecology, connectivity is a function of the dispersal ability of species and the area, quality and spatial configuration of patch types (Hodgson et al. 2009, Berkström et al. 2012, Olds et al. 2012a, Pittman 2018). Connectivity plays a key role in determining the distribution of biota across a range of taxa in marine systems (Jordán-Dahlgren 2002, Mumby 2006, Ayre et al. 2009, Huijbers et al. 2013, Swadling et al. 2019), as it is crucial for regulating metapopulation dynamics, with more connected patches experiencing greater immigration (Grober-Dunsmore et al. 2009, Sheaves 2009). Further, connectivity is essential for ensuring ecosystem functioning (e.g. nutrient subsidies and herbivory) and population resilience (Clark et al. 2009, Davis et al. 2014, Hyndes et al. 2014, Swindells et al. 2017, Martin et al. 2018). The role of connectivity in mediating species distributions and ecosystem functioning means it is an important consideration for management strategies, such as identifying the optimal location and spacing for marine reserve networks to protect key habitats and movement corridors (Allison et al. 1998, Mumby 2006, Olds et al. 2016, Weeks 2017, Friesen et al. 2019) and optimising coastal seascape restoration and creation (Gilby et al. 2018a, Duncan et al. 2019, Gilby et al. 2019).

Coastal seascapes are heterogeneous environments containing a mosaic of various patch types (e.g. reefs, seagrass, mangroves and sand) which are connected through biological, physical and chemical processes (Grober-Dunsmore et al. 2009). Fish act as important mobile links connecting coastal patch types and populations across multiple spatial and temporal scales (Irlandi and Crawford 1997, Lundberg and Moberg 2003, Pittman and McAlpine 2003, Hyndes et al. 2014). For example, numerous species of fish exhibit a triphasic life-cycle where they recruit to inshore habitats (e.g. seagrass and mangroves) following a pelagic larvae stage, and then perform ontogenetic migrations to adult habitats such as reefs once they reach a certain age or size-class (Pittman and McAlpine 2003, Elliott et al. 2007, Nagelkerken 2009, Sambrook et al. 2019). In addition, many mobile fish connect patches during tidal, diel, monthly or seasonal movements in search of food and refugia or to spawn (Pittman and McAlpine 2003, Green et al. 2015). The availability, or access to, these adjacent patch types is dependent on seascape structure, with certain attributes either facilitating (patches in close proximity or presence of habitat corridors) or hindering movement (no patches nearby or presence of a barrier) (Grober-Dunsmore et al. 2009). Therefore, the distribution of many fishes can be explained by the spatial context of patch types and seascape structure. For instance, reefs close to large areas of seagrass have been reported to support greater abundance and species diversity relative to more isolated reefs in both tropical (Dorenbosch et al. 2005, Grober-Dunsmore et al. 2007, Campbell et al. 2011, Berkström et al. 2012, Olds et al. 2012b; Berkström et al. 2020) and temperate (Rees et al. 2018, Swadling et al. 2019) seascapes. This increase in abundance and diversity has been attributed to seagrass areas acting as “source” habitats and enhancing the recruitment of fishes to nearby reefs. Alternatively, increased biodiversity may occur when seagrasses are adjacent to reefs due to more resources being available in the seascape for mobile fish (i.e. landscape complementation and supplementation; Dunning et al. 1992), such as predatory Haemulids or Lutjanids that feed in seagrasses at night (Nagelkerken et al. 2000, Beets et al. 2003, Appeldoorn et al. 2009).

The movement of organisms has been categorised into four components, but this can be expanded to include seascape structure (Nathan et al. 2008, Pittman 2018). The four components of movement proposed by Nathan et al. (2008) include; 1) the internal state of the organism compelling it to move (e.g. foraging and reproduction), 2) the movement ability of the individual or its aptitude for locomotion/transport, 3) the organisms navigational ability in time and space, and 4) external influences, such as environmental signals and resource distribution. When considered within a seascape framework, seascape structure incorporates many of the external factors determining movement, particularly for mobile species (Fig. 1.2; Pittman 2018). The effect of seascape structure on movement decisions, however, is dependent on species traits such as its capacity to move and its internal state (Fig. 1.2). For example, the movements of species between patch types may decrease when patches are further apart due to energetic constraints, difficulties in navigation or exposure to predation when migrating (Zollner and Lima 1999, Grober-Dunsmore et al. 2009, Turgeon et al. 2010, Ryan et al. 2012, Nagelkerken et al. 2015). Certain species can also create seascape features during their movements or activities (i.e. external dynamics; Fig. 1.2), such as stingrays feeding in seagrass causing rounded depressions and the removal of seagrass fronds (Orth 1975, Howard et al. 1977). Therefore, the conceptual model of movement proposed by Nathan et al. (2008) and later adapted by Pittman (2018) can be further modified to incorporate these relationships as seen in Figure 1.2.

Connectivity can be quantified using metrics that fall into three main categories as suggested by Calabrese and Fagan (2004). Firstly, structural connectivity uses the spatial arrangements of physical structures in the seascape to infer connectivity with limited knowledge on the scale of movements. Secondly, potential connectivity combines some information on species movements with seascape configuration. And finally, connectivity can be quantified as actual connectivity which requires techniques that quantify the movement pathways across the seascape. The majority of seascape studies to date have used structural connectivity metrics (i.e. patch area and isolation) to explore correlations with observed distribution and abundance data (e.g. Grober-Dunsmore et al. 2007, Olds et al. 2012b, Swadling et al. 2019). Such methods are popular as they can identify key fish habitats and provide surrogates for multispecies conservation in a simple and cost-effective manner, making them practical for management (Ward et al. 1999, Dalleau et al. 2010, Olds et al. 2014).

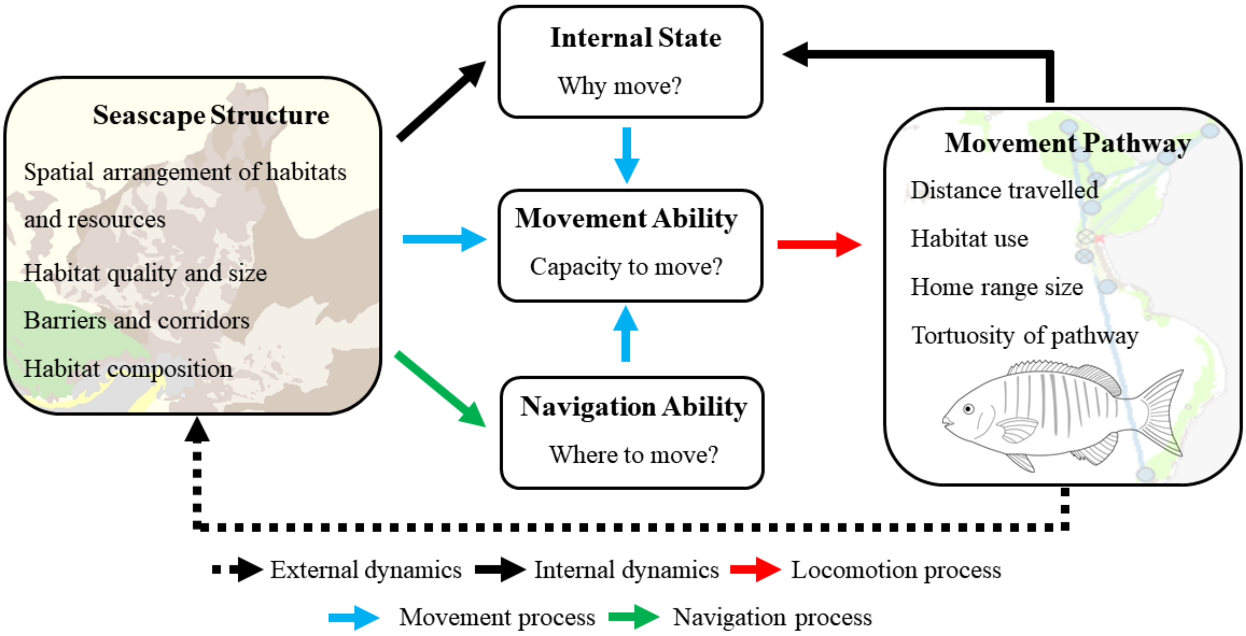


Figure 1.2 A conceptual framework for the movement pathway selected by an organism and the influence of seascape structure adapted from Nathan et al. (2008) and Pittman (2018). Relationships between components and their effects on one another are represented by arrows. Definitions: Navigation process is the navigational ability of the organism at its current location; Locomotion process is the speed and direction of movements produced; Movement process refers to the capacity of an individual to move at its current location, internal state and navigational ability.

Whilst quantifying connectivity using structural metrics is useful, this method infers movement pathways and provides limited information on actual connectivity. Therefore, current understanding on the movement of many fish species at different life-stages is largely conceptual. This is especially true for the ontogenetic dispersal of juveniles from nursery areas to adult habitats, with most information coming from studies testing for correlations between structural connectivity metrics and observational data of abundance and/or size classes (Dorenbosch et al. 2005, Grober-Dunsmore et al. 2007, Olds et al. 2012b, Rees et al. 2018, Swadling et al. 2019, Berkström et al. 2020). Other methods have been used to provide a more quantitative estimate on the spatial scale that juvenile fish disperse from nursery areas, including mark-recapture (Morton et al. 1993, Zeller et al. 1996, Verweij et al. 2007, Wakefield et al. 2011) and otolith chemistry (Yamashita et al. 2000, Forrester and Swearer 2002, Gillanders 2002, Gillanders 2005, Hamer et al. 2005, Reis-Santos et al. 2015, Schilling et al. 2018). For example, Gillanders (2002) used otolith chemistry to demonstrate that the majority (89%) of a key fisheries species in Australian waters, pink snapper (*Chrysophrys auratus*), caught on coastal reefs in the Sydney region used nearby estuaries as nursery areas. These techniques highlight the value of certain nursery areas to fish populations and provide some estimate of actual connectivity in the seascape, but they do not quantify fish movements over spatial scales appropriate to reconstruct detailed movement pathways. Therefore, several fundamental questions remain about how juvenile fish connect patch types across the seascape such as the spatial and temporal scales over which they disperse from nurseries to adult habitats, the importance of this connectivity for fisheries conservation strategies and which methods can be used to effectively track juvenile fish movements. Examining such questions using experimental or quantitative methods in a seascape framework will provide a better understanding of connectivity and the mechanisms underpinning biodiversity patterns. One method with the potential to achieve this is acoustic telemetry.

1.3 Acoustic telemetry

Quantifying the movement of fauna in aquatic systems is challenging. The spatial ecology of fishes has historically been investigated using methods such as visual observations (Beets et al. 2003), extractive techniques such as net or trap sampling (Guillard 1998, Hohausová et al. 2003, Jelbart et al. 2007, Clark et al. 2009), chemical isotopes (Gillanders 2002, Elsdon et al.

2008), biological tags (e.g. parasites; Lester et al. 2001, Mosquera et al. 2003) or capture-recapture tagging (Morton et al. 1993, Barrett 1995, Gray et al. 2012, Fowler et al. 2018). The development of biotelemetry represents a significant progression on these techniques, allowing for the movement of marine organisms to be quantified in detail both affordably and time efficiently (Rutz and Hays 2009, Donaldson et al. 2014, Hussey et al. 2015, Wilmers et al. 2015).

Acoustic telemetry (Box. 1.1) is among the most popular biotelemetry methods currently available to track fish movements (Donaldson et al. 2014, Hussey et al. 2015, Taylor et al. 2017a). Since its inception in the early 1970's, acoustic telemetry in aquatic ecosystems has experienced rapid growth and innovation, with the technology becoming more accessible, smaller and increasingly reliable (Thorstad et al. 2013, Donaldson et al. 2014, Taylor et al. 2017a). Acoustic telemetry has since become widespread in marine ecology and has been used to track the movement of a range of species from smaller, less mobile fish such as razorfish and Serranids (March et al. 2010, Alós et al. 2011, Aspillaga et al. 2021) to large, highly mobile fish such as marlin (Block et al. 1992), white sharks (McAuley et al. 2017, Bruce et al. 2019) and whale sharks (Rohner et al. 2020). Acoustic telemetry has revolutionised fisheries science and conservation by providing critical insights into the habitat use, population dynamics, migration patterns, physiology, behaviour, and inter-specific interactions of fishes (Donaldson et al. 2014, Hussey et al. 2015, Crossin et al. 2017). The findings from many acoustic telemetry studies highlight how fish move across the seascape, particularly when combined with reliable, high resolution seafloor maps and therefore provide many opportunities to address questions relevant to the field of seascape ecology, although most studies fail to do this.

Box 1.1. The fundamentals of Acoustic Telemetry

Acoustic Transmitters

Acoustic transmitters (i.e. acoustic tags) are miniature mechanical devices that can be attached externally or surgically implanted within organisms. These tags release acoustic signals as omni-directional pressure waves at a pre-determined delay and contain a unique identifier or code. There are a range of acoustic tags available, and the selection of tag is based on the ecological objective of the study and a trade-off between size, battery life and the frequency that the tag emits acoustic signals (referred to as tag delay). Tags can also contain accelerometers and other sensors (depth, temperature and predation) to combine with presence-absence data to provide a more complete picture on the spatial ecology of species.

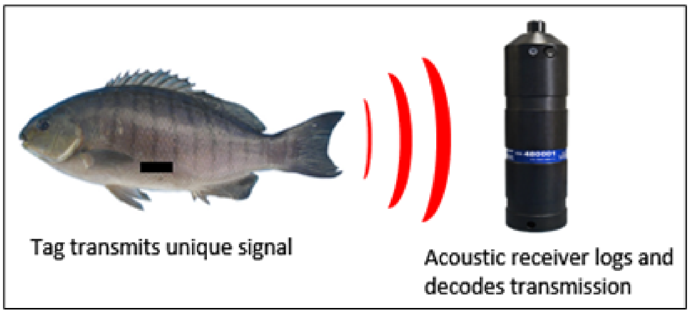
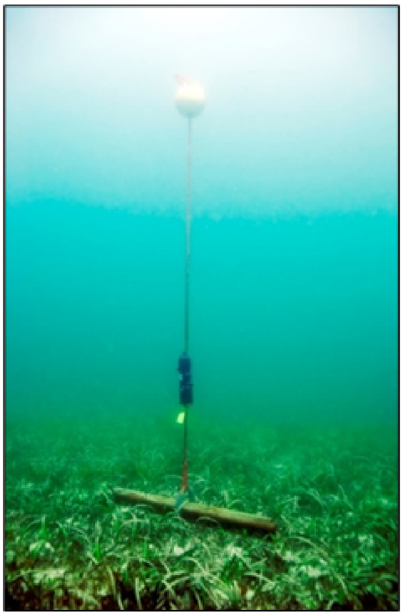


Figure 3. *Above*: The operational basics of acoustic telemetry. *Below*: An acoustic receiver affixed to a submerged mooring. Picture courtesy of Dr. Nathan Knott.

Acoustic Receivers

Acoustic receivers are hydrophones submerged in the aquatic environment that record and log the signals from acoustic tags. Receivers can be handheld to track a tagged individual from a vessel (active tracking) or fixed to some form of structure (passive tracking). Active tracking records the fine-scale movement paths of tagged individuals whereas passive tracking determines if an individual was present or absent in an area. Multiple receivers can be placed to form a passive acoustic array to cover areas or habitats relevant to a studies objective. Passive methods can also be used to track the fine-scale movements of individuals using positioning systems. This is achieved by triangulating the location of a tagged fish detected by three or more receivers with overlapping detection ranges (e.g. Vemco Positioning System). Technological advances in acoustic receivers mean they can now be deployed at great depths (> 100 m) and data can be remotely downloaded from the surface.



1.4 Acoustic telemetry and fish movements within seascapes

Acoustic telemetry has been commonly used to determine the habitat use and connectivity of adult, large-bodied fishes. Habitat use has been explored by quantifying residency to certain areas/patch types, using habitat selection indices, or by superimposing movement pathways or home-ranges from utilisation distributions (UDs: Box 1.2) onto benthic seascape maps (Lowry and Suthers 1998, Eristhee and Oxenford 2001, Lowe et al. 2003, Espinoza et al. 2011, Hitt et al. 2011). This research has revealed that many fishes have habitat preferences (Topping et al. 2005, Guttridge et al. 2015, Earl et al. 2017, Pillans et al. 2017) and species once considered to be highly mobile show residency or site-attachment to relatively small areas for periods of time (Ferguson et al. 2013, Harasti et al. 2015, Fetterplace et al. 2016, Novak et al. 2020). A number of species have also been observed to regularly connect patch types through their movements whilst foraging, seeking shelter or spawning (Luo et al. 2009, Claisse et al. 2011, Ferguson et al. 2013, Gannon et al. 2015, Green et al. 2015, Murchie et al. 2015, Taylor et al. 2018a). For instance, some piscivorous fish perform daily crepuscular migrations from reefs to adjacent seagrass patches (Verweij and Nagelkerken 2007, Appeldoorn et al. 2009, Green et al. 2015, Honda et al. 2016, Taylor et al. 2018a). These daily movements of piscivores have been attributed to foraging behaviour on adjacent seagrass meadows, which are highly productive and contain large amounts of prey items. Additionally, a range of species have been shown to move from day-time home ranges to night-time locations (Eristhee and Oxenford 2001, Claisse et al. 2011, Marshell et al. 2011, Ferguson et al. 2013). It has been proposed that these night-time locations are used for shelter because they are often structurally complex patch types such as rugose reefs or vegetated areas that offer protection (Claisse et al. 2011, Marshell et al. 2011). For example, Claisse et al. (2011) reported that yellow tang (*Zebrasoma flavescens*) exhibits crepuscular migrations along consistent corridors of up to 600 m between daytime foraging areas and night refuge sites.

There have been numerous studies that have observed fish moving along specific habitat corridors (Rhodes et al. 2012, Murchie et al. 2015, Hall et al. 2019, Hayden et al. 2019). For instance, Murchie et al. (2015) reported tagged bonefish (*Albula vulpes*) on the island of Grand Bahama move along a canal that traverses the island to reach spawning grounds, instead of migrating around the island's periphery. It is critical for research to continue identifying the connections between patch types and specific corridors used during daily and life-cycle movements, as this information has significant ramifications for designing conservation strategies, as shown in landscape ecology (Turner 2005, Lindenmayer et al. 2008).

Far fewer studies have explicitly quantified the movement of juvenile fish using acoustic telemetry, which is likely a result of acoustic transmitters being too large for use in small fishes. Therefore, current understanding on the habitat use of juveniles and their movement from nursery areas to adult populations remains unclear. The limited information available from acoustic telemetry on juvenile fish movements is predominantly for larger bodied teleosts (e.g. *Argyrosomus japonicus*; Childs et al. 2015, Taylor et al. 2017b) and elasmobranchs (Heupel and Hueter 2001, Weng et al. 2007, Simpfendorfer et al. 2010, Chin et al. 2016, Bruce et al. 2019, Hutchinson et al. 2019, Bangley et al. 2020). In contrast, there is a paucity of data for juvenile fishes of small body size (but see Furey et al. 2013, Huijbers et al. 2015, Grant et al. 2017). Huijbers et al. (2015) provides one study that has used acoustic telemetry to provide direct evidence of ontogenetic movements of juvenile fish (< 30 cm total length) from known nursery areas (i.e. a sheltered embayment in Curaçao) to coral reefs. A key finding of their study was that a proportion of juvenile schoolmaster snapper (*Lutjanus apodus*) permanently move to nearby coral reefs whilst other individuals appeared to perform exploratory movements to nearby reefs before returning to nursery areas. The lack of information on the movements of juvenile fish is undoubtedly due to the difficulties of implanting acoustic tags within small fish (Jepsen et al. 2005, Thorstad et al. 2009), which is constrained by tag size.

There is a general notion that is widely accepted in the telemetry community that excess mortality occurs when tagging fish if the tag to body mass ratio exceeds 2% (i.e. the 2% rule) (Jepsen et al. 2005). However, there is increasing evidence to challenge the 2% rule, with many species unaffected by the surgical implantation of tags weighing up to 12% of their body mass (Brown et al. 1999, Childs et al. 2011, Smircich and Kelly 2014, Klinard et al. 2018). Regardless, caution is still warranted when tagging small-bodied fishes, and the increasing miniaturisation of acoustic tags now offers researchers the opportunity to begin tracking juvenile teleosts of smaller sizes.

Research investigating the movement of fish between patches has largely used presence-absence data from passive telemetry to describe connectivity. Novel techniques now exist that can be used to extend beyond simply describing patterns of connectivity and explicitly test movement-seascape relationships with acoustic data collected using passive acoustic telemetry (Box 1.2; Pittman 2018, Whoriskey et al. 2019). For example, the seascape within a fish's home-range calculated using UDs can be analysed with spatial patterns metrics to deduce how seascape structure influences movement behaviour (Hitt et al. 2011, Dance and Rooker 2015). Another statistical technique beginning to be frequently applied to interpret telemetry data is network analyses. Indeed, network analyses provide researchers the ability to test how patch type, size and isolation influence movements (Jacoby et al. 2012, Finn et al. 2014, Espinoza et al. 2015, Lédée et al. 2015, Becker et al. 2020). An example of this is Espinoza et al. (2015), who examined the degree of connectivity of several shark species in the Great Barrier Reef using network analysis. The ability of sharks to migrate between habitats was dependent on the level of isolation of patch reefs, however this was species specific, with bull sharks (*Carcharhinus leucas*) showing greater mobility and connecting more isolated reefs than grey reef (*Carcharhinus amblyrhynchos*) and silvertip (*Carcharhinus albimarginatus*) sharks. Network analyses show great promise for testing movement-seascape hypotheses in comparison to more “conventional” analyses such as KUDs, as it can identify certain patch types and corridors important for maintaining connectivity (Lédée et al. 2015, Engelhard et al. 2017). Further, network analyses can be used to model the effects of habitat loss on connectivity patterns (Jacoby et al. 2012, Jacoby and Freeman 2016), which is important considering the increased pressure on marine systems from anthropogenic stressors (Halpern et al. 2008, Crain et al. 2009, Creighton et al. 2015).

Whilst acoustic telemetry provides a great opportunity to quantify the movements of fish, some limitations remain (Donaldson et al. 2014, Kessel et al. 2014, Brownscombe et al. 2019). One of the most notable considerations for passive acoustic telemetry is the variability and magnitude of the detection range of acoustic receivers within arrays (Kessel et al. 2014, Huveneers et al. 2016, Brownscombe et al. 2020). The detection range of acoustic receivers is defined as the maximum distance in which the acoustic signal of tags can be effectively detected and decoded (Kessel et al. 2014, Brownscombe et al. 2020). The detection range of receivers varies in time and space because acoustic signals are attenuated, refracted or lost as they travel in water, blocked by physical barriers or muffled by environmental and biological noise, all of which corrupt the transmitted code (Cagua et al. 2013, Gjelland and Hedger 2013, Kessel et al. 2014, Huveneers et al. 2016, Selby et al. 2016). Detection range can also vary due to the specifications of an acoustic tag, with higher powered tags detected over greater distances (How and de Lestang 2012, Cagua et al. 2013, Klinard et al. 2019), although this comes with the trade-off of larger tag sizes. False detections by receivers can also occur when signals are altered by external noises but still decoded by a receiver, or when transmissions from multiple tags operating on the same frequency overlap and collide (Simpfendorfer et al. 2015, Brownscombe et al. 2020). Therefore, the tag selected for a study and its transmission delay are important considerations when undertaking telemetry studies.

Box 1.2. Analytical approaches for exploring acoustic movement data in a seascape framework

Maximum Linear Dispersal (MLD)

MLD can be simply defined as the maximum distance a fish travels over a given time. For passively collected data, MLD can be used to identify certain seascape features acting as a barrier to movements, if certain habitats are used disproportionately by fish (i.e. show residency), and can be binned through time to determine the frequency of inter-habitat movements.

Examples: (Ferguson et al. 2013, Espinoza et al. 2015, Pillans et al. 2017)

Utilisation Distribution (UD)

UDs are a type of kernel density estimation used to quantify and visualise 2-dimensional space use from acoustic telemetry data. UD methods compute the probability that an individual is located within an area over time. There are several UD techniques, such as Minimum Convex Polygons, Kernel Utilisation Distributions or Local Convex Hulls that calculate areas where movements are concentrated by placing boundaries around the space use of an animal (e.g. 50% and 95% use areas). Other extensions of UDs include Brownian Bridge movement models that incorporate random walks between consecutive positions or Movement-based Kernel Density Estimates considering movement trajectories and habitat use.

Examples: (Topping et al. 2005, Hitt et al. 2011, Furey et al. 2013)

Network Analysis

Network analysis (NA) is a relatively nascent method to evaluate connectivity across seascapes with telemetry data. NA is rooted in graph theory and visualises animal movements as nodes (receivers or habitat patches) connected by edges (movements). NA can be constructed from acoustic data and combined with seascape structure to illustrate the flow of individuals across the seascape and space-use of individuals. NA techniques can provide valuable information not available using traditional methods (e.g. UDs) such as weighted directional movements that highlight corridors of movement.

Examples: (Jacoby et al. 2012, Finn et al. 2014, Espinoza et al. 2015, Becker et al. 2020)

Movement Pathway Analysis

Movement pathway analysis examines the movement and trajectory of animals at the path-level to determine the causes and behaviours of animals moving over space. Movement pathway analysis can be used to deduce differences in behaviours by statistically scrutinising the angles and lengths of movement pathways against models assuming behavioural modes such as foraging, fleeing or transiting (referred to as "state space models"). Movement pathway analysis can be overlaid on benthic seascape maps to associate variations in movement behaviour or pathway tortuosity with certain seascape features. When doing this, however, it is imperative that the extent and grain of the map be appropriate for the movements of the studied individual, and this may be species specific.

Examples: (Papastamatiou et al. 2009, Tilley et al. 2013, Alós et al. 2016, Wells et al. 2018)

The environmental and biological conditions that effect the detection range of acoustic receivers differ between systems and patch types, making *in situ* acoustic range tests an essential pre-requisite for telemetry studies to determine the appropriate array design and data interpretation (Kessel et al. 2014, Brownscombe et al. 2020). Another important consideration to incorporate into acoustic range tests is the behavioural traits of species that could contribute to variation in detection ranges, such as animals sheltering within refugia (e.g. rock crevices or aquatic vegetation) (Baktoft et al. 2015, Weinz et al. 2021). However, the majority of published acoustic range tests fail to incorporate nuances in how tagged animals use habitat as they only examine variations in detection performance using stationary tags in the water column (Kessel et al. 2014, Huveneers et al. 2016, Reubens et al. 2018, Brownscombe et al. 2020). The failure to incorporate information on receiver performance and range within a study creates the potential for erroneous conclusions to be deduced on the movement behaviour of tagged individuals (Payne et al. 2010).

1.5 Implications for marine management

Fisheries production is highly dependent on habitats (Creighton et al. 2015, Raoult et al. 2018, Taylor et al. 2018b, Jänes et al. 2020), meaning resource managers require information on key fish habitats and the connections between them to develop policies (CBD 2011; Crossin et al. 2017; NSW MEMA 2018). Such habitat management strategies include the protection of key fish habitat to mitigate any habitat loss or damage resulting from human stressors and enhancing, restoring or creating (e.g. offsets) habitats (Beck et al. 2001, Creighton et al. 2015, Fitzsimons et al. 2015, Gilby et al. 2018a, Jacob et al. 2018). Information on how fish interact with habitats within the seascape gathered using acoustic telemetry can help managers prioritise areas of habitats to protect (Crossin et al. 2017). For example, Simpfendorfer et al. (2010) quantified the fine-scale movement and habitat use of the critically endangered smalltooth sawfish (*Pristis pectinata*) and found that juveniles had small home-ranges located in shallow mud/sand banks lined with mangrove shorelines. Therefore, conservation of the species should target the protection of areas containing these patch types. Acoustic telemetry has also been used to highlight the success of habitat restoration projects (Espinoza et al. 2011, Brooks et al. 2017, Hall et al. 2019). By combining acoustic telemetry and population surveys (i.e. seining and long-lining), Espinoza et al. (2011) demonstrated that juvenile gray smooth-hound sharks (*Mustelus californicus*) were using a newly restored Californian estuary and that the system provided suitable resources for feeding and growth. Improved knowledge on fish movements across varying spatiotemporal scales will assist managers to better protect key habitats for fisheries production or threatened species and to develop effective restoration strategies.

Marine Protected Areas (MPAs) are being used worldwide to protect and conserve the biological diversity and social values of marine ecosystems from anthropogenic stressors (Spalding et al. 2008, Gaines et al. 2010, Edgar et al. 2014, Knott et al. 2021). To be successful in conserving fish populations, MPAs must be appropriately sized and located to incorporate the areas fish use regularly during at least part of their life-cycle (Kramer and Chapman 1999, Grüss et al. 2011). Information on the movement and connectivity patterns of fishes within the seascape is therefore essential to both assess the efficacy of currently established MPAs and to assist the design of future “no-take” marine reserves. This is particularly true for the dispersal of juvenile fish from nursery areas to adult habitats, as this will determine the optimal design to protect fish throughout their life-histories (Grüss et al. 2011). For instance, if juvenile fish disperse from nurseries to nearby adult habitats, then reserves should be designed to cover both habitats within their boundaries and protect these linkages. Alternatively, if juveniles disperse large distances to adult habitats, then networks of spatially discrete reserves may be more appropriate to conserve fish populations. Incorporating nursery areas within reserves could also be used to prevent the loss of these habitats and to promote adjacent fisheries, as the ‘spillover' (i.e. dispersing over reserve boundaries) of individuals will ensure adequate recruitment to adult habitats where fishing is permitted (Gell and Roberts 2003, Grüss et al. 2011). The importance of connectivity for MPA design is further emphasised by recent research highlighting that both academic scientists and resource managers identified that the spatial scales of connectivity within the seascape and its impact on management actions (e.g. MPAs or habitat restoration) is a high priority research question for future work in the field of seascape ecology (Pittman et al. 2021).

1.6 Thesis aims and structure

There is a clear need for information on the mechanisms underpinning patterns of biodiversity and ecological processes that can be deduced using a seascape ecology framework. Central to this is the movement of fish as it is a key determinant of connectivity and the distribution of species. Furthermore, understanding the movement and connectivity of fishes will assist the identification of key fish habitats and the implementation of management initiatives such as MPAs. This is critically needed given that the continued and pervasive degradation to the marine environment has the potential to disrupt linkages across the seascape. In this thesis, I investigated fish movements and connectivity between patch types using both observational techniques and acoustic telemetry. The overarching aims of this thesis include 1) examining the movement patterns and habitat use of reef-associated fish at varying life-stages, 2) quantifying the connectivity between nursery areas and adult habitats for temperate reef-associated fish, and 3) assessing the importance of fish movements and connectivity for spatial management strategies, such as MPAs.

The specific aims addressed in each chapter were:

Chapter 2: "*Over what spatial scales do estuarine nursery areas contribute juvenile fish to rocky reefs and how does this affect the abundance and size of the population?*" In this chapter, I examined how the relative abundance and body length of three targeted fish species (*Chrysophrys auratus*, *Pseudocaranx georgianus* and *Nemadactylus douglasii*) on coastal rocky reefs varied in relation to the proximity and size of the nearest estuary. Based on previous research showing *C. auratus* to be dependent on estuaries as nurseries, I predicted that the species would be smaller and more abundant on reefs close to estuaries due to increased recruitment of juveniles. In contrast, I predicted that the abundance and length of the other two species (*P. georgianus* and *N. douglasii*) would not be influenced by the proximity or area of estuaries as these species are not estuarine dependent. As a network of marine reserves exist across the study area, I also assessed whether reserve effects were influenced by proximity to estuaries. I predicted that reserves would contain greater abundances of each fish species, but *C. auratus* abundance would be greatest in reserves closest to estuaries due to the enhanced recruitment.

Chapter 3: "*Is the detection range of acoustic receivers impacted when tagged fish are within the seagrass canopy?"* Range tests of acoustic receivers are an essential prerequisite prior to conducting telemetry projects. However, there has been no formal assessment of the performance of acoustic telemetry within seagrass patch types or any consideration on how the sheltering behaviour of fish within seagrass fronds affect the transmission of acoustic signals. In this chapter, I performed a novel range test where acoustic transmitters were located within and above the seagrass canopy to determine the impacts on the detection range of receivers and the efficacy of a Vemco Positioning System (VPS; Box 1.1). I predicted that there would be a substantial decrease in detection range and fewer positional estimates from the VPS when transmitters were ensconced in seagrass. In addition, I also predicted that the detection range of receivers would be influenced by environmental conditions (i.e. wind, time of day, background noise, atmospheric pressure, receiver tilt and depth).

Chapter 4: "*Do juvenile reef-associated fish show residency within seagrass nursery areas and how far do they disperse to adult habitats?"* The aim of this chapter was to quantify the movement patterns of juvenile fish belonging to two targeted species (*Acanthopagrus australis* and *Girella tricuspidata*) within their nursery areas (i.e. seagrass patches) and their dispersal to adult reef habitats using acoustic telemetry. I predicted both species would show residency to their capture location in seagrass nursery areas. I further predicted that both species would move to rocky reef habitats directly adjacent nurseries and not reefs farther afield. This prediction was formed from previous research finding higher abundance and diversity of fish on reefs close to seagrass in the study area, which was used to infer connectivity (Rees et al. 2018, Swadling et al. 2019). I also assessed the scale of these movements in relation to the size of current no-take marine reserves and identified if individuals crossed reserve boundaries into fished areas.

Chapter 5: "*Do fish show general movement patterns across seascapes with different environmental conditions?"* In this chapter I quantified the movement patterns of adult *Girella tricuspidata* on rocky reefs along a wave exposed coastline. I predicted that individuals would exhibit strong residency or site-attachment like those previously reported on reefs in a coastal embayment. I also predicted that the species movements on coastal reefs would be different to those reported from estuarine systems where fish are exposed to large fluctuations in physico-chemical conditions that effectively force them to move. I also examined how the movement of adult *G. tricuspidata* varies with environmental conditions, predicting that individuals will be less mobile at night and in stochastic weather events such as storms and large swells.

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Chapter 2: Seascape connectivity of temperate fishes between estuarine nursery areas and open coastal reefs

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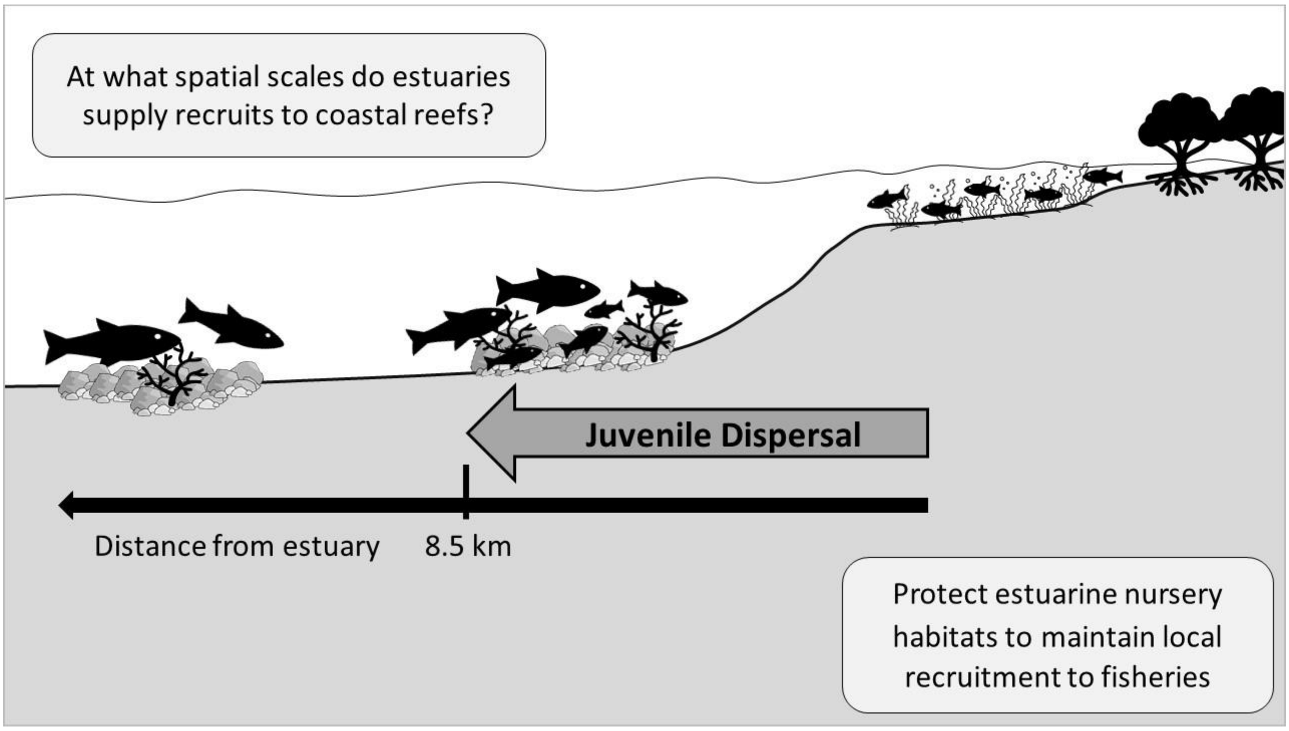

Plate 2.1 Graphical abstract for Chapter 2.

2.1 Introduction

The ecological and economic importance of estuaries as nursery areas for coastal fishes is widely recognised (Beck et al., 2001; Barbier et al., 2011; Sheaves et al., 2015), yet the spatial extent over which estuaries influence fish populations along open coastlines is poorly quantified. Many species extracted in coastal fisheries are known to recruit as larvae/juveniles to estuaries where they benefit from physico-chemical conditions favourable to growth, high availability of food and refugia before migrating to adult populations in coastal habitats (Beck et al., 2001; Potter et al., 2015). Determining the spatial scales over which nursery areas contribute recruits to adult populations is critically needed to better measure population dynamics, identify relevant spatial scales for management, understand the ecosystem services provided by nursery habitats and determine target habitats for conservation which will provide recruits to exploited fish populations (Beck et al., 2001; Lipcius et al., 2008). This is particularly important for targeted species that use estuaries as nursery areas, as estuarine systems are experiencing degradation worldwide from anthropogenic stressors such as overdevelopment, pollution, and climate change (Barbier et al., 2011). This degradation to estuaries could significantly disrupt the lifecycles of estuarine dependent species and reduce overall recruitment (Meynecke et al. 2008; Sheaves et al., 2014). Quantifying supply-side relationships between estuarine nurseries and coastal populations should allow us to predict the impacts of estuary degradation on broader fish metapopulations and develop mitigation or remediation strategies to avoid these costly and damaging effects in the future (Kennish, 2002; Meynecke et al. 2008; Sheaves et al., 2014).

Research using observational techniques, natural tags (e.g. otoliths, parasites, and stable isotopes) or mark-recapture methods has shown that many species preferentially disperse from estuarine nurseries to nearby reefs relative to distant ones (Olson & Pratt, 1973; Morton et al., 1993; Gillanders, 2002; Rees et al., 2021). For example, Gillanders (2002) used otolith chemistry to show that the majority (89%) of *Chrysophrys auratus* captured on coastal reefs in the Sydney region originated from the closest estuary. Examination of the abundance and size-structure of fishes provides a complimentary approach to studies of natural tags to better understand connectivity between estuaries and adjacent coastal habitats (Gillanders et al., 2003). For instance, Rees et al. (2021) reported that juvenile *C. auratus* had a higher probability of occurrence on reefs near large estuaries. However, they modelled this relationship using the presence-absence of categorical size-classes and did not assess the scale of connectivity between estuaries and reefs. Therefore, the distance at which recruits are supplied from estuaries to coastal reefs remains poorly resolved. An alternative method to better quantify the scale of connectivity between habitats is to model fish abundance and body length as continuous variables (Galaiduik et al., 2017). Such an approach would enable inferences on how far juveniles disperse to coastal reefs across the seascape, through an increase in fish length and a decrease in abundance as reefs get further from estuaries. Similar methods have been used to quantify connectivity between seagrass nursery areas and reef habitats (Nagelkerken et al., 2017; Rees et al., 2018; Swadling et al., 2019; Berkström et al. 2020).

No-take marine reserves (hereafter referred to as NTMR) are used globally to conserve marine biodiversity by reducing anthropogenic impacts to the marine environment (Halpern & Warner, 2002; Gaines et al., 2010). There is, however, only a nascent understanding on how connectivity influences NTMR performance (Olds et al., 2016). Close proximity to nursery habitats has been assumed to provide strong connectivity by offering a highly connected source of recruits which may enhance the effect of NTMRs (Nagelkerken et al., 2012; Olds et al., 2013). For example, Olds et al. (2013) observed enhanced reserve effects on targeted fishes on protected coral reefs close to mangrove nurseries in comparison to more isolated protected reefs that experienced lower recruitment of nursery dependent species. Despite this evidence, and recommendations in the literature to incorporate connectivity into NTMR design (Olds et al., 2016), there are few examples where connectivity has been assessed to evaluate ecological patterns within NTMRs.

In this study, we examined relationships between the relative abundance and size-structure of fishes on temperate coastal rocky reefs in relation to the proximity and size of estuaries. We collected these data using Baited Remote Underwater Videos Systems (BRUVS), across an entire temperate bioregion (the Batemans Marine Bioregion; 34° 35’S to 36° 48’S) in south-eastern Australia. As a network of NTMRs exists across the bioregion, we also assessed for reserve effects and whether differences in fish abundance and size between reserve and non-reserve sites are influenced by the proximity and size of estuaries. We focussed on three species harvested in both recreational and commercial fisheries in the bioregion; pink snapper (*Chrysophrys auratus*), grey morwong (*Nemadactylus douglasii*) and silver trevally (*Pseudocaranx georgianus*) (Stewart et al., 2015; West et al., 2015). All species have similar adult body size, but disparate life-histories, allowing for a comparison among fishes with differing estuarine dependency. Specifically, the sparid *C. auratus* has an estuarine ontogenetic phase, remaining in estuaries for 1-2 years and reaching lengths between ~180-220 mm before migrating to coastal reefs (Bell & Worthington, 1992; Ferrell & Sumpton, 1997); the carangid *P. georgianus* is considered an estuarine opportunist, with adults and juveniles found in both estuarine and coastal waters (Farmer et al., 2005; Fowler et al., 2018); and finally the cheilodactylid *N. douglasii* is a reef specialist and is not known to use estuaries as nursery habitats (Stewart & Hughes, 2009). We therefore predicted that the estuarine dependent *C. auratus* would be more abundant and smaller on reefs close to large estuaries due to the presence of recruits < 220 mm. In contrast, we predicted that the abundance and size-structure of species less reliant on estuarine nurseries (i.e. *N. douglasii* and *P. georgianus*) would not be correlated to the proximity or area of estuaries.

2.2 Methods

We sampled 46 rocky reef sites along a 417 km length of coastline in the Batemans Marine Bioregion in south-eastern NSW, Australia (Fig. 2.1). The seascape of the bioregion, like most temperate coastal marine environments, is comprised of coastal rocky reefs and estuaries containing vegetative patches (primarily seagrass and mangroves), interspersed in a matrix of unconsolidated soft sediment. These patch types are present throughout the bioregion but vary spatially in their coverage and arrangement. Estuarine patch types important for fish populations (seagrass, mangroves and saltmarshes) have experienced losses in NSW waters and face a range of anthropogenic stressors which include development and land use changes (Meehan & West 2000, Saintilan & Wilton 2001, Harty & Cheng 2003, Williams & Thiebaud 2007), boating activities and infrastructure (Fyfe & Davis 2007, West 2011, Glasby & West 2018), trampling by humans and livestock (Ross 2006) and events associated with climate change such as droughts or sea level rise (Saintilan et al. 2014, Davis et al. 2016, Scanes et al. 2020). The bioregion contains two multi-use marine parks, Batemans Marine Park and Jervis Bay Marine Park with replicated NTMR (where it is not permitted to harm or remove animals) along with habitat protection zones and general use zones where fishing is allowed (Fig. 2.1).

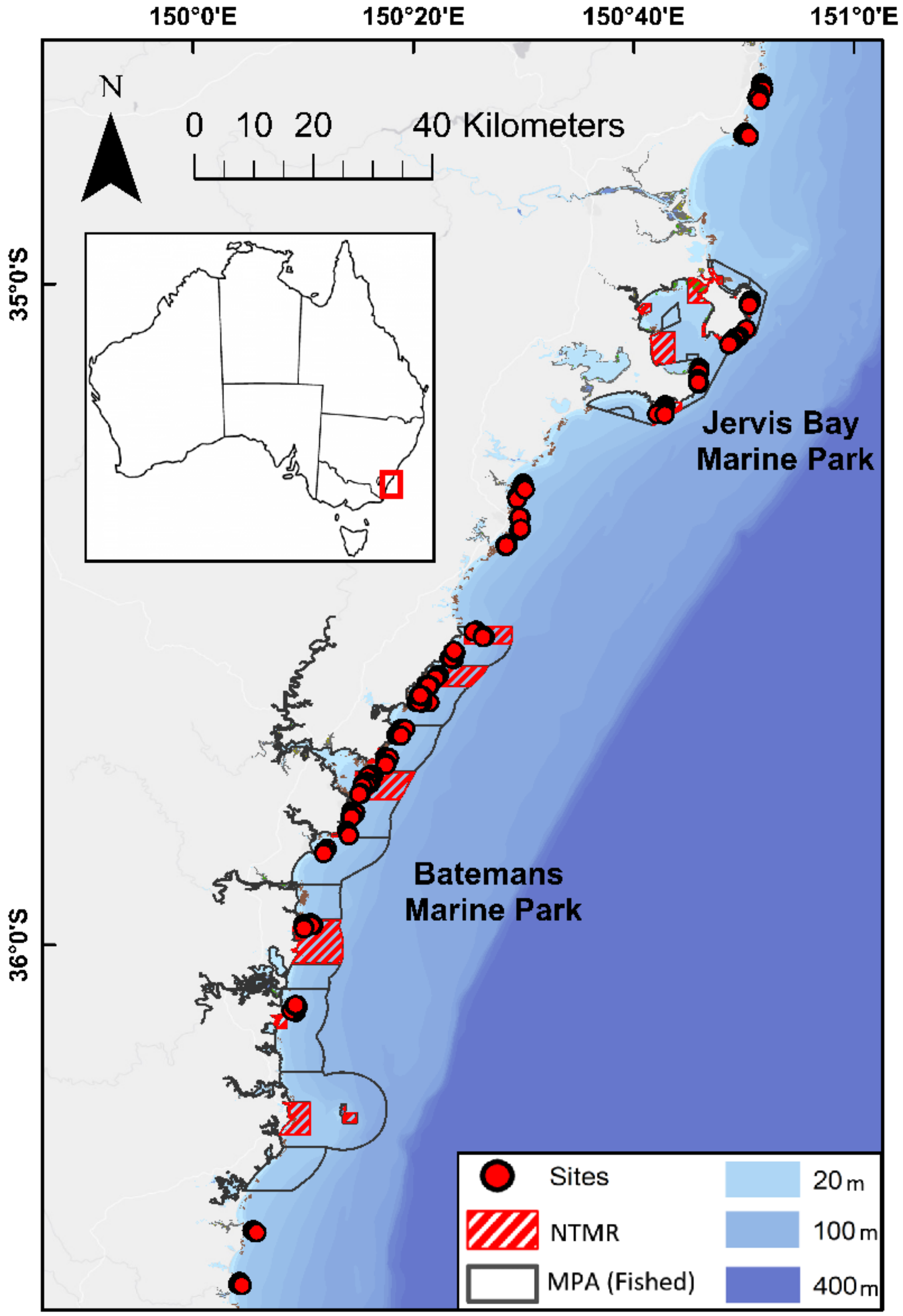

Figure 2.1 Locations of the 629 stereo-BRUV deployments across the Batemans bioregion in South-Eastern Australia. The locations of the two Marine Parks (MPA) and their no-take marine reserves (NTMR) are included.

2.2.1 Fish assemblage sampling and video analysis

Rocky reef fish assemblages were sampled using BRUVS, with a total of 629 BRUVS deployed across the 46 reef sites (Fig. 2.1). At each site, BRUVS were deployed on rocky reefs simultaneously in groups of four during the austral Winter and Spring of 2010, 2011, 2015 and 2016. The BRUV deployments in this study were completed for a larger project, specifically the NSW state-wide BRUV monitoring program undertaken by NSW Fisheries Research (see Knott et al. 2021). Sites were positioned to representatively sample fish assemblages across reefs throughout the bioregion and were located at various distances from estuaries, meaning these data were suitable for investigating relationships between fish assemblages and estuarine connectivity. The BRUVS were baited with ~500 g of crushed pilchards (*Sardinops sagax*), deployed for a minimum of 30 minutes, and separated by 200 m (Malcolm et al., 2007; Harasti, Malcolm, et al., 2015). Rocky reef sites ranged from 15-36 m in depth and contained numerous species targeted in fisheries, including *C. auratus*, *N. douglasii* and *P. georgianus* (Kelaher et al., 2014; Knott et al., 2021).

The BRUVS were constructed as described in Malcolm et al. (2007) and consisted of a video camera (digital Canon HG21 or HFG10/25) attached to a galvanised metal frame with a 1.5 m horizontal bait arm. In 2015 and 2016, stereo-BRUVS were used, and these systems had two calibrated cameras on each frame which record simultaneously allowing for accurate measurements of fish lengths. The 30-min videos from each BRUV deployment were analysed using EventMeasure software (SeaGIS Pty Ltd). Fish that entered the field of view within 5 m of the camera were identified to the species level where possible. A relative abundance measure (MaxN) was calculated for each species, which was defined as the maximum number of a given species observed in a single frame during the 30-minute deployment. For the stereo-BRUVS deployed in 2015 and 2016, the fork length (FL) of the three study species was measured at the time of MaxN for each species. The number of lengths obtained for the three species (320 to

356 measurements) and deployments (n= 326) fit the recommended levels to determine accurate size-structure of fish populations using stereo-BRUVs (Weerarathne et al., 2021). Stereo-BRUVS were calibrated before and after each sampling period to ensure accurate length estimates.

2.2.2 Quantifying spatial metrics

The distance to the nearest estuary from each BRUV deployment was quantified as Euclidean distances in ArcGIS version 10, along with the area of estuary surrounding each deployment at two spatial scales, 10 and 20 km, measured as radii centred over each deployment (n= 629). Only open estuaries defined by Roy et al. (2001) were selected for analyses. Intermittently closed and open lakes and lagoons are present throughout the bioregion but were excluded because there is limited information available on their episodic opening and closing. Therefore, we could not be certain if they could be contributing individuals to coastal populations at the time of sampling. Reef sites were positioned within fished areas or NTMR (i.e. unfished areas) across the bioregion and fishing status was included as an explanatory variable because it has been demonstrated to significantly affect the abundance and size of reef-associated fishes (Halpern & Warner, 2002; Malcolm et al., 2018; Knott et al., 2021). Sites in fished areas and NTMRs were distributed across similar distances from estuaries throughout the bioregion (Fig. A1.1). The accessibility of reefs by fishers, measured as the distance to boat ramps, was consistent across the bioregion (Fig. A1.2) and not collinear with estuary proximity (Pearson correlation r= 0.08, P= 0.3). The depth of each deployment was also recorded.

2.2.3 Statistical analyses

We used generalised additive mixed models (GAMMs) to understand correlations between the proximity and area of estuaries in combination with fishing status and sampling year and the abundance and body length of reef-associated fish (Hastie & Tibshirani, 1987). GAMMs were selected because they are suitable for predicting complex non-linear relationships between species distribution data and environmental predictors whilst taking into account random effects (Guisan et al. 2002; Zuur et al. 2009). In addition, GAMMs have previously shown great utility for modelling fish abundance and length data to explore relationships with seascape structure (Galaiduk et al. 2017; Swadling et al. 2019; Berkström et al. 2021). Preliminary data exploration was used to assess homogeneity and collinearity between predictor variables (Zuur et al., 2009). Estuary area was square root and log(x + 1) transformed at the 10 and 20 km scales respectively to normalise their distribution. A full-subset approach was used to fit all possible combinations of explanatory variables that were not collinear (i.e. Pearson’s correlations < 0.28) to models (Fisher et al., 2018). All models were fitted with a maximum of three predictors and the smoothing parameter was limited to a simple spine (k= 5) to prevent overfitting and create conservative, ecologically relevant models (Fisher et al., 2018). Site was included within models as a random effect to increase inferential power and account for overdispersion and spatial autocorrelation (Harrison, 2014). The depth of deployments and sampling year were also included as predictor variables. Interactions were permitted in models between factors, and between factors and continuous predictors (e.g. between fishing status and distance to estuary). The model residuals did not show evidence of spatial autocorrelation using Morans *I* and spline correlograms (Fig. A1.4 - 6).

Fish response variables were not transformed as the selection of appropriate error distributions in GAMMs account for non-normal distributions of the data. GAMMs for species lengths were fitted with gaussian distributions while models of abundance used a tweedie distribution to account for the large number of zeroes (Tweedie, 1984). The lengths for a given species recorded from a single stereo-BRUV deployment are not independent of one another so deployment number was included as an observation-level random effect into models for body length (Harrison, 2014). Model selection was based on the Akaike information criterion for small sample sizes (AICc), with the best model having the lowest AICc (Burnham & Anderson, 2002). When multiple candidate models occurred within ±2 AICc of the best model, the most parsimonious model(s) with the fewest predictors was selected. R^2 values were used to indicate the predictive power of each model. Summed AICc weights were used to determine the relative importance of predictor variables across the full set of models (Anderson & Burnham, 2002).

Length frequency distributions were used to compare the body lengths of *C. auratus, P. georgianus* and *N. douglasii* on reef sites “close” or “distant” from estuaries. Reefs were categorised as either close or distant based on whether they were below or above the mean distance of reefs (~8,500 metres) from an estuary. A Kolmogorov-Smirnov two-sample test was used to compare length distributions between close and distant reefs. The Kolmogorov-Smirnov two-sample test was conducted using 100,000 simulations to account for the small sample sizes. All statistical analyses and plots were performed using the statistical computing program “R” (R Core Development Team, 2018) and the packages FSSGAM 1.11 (Fisher et al., 2018), mgcv (Wood, 2015), gamm4 (Wood & Scheipl, 2014) and ggplot2 (Wickham, 2016).

2.3 Results

The distance to estuary, fishing status and sampling year were the most important predictors for the abundance and length of the three study species, however relationships were highly species specific (Table 2.1; Fig. 2.2). Full subsets analysis identified an interaction between fishing status and the year sampled on the lengths of all species (Table 2.1). There were no interactive effects between fishing status and either the size or distance to estuary in any models within ± 2 AICc of the top model for species abundance and length (Table A1.1).

Table 2.1 Best generalised additive mixed models (GAMMs) predicting the abundance and length of the study species. All models within ± 2 AICc values are presented in Table A1.1. * denotes an interaction between variables.

Response		**edf**	**wAICc**	**AICc**	**R^2**	**Best model(s)**
Species abundance (MaxN)	*Chrysophrys auratus*	38.06	1	3690.23	0.28	Distance to estuary + Status*Year
	Nemadactylus douglasii	25.93	0.229	608.84	0.16	Distance to estuary + Estuarine area (20 km)
		25.89	0.199	609.12	0.16	Distance to estuary + Status
	Pseudocaranx georgianus	33.78	0.21	2445.61	0.11	Estuarine area (10 km) + Year
Species lengths	*Chrysophrys auratus*	8	0.751	3867.85	0.14	Distance to estuary + Status*Year
	Nemadactylus douglasii	8	0.45	3466.7	0.06	Distance to estuary + Status*Year
		8	0.26	3467.81	0.05	Estuarine area (10 km) + Status*Year
	Pseudocaranx georgianus	8	0.3	3178.35	0.001	Depth + Status*Year
		8	0.27	3178.56	0.002	Distance to estuary + Status*Year
		8	0.2	3178.83	0.0001	Estuarine area (10 km) + Status*Year

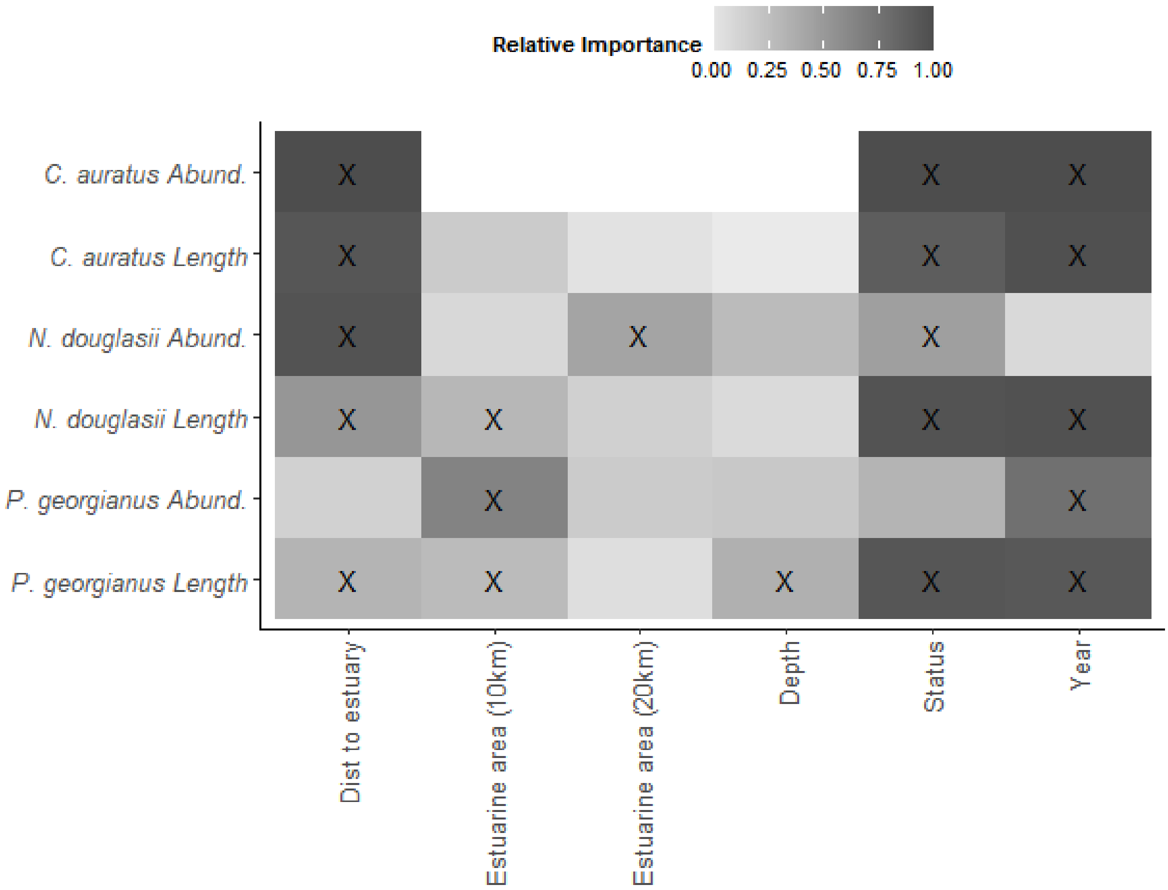

Figure 2.2 Relative importance scores from the full-subsets analyses exploring the effect of predictor variables on the abundance and length of the study species. The X labels illustrates variables selected in the most parsimonious model(s)

The abundance of *Chrysophrys auratus* exhibited a non-linear relationship with distance to estuary, decreasing from an average MaxN of four on reefs directly adjacent to an estuary to one individual on reefs 4 km from estuaries. The predicted MaxN of *C. auratus* then increased to three on reefs 11 km from estuaries before declining again to a MaxN of one (Fig. 2.3a; R^2= 0.28). Higher abundances of *C. auratus* were also observed in NTMRs compared to fished areas and abundance in each zone gradually increased through time (Table 2.1; Fig. 2.3a). As predicted, the abundance of *Nemadactylus douglasii* exhibited no clear relationship with distance to estuary with only small increases at both 2.5 and 11 km. Both *C. auratus* and *N.*

douglasii exhibited peaks in abundance on reefs ~11 km from estuaries which corresponded with a high proportion of BRUV deployments within NTMRs in comparison to fished areas and likely represent a reserve effect rather than an increase in abundance due to the distance from estuary. The abundance of *N. douglasii* remained consistent with estuarine area at the 20 km scale (Table 2.1; Fig 2.3b; R^2= 0.16). There was an alternate parsimonious model within ± 2 AIC of the best model for *N. douglasii* abundance, which contained the distance to estuary and indicated a greater abundance in NTMRs compared to fished areas (Table 2.1; Fig. A1.3a). The abundance of *Pseudocaranx georgianus* slightly decreased with greater area of estuary at the 10 km spatial scale, although this was a very marginal effect. The abundance of *P. georgianus* was also greater in 2015 and 2016 when compared to 2010 and 2011 (Table 2.1; Fig. 2.3c; R^2= 0.11).

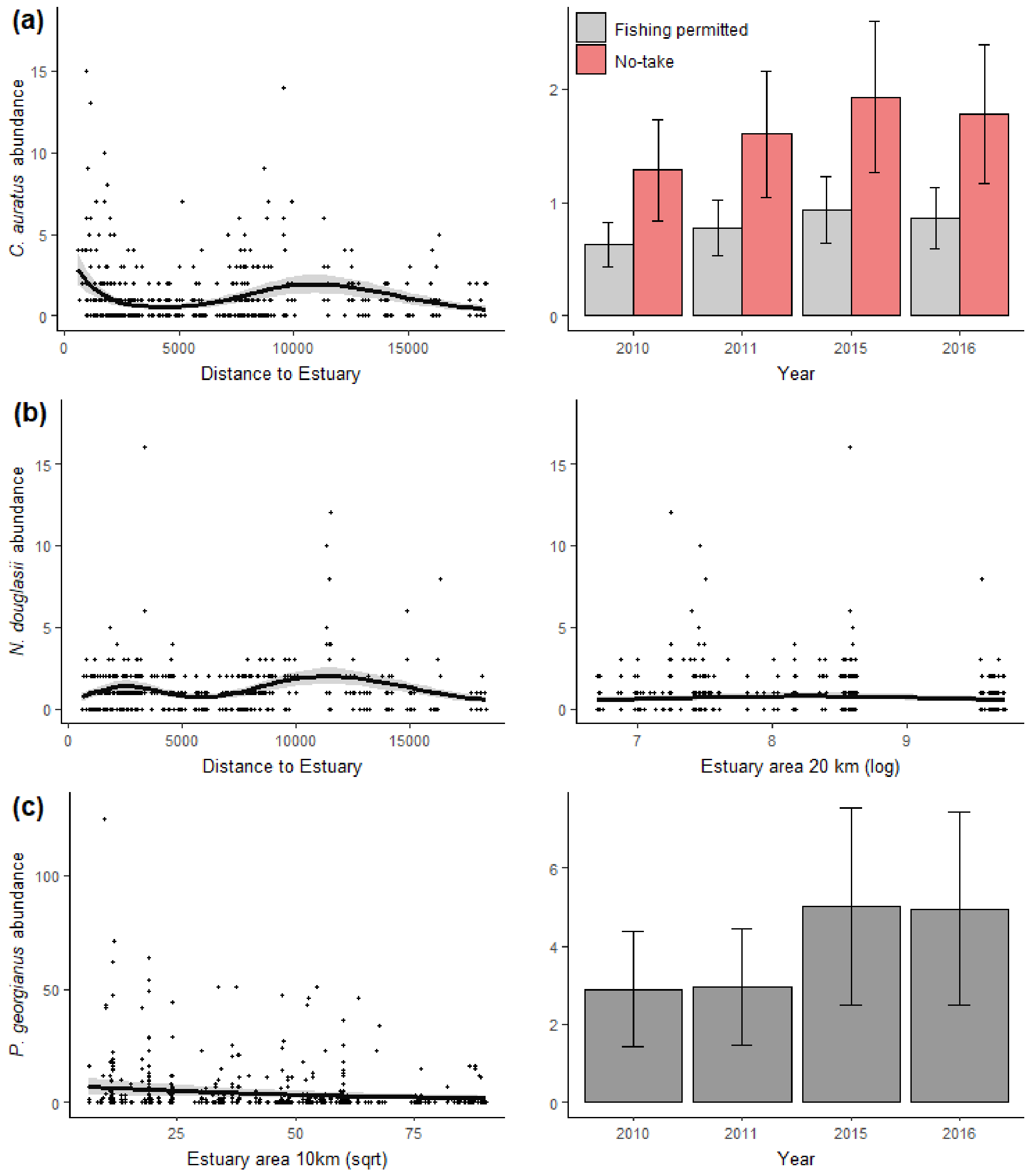

Figure 2.3 Relationships between explanatory variables and the abundance of a) *Chrysophrys auratus*, b) *Nemadactylus douglasii*, and c) *Pseudocaranx georgianus*. Fitted GAMM prediction curves (solid line) are included, and ribbons and error bars represent ± standard error. Grey bars = areas where fishing is permitted and red bars = 'no-take' marine reserves. Distance to estuary is measured in metres.

The average body length of *C. auratus* increased with the distance from estuary, plateauing at ~260 mm until reefs were 8.5 km from estuaries and then increasing substantially to ~350 mm on reefs > 15 km from estuaries (Table 2.1; Fig. 2.4a; $R^2 = 0.14$). The length of *N. douglasii* increased from 320 mm to 350 mm as reefs became more isolated from estuaries (Fig. 2.4b), although this relationship had low explanatory power ($R^2 = 0.06$; Table 2.1). There was also an increase in the length of *N. douglasii* with estuarine area at the 10 km scale (Table 2.1; Fig. A1.3b). The predicted average length of *P. georgianus* decreased from 280 mm to 250 mm as depth increased from 17 to 22 m, before plateauing around 255 mm (Table 2.1; Fig. 2.4c). There was little effect of estuaries on the length of *P. georgianus* with these relationships having small effect sizes and explaining little variation ($R^2 < 0.002$; Table 2.1; Fig. A1.3).

The length of *C. auratus* demonstrated the strongest response to status and year, being larger in NTMRs in comparison to fished zones and length also increased in both zones through time (Fig. 2.4a). Both *N. douglasii* and *P. georgianus* were larger on reefs in NTMRs compared to those in fished areas in 2015 (Fig. 2.4). However, *N. douglasii* length on fished reefs increased in 2016 so there were marginal differences between management zones (Fig. 2.4b). Further, *P. georgianus* length in NTMRs decreased in 2016 to sizes comparable to fished areas (Fig. 2.4c).

Length frequency histograms provided further characterisation of the differences in length distributions of each species on reefs “close” and “distant” from estuaries (Fig. 2.5). The length distributions of *C. auratus* was significantly larger on reefs distant from estuaries (KS test: D= 0.23, $P < 0.001$; Fig. 2.5a). The modal length of *C. auratus* was much smaller on reefs close to estuaries, indicating the presence of many more juveniles, while large individuals greater than the minimum legal length of the species (i.e. > 300 mm total length (TL) or > 260 mm FL; Ferrell & Sumpton, 1997) were more evenly distributed across the bioregion (Fig. 2.5a). The length distributions of *N. douglasii* and *P. georgianus* were not significantly different between reefs that were close versus distant from estuaries (K-S test: $P > 0.05$).

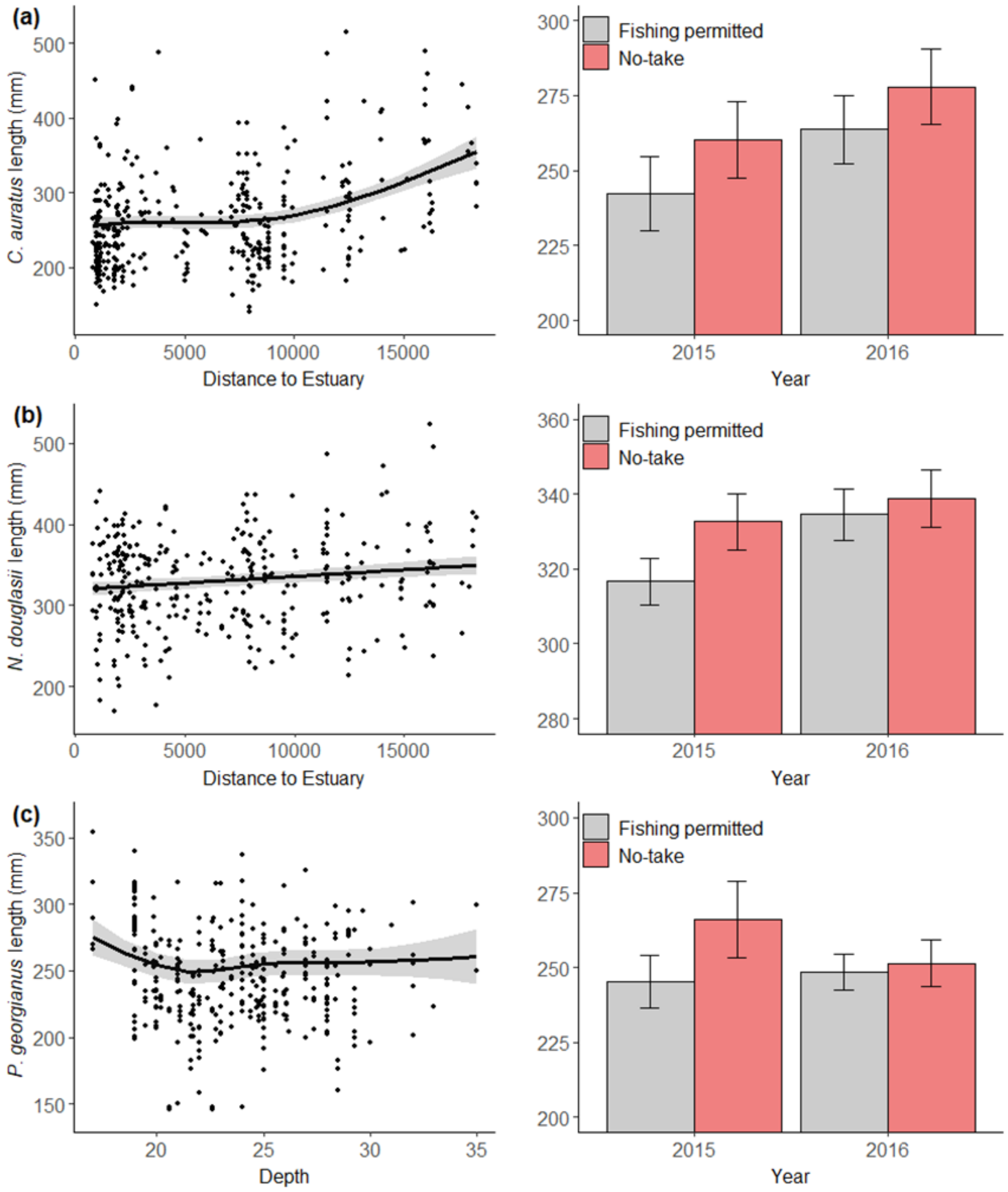

Figure 2.4 Relationships between explanatory variables and the fork length (mm) of a) *Chrysophrys auratus*, b) *Nemadactylus douglasii*, and c) *Pseudocaranx georgianus*. Fitted GAMM prediction curves (solid line) are included, and ribbons and error bars represent ± standard error. Grey bars = areas where fishing is permitted and red bars = 'no-take' marine reserves. Distance to estuary is measured in metres.

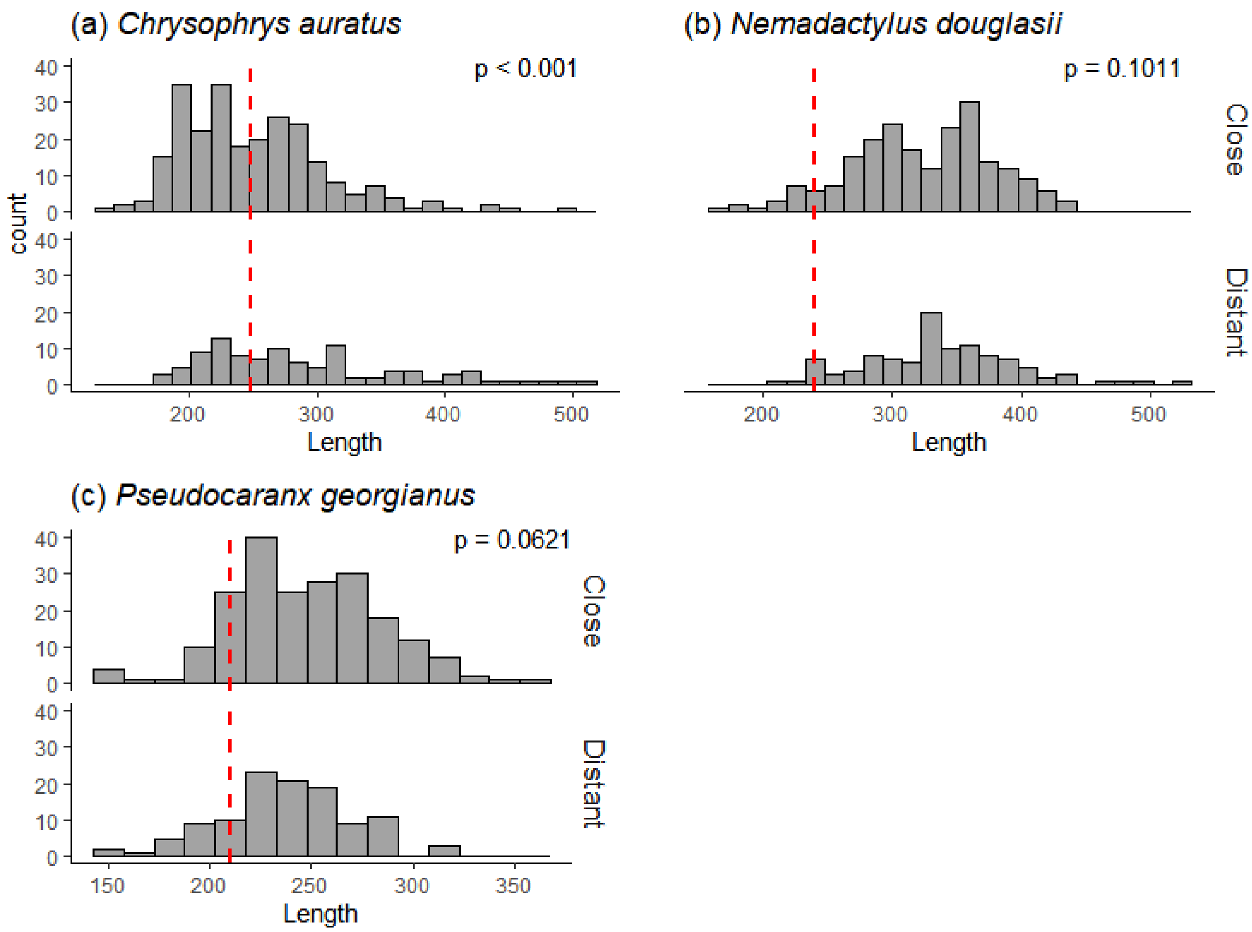

Figure 2.5 Length distributions for the fork lengths (mm) at reefs close and distant from estuaries for a) *Chrysophrys auratus*, b) *Nemadactylus douglasii*, and c) *Pseudocaranx georgianus*. The dashed red line highlights the approximate body length when the species reaches maturity. The *P* values are the result of a Kolmogoroc-Smirnov two-sample test.

2.4 Discussion

Although considered fundamental to the replenishment of fisheries worldwide and the maintenance of metapopulations, there are generally few quantitative estimates on the potential recruitment subsidy from estuarine nurseries to coastal adult populations and this has led to their importance being questioned (Sheaves 2017; Sheaves et al. 2020). We present one of the few empirical studies quantifying the spatial scale that estuarine nursery habitats contribute individuals to coastal reef-associated fish populations. A key finding was that the abundance and length of a highly important species for recreational and commercial fisheries in temperate waters, *Chrysophrys auratus*, is heavily influenced by distance to estuaries across more than 400 km of temperate coastline. Effects on abundance generally occurred up to 2 km from estuaries whereas the species length was consistently smaller on reefs within 8.5 km from estuaries. The validity of this interpretation is highlighted by no distinct relationship being found between estuarine proximity or area the distribution of *Nemadactylus douglasii* and *Pseudocaranx georgianus*, two species that are considered not to be dependent on estuaries as nursery habitats.

Previous research has highlighted that estuaries are an important source of recruits for *C. auratus* and there is evidence that adults of the species inhabiting reefs in NSW originate from nearby estuaries (Gillanders, 2002; Rees et al., 2021). We observed smaller *C. auratus* on reefs close to estuaries, which is consistent with the species performing ontogenetic migrations from estuarine nurseries to nearby open coastal rocky reefs. We extend previous research, however, by combining continuous fish length data from stereo-BRUVs with seascape maps to reveal that the supply of recruits from estuaries occurs disproportionately across small spatial scales, with individuals < 220 mm FL (and approximately 1-2 years of age) found largely on reefs within 8.5 km from estuaries. These findings contrast with studies from other regions of Australia (i.e. Victoria, South Australia and Western Australia) analysing the chemical compositions of otoliths for *C. auratus* that have found coastal embayments contribute juveniles/subadults to reefs at much broader scales, across 10’s to 100’s of kilometres (Fowler et al., 2005; Hamer et al., 2005; Hamer et al., 2011). For example, Hamer et al. (2005) reported that Port Phillip Bay in Victoria supplied 60% of subadult (i.e. 1-2 years) *C. auratus* captured on reefs 60 km away. The strong connectivity between estuarine and coastal populations of subadult *C. auratus* is important considering any declines in estuary health and nursery quality will have the potential for negative impacts on the number of recruits entering nearby coastal fisheries.

Importantly, we observed large adult *C. auratus* to be distributed uniformly across the bioregion, irrespective of reef proximity to estuaries. The predicted increase in size far from estuaries was caused by the lack of smaller individuals on distant reefs rather than an increase in the observed lengths. Previous analysis of the otolith chemistry of this species in South Australia and Victoria has suggested that they are highly mobile between the ages of 3 to 5 years, where they redistribute themselves across the coastline (Fowler et al., 2005; Hamer et al., 2011). Given that 3+ year old (approximately ≥ 300 mm FL; Ferrell & Sumpton, 1997; Stewart et al., 2011) *C. auratus* were evenly distributed on reefs along the coastline in the current study, we contend that the species is also highly mobile in this age class within the Batemans Marine bioregion. We suggest that *C. auratus* predominantly move out of estuaries at around 1 to 2 years (i.e. ~180-220 mm FL) to reefs adjacent (< 8.5 km) estuaries and over the next few years move to reefs farther afield resulting in the even distribution of older size-classes (i.e. > 300 mm FL) across the bioregion. This may be linked to a shift in diet through ontogeny, with the species expanding its diet to larger items such as crabs, bivalves and teleosts as they grow (Usmar, 2012). The movement of *C. auratus* through ontogeny is poorly understood, but adults and subadults have been reported to show residency on coastal reefs in NSW for at least one-year post-tagging (Harasti, Lee, et al., 2015). Future studies using direct, quantitative techniques such as acoustic telemetry is necessary to provide more detail on the connectivity of *C. auratus*, and other estuarine dependent fishes, across coastal seascapes.

As predicted, the length and abundance of *N. douglasii* and *P. georgianus* showed little relationship to estuarine proximity which supports the hypothesis that these species do not rely on estuaries as nurseries. While observations of juvenile *P. georgianus* within estuaries suggest they use these areas as nurseries, the species is highly mobile and inhabit numerous shallow coastal patch types, such as soft-sediments and reefs (Rowling & Raines, 2000; Farmer et al., 2005; Fowler et al., 2018). Therefore, if a significant proportion of the species recruits directly to coastal reefs or other nearshore patch types and regularly move over large areas, the influence of estuaries on the structure of the population would be limited and difficult to assess using indirect (i.e. observational) techniques. The lack of effect for estuarine proximity on the distribution of *N. douglasii* and *P. georgianus* highlights that our findings for *C. auratus* are likely driven by ontogenetic dispersal, rather than other processes altering assemblages such as estuarine plumes that influence productivity and recruitment on nearby reefs (Grimes & Kingsford, 1996; Connolly et al., 2009).

Connectivity between nursery and adult habitats has been found to enhance the ability of NTMRs to promote the abundance of fish in tropical seascapes (Nagelkerken et al., 2012; Olds et al., 2013). In the current study, however, we found no interactions between reserve effects and the distance to estuary for any species. This is particularly surprising for *C. auratus*, as we expected based on previous literature that greater rates of immigration from estuaries to nearby protected reefs would promote higher abundances within these NTMRs. The relationship between the abundance of *C. auratus* within NTMRs and connectivity is likely due to subadults dispersing to reefs prior to being targeted by fishers as these individuals are below the legal-size limit in NSW of 300 mm (TL). Therefore, these individuals are protected from fishing pressure on reefs in both fished and NTMRs which would reduce the apparent reserve effect. Conceptually, the connectivity between estuaries and reefs may still be important as NTMRs located adjacent to estuaries will offer protection to a range of *C. auratus* size classes and are supplied with more recruits than those reserves far away. The network of NTMRs within the bioregion did appear to provide conservation benefits to *C. auratus* populations irrespective of their spatial context to estuaries, with larger and more abundant *C. auratus* observed within reserves compared to fished areas, and this difference increased through time. Similar responses to protection by *C. auratus* have been reported in previous research in Australia (Harasti et al., 2018; Malcolm et al., 2018), including in the Batemans bioregion (Kelaher et al., 2014; Knott et al., 2021), and in New Zealand (Edgar et al., 2017). NTMR effects in the bioregion for *N. douglasii* and *P. georgianus* occurred but were more variable than those observed for *C. auratus*.

This study provides quantitative data on the spatial scales over which estuaries contribute individuals to coastal reefs and the consequences for the distribution of species. Specifically, these data suggest that local estuaries are an important source of *C. auratus* recruits for nearby open coastal rocky reefs. This is significant considering that globally, numerous species of fish with high socio-economic value have been reported to be estuarine dependent as juveniles before migrating to offshore populations as adults (Vasconcelos et al., 2008; Tournois et al., 2017; Santos et al., 2019). Future research in other geographic regions is therefore imperative to understand the relative contributions of estuarine nursery areas to coastal fisheries and the scale over which they supply juveniles to offshore marine populations. The need for this information is further underscored by the continued stress placed on estuaries by anthropogenic processes which threatens to reduce the nursery function of these systems (Meynecke et al. 2008; Potter et al., 2015; Rees et al., 2021). For example, if localised recruitment occurs for these species, then the degradation and loss of habitats within estuaries may pose a threat to the health and productivity of coastal fish populations by disrupting linkages essential for the maintenance of metapopulations. Indeed, this would have serious social and economic consequences. Protecting or restoring estuarine systems should therefore be a priority for management to ensure the conservation of ecological functions and to sustain adequate recruitment for species with estuarine dependency.

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Chapter 3: Seagrass canopies and the performance of acoustic telemetry: Implications for the interpretation of fish movements

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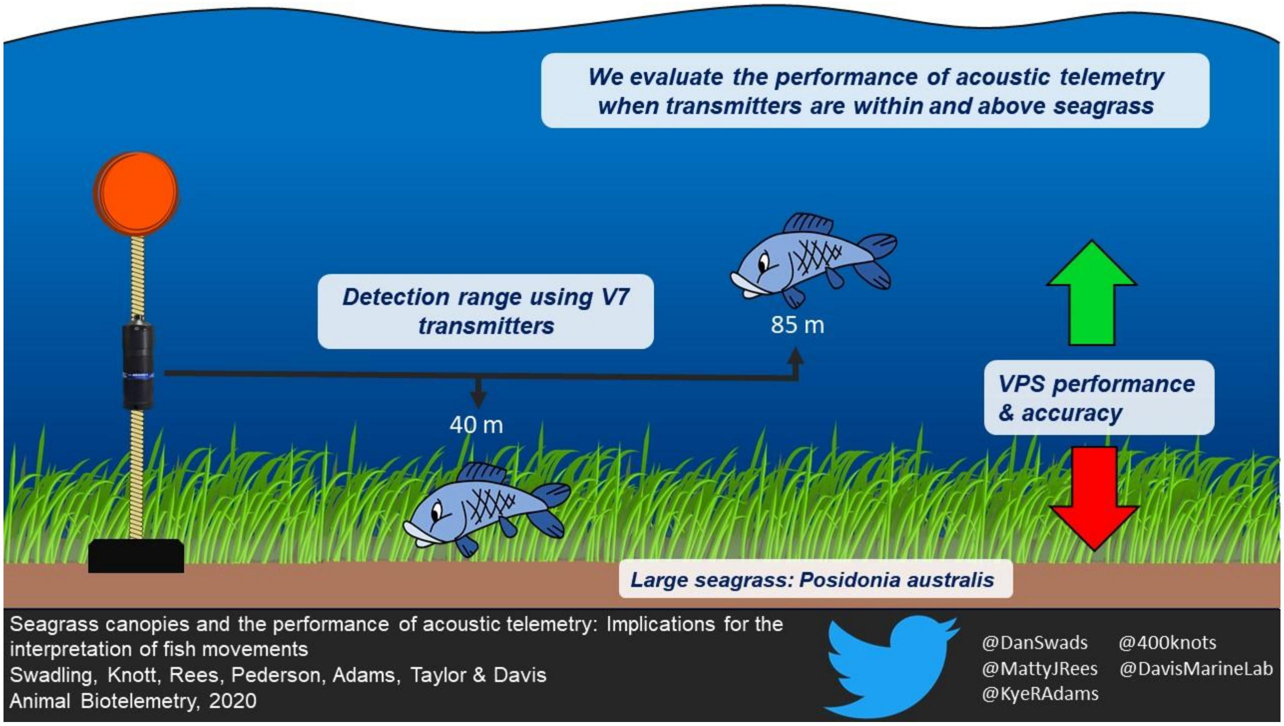

Plate 3.1 Graphical abstract for chapter 3.

3.1 Background

Acoustic telemetry is used to quantify the movement patterns of marine fauna (1-3), however assessments on the performance of telemetry among different habitats is limited (4-7). A key factor affecting the performance of acoustic telemetry is the detection range of a receiver (5). The ‘detection range’ is defined as the maximum distance where a certain proportion of transmissions, generally 50%, are detected by a receiver (5). Quantifying the factors affecting the detection range in various systems is essential to guide the spatial arrangement of receiver arrays and help interpret the movement and behaviour of tagged individuals (5, 8-10). Further, information on detection ranges can prevent studies drawing inaccurate conclusions on fish movements that would misinform management (5, 10). The detection range of receivers is often assumed, and few studies have conducted *in situ* range tests of acoustic equipment. Consequently, there is a paucity of data available for the performance of acoustic equipment in many habitats or environmental conditions.

Understanding the detection range is particularly relevant when arrays are designed as positioning systems (e.g. Vemco Positioning System – hereafter called VPS). Positioning systems allow for the fine-scale movements of tagged individuals to be determined within metres. These systems are becoming a popular tool in both marine and freshwater systems to elucidate activity and patterns of habitat use (11-13). In a VPS, positions are triangulated through measuring the differential time of arrival of pings from a transmitter detected simultaneously by three or more receivers with overlapping detection ranges (11, 14, 15). The successful application of positioning systems is dependent on receivers being spaced to maximise the likelihood of multiple receivers detecting a transmitter and the speed of sound being relatively consistent throughout the habitat. Therefore, information on the detection range of receivers *a priori* is critical to determining the geometry to be employed in VPS systems.

Determining the detection range can be difficult, and it is temporally variable and dependent on several factors including attenuation and refraction of acoustic signals and spreading losses with increasing distance (5, 7, 16, 17). Further, environmental variables such as water properties (e.g. temperature and salinity) and physical barriers can increase attenuation or obstruct the transmission of acoustic signals (4, 6, 7, 17-19). Noise from anthropogenic and natural sources, for example snapping shrimp, wind generated waves, boats or depth sounders can interactively contribute to variation in detection range and create background noise which disrupts the decoding of signals by receivers (4, 9, 10). The behavioural traits of tagged individuals can also contribute to variation in detection ranges, such as animals sheltering within refugia (e.g. rock crevices or aquatic vegetation) at regular diurnal intervals (20). These factors have contributed to the variable performance of acoustic telemetry reported in the literature (5, 7). This creates a need to conduct acoustic range testing prior to commencing research in specific habitats or systems, and to account for this variation in array design and data analyses (7, 10).

One common habitat where the relationships between the performance of acoustic telemetry and environmental variables are poorly understood is seagrass meadows. Seagrasses are structurally complex and productive habitats containing high levels of biodiversity and play an important role in ecosystem functioning (21-23). The spatial distributions of numerous fish species captured in both recreational and commercial fisheries are linked to seagrass meadows as fish use the habitat for foraging, shelter or as nurseries (13, 24-26). Seagrass meadows, however, are under increasing pressure from anthropogenic activities and have been declining at alarming rates (27, 28). Protecting seagrass meadows is therefore a focus of conservation strategies and fisheries management (29), making them an important system in which to study the movement and behaviour of organisms. This has undoubtedly contributed to the increasing number of studies investigating the movement of fishes within seagrass (13, 30-33), but no studies have quantitatively assessed the performance of a VPS or receivers in this habitat. Seagrass meadows contain a suite of unique conditions that pose challenges for the performance of acoustic telemetry. Most notably, the Oxygen produced in photosynthesis by the plants and either stored in aerenchyma or emitted as bubbles can attenuate acoustic signals and alter sound wave velocity, thereby affecting VPS performance and error (34, 35). Furthermore, many fish species are known to regularly position themselves within the seagrass canopy to rest, shelter from predators or stalk prey (36). The consequence of these behaviours could include attenuation or obstruction of acoustic transmissions by seagrass leaves.

This study quantitatively evaluates the performance of acoustic telemetry within seagrass habitats. Specifically, we compare detection ranges for transmitters within and above the seagrass to determine impacts on the performance of a VPS. We also assess the effects of a number of environmental factors commonly measured in range tests on the performance of acoustic receivers, such as meteorological conditions (i.e. wind, rain and atmospheric pressure), depth, time of day, ambient noise (69 kHz) and water temperature. The overarching goal of this research was to determine how the performance of acoustic telemetry is affected by fish moving amongst *Posidonia australis*, a large, robust seagrass species that grows to a width of 2cm and a length of 60cm. This information will ascertain the appropriate spatial configuration of receivers forming a VPS and arrays in seagrass.

3.2 Results

VPS performance was substantially reduced when transmitters were positioned within the seagrass (Fig. 3.1). The positional accuracy of the VPS significantly improved when transmitters were positioned above the seagrass (2.2 m) compared to when transmitters were within seagrass (2.7 m) ($P < 0.01$; Fig. 3.1a). There was also substantially more variation in the positional accuracy of transmitters within the seagrass (1.7 - 5.26 m) than above it (1.7 - 2.74 m). Transmitters located above seagrass were positioned with significantly better precision (0.45 m) in contrast to those within seagrass (0.9 m) ($P < 0.001$; Fig. 3.1b). The greatest impact of a transmitters position relative to the seagrass canopy on VPS performance was on the proportion of successful number of positions per day (i.e. daily system efficiency), which significantly decreased from 30.9% for transmitters above the canopy to 5.9% when they were within seagrass ($P < 0.01$; Fig. 3.1c).

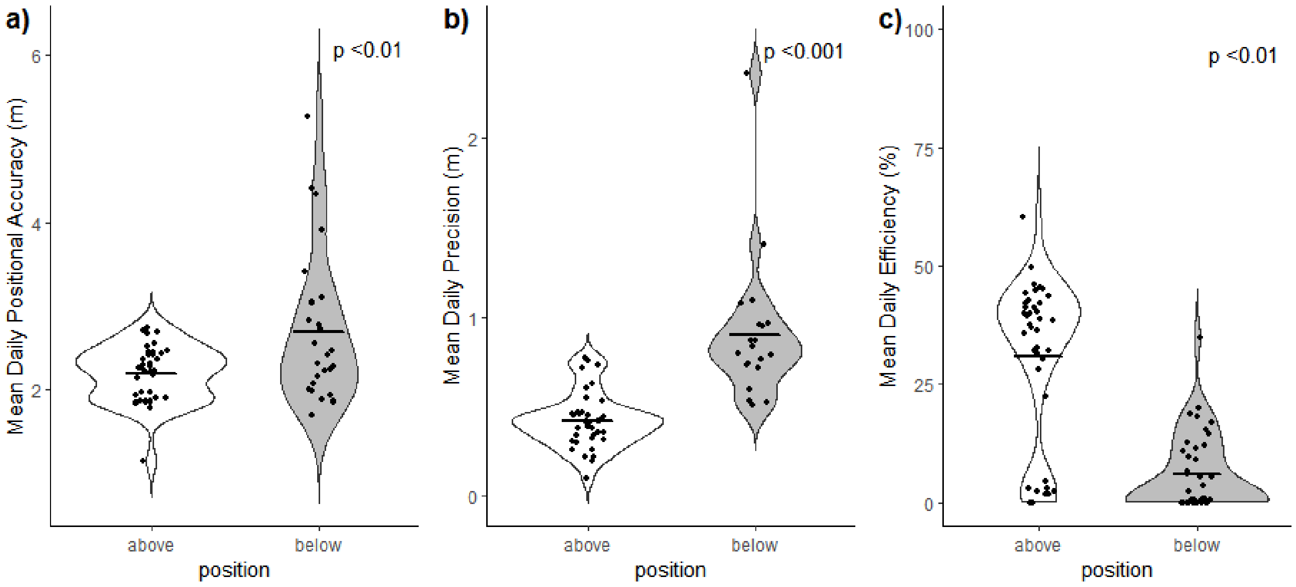

Figure 3.1 Distributions of the mean daily a) positional accuracy (m), b) precision and c) system efficiency (%) for the transmitters above and within seagrass (x-axis). Data points represents the raw values, violin plots illustrate the probability density and the black line is the mean.

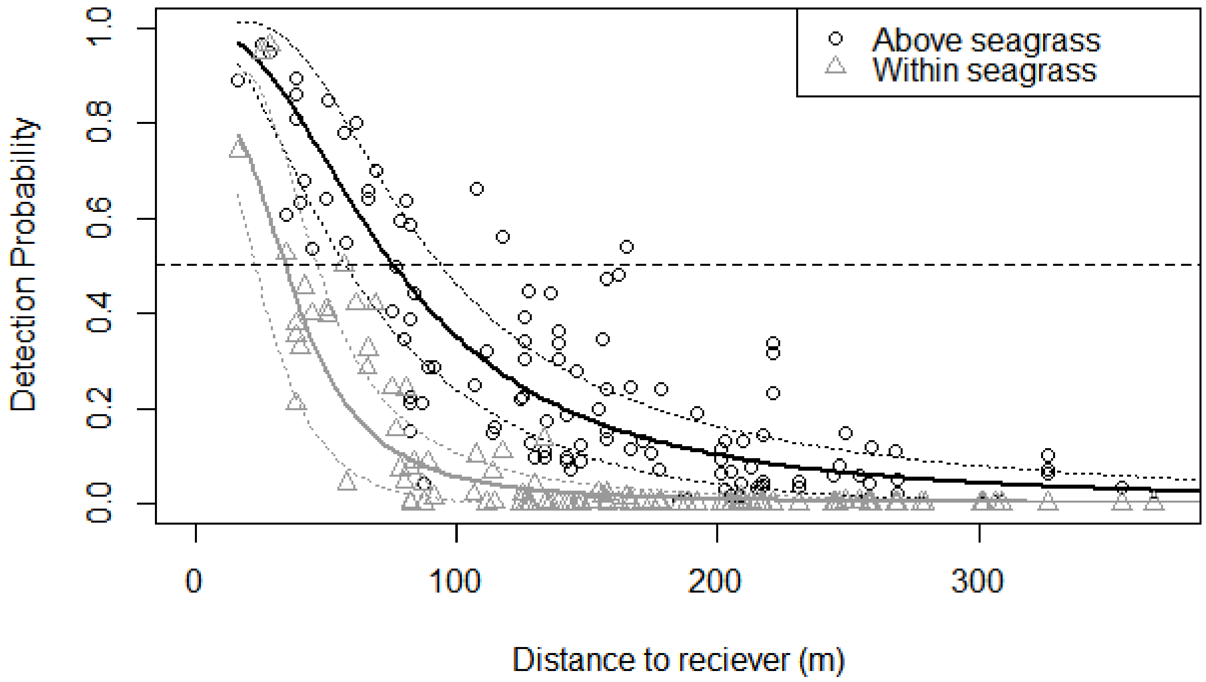

Figure 3.2 Modelled detection probability for each deployment period at varying distances between transmitters and receivers. Black dots represent transmitters above seagrass and grey triangles illustrate transmitters within seagrass. Solid lines illustrate the prediction of the model and dashed lines define the standard error. The horizontal dashed line indicates the working detection range (i.e. 50% probability of detecting a transmitter) of acoustic receivers.

Detection probability was significantly reduced when transmitters were positioned within the seagrass compared to above ($t_{125} = 12.56$, $P < 0.001$). The working detection range of acoustic receivers (i.e. distance where 50% of transmissions were detected) more than halved from ~85 m for transmitters above the seagrass to ~40 m when they were located amongst the seagrass (Fig. 3.2). For transmitters within seagrass, 10% of detections were recorded at ~90 m from the receiver and the detection probability decreased to 0 at 150 m (Fig. 3.2). In comparison, transmitters above seagrass had a 10% probability of detection at ~200 m from the receiver (Fig. 3.2). We therefore estimate the maximum workable detection range to be 90 m and 200 m for the transmitters located within and above the seagrass, respectively. However, fish implanted with V7 transmitters with a fixed delay of 180 s would have to be resident within these distances for an average of 30 minutes to be recorded.

Variation in the detection probability of the internal transmitters in the VR2Tx receivers was best explained by the distance to receiver, average wind speed and hour of day (R^2= 0.45; Fig. 3.3). Considering that acoustic signals attenuate over distance, it was expected that distance from the receiver would be an important variable for predicting detection probability. The detection probability of the internal transmitters was high (> 0.8) up to 200 m but declined beyond this distance (Fig. 3.3). The working detection range of acoustic receivers detecting the internal transmitters was ~260 m (Fig. 3.3). Detection probability was found to negatively correlate with average wind speed, decreasing from 0.9 in conditions of no wind to 0.75 when wind gusts reached 50 km hr^{-1} (Fig. 3.3). A strong diurnal pattern in detection probability was also observed, increasing from 0.55 at midnight to 0.80 in the middle of the day (Fig. 3.3). It was notable that a strong diurnal pattern was also found for the mean environmental noise at 69 kHz which peaked at 710 mV at night and decreased to 520 mV at 1500 hours (Fig. 3.4)

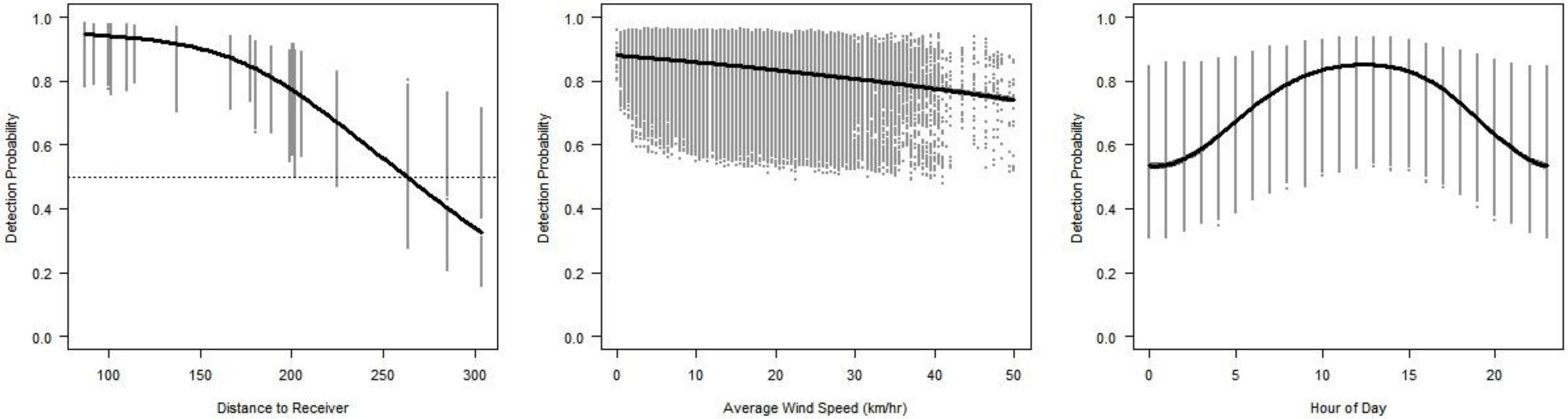

Figure 3.3 Relationships for the model of environmental variables found to predict the detection probability of the internal VR2Tx transmitters from a GAMM. Solid lines illustrate the prediction of the model, and the dashed areas define the 95% confidence intervals around the fitted values. The horizontal dashed line in the distance to receiver plot represents the working detection range (i.e. 50% of transmissions received).

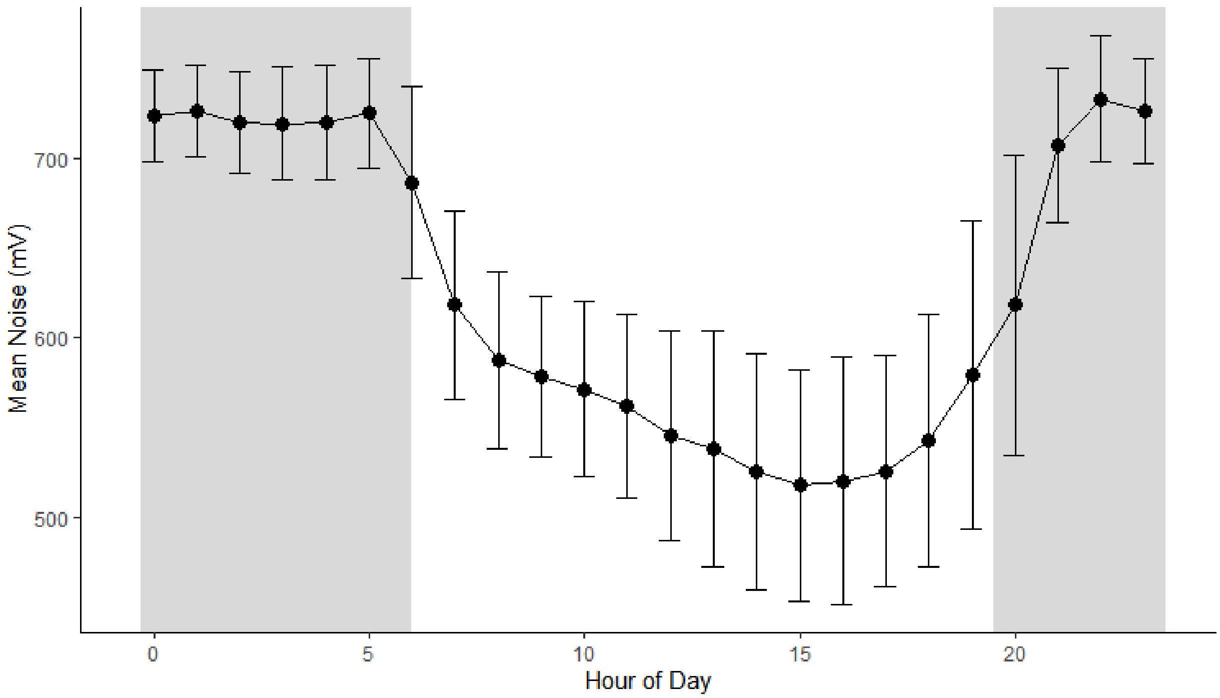

Figure 3.4 Noise (mV) at 69 kHz calculated at all three VR2Tx receivers for each hour of the day. Solid dots represent the mean hourly value and error bars are ± standard deviation. Shading indicates nocturnal hours between 19:30 - 06:00.

3.3 Discussion

This study provides clear evidence that the seagrass canopy represents an obstacle to the transmission of acoustic signals and can substantially reduce the performance of a VPS and acoustic receivers. The positional accuracy, precision and the system efficiency of the VPS was significantly poorer when transmitters were within the seagrass compared to those positioned above the canopy. The reduced VPS performance was ascribed to a decrease in detection range for transmitters amongst seagrass, with the distance at which 50% of detections were recorded declining from 85 to ~ 40 m. Further, detection probability varied temporally, with fewer detections found in high wind conditions and at night. Other range testing studies have reported similar temporal variations in response to wind and time of day (4, 6, 10, 18), however these were performed in reefs, lakes and open habitats such as soft sediments and not in seagrass meadows. Overall, our findings highlight that VPS performance and detection range may be significantly reduced for fish residing in seagrass habitats, particularly if they are routinely sheltered amongst seagrass such as juveniles or cryptic species. These results demonstrate the importance of performing *in situ* acoustic range tests that consider how fish use habitats for creating effective receiver arrays and interpreting movement data.

Previous research has highlighted that topographic features and vegetation obstructing the line of sight between a receiver and transmitter can reduce the performance of acoustic telemetry (5, 19, 37–39). For instance, in coral reef systems the topography of the substrate has been reported to reduce the detection range of acoustic receivers by up to 70% (38). In the present study, seagrass leaves obstructing the line of sight of receivers were observed to reduce detection range. For transmitters positioned in the water column above seagrass, the 50% detection range of receivers was 85 m which is comparable to previous studies using the same model transmitter (i.e. V7) in coral reef habitats (60–120 m) (18, 40). When transmitters were placed within the seagrass canopy, however, the distance at which 50% of detections were recorded decreased by over half to 40 m and no detections were recorded beyond 150 m. The blades of *Posidonia australis* are large and robust and therefore present a substantial obstacle that impedes or absorbs the acoustic signals reaching receivers.

The ability of the VPS to position a transmitter is dependent on at least three receivers simultaneously detecting an acoustic signal travelling at a known speed. Given that the probability of detecting a transmitter decreased when it was amongst the seagrass, it is unsurprising that the daily system efficiency of the VPS was significantly lower for transmitters within (5.9%)

compared to above (30.9%) the seagrass. It is also notable that no positions could be calculated for transmitters outside of the VPS boundary. The relatively low percentage of positions by the VPS for both the above and within seagrass transmitters could also result from the high levels of 'in-band' noise recorded in the system. The noise levels during the day were high enough to impact the ability of a receiver to detect an acoustic signal (i.e. 450–650 mV) and the extreme noise levels at night would drastically decrease receiver performance (> 650 mV). The accuracy of positions was reasonable (2–3 m) for both the transmitters above and within seagrass and corroborates estimates reported in marine and freshwater systems (< 5 m) (14, 15, 37). The positional accuracy and precision of the VPS, however, were significantly different when transmitters were within seagrass. Furthermore, the positional accuracy of the VPS for transmitters within seagrass had a much higher variance than those above seagrass. It is possible that the poorer accuracy and precision recorded for transmitters within seagrass was caused by the acoustic signal being refracted by seagrass leaves and therefore taking a longer time to travel between receivers (41). Alternatively, the acoustic signal may be attenuated or change speed as it travels through the plant tissue, the gas contained within the seagrass and the oxygen bubbles collected on the leaves. Overall, our findings suggest that a VPS in seagrass will provide a low system efficiency, particularly if fish ensconce in seagrass for periods of time, although any positions should have a reasonable accuracy and precision.

Detection probability of the internal VR2Tx transmitters was lower in high wind conditions and at night. Wind speed has previously been reported to negatively affect detection range, particularly in shallow water habitats (4, 42). Wind influences sound propagation as it generates surface waves which create noise and air bubbles that penetrate the upper water column (4–6). We also observed a strong diel pattern, with detection probability increasing during the day and declining at night.

Similar observations have been made in previous studies in reef systems and attributed to biological noise (6, 10, 18, 38). Although we cannot explicitly state the exact mechanism behind the observed diurnal patterns, noise at the 69 kHz frequency was exceptionally loud (> 650 mV) at night and likely originates from biological sources. For example, invertebrates commonly found in seagrass such as snapping shrimp (*Alpheus* spp.) are nocturnally active and create background noise (43, 44). This background noise has been suggested to mask acoustic signals and interfere with a receiver's ability to translate pings to detections (9, 10, 45). These findings highlight the importance of considering environmental conditions when designing arrays and analysing movement patterns from detection data (10).

While studying acoustic telemetry performance under varying abiotic and biotic conditions is important, it is equally relevant to recognise how to address confounding factors when implementing telemetry research (4, 42). The findings of this study emphasise the importance of considering the effects of how fish use structurally complex vegetated habitats on VPS and receiver performance when designing telemetry studies. For instance, tracking fish species known to move regularly within the water column will require a different receiver configuration when compared to tracking species that regularly shelter amongst seagrass. Our results suggest that receivers must be tightly spaced in our system when using V7 transmitters, ~ 40 m for a VPS and 80 m in receiver arrays to ensure that fish moving within seagrass have a 50% chance of being detected. However, detection ranges will vary with location and are dependent on local environmental conditions. We therefore strongly advocate that all telemetry studies perform *in situ* range tests rather than infer detection ranges to determine the adequate spacing of receivers. In addition, studies should include multiple sentinel transmitters in receiver arrays placed within and above the seagrass to quantify variations in detection probability through time (4, 5, 7, 10). This information on the spatiotemporal variation of detection probabilities can be incorporated into statistical analyses to improve confidence in the interpretation of fish movement patterns and behaviour (7, 10). Furthermore, understanding detection range over spatiotemporal scales can guide the positioning of receivers to maximise coverage over habitats or areas relevant to scientific questions and therefore increase the economic efficiency of research (6). The performance of acoustic telemetry in seagrass habitat will also vary with the model of transmitter selected. For example, in the current study the internal VR2Tx transmitters were equivalent to a low powered V16 transmitter and increased the 50% detection range of receivers to ~ 260 m when above seagrass (compared to 85 m for the lower powered V7 transmitters). It is likely that higher-powered transmitters would also have an increased detection range when amongst the seagrass compared to low-powered transmitters. However, the attenuation rate of acoustic signals emitted by high-powered transmitters within seagrass remains unclear and the influence of this on detection ranges should be explored in future acoustic range tests. It is noteworthy that higher output transmitters are intrinsically large due to increased battery size and would not be as appropriate as the V7 model for tracking the smaller cryptic species or juveniles commonly found in seagrass meadows (e.g. the 2% rule; (46)).

3.3.1 Conclusion

In conclusion, we have provided the first evidence that the performance of a VPS and acoustic receivers is greatly reduced when transmitters are within the seagrass. The reduced performance observed in the VPS can be attributed to declines in detection range when transmitters are amongst seagrass. In addition, detection probability was found to decrease in high wind conditions and at night, which corroborates previous range testing studies in other habitats. We strongly support recommendations for performing acoustic range tests as a prerequisite for acoustic telemetry studies and the incorporation of multiple sentinel transmitters (i.e. stationary transmitters) within arrays to quantify temporal changes in detection probability (4, 5, 7, 10). Incorporating range testing and sentinel transmitters into studies will allow researchers to better understand any assumptions made when estimating the home ranges or habitat associations of fishes (6). Future research is necessary to explore if similar patterns in detection probability occur for transmitters within other seagrass species possessing different morphologies *to P. australis*, such as those with smaller leaves (e.g. *Zostera* spp.) as these may represent less of an obstacle to acoustic signals. Future range testing studies should also consider the effect of a fish's behaviour on the performance of acoustic telemetry in other habitat types, such as fish sheltering within reef crevasses or being buried within soft sediments (47).

3.4 Methods

3.4.1 Study area

The study was conducted in Jervis Bay Marine Park (JBMP; 35.06203° S, 150.73419° E) on the south coast of New South Wales (NSW), Australia (Fig. 3.5). JBMP incorporates a large acoustic array consisting of approximately 60 receivers which has been used to track a range of fish species over the past ~ 10 years (48, 49). The seascape of JBMP is dominated by rocky intertidal and subtidal reefs, seagrass meadows and soft sediments. The seagrass selected for this study was *Posidonia australis* (Hook.f.), a species endemic to temperate Australia that forms large meadows within JBMP. *P. australis* is a long leaved, slow-growing seagrass of high conservation significance due to population declines and has been listed as endangered at six locations in NSW (28, 50).

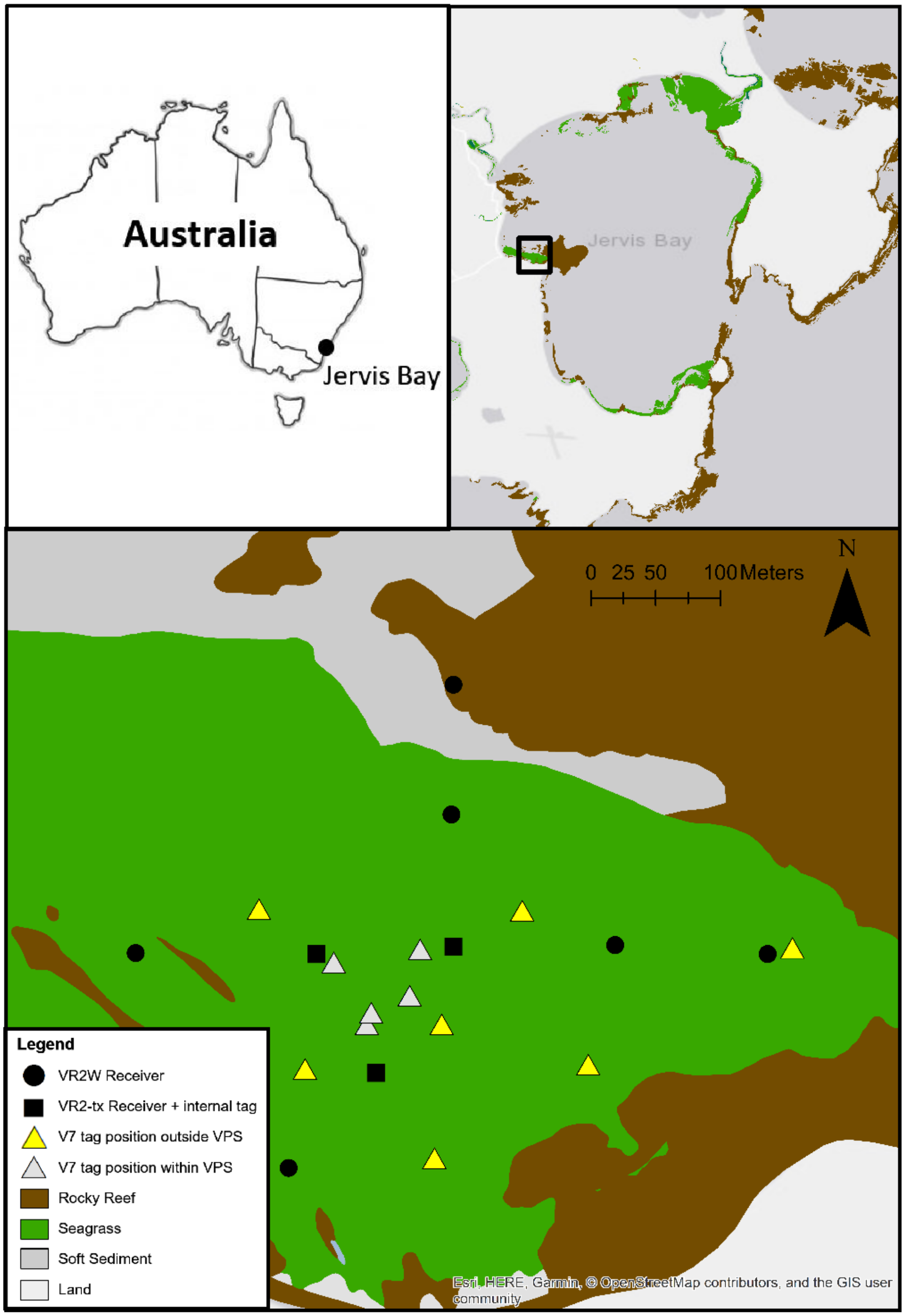

Figure 3.5 Map of the location of Jervis Bay, NSW, Australia showing the major habitats and the positions of the VPS, additional receivers and transmitters.

3.4.2 Experimental design

In November 2017, three VR2Tx acoustic receivers (VEMCO Ltd Canada, Nova Scotia) were deployed to form a VPS within a large seagrass bed at Plantation Point in JBMP (Fig. 3.5). The three receivers were placed in a triangular formation and separated by 150 m on fixed moorings (Fig. 3.5). An additional six VR2W acoustic receivers (VEMCO Ltd Canada, Nova Scotia) were deployed in a cross formation 150 m apart to allow for a range of distances between the receivers and transmitters placed within the array (Fig. 3.5). The nine receiver moorings were deployed at depths ranging from 2.4 to 9 m and were comprised of a section of railway line (50 kg) and a subsurface polystyrene buoy attached to a rope which maintained receivers in an upright position (hydrophones oriented to the surface). Receivers were fixed to the mooring a minimum of 1 m below the buoy to avoid blocking the hydrophone.

Range testing was performed using two different models of acoustic transmitters. First, four VEMCO V7-4x 69 kHz range test transmitters (power output 136 dB, fixed delay 180 s) were used to test the effect of submersion within seagrass on the performance of the VPS and acoustic receivers. These four V7-4x range testing transmitters were attached to two transportable moorings, respectively. These moorings were 2 m in height and comprised a six-pound dive weight with a subsurface polystyrene buoy attached to polypropylene rope. The V7-4x transmitters were placed either 15 cm or 145 cm from the base of the mooring to ensure that one transmitter was within the seagrass while the other was above the canopy (Fig. 3.6). Each pair of transmitters were located either within or outside of the VPS (Fig. 3.5). The transmitters within the VPS were relocated to five positions across two 4-week periods. The transmitters outside of the VPS were relocated to different positions generally every 7 days over two 4-week periods during November–December 2017 and March 2018 (one deployment was for a 2-week period due to poor weather).

The locations of each V7 transmitter pair within and outside the VPS were spatially balanced using ArcGIS version v. 10 and ranged from 2.3 to 6 m in depth. Second, the three VR2Tx receivers each had an internal transmitter set to high power (154 dB) and a 300-s fixed delay, which is comparable to the output of a V16-4L transmitter (150–162 dB). These internal VR2Tx transmitters were deployed from November 2017 to April 2018 at depths ranging between 3.5 and 5 m and were used to investigate the influence of environmental variables on array performance over a broader temporal scale.

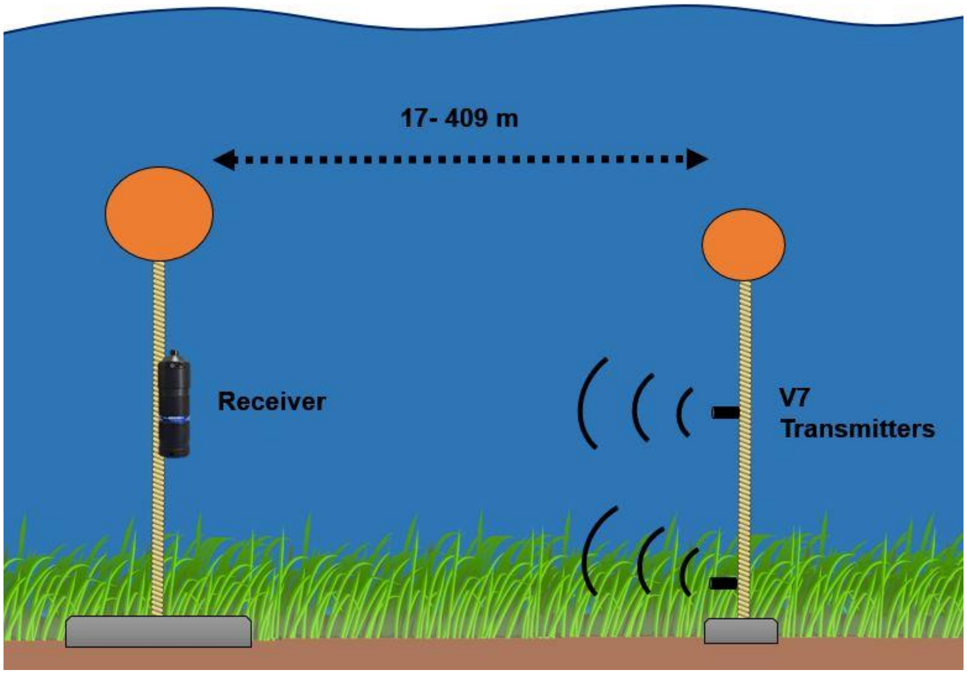

Figure 3.6 Schematic of a VR2W acoustic receiver station (left) and two transmitters (V7-4x) suspended either above (145cm) and within (15cm) the seagrass.

The distance between each transmitter location and receiver was calculated in R using the GPS locations and the ComputeDistance function in the package VTrack (51). Meteorological conditions were recorded by the Australian Bureau of Meteorology (BOM) at the Point

Perpendicular meteorological station 10.5 km from the study site. Four meteorological variables were included in our analyses; wind speed and direction, precipitation and air pressure. Each meteorological variable was recorded every 30 min and averaged to get an hourly value. The VR2Tx receivers recorded water temperature, receiver tilt and the ambient noise levels at 69 kHz (the operational frequency of the acoustic transmitters) every 10 min (Table 3.1). Each metric recorded by the VR2Tx receivers was averaged to provide an hourly mean. A variety of environmental conditions were encountered during the study period (Table 3.1), but as variation in receiver tilt was found to be negligible it was excluded from subsequent analyses.

Table 3.1 The minimum and maximum values of environmental conditions

Variable	Source	Min. value	Max. value
Precipitation (mm)	BOM	0	8.7
Wind speed (km/hr)	BOM	0	50
Wind direction (°)	BOM	0.5	359.5
Atmospheric pressure (Pa)	BOM	996.95	1030.25
Depth of receivers (m)	Depth sounder	2.4	9
Temperature (°C)	VR2Tx sensor	13.4	25
Noise 69 kHz (mV)	VR2Tx sensor	290	803.3

3.4.3 Statistical analyses

The detection probability for each receiver and V7 transmitter combination was calculated as the total number of recorded detections for each deployment period over the number of expected detections. The detection probability of the internal VR2Tx transmitters was calculated as the number of recorded detections for each transmitter per hour divided by the number of expected detections (i.e. 12 detections). Days when the transmitters were relocated or deployed were excluded from the analyses. The influence of distance on the detection probability of transmitters above and within seagrass was estimated by fitting a logistic regression. A paired-sample t test was used to evaluate differences in the number of detections for transmitters "above" versus "within" seagrass over the entire deployment period.

The VPS used three acoustic receivers (VR2Tx) to triangulate the x–y positions of transmitters (52). Positions calculated by the VPS were based on the differential time of arrival of acoustic transmissions travelling at a known speed that were simultaneously detected by all three receivers (11, 15). The speed of sound was quantified from the temperature and salinity of the water (8). The internal clocks of the VPS receivers were synchronised using the internal VR2Tx sync transmitters that emitted pings at known times (11, 15). Time synchronisation of the receivers is necessary to accurately calculate differences in the time of arrival and account for time drift in the receiver's clocks. Differences in the time of arrival of transmissions between receivers were then converted to differences in range and used in a hyperbolic positioning algorithm to generate an x–y position (52).

Three metrics for VPS performance were calculated: (1) positional accuracy, (2) precision, and (3) system efficiency (37). Positional accuracy was measured as the Euclidean distance between the position estimated by the VPS and the GPS position of the transmitters. Precision represented the variability of positional accuracy and was the standard deviation of the mean daily positional accuracy. System efficiency was calculated as the proportion of successful estimated positions (i.e. number of positions/expected number of positions) by the VPS. These metrics were calculated and averaged to give a daily value for each day the transmitters were in the water, excluding the days during which transmitters were relocated. Generalised linear models (GLMs) were used to test the influence of a transmitter's position above or within the seagrass canopy on the mean daily positional accuracy, precision and system efficiency. GLMs for daily system efficiency were fitted with a binomial distribution and a gamma distribution was used for daily accuracy and precision.

Relationships between the detection probability of the internal VR2Tx transmitters and environmental variables were examined using generalised additive mixed models (GAMMs) (53, 54). Prior to analysis, collinearity between explanatory variables was assessed using Pearson's pairwise correlation coefficients and Variance Inflation Factor (VIF). GAMMs were constructed using a full-subset approach to provide all possible model combinations (55). GAMMs were fitted using a beta distribution with receiver ID as a random effect to account for the lack of independence between receivers. Models were restricted to a maximum of three explanatory variables and excluded variables with a Pearson's correlation greater than 0.28 to avoid issues with collinearity (55, 56). These parameters were selected to prevent overfitting and develop conservative, interpretable models. Average wind direction and hour of day were fitted using cyclic smooths to account for their circular nature (55). Akaike Information Criterion corrected for small sample sizes (AICc) was used to compare models, with the best fitting model containing the lowest AICc (57). No alternate candidate models were within ± 2 AICc of the best model. All statistical analyses and plots were developed using the statistical computing program R (58) and the functions; FSSGAM 1.11 (55), mgcv (59), ggplot2 (60), visreg (61) and gamm4 (62).

3.4.4 Abbreviations

VPS: Vemco Positioning System; BOM: Bureau of Meteorology; GPS: Global Positioning System; JBMP: Jervis Bay Marine Park; NSW: New South Wales; ID: Identification; GLM: Generalised Linear Models; GAMM: Generalised Additive Mixed Models; AICc: Akaike Information Criterion corrected for small sample sizes.

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Chapter 4: Consequences of juvenile fish movement and seascape connectivity: Does the nursery-role concept need a rethink?

This chapter has been prepared for submission to ***Ecological Applications***.

At the time of writing, a small number of receivers (4) in the Jervis Bay Marine Park receiver array had not been downloaded because fieldwork was delayed by COVID-19 restrictions. However, enough receivers were downloaded to provide results and I am confident that any data on the receivers yet to be collected will not affect the conclusions drawn in this chapter. The remaining data will be collected and analysed before this chapter is submitted for publication.

Plate 4.1 School of luderick (*Girella tricuspidata*) and yellowfin bream (*Acanthopagrus australis*) on a reef adjacent to seagrass in the Hare Bay sanctuary zone in Jervis Bay Marine Park, Australia.

4.1 Introduction

Nearshore patch types provide important nursery areas for harvested fish species and are essential for maintaining the sustainability of fisheries worldwide (Beck et al. 2001, Heck Jnr et al. 2003, Sheaves et al. 2015). Nursery areas are generally defined as discrete or homogenous patch types that provide benefits to juveniles (i.e. increased survival and growth) and contribute a disproportionate number of recruits to adult populations (Beck et al. 2001, Heck Jnr et al. 2003, Dahlgren et al. 2006). For example, seagrasses are thought to play an important role as nurseries for juveniles of numerous reef-associated fish before they disperse to adult populations once a certain age or size-class is reached (Heck Jnr et al. 2003, Pittman and McAlpine 2003, Sambrook et al. 2019). Defining nursery areas as discrete patch types may be too simplistic because many species are found in multiple patch types at juvenile life-stages and have the potential to connect these patches with their movements (Sheaves et al. 2006, Nagelkerken et al. 2015, Litvin et al. 2018). Therefore, it has been suggested that the nursery-role concept should consider nursery areas as spatially explicit seascapes of connected patch types (i.e. “seascape nurseries”) (Nagelkerken et al. 2015, Perry et al. 2018, Pittman et al. 2021). However, there is currently limited information on the movement patterns and connectivity of juvenile fishes and these data are essential to properly understand whether the nursery-role concept needs to be refined and to quantify the contribution of nursery habitats to adult populations (Beck et al. 2001, Dahlgren et al. 2006, Nagelkerken 2009, Nagelkerken et al. 2015, Sheaves et al. 2015). The need for this information is underscored by the global loss of nearshore vegetated habitats due to anthropogenic stressors (Waycott et al. 2009, Li et al. 2018, Dunic et al. 2021). This degradation has the potential to disrupt linkages between patch types and the number of recruits entering coastal fisheries (Barbier et al. 2011, Sheaves et al. 2014, Li et al. 2018).

There is increasing evidence highlighting that juvenile dispersal from nursery areas may occur at greater rates to nearby adult populations than those further afield, however there are few examples of this dispersal being directly quantified. Instead, current understanding on the spatiotemporal scale of ontogenetic habitat shifts comes largely from observational studies inferring movements from changes in abundances or size classes between patch types (Dorenbosch et al. 2005, Grober-Dunsmore et al. 2007, Olds et al. 2012, Nagelkerken et al. 2017, Swadling et al. 2019, Berkström et al. 2020, Rees et al. 2021), natural tags such as otolith microchemistry, parasites, and stable isotopes (Olson and Pratt 1973, Gillanders 2002, Hamer et al. 2005, Russell et al. 2021) or mark-recapture studies (Morton et al. 1993, Gray et al. 2012). For instance, Swadling et al. (2019) observed a higher abundance and diversity of fish on reefs close to large seagrass patches and attributed this to a greater number of recruits dispersing to reefs from adjacent seagrass nurseries. Whilst useful for providing evidence of dispersal, such methods do not provide a detailed mechanistic understanding of movement pathways. Therefore, they are inappropriate to explicitly establish the spatial scales over which fish perform ontogenetic habitat shifts and determine whether this dispersal occurs abruptly or as a stepwise process where individuals slowly move from nursery areas toward reefs as they become larger.

Acoustic telemetry provides the opportunity to quantify the movement, space-use and connectivity of juvenile fishes (Donaldson et al. 2014, Hussey et al. 2015, Taylor et al. 2017a). Studies adopting acoustic telemetry have largely focussed on tracking the movement of adult fish across a range of spatial and temporal scales, providing valuable insights into species movement ecology and helping inform marine management and conservation (Donaldson et al. 2014, Crossin et al. 2017, Taylor et al. 2017a). Acoustic tracking of smaller fish has been limited by transmitter (i.e. tag) size because high tag size to body mass ratios can have negative effects on fish health and behaviour

(Jepsen et al. 2005, Brown et al. 2006, Thorstad et al. 2013). Consequently, literature tracking juvenile fish movements in the marine environment has generally been restricted to species with large (e.g. > 30 cm) body sizes (Childs et al. 2015, Taylor et al. 2017b, Murray et al. 2018, Staveley et al. 2019, Duffing Romero et al. 2021, Kendall et al. 2021, Stamp et al. 2021) including elasmobranchs (Simpfendorfer et al. 2010, Knip et al. 2011, Chin et al. 2013, Bangley et al. 2020, Martins et al. 2020). Advances in technology leading to the miniaturisation of acoustic transmitters means research tracking the movement of small marine fishes (< 20 cm), including juvenile life-stages, is increasing (Pursche et al. 2014, Huijbers et al. 2015, Aspillaga et al. 2021, Barcelo-Serra et al. 2021, Matley et al. 2021).

Marine Protected Areas (MPAs) have been established worldwide to conserve biological diversity and social values (Spalding et al. 2008, Gaines et al. 2010, Hernandez et al. 2021), and there is growing evidence highlighting their benefits to harvested fishes (Edgar et al. 2017, Malcolm et al. 2018, Goetze et al. 2021, Knott et al. 2021). To provide effective conservation benefits to fishes, MPAs must be appropriately sized and located to incorporate the habitats used during species daily movements or life-cycle migrations (Kramer and Chapman 1999, Grüss et al. 2011, Weeks et al. 2017). If MPAs are too small or do not contain important fish habitat, individuals will likely cross reserve boundaries and be exposed to fishing pressure or key habitats may be lost or degraded (Kramer and Chapman 1999, Grüss et al. 2011, Pittman et al. 2014). Knowledge of the movement patterns of fishes will therefore assist the design, management and assessment of MPAs to ensure they are effective (Crossin et al. 2017, Weeks et al. 2017). There is a particular need for information on the dispersal and connectivity of juvenile fishes, as this will guide the design of MPAs to protect species throughout their entire life-history (McCook et al. 2009, Grüss et al. 2011). For instance, if fish use multiple patch types as juveniles and perform small-scale dispersal from nursery areas to adjacent adult populations, then singular reserves should be designed to cover these patches within their boundaries to protect these linkages. Alternatively, if juveniles disperse to adult populations over large distances, then MPA networks positioned along the coast may be more appropriate. Identifying and including nursery areas within MPAs could also be used to promote the sustainability of adjacent fisheries, as the spill-over of individuals across reserve boundaries should ensure adequate recruitment to targeted populations (Lizaso et al. 2000, Gell and Roberts 2003, Halpern et al. 2009, Grüss et al. 2011).

In this study, we used acoustic telemetry to quantify the movement and connectivity of juvenile fish belonging to two species important for commercial and recreational fisheries, luderick (*Girella tricuspidata*) and yellowfin bream (*Acanthopagrus australis*), over an area of 120 km^2 in Jervis Bay Marine Park (JBMP), NSW, Australia. Both species reside in seagrasses as juveniles, and adults are commonly found on shallow coastal reefs (Curley et al. 2013). The specific aims of this study were to: 1) determine if juvenile fish exhibit site-attachment to seagrass ‘nursery’ areas or if they use a mosaic of patch types (i.e. seascape nurseries), 2) quantify the scale of ontogenetic habitat shifts between seagrass and rocky reefs, and 3) assess the movement and dispersal of juveniles in relation to current zoning within an existing MPA. We predicted that juveniles would show small-scale movements and site-attachment within nursery areas (defined in this study as seagrass patches). However, this would be dependent on body size, with fish expanding their home-ranges as they grow and become larger prior to permanent dispersal to adult habitats. We also predicted that both species would demonstrate ontogenetic habitat shifts in greater numbers to reefs adjacent to nursery areas compared to those further away. This prediction was founded on existing research in Jervis Bay reporting higher abundances and diversity of fish (including luderick and yellowfin bream) on reefs close to seagrass, providing qualitative evidence of dispersal from nursery habitats (Rees et al. 2018, Swadling et al. 2019). Finally, we predicted that fish would show strong retention within current no-take marine reserve zones, given the anticipated small-scale movements of fish both within seagrass nurseries and to adult reef habitats.

4.2 Methods

4.2.1 Study Site

The study was completed in Jervis Bay (35°8’S 150°43’E), which is a large coastal embayment in south-eastern Australia spanning 120 km^2 (Fig. 4.1). The embayment is dominated by oceanic conditions and contains a mosaic of intertidal and subtidal rocky reef, seagrass and unconsolidated soft sediments, plus tidal creeks with seagrass, mangrove (*Avicennaia marina* and *Aegiceras corniculatum*) and saltmarshes (*Sarcocornia quinqueflora* and *Sporobolus virginicus*) also feeding into the Bay (Fig. 4.1). The predominant species of seagrass within the embayment is *Posidonia australis*, a slow growing, persistent species with large strap-like leaves (30-60 cm long and 6-14 mm wide). Populations of *P. australis* are listed as endangered in six NSW estuaries, however this does not include meadows in Jervis Bay as rates of decline for the species here are relatively low (West 2010; West and Glasby 2021). Other species of seagrass are also found within Jervis Bay, although mainly within the tidal creeks, and these include *Zostera muelleri* subsp. *capricorni* (Ascherson) and *Halophila* species which are both smaller than *P. australis* and have transitory meadows that are more resistant to disturbances (Kilminster et al. 2015). Jervis Bay forms the central area of JBMP, which contains multiple “no-take” marine reserves (hereafter referred to as NTMR, also known locally as sanctuary zones; Fig. 4.1) where it is not permitted to remove or harm marine biota. The remainder of the Bay is zoned to allow recreational fishing and some forms of commercial fishing.

4.2.2 Fish collection and acoustic tagging

Fish were captured using hook and line in JBMP between August 2018 and February 2020 (Table 4.1). Tagging was concentrated within the Hare Bay NTMR (i.e. Hare Bay and Carama Inlet), but also occurred at other locations including Currambene Creek (i.e. Woollamia and Myola) and Moona Moona Creek (Fig. 4.1). It was notable that all luderick were below the size that the species reaches sexual maturity (i.e. 286 – 295 mm; Gray et al. 2012), whereas 7 of the 20 yellowfin bream were expected to be reproductively mature (i.e. > 220 mm; Pollock 1985, Curley et al. 2013). We elected to tag a range of size-classes (Table 4.1; Table A2.1) to explore whether juvenile fish mobility increased with size and to allow the best chance of quantifying the dispersal of individuals, given that the size or age class the species perform ontogenetic habitat shifts is unknown.

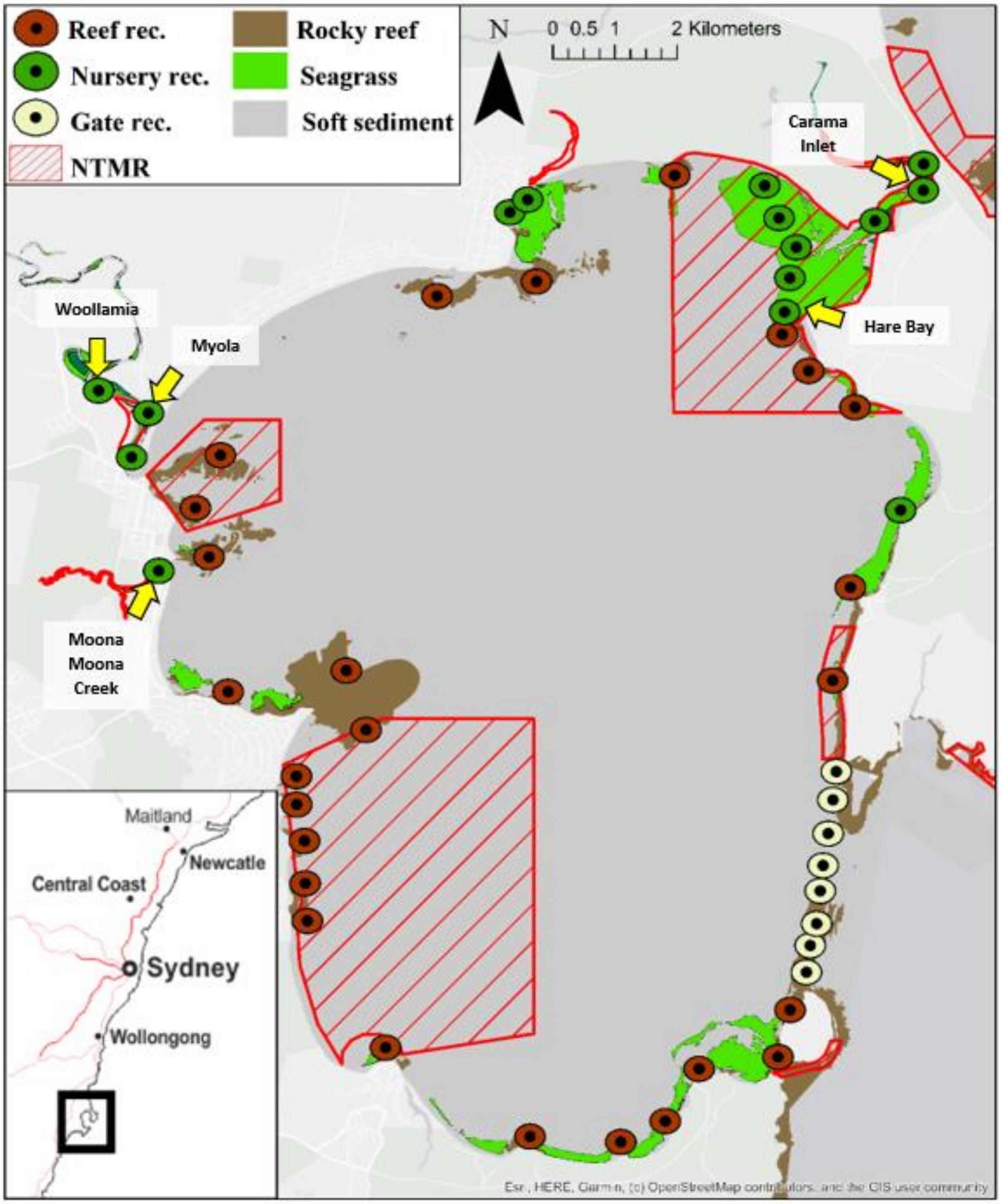


Figure 4.1 Map of Jervis Bay Marine Park (insert shows location on NSW coastline) and the dominant patch types. Receiver stations within the array are depicted and coloured based on whether they are in seagrass "nursery" patches (dark green), reef patches (russet) or part of the acoustic gate at the bays entrance (yellow). The general location of fish capture/release (see Table A2.1) are represented by yellow arrows. No-take marine reserves (NTMR) are illustrated by areas of red cross hatching. Please note that Wollamia and Myola are both located within Currambene Creek.

Table 4.1 Summary data for the 53 tagged individuals. Values for fork length, number of detections and days at liberty represent the means ± standard deviation and in parentheses are the minimum and maximum values observed.

Species	**Location**	**Tagging year**	**n**	**Fork length (mm)**	**Number of detections**	**Days at liberty**
Luderick	Hare Bay	2018	13	181.2 ± 18.1 (146 - 216)	1740.7 ± 1203.5 (193 - 4975)	322.3 ± 152.9 (26 - 409)
Luderick	Currambene Creek	2019	15	182.3 ± 23.8 (145 - 231)	16061.3 ± 24530.5 (0 - 86496)	321.4 ± 112.3 (55 - 413)
Luderick	Moona Moona Creek	2019	5	169.2 ± 9.45 (160 - 185)	71664.2 ± 56862.3 (5723 - 145700)	247.8 ± 191.8 (6 - 409)
Yellowfin Bream	Hare Bay	2019	9	244.9 ± 41.3 (166 - 298)	3133 ± 2393 (622 - 7880)	363.4 ± 86.9 (155 - 409)
Yellowfin Bream	Carama Inlet	2019 / 2020	11	193.2 ± 40.6 (145 - 284)	9815.8 ± 11394.4 (420 - 35711)	340.63 ± 118.9 (7 - 409)

All fish were captured in or directly adjacent to seagrass patches and were surgically implanted with Vemco V7-4x acoustic tags (7 mm diameter, 18 mm length, 0.7 g weight in water, ~400 d battery life: Innovsea, NS, Canada). These coded tags were programmed to randomly emit a unique signal every 180 – 240 seconds at a frequency of 69 kHz. Prior to the surgical implantation of acoustic tags, fish were placed in an aerated 50 L holding tank for a minimum of 15 mins to recover from capture and were visually examined for general health and condition. Fish were then anaesthetized using 60 mg L^{-1} Aqui-S® solution before being transferred to a wetted cradle for surgery. A 10 mm incision was made in the ventral surface of the fish toward the rear of the peritoneal cavity in which the tag was inserted. Before surgery, all surgical equipment and acoustic tags were treated with povidone-iodine antiseptic (Betadine® solution) to prevent infection. Once the tag was inserted, the wound was sutured using one to two dissolving stitches tied with a double surgeon’s knot. Fish were then transferred to another aerated 50 L holding tank and monitored for 30 minutes before release at the capture site.

4.2.3 Acoustic monitoring array

An array of 49 Vemco VR2W and VR2tx acoustic receivers was established within JBMP to passively track tagged fish (Fig. 4.1). The JBMP array is operated and maintained by the NSW Department of Primary Industries and collaborators (University of Wollongong and Macquarie University), and the resultant data are stored in the Integrated Marine Observing System Animal Tracking Facility Database (https://animaltracking.aodn.org.au/; Hoenner et al. 2018). Acoustic receivers in the array are strategically placed to provide detection coverage on almost every reef within Jervis Bay, along with the seagrass and creeks where fish were tagged in the current study. In addition, an acoustic gate across the mouth of Jervis Bay was present to allow for the detection of any fish leaving or entering the Bay (Fig. 4.1). Acoustic receivers were separated by a minimum of 500 m and placed no further than 300 m from the shoreline. Most acoustic receivers were attached to rope moorings which consisted of sections of railway lines (~50 kg) and a subsurface polystyrene buoy that maintained receivers in an upright position (hydrophones oriented to the surface). Receivers were fixed at least 1 m below the buoy and 2 m above the sea floor. The exceptions were the receivers within the creeks of depths less than 3 m, where receivers were attached to moorings with shorter ropes or on star pickets embedded within the substratum. Receivers were collected and the moorings cleaned every 12 months. The detection range of receivers has previously been determined to be 85 m for V7 acoustic transmitters above the canopy in seagrass meadows in Jervis Bay and 40 m when submerged within seagrass fronds (Swadling et al. 2020).

4.2.4 Data processing

Detection data for tagged individuals were corrected for time drift and then filtered to remove any detections that occurred less than 180 s apart, which was the minimum tag ping rate.

Detections within 180 s of each other were assumed to be suspect and classified as false detections caused by tag collisions and interference from background noise (Simpfendorfer et al. 2015). In addition, fish that were recorded on receivers for less than 10 days, had fewer than 50 detections and were not detected leaving the Bay (i.e. not detected on receivers in the gate or arrays outside of JBMP) were removed from subsequent analyses (Stocks et al. 2015, Moulton et al. 2017). These criteria led to the exclusion of four fish (Luderick 16, 29, 32 and Bream 2; Table A2.1).

4.2.5 Home-range estimation

The home-range of tagged fish was estimated using the Brownian Bridge Movement Model (BBMM) to calculate utilisation distributions (UD). The BBMM was selected over other UD methods as it models the probability of a tagged individual being in an area from its start and end locations, the time elapsed between detections and the speed travelled between successive detections (Bullard 1991, Horne et al. 2007). BBMM also incorporates location error, an important caveat in acoustic telemetry where the successful detection of an individual is dependent on them being within a receiver's detection range (Kessel et al. 2014, Huveneers et al. 2016, Swadling et al. 2020). Estimates of locations for the BBMMs were produced using a mean position algorithm to create centres of activity for each fish (Simpfendorfer et al. 2002). Two smoothing parameters were required to create the BBMM (Horne et al. 2007). Firstly, the Brownian motion variance parameter (σ^2_m) estimates the variance in a fish's position between two points using a maximum likelihood approach. Secondly, the location error was also required, and this was set as the predicted receiver detection range of 85 m estimated in **Chapter 3**. Home-range estimates derived from BBMMs were calculated as 50% (core home range) and 95% (home range extent) UDs using the adehabitatHR package (Calenge 2006).

4.2.6 Network analysis

Network analysis was used to further explore patterns of movement and connectivity of tagged individuals within the JBMP array. Network analyses offer a complimentary approach to traditional metrics modelling activity spaces (e.g. UDs) from passive telemetry data (Finn et al. 2014, Jacoby and Freeman 2016). The method is embedded within graph theory and investigates relationships between nodes (acoustic receivers) that are connected by edges (fish movements), with all the combined edges represented as a network (Finn et al. 2014, Jacoby and Freeman 2016). Network analysis is a powerful analytical tool that can identify movement corridors and pathways connecting patch types often overlooked in typical space-use metrics (Lédée et al. 2015, Becker et al. 2016, Whoriskey et al. 2019).

To assess habitat use, we created non-square matrices from the detection data that counted the frequency of habitat use by individual tagged fish (Heupel et al. 2019). Frequency of habitat use was calculated by dividing the sum of detections by the number of receivers located in each patch type. Receivers were divided into five main patch types that included creeks, seagrass in Hare Bay, distant seagrass patches and rocky reef patches either adjacent or distant to the seagrass (i.e. nursery area) where fishes were released. For fish tagged in Hare Bay (Fig. 4.1), the seagrass patch was separated into two sub-categories: eastern and western Hare Bay. This allowed for an assessment on whether fish showed site-attachment to specific areas of seagrass within Hare Bay or if they regularly venture across the this large seagrass meadow. Bipartite habitat networks were created from the non-square matrices to visually represent the habitat use of each fish.

To assess the connectivity of fish between habitats, directed and weighted movement networks were formed from square movement matrices. The colour of nodes (i.e. receivers) illustrated the proportion of detections recorded for a given fish and the colour of the edges was weighted by the number of movements between nodes (i.e. connectivity). All nodes were placed in their actual (latitude and longitude) locations to assist with the interpretation of “real world” space-use and connectivity. Each network was tested against 10,000 randomly generated network structures to determine whether fish exhibited non-random movement patterns. Random networks for each individual were generated using a link re-arrangement approach via bootstrapping (Croft et al. 2011) while retaining the same degree of distribution from the original network. Network-level metrics (i.e. degree, betweenness, closeness and transitivity) were then calculated from each randomly generated graph and tested against metrics from the original network using a one-sample Wilcoxon signed rank test (α= 0.05).

Core use receivers (CUR) were quantified to further define highly visited areas within each network following the methodology of Becker et al. (2016). Centrality degree (i.e. the total number of ingoing/outgoing movements from a receiver) was used to rank the receivers within individual networks, with receivers below 50% identified as a CUR. Centrality degree was selected as it is comparable to other UD techniques estimating the frequency an area was used and would therefore compliment the results of the core-use areas found using BBMM. However, it is notable that while both network analyses and BBMM produce similar results for core-use areas, network analysis has been suggested to overestimate the extent of home ranges (95% UDs) (Lédée et al. 2015).

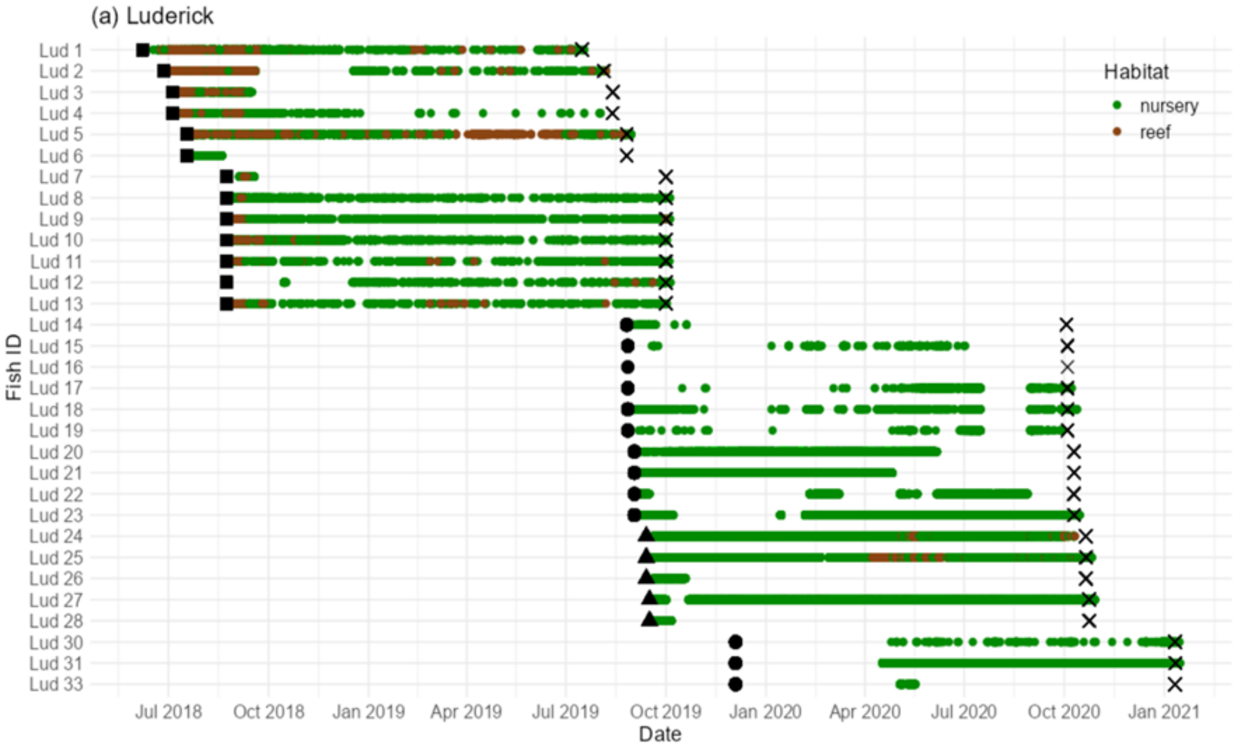
4.2.7 Modelling patterns of space use and connectivity

Generalised Additive Mixed Models (GAMMs) were used to test whether observed movement patterns (i.e. core and extent home ranges and number of edges and nodes in networks) varied between species, the fork length of fish and the release location of individuals. Preliminary data exploration was performed to assess for potential outliers, normality of the data and collinearity between the explanatory variables (Zuur et al. 2009). Models were fit with the transmitter ID as a random factor to account for the repeated-measures nature of the data. Akaike Information Criterion corrected for small sample sizes (AICc) was used to compare models, with the best fitting model containing the lowest AICc and fewest variables (Burnham and Anderson 2002). All analyses and plots were created using the statistical computing program R (R Core Development Team 2018) and the packages igraph (Csardi and Nepusz 2006), Vtrack (Campbell et al. 2012), glatos (Holbrook et al. 2017), mgcv (Wood and Wood 2015) and ggplot2 (Wickham 2016).

4.3 Results

4.3.1 General findings

We tracked 33 luderick and 20 yellowfin bream between August 2018 and May 2021, recording a total of 712,552 filtered detections within the JBMP array. There were 19 luderick (57%) and 14 yellowfin bream (70%) still being detected within the array at the expected date the transmitters would cease functioning (i.e. ~404 days from deployment; Fig. 4.2). The number of days fish were detected in the array was best explained by fork length, with an increase observed from 120 days for fish 150 mm FL to ~220 days at 250 mm FL before plateauing (Fig. 4.3). However, this model had low explanatory power (R^2= 0.09; Table 4.2). It was notable that multiple luderick tagged in Currambene Creek had large gaps in detection histories between December 2019 to April 2020 (Fig. 4.2a) and this can be attributed to the loss of a receiver. No fish were observed to permanently leave Jervis Bay, with none detected passing through the gate or on external acoustic arrays; only one fish was detected on the gate receivers before returning to its release location (Bream 10; Fig. 4.2, A2.5).


(a) Luderick

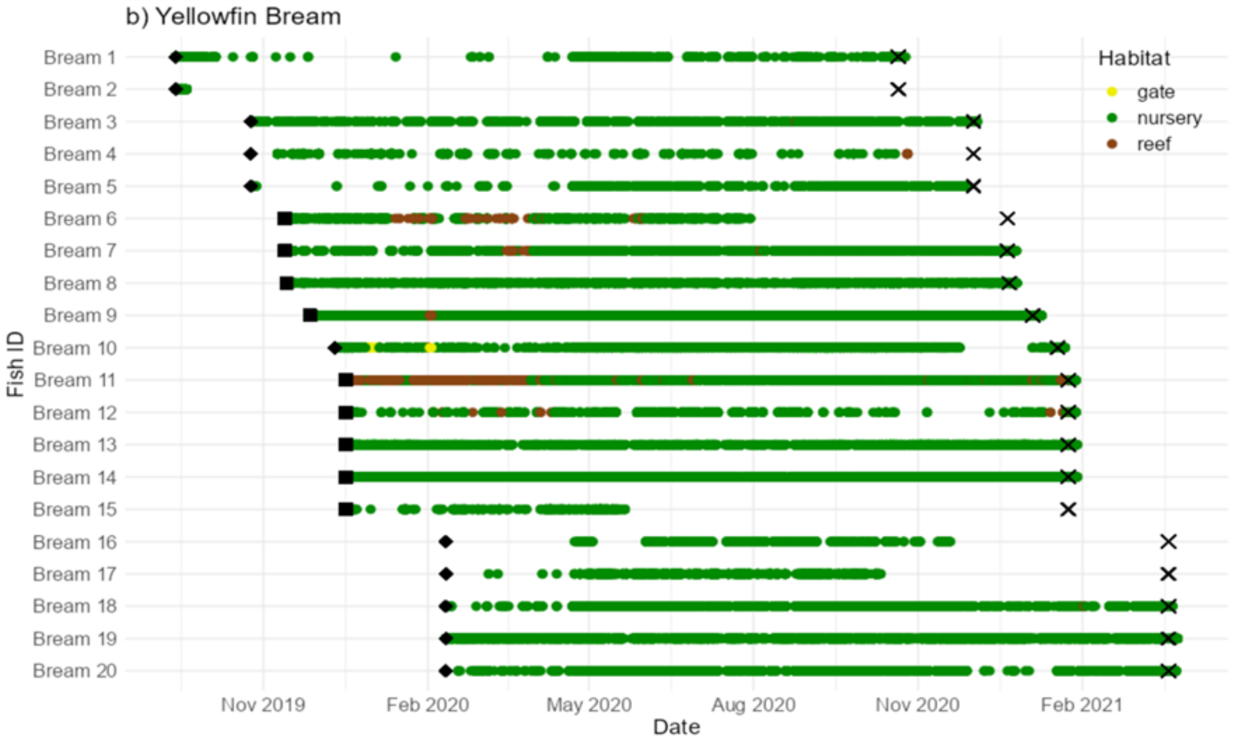

b) Yellowfin Bream

Figure 4.2 Detection history over the study period for tagged a) luderick and b) yellowfin bream at receivers in seagrass “nurseries” (green dots), rocky reefs (brown dots) or the acoustic gate (yellow dots). Tag deployment is represented by the black dots, with shape referring to release locations; black squares = Hare Bay, black circles = Currambene Creek, black triangles = Moona Moona Creek, black diamonds = Carama Inlet. Crosses indicate the anticipated date on which battery failure occurred. Fish with no detections are not included.

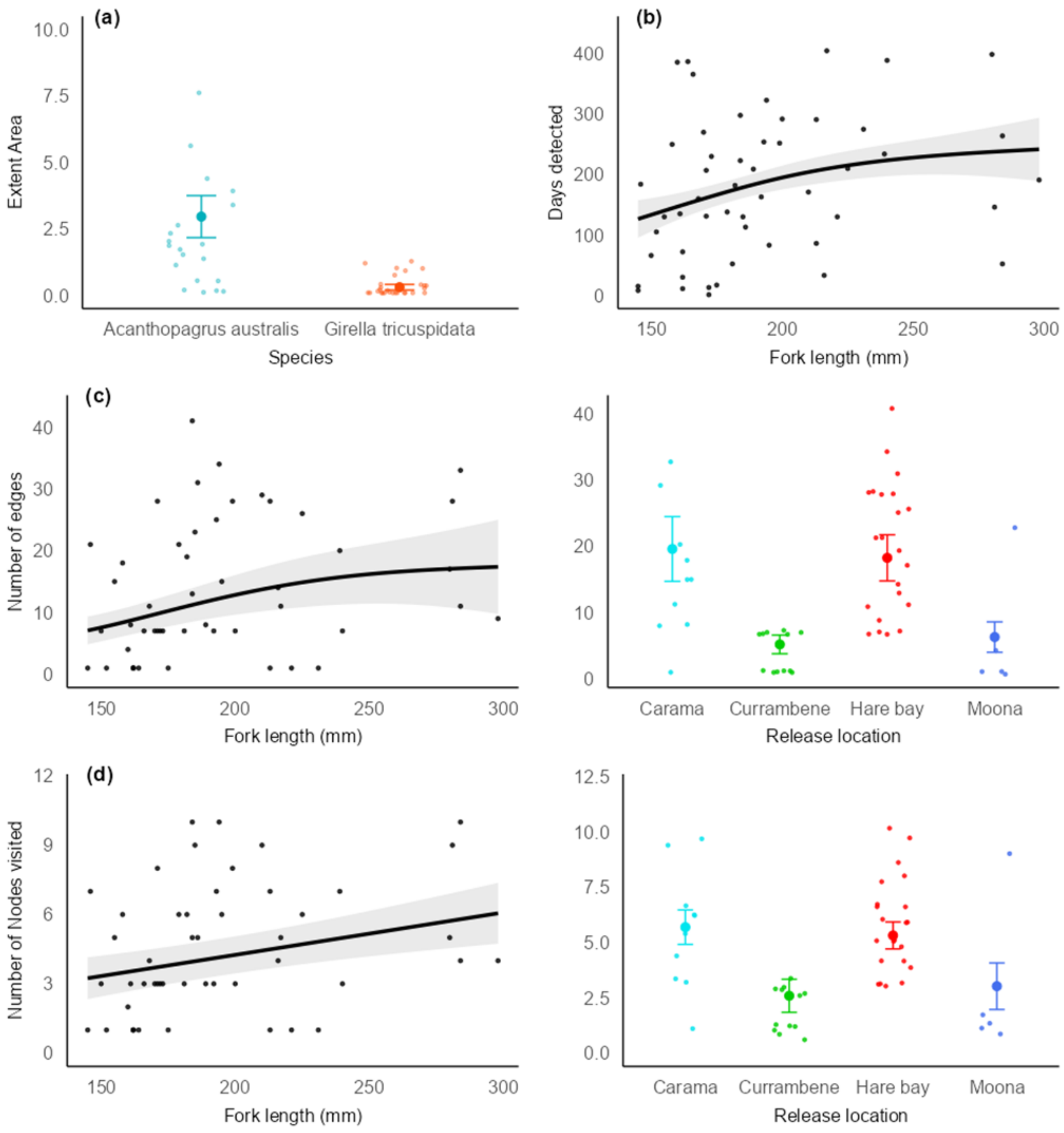


Figure 4.3 Predictions from the best fitting generalised additive mixed model for a) the extent area home-range (i.e. 95% BBMM), b) the number of days detected within the array, c) the number of edges within a network, and d) the number of nodes visited within a network. The solid lines are fitted prediction curves and ribbons and error bars represent ± standard error.

Table 4.2 Model candidates within ±2 AICc for explaining the movement patterns of tagged fish. The Akaike information criterion corrected for small sample sizes (AICc), difference between the lowest Akaike information criterion corrected for small sample sizes (ΔAICc), variance explained (R^2) and effective degrees of freedom (EDF) are reported for model comparison. Models in bold represent the most parsimonious models.

Response	**Best model (s)**	**df**	**AICc**	**ΔAIC**	**R^2**
Core area (50% BBKUD)	**Null (~ tag ID)**	**1**	**33.36**	**0**	**<0.01**
Extent area (95% BBKUD)	~ Species + Fork length	4	117.33	0	0.5
	~ Species	**3**	**117.99**	**0.66**	**0.47**
Number of days detected	**~ Fork Length**	**3.4**	**631.5**	**0**	**0.09**
	~ Species + Fork length	4.1	631.65	0.15	0.11
	~ Species + Fork length + Release location	7.7	632.67	1.17	21.7
	~ Fork length + Release location	6	632.68	1.18	18.7
Number of nodes visited	~ Fork length + Species + Release location	7	222.06	0	0.46
	~ Fork length + Release location	**6**	**223.06**	**1**	**0.45**
Number of edges	**~ Fork length + Release location**	**7**	**332.58**	**0**	**0.53**

4.3.2 Species home ranges

Both luderick and yellowfin bream were estimated to have comparatively small home ranges (Fig. 4.4, 4.5; Table A2.1). Core-use areas were not found to correlate with predictor variables (Table 4.2) and ranged from 0.018 to 0.25 km^2 (mean = 0.04 km^2 ± 0.04; Fig. 4.4) for luderick and 0.02 to 0.84 km^2 (mean = 0.19 km^2 ± 0.21; Fig. 4.5) for yellowfin bream (Table A2.1). Core-use areas for both species were generally focussed on stations within seagrass habitats, particularly around those closest to release locations suggesting a degree of site-attachment. Factor ‘Species’ was found to predict the extent of home ranges, with yellowfin bream moving over larger areas than luderick (R^2= 0.45; Table 4.2; Fig. 4.3a, 4.4, 4.5). There were also some minor differences in the extent of home ranges between release locations, although these were not identified in the top model (Table 4.2). Specifically, luderick released in creeks moved over smaller areas (Currambene Creek mean = 0.13 km^2 ± 0.07 & Moona Moona Creek mean = 0.16 km^2 ± 0.12) in comparison to those in Hare Bay (mean = 0.64 km^2 ± 0.41; Fig. 4.4). In contrast, yellowfin bream released in Carama Inlet moved over larger areas (mean = 3.02 km^2 ± 2.2) than those in Hare Bay (mean = 1.4 km^2 ± 1.39; Fig. 4.5).

4.3.3 Species networks: Habitat use and connectivity

All metrics calculated from the observed movement networks were significantly different from those generated by random networks ($P < 0.001$). Therefore, networks quantified for all fish were considered non-random and used in the analyses. The number of edges and nodes in individual movement networks was found to differ with the size of fish and release locations (Table 4.2). Specifically, the number of edges and nodes in movement networks increased with fork length, suggesting larger fish were more mobile (Fig. 4.3c-d). Fish released in Carama Inlet and Hare Bay also had a higher number of edges and nodes than those from Currambene and Moona Moona Creeks, providing further support to the results from the BBMMs that these fish used larger areas (Fig. 4.3c-d).

Fish were observed to use the seagrass habitats where they were released disproportionately more than other habitats. This was evident by the high frequency of use illustrated in habitat networks (Fig. 4.6) and both the large number of CURs and high proportion of detections at the station nearest to release sites in the movement networks (Fig. 4.7, A2.2-2.5). It was notable, however, that luderick released in Hare Bay were primarily detected in the eastern section of this large seagrass habitat, whereas yellowfin bream moved more widely across the seagrass in Hare Bay (Fig. 4.6, A2.4-2.5).

There were strong linkages between Hare Bay and Carama Inlet, with many fish detected moving in and out of this creek system (Fig. 4.7, A2.2-2.5). This included nine luderick and five yellowfin bream tagged in Hare Bay moving up to 2 km into Carama inlet before returning to the Bay (Fig. A2.2-2.5). In addition, all but one yellowfin bream released in Carama Inlet were observed to egress into Hare Bay, where they showed wide-ranging movements before returning to the creek (Fig. 4.7, A2.5). Movements into the Bay were less frequent for luderick released in creeks. No fish from Currambene Creek were detected moving into the Bay, although several fish made repeated movements within this system (Fig. 4.7, A2.3). Two luderick from Moona Moona Creek were detected leaving this creek system into the Bay (Fig. A2.4).

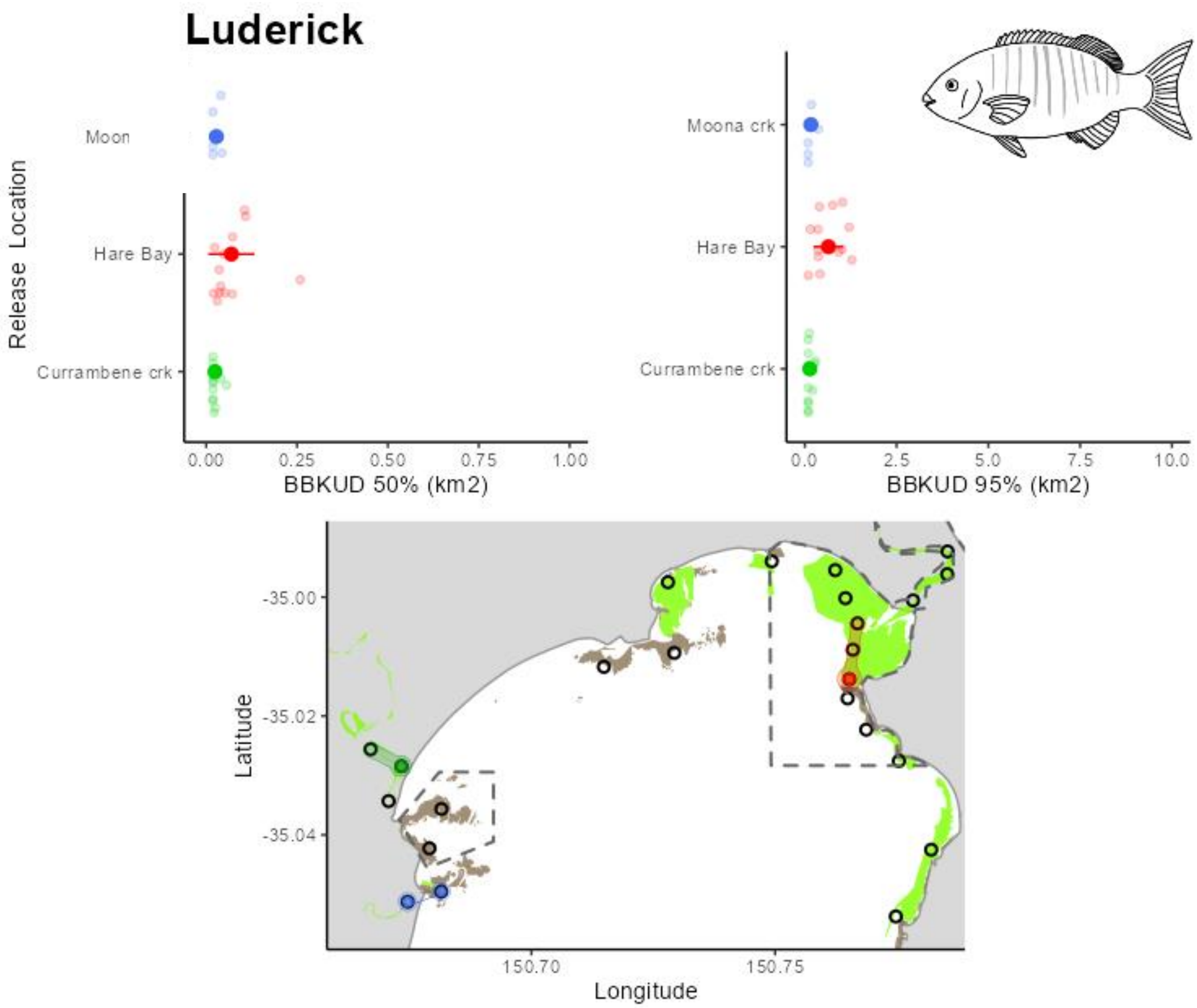


Figure 4.4. Comparison of core (50% BBMM) and extent (95% BBMM) home ranges for luderick tagged at different sites within Jervis Bay Marine Park. Points represent the mean values and bars are ± standard deviation. Maps illustrate spatial representations of the 50% (filled dark polygons) and 95% utilisation distributions (filled light polygons) using Brownian bridge movement models for a representative individual tagged at each different site. Dashed areas illustrate no-take marine reserves. Habitats (e.g. seagrass and reef) are depicted as seen in Figure 4.1.

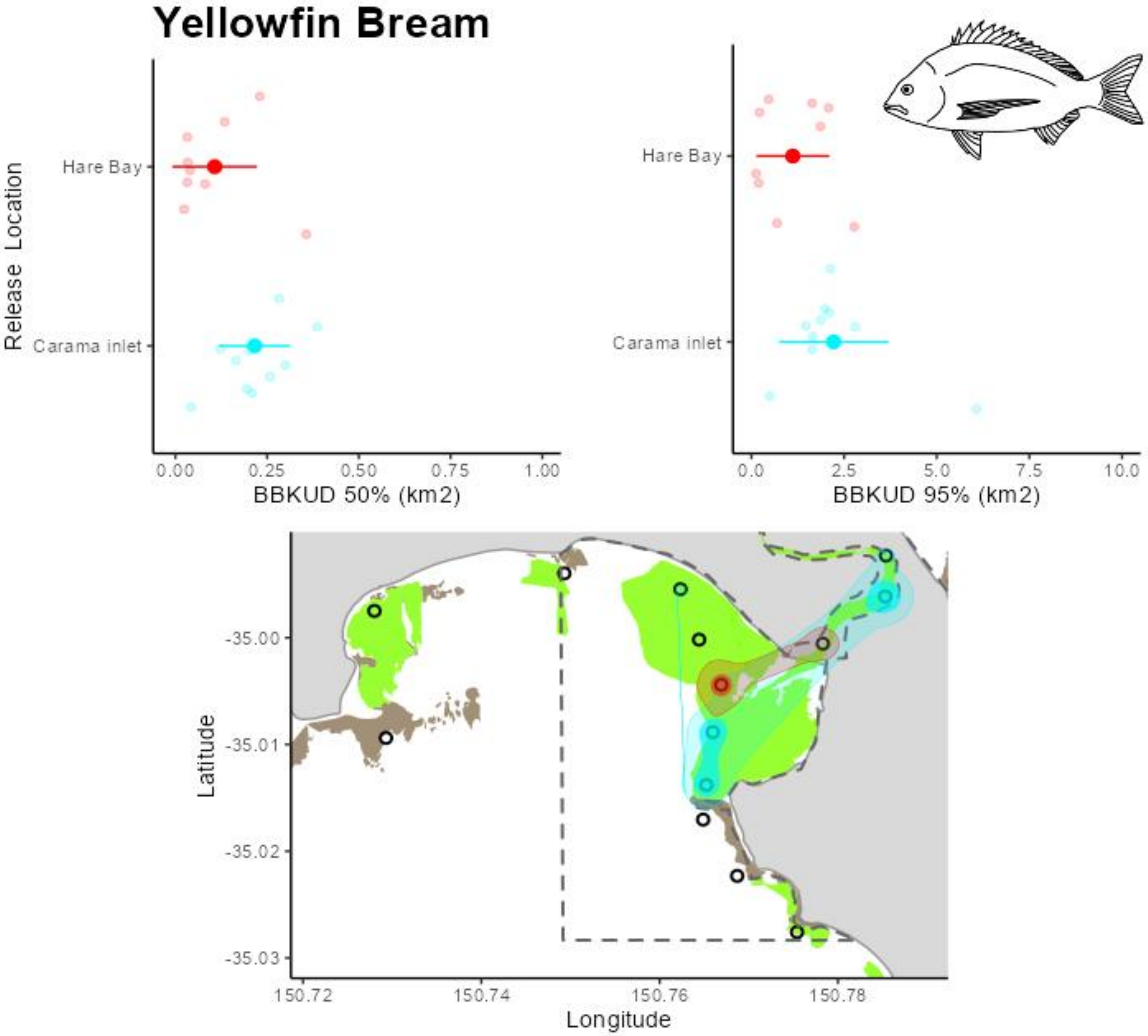
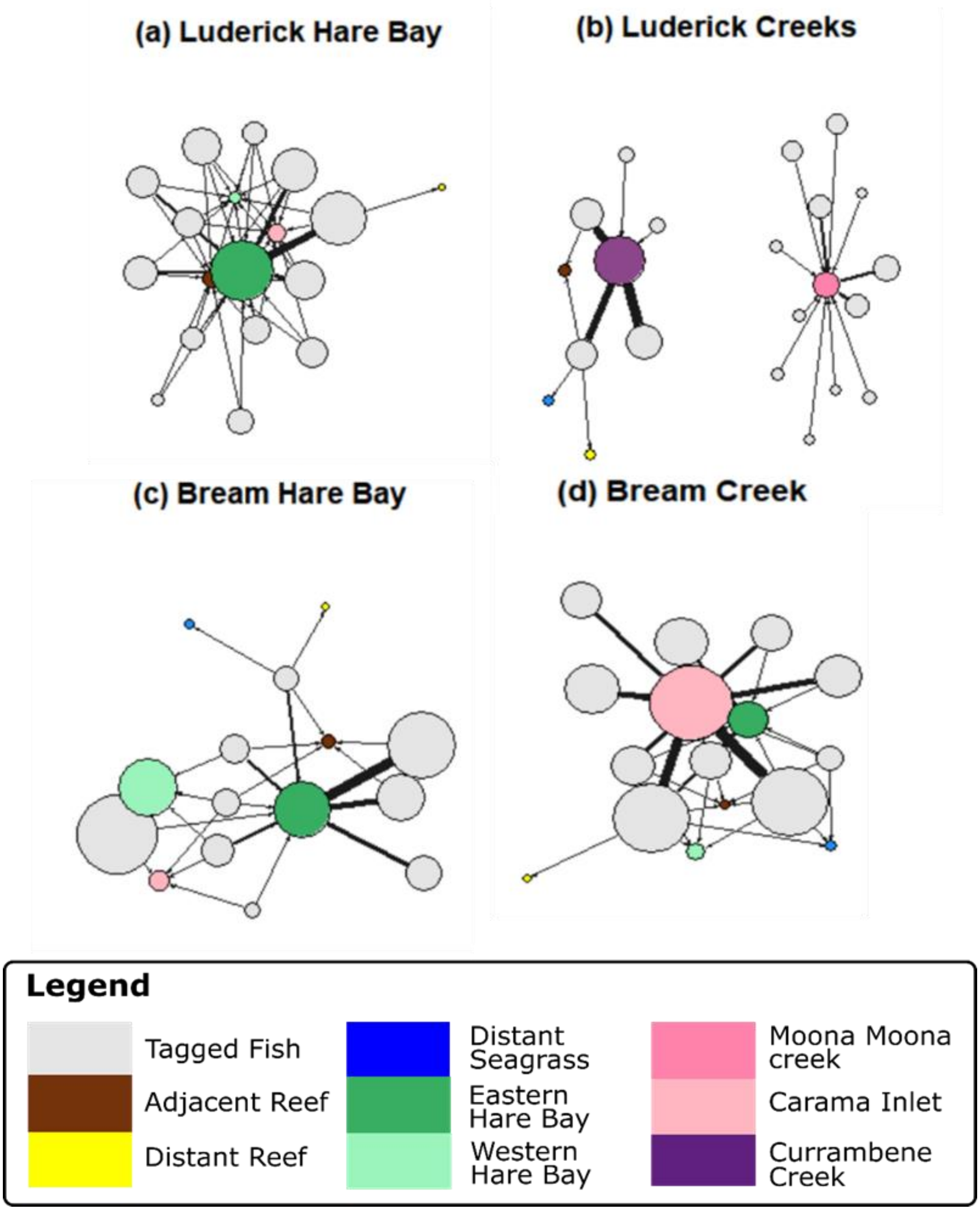


Figure 4.5. Comparison of core (50% BBMM) and extent (95% BBMM) home ranges for yellowfin bream tagged at different sites within Jervis Bay Marine Park. Points represent the mean values and bars are ± standard deviation. Maps illustrate spatial representations of the 50% (filled dark polygons) and 95% utilisation distributions (filled light polygons) using Brownian bridge movement models for a representative individual tagged at each different site. Dashed areas illustrate no-take marine reserves. Habitats (e.g. seagrass and reef) are depicted as seen in Figure 4.1.


(a) Luderick Hare Bay

(b) Luderick Creeks

(c) Bream Hare Bay

(d) Bream Creek

Figure 4.6 Species habitat networks for luderick and yellowfin bream tagged in either Hare Bay or creeks. In b), the left network represents luderick released in Moona Moona Creek and the right are luderick from Currambene Creek. The size of the grey nodes is representative of the number of detections recorded for an individual fish whilst habitat node size is proportionate to the frequency a patch type was used by fish. Edge size is scaled by the number of detections an individual was recorded in a patch type.

Individual movement networks revealed that both species frequently visited reef habitats adjacent to seagrass nursery areas. These reef-ward movements were predominantly observed for luderick and yellowfin bream released in the Hare Bay NTMR, where they moved 100's m to km's from seagrass meadows to nearby rocky reefs (Fig. 4.7, A2.2, A2.5). The two-luderick detected emigrating out of Moona Moona Creek also regularly visited reef habitat, repeatedly moving ~500 m to the reef at the mouth of this tributary (Fig. S4). There was some evidence of larger scale movements from seagrass habitats to reefs around the Bay, with one luderick and four yellowfin bream detected on reef habitats up to 10 km from release sites (Fig. A2.2, A2.5). Importantly, no fish were detected to permanently disperse to reef habitats and instead appeared to visit reefs for short periods of time before returning to the sites where they were released. One luderick (Luderick 24) had remarkable movement patterns during the last 10 days that it was detected, moving up to 15 km into the North of Jervis Bay twice (Fig. A2.4).

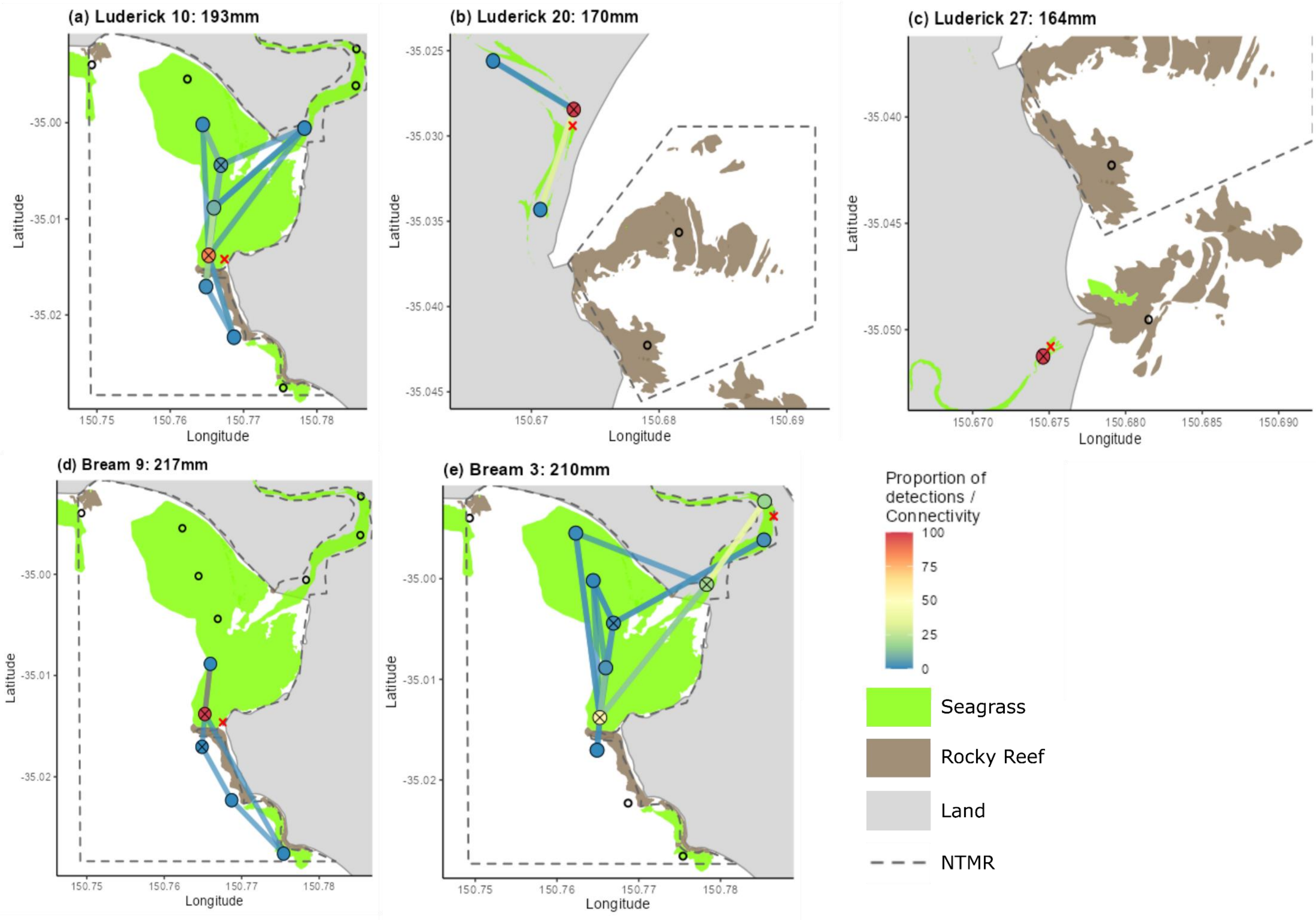

(a) Luderick 10: 193mm
(b) Luderick 20: 170mm
(c) Luderick 27: 164mm
(d) Bream 9: 217mm
(e) Bream 3: 210mm
Latitude
Longitude
-35.00
-35.01
-35.02
150.75
150.76
150.77
150.78
-35.025
-35.030
-35.035
-35.040
-35.045
150.67
150.68
150.69
-35.040
-35.045
-35.050
150.670
150.675
150.680
150.685
150.690
Proportion of detections / Connectivity
100
75
50
25
0
Seagrass
Rocky Reef
Land
NTMR

Figure 4.7 Individual movement networks showing connectivity and space use in JBMP for a representative fish from a) luderick released in Hare Bay, b) luderick released in Currambene Creek, c) luderick released in Moona Moona Creek, d) yellowfin bream released in Hare Bay and e) yellowfin bream released in Carama Inlet. The colour of nodes illustrates the proportion of detections at a given receiver and edge colour shows the number of movements (i.e. connectivity) between receivers. Empty black circles show the non-visited receivers. The red 'x's are the release location of fish and black crosses on receivers represent core-use receivers.

4.3.4 MPA use

The vast majority of fish tagged within the Hare Bay NTMR (i.e. n = 33) were never detected outside of this reserve. Only one luderick and four yellowfin bream were detected to cross the reserve boundary, where they mostly spent short durations (1 to 2 days) outside the NTMR (Fig. A2.1, A2.2, A2.5). However, the one luderick (Luderick 5) was consistently detected outside of the NTMR over a 3-month period before returning to Hare Bay (Fig. A2.1). Two yellowfin bream moved into a different NTMR, moving from Hare Bay NTMR to the Groper Coast NTMR (Fig A2.5).

4.4 Discussion

Assessing the habitat use and movement of juvenile fish will lead to a more sophisticated understanding of fish-habitat relationships and seascape connectivity. This study offers novel insights into the movement and connectivity patterns of juvenile fish belonging to two targeted species, luderick (*Girella tricuspidata*) and yellowfin bream (*Acanthopagrus australis*) in a temperate Marine Park. Although juveniles of both species exhibited site-attachment to seagrass habitats as we had predicted, many made wide-ranging movements across large areas of seagrass and to adjacent habitats and there was evidence of larger fish having increased mobility. As predicted, there was strong connectivity between seagrass and adjacent rocky reef habitats, with a higher number of fish detected moving to nearby reefs than those far away. However, these reef-ward movements were unexpectedly not unidirectional ontogenetic habitat shifts, and fish instead made frequent visits to adjacent reefs before returning to seagrass. There was also no observed export of individuals to populations along the open coast, with no fish recorded leaving the JBMP array. Overall, these findings have important implications for the definition of nursery areas and provide quantitative data to support the inferred connectivity of juvenile fish from seagrass habitats to adjacent reefs made by previous observational studies (Dorenbosch et al. 2005, Olds et al. 2012, Rees et al. 2018, Swadling et al. 2019; Berkström et al. 2020).

Numerous fish species perform ontogenetic habitat shifts connecting juvenile populations in vegetated nearshore habitats to adult populations on reefs, yet the spatiotemporal scale of this dispersal has remained unclear (Pittman and McAlpine 2003, Sambrook et al. 2019). We provide some of the first telemetry data demonstrating that juvenile fish move from seagrass to rocky reef habitats across relatively small spatial scales (100's m to km's). Contrary to expectations however, these seagrass-reef movements were not permanent, and fish made repeated short visits to reefs before returning to the seagrass areas from which they were released. When considering that larger individuals appeared to be more mobile, it is possible that as fish grow, they perform exploratory movements outside of their normal home-ranges to adjacent reefs prior to permanently dispersing. This "area expansion" behaviour where juvenile fish move to adult habitats and then return to nursery areas has been previously observed in telemetry studies (Childs et al. 2008, Huijbers et al. 2015, Murray et al. 2018, Stamp et al. 2021). For example, Murray et al. (2018) reported that juvenile Leerfish (*Lichia amia*) tagged in South Africa routinely made excursions out of estuaries to open coastal areas and attributed this to exploratory behaviour before a permanent ontogenetic habitat shift. Such a life-history strategy would allow later stage juveniles to access the resources they require without the costs of permanently dispersing. Alternatively, the lack of permanent dispersal over the timescale of the current study (~404 days) may also suggest that many fish can remain in seagrass as adults and fewer fish perform explicit ontogenetic shifts to reef habitats than previously theorised. Indeed, this is supported by the larger mature yellowfin bream tagged in this study showing site-fidelity to seagrass habitats and previous observations of adults of both species being present in seagrass in Jervis Bay (Kiggins et al. 2018, Rees et al. 2018). It would be significant if few individuals permanently disperse to adult populations on reefs because it would suggest that these species may exist as a metapopulation, with a large proportion being a non-dispersing subpopulation. Seagrass patches have also been identified to play an important role as habitat at different life stages (e.g. both juvenile and adults) for other targeted reef-associated fish species in tropical seascapes (Beets et al. 2003; Hitt et al. 2011, Honda et al. 2016, Ebrahim et al. 2020). For example, Ebrahim et al. (2020) reported that adult shoemaker spinefoot (*Siganus sutor*) in the Seychelles display small movements, focussed mainly on mosaics of seagrass and coral. This was significant, because previous studies had identified seagrass only being important for the species as nursery area and not habitat for adults (Gell & Whittington, 2002, Kimerei et al. 2011).

Identifying nursery habitat is essential for conservation and management strategies, but current definitions of nurseries may be too static as they do not incorporate seascape connectivity (Sheaves et al. 2006, Nagelkerken et al. 2015, Sheaves et al. 2015, Litvin et al. 2018). In the current study, we reveal that whilst both juvenile luderick and yellowfin bream tagged at several sites in Jervis Bay exhibit strong site-attachment to specific areas of seagrass habitat, they can show wide-ranging movements and connect a mosaic of different patch types when in close proximity. For instance, fish tracked in the Hare Bay NTMR frequently moved across large areas of seagrass, into creeks (i.e. Carama Inlet) and directly adjacent reefs. We therefore propose that juvenile fish are not bound to certain patch types (e.g. seagrass) and that they can use multiple patches when they are spatially connected to access food or shelter (i.e. landscape supplementation; Dunning et al. 1992). Furthermore, the use of multiple patch types as nursery areas has important ecological consequences as juveniles could act as an important link between patches by transfering nurtients (Lundberg & Moberg 2003, Heck et al. 2008) .These findings suggest that the current framework for defining nursery habitats as discrete or homogenous patch types is too simplistic, and that the nursery-role concept should be refined to view nurseries as a combination of patch types that juvenile fish regularly use and visit during juvenile and subadult life stages. This “seascape nursery” approach offers a more realistic definition of nursery areas and would assist resource managers to identify appropriate areas for management actions (Nagelkerken et al. 2015, Sheaves et al. 2015, Pittman et al. 2021).

The site-fidelity of fish released in an existing NTMR in the current study meant that few individuals were detected crossing reserve boundaries. This finding adds to the growing literature demonstrating that many fishes have small home-ranges and remain inside of NTMRs over relatively long time periods (Pittman et al. 2014, Harasti et al. 2015, Lee et al. 2015, Legare et al. 2015, Aspillaga et al. 2016, Ferguson et al. 2016, Kendall et al. 2017, Novak et al. 2020). Strong retention within NTMRs have been previously observed for adult luderick in JBMP (Ferguson et al. 2013, Ferguson et al. 2016) and multiple species belonging to Sparidae in Australia (Harasti et al. 2015) and abroad (Parsons et al. 2003, March et al. 2011, La Mesa et al. 2013, Abecasis et al. 2015). For example, Harasti et al. (2015) reported that juvenile and adult pink snapper (Sparidae: *Chrysophys auratus*) displayed site fidelity to a NTMR in NSW for up to 1249 days. While five fish in the current study moved across reserve boundaries, all returned to the NTMR where they were released after spending between 1 day to 3 months in fished waters. These movements provide evidence of spill-over from the NTMR into adjacent fished populations which can influence biodiversity, productivity and ecological functioning (McClanahan and Mangi 2000, Halpern et al. 2009, Weigel et al. 2014, Di Lorenzo et al. 2020).

The utilisation of multiple patch types and the gradual increase in species home range with size has important yet rarely considered implications for the design of MPAs (Carr et al. 2017, Balbar and Metaxas 2019). Currently, there are few examples where connectivity and ontogenetic habitat shifts are considered in spatial conservation strategies (but see Weeks 2017, Balbar and Metaxas 2019, Friesen et al. 2019), which is undoubtedly due to the paucity of empirical data on the movement of fishes across the seascape at various life-stages. For instance, Balbar and Metaxas (2019) reported that for 746 MPAs located across six countries, only 11% considered connectivity as an ecological criterion by managers designing them. In the face of limited information, MPAs are often designed to protect a portion of the patch types in an area (i.e. habitat representation) (Sala et al. 2002, Airamé et al. 2003, Rondinini 2011, Hernandez et al. 2021), with little understanding of how they are connected through processes such as animal movement. A shift in the perception of nursery areas from individual patch types to a seascape mosaic as advocated by our findings, and those from previous studies (Pittman et al. 2007, Sheaves et al. 2006, Nagelkerken et al. 2015, James et al. 2019; Cheminée et al. 2021), highlight that simply representing patches within MPAs may be misguided. Instead, it may be more appropriate for MPA design to protect areas where there are different patch types in close proximity. This strategy should incorporate connectivity within MPA boundaries and maximise conservation benefits by protecting a large proportion of the population during their movements. It would also safeguard key fish habitats (e.g. seagrasses, mangroves, saltmarshes) that are currently under pressure globally (Waycott et al. 2009, Li et al. 2018, Dunic et al. 2021). Similar recommendations have been made in previous studies (Pittman et al. 2007; McCook et al. 2009, Olds et al. 2016), including recently in a set of “rules of thumb” for designing MPA networks that incorporate connectivity outlined by the International Union for Conservation of Nature (IUCN) (Lausche et al. 2021)

Understanding variation in movement patterns and connectivity at the species and individual level has been gaining increased attention in both terrestrial and marine biomes (Taylor et al. 2017a, Andrzejaczek et al. 2020, Dwyer et al. 2020, Hertel et al. 2020, Hilty et al. 2020, Shaw 2020). In the current study, there were some differences in species movements, with yellowfin bream having larger home-ranges than luderick. We also found substantial individual variation in movement patterns, which was largely driven by release location. Specifically, fish tagged in Currambene and Moona Moona Creek had restricted movements and smaller networks, due to the limited number of individuals moving out of these creeks and into Jervis Bay. It is worth noting that we may have underestimated the space-use of individuals within these creek systems, as fish could have moved upstream and not been detected. Our findings also indicate that larger individuals may be more mobile, and this is a common trend reported throughout the literature for various species (Kramer and Chapman 1999, Nash et al. 2015). Future research is required to better understand the processes underpinning the drivers of fish movements and causes of individual variation due to its importance in population dynamics and informing management and conservation strategies. Furthermore, information on the traits of different species, including their movements, also assist the design of spatial management strategies to reach varying conservation objectives (Miatta et al. 2020).

There are several reasons why some fish were not detected throughout the entire study period. Firstly, the detection range of receivers for V7 transmitters in seagrass patches is low, particularly when fish are ensconced in seagrass (Swadling et al. 2020). Indeed, this may explain why smaller fish were detected on fewer days, because these individuals may be more likely to exhibit cryptic behaviour and shelter amongst the seagrass fronds. It is also possible that fish were present within the array or emigrated to the open coast without being detected, but it seems improbable because the preferred habitats of the study species were well covered by receivers and no fish were detected on external arrays. Using higher powered tags would increase the detection range and allow any diurnal patterns in juvenile movements to be elucidated, as we were unable to test for this due to poor detection ranges at night (Swadling et al. 2020). However, higher power comes with an increase in tag size, which would not be suitable for tracking small juvenile fish. Another explanation for the loss of tags in the array is that fish may have experienced natural mortality, such as predation. For example, the abrupt changes in movement patterns made over the final 10-day detection period for Luderick 24 was probably due to a predation event. It would be worth future studies tracking juvenile fish to adopt tags with predation sensors (i.e. "predation tags") to provide an estimate on the frequency of these events (Weinz et al. 2020). Furthermore, mortality due to fishing was predicted to be low as there is minimal illegal fishing in the Hare Bay NTMR and the study animals were generally under the legal size for the species.

Our results demonstrate that juveniles belonging to two co-occurring species which are important in both commercial and recreational fisheries show site-attachment to seagrass habitats, but frequently move between different areas such as creeks and rocky reefs. The routine use of multiple patch types by juvenile fish has important ramifications for the nursery-role concept, highlighting the need to move away from defining nursery areas as discrete patch types and instead consider them as mosaics of functionally connected patches within the seascape (i.e. seascape nurseries). Although fish were detected moving to rocky reefs adjacent to seagrass at greater rates than to reefs further away, these movements did not represent a permanent dispersal to adult populations, with many individuals making repeated visits to reefs. These movements to reef are thought to be driven by exploratory movements as fish grow, which would correspond to changing resource requirements, maturation, and reduced predation risk (Kimirei et al. 2013, Grol et al. 2014). Overall, gaining a more quantitative understanding on the movement patterns and connectivity of juvenile fish across the seascape, including habitat-use and the spatiotemporal scale of ontogenetic habitat shifts, is important for improving knowledge on species-habitat relationships and to better inform resource managers and assist the design of sound and effective MPAs.

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Chapter 5: Assessing generality in movement patterns for a targeted fish: home range and residency of Luderick (*Girella tricuspidata*) on open coastal reefs

This chapter has been written to be submitted to ***Fisheries Research***. The receivers in the Bendalong array were scheduled to have their final download in mid-2021, however this was delayed due by COVID-19 restrictions. Despite this, the data in this chapter is of a considerable time scale (~19 months) and the remaining data will be collected and analysed before this chapter is submitted for publication.

Plate 5.1 Commuting to our study site on the south side of Bendalong Point for a day of fish tagging.

5.1 Introduction

Understanding generalities in patterns and processes is fundamental in ecology as it enables the prediction of relationships across systems (Lawton, 1999; Underwood et al. 2000; Knapp et al. 2004). However, the tradition of single-site experiments has largely hindered our ability to conceive generalisations of ecological phenomena, as this requires repeated testing and the production of consistent, predictable outcomes (Borer et al. 2014). Acoustic telemetry is rapidly developing and is becoming a popular method to quantify the spatial and behavioural ecology of marine fauna (Donaldson et al. 2014; Hussey et al. 2015), yet there are few examples where repeated tests have been conducted to assess the generality of species movements across various systems. Instead, generalities of movement patterns are usually founded from meta-analyses (e.g. Green et al. 2015, Nash et al. 2015), but this may be misguiding because it means they are developed from studies of different species or contrasting methodological designs (e.g. acoustic arrays of differing configurations; Gates, 2002; Gurevitch and Mengersen, 2010). Gaining a better grasp on the drivers and scales of species movements in varying environmental contexts through replicated studies is essential to understand whether tracking data can be used to confidently guide the design of conservation and management strategies (Kramer and Chapman, 1999; Grüss et al. 2011).

Abiotic factors can be key drivers in the movement of fish across several temporal scales, including stochastic disturbances like weather events, or across days, seasons, and years (Meyer et al. 2007; Childs et al. 2008; Payne et al. 2013; Aspillaga et al. 2016; Bacheler et al. 2019). Such abiotic factors vary between patch types, which can result in intraspecific variation in the spatial ecology of species in different spatial contexts (Schlaff et al. 2014; Bradley et al. 2020). For instance, the movement of fish in estuaries have been linked to changes in salinity, turbidity and temperature

(Childs et al. 2008; Payne et al. 2013; Payne et al. 2015) whereas oceanic conditions such as swell or storms may have a larger influence on fish along the open coast (Stocks et al. 2015; Aspillaga et al. 2016; Bacheler et al. 2019). Few studies, however, have been replicated for species across different environmental systems and this represents a key challenge for developing generalisations in their response to various abiotic factors. Another challenge for developing generalisations in species spatial ecology are intrapopulation differences in movement patterns that are independent of environmental context (i.e. personalities) (Harrison et al. 2015, del Mar Delgado et al. 2018, Villegas-Rios et al. 2018, Papastamatiou et al. 2022). Many species do show repeatable movement patterns that can be placed within collective behavioural traits even despite differences due to individual fish movements (Kessel et al. 2016, Ferguson et al. 2013, Taylor et al. 2018, Stamp et al. 2021, Aspillaga et al. 2021). For example, many species of fish exhibit partial migration, where a fraction of the population perform migrations, but the remainder show residency to an area (Chapman et al. 2012, Gray et al. 2012, Papastamatiou et al. 2013, Childs et al. 2015, Winter et al. 2021)

In this study, we explore movement patterns using luderick (*Girella tricuspidata*; Quoy & Gaimard) as a study species to determine if reliable generalisations can be formulated. Luderick are a predominantly herbivorous Girellid commonly found on rocky reefs and in estuaries across south-eastern Australia and northern New Zealand where they are targeted in commercial, recreational and indigenous fisheries (Kingsford et al. 1991; Curley et al. 2013; Schnierer and Egan, 2016). Luderick movement patterns have been studied (Gray et al. 2012; Ferguson et al. 2013; Cadiou, 2016; Ferguson et al. 2016), but the generality of their spatial ecology is yet to be determined. There is a paucity of movement data for luderick on coastal rocky reefs along wave dominated coastlines, despite these areas being a key habitat for adults (Kingsford, 2002). Acoustic tracking of both adult and juvenile luderick in a coastal embayment (i.e. Jervis Bay) has demonstrated the species to be highly site-attached, with fish remaining at reefs and seagrass areas for substantial time periods, with some short-term (~1-3 days) movements to adjacent areas before returning to release locations (Ferguson et al. 2013; Ferguson et al. 2016; **Chapter 4**). Adult fish within this coastal embayment also showed diurnal movement patterns where they were active during the day and sheltered at night. This contrasts with the findings of research quantifying luderick movements within three large estuaries in NSW, where fish were observed to show little residency and moved widely around the estuarine system or egressed to the open coast (Cadiou, 2016). Furthermore, changes in the species movement behaviour due to prevailing meteorological conditions remains unclear, although it has been speculated that they may seek shelter in storm events (Ferguson et al. 2013). In this study, we predicted that luderick on open coast rocky reefs would show similar movements to those previously observed within a coastal embayment and exhibit a high degree of site-attachment during ‘normal’ sea conditions and show distinct diurnal patterns of movement. This behaviour would then be punctuated by sheltering in calmer or protected areas during storm conditions. We propose this behaviour will be different from that observed in estuaries where substantial changes in physico-chemical conditions may effectively force fish to be more mobile and egress from estuaries to disperse to other areas (Cadiou, 2016).

5.2 Materials and methods

5.2.1 Study site

This study was performed along a ~12 km stretch of wave exposed coastline in Bendalong, south-eastern NSW, Australia (35.2191° S, 150.4864° E; Fig. 5.1). The coastline consists of intertidal and subtidal rocky reefs which are separated by expanses of soft sediments (Fig. 5.1). The study area is dominated by oceanic conditions with minimal estuarine input and experiences relatively stable water quality.

An array of 10 VR2W acoustic receivers (Innovsea, NS, Canada) were deployed on reefs across the study area in July 2018. The receivers were deployed on, or directly adjacent to, rocky reefs at depths ranging from 5 – 13 m. The range of the receivers was assumed to be 300 m based on previous research from nearby arrays on similar rocky reefs (i.e. Jervis Bay; Ferguson et al. 2013). The moorings were positioned no more than 250 m from the shoreline and were separated by a minimum of 1,000 m or a physical feature (e.g. headlands, bomboras or shallow reefs which would block acoustic signals between receivers). This receiver spacing is comparable to the array located within Jervis Bay Marine Park, where luderick have been tracked previously (Ferguson et al. 2013, Ferguson et al. 2016) and should therefore allow a comparison of the species movement patterns between systems. Receiver moorings comprised a section of railway line (60-100 kg) connected to a subsurface polystyrene buoy with a rope. All receivers were cable tied to the rope with the hydrophone orientated in an upright position, a minimum of 1.5 m from the seabed and 1 m below the subsurface buoy. The receivers were downloaded, and the moorings checked in June 2019 and March 2020. It is noteworthy that there are several acoustic receiver arrays adjacent to the study site that form the Australian Animal Tagging and Monitoring System (AATAMS, see https://animaltracking.aodn.org.au/) along south-eastern Australia. Therefore, if fish tagged in the current study moved to the north or south, they should theoretically be detected by these arrays.

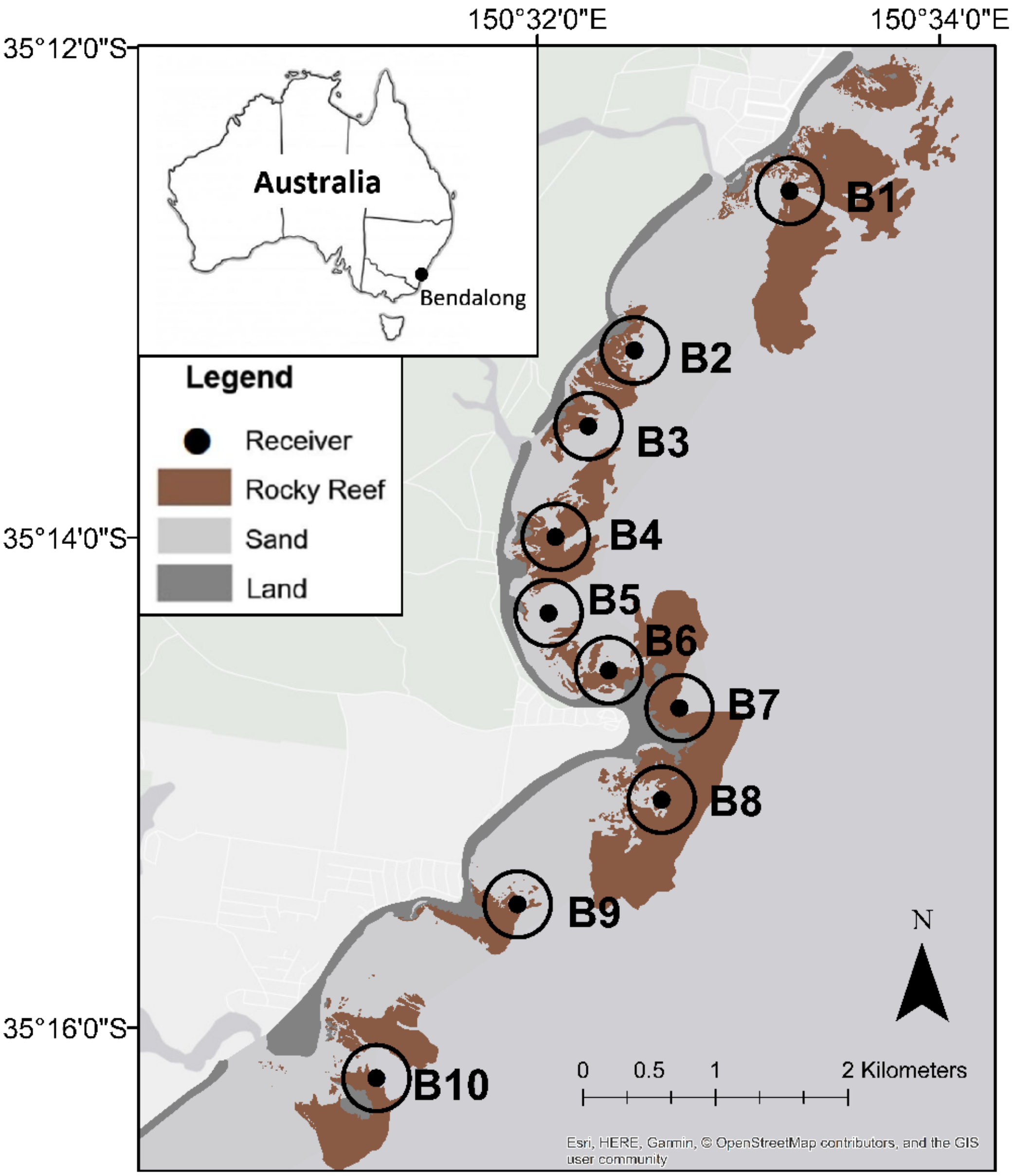

Figure 5.1 Map of the study area (Bendalong region, NSW, Australia) showing the configuration of the acoustic receivers (black dots) deployed over the 18-month study period. Circles surrounding each receiver illustrate a 300 m detection area. Areas of rocky reef (brown) and unconsolidated soft-sediment (light grey) are depicted.

5.2.2 Fish collection and tagging

A total of 10 adult luderick (*Girella tricuspidata*) were captured and internally tagged with Vemco V9-2H coded transmitters (27.5 mm length, 9 mm diameter, 2.7 g in water, battery life 912 days) possessing a nominal delay of 120-180 s. Luderick were caught in August and September of 2018 from rock platforms at depths < 4 m using rod and line, with a circle hook baited with *Ulva* spp. All fish were larger than the legal-size limit (270 mm for NSW waters) and were likely to be sexually mature, with individuals ranging from 275 mm to 350 mm fork length (Table A3.1; Gray et al. 2012). Fish were captured and tagged in the centre of the array (i.e. B7 and B8; Table 5.1; Fig. 5.1) so that if any fish moved in a north or south direction, they would have a high probability of being detected. The surgical procedure in this study followed an established technique used effectively in previous studies (**Chapter 4**; Ferguson et al. 2013; Fetterplace et al. 2016). Upon capture, fish were placed in an aerated 50 L holding tank for a minimum of 15 mins to recover and were visually examined for general health and condition. Fish were then anaesthetized using 60 mg L^{-1} Aqui-S® solution before being transferred to a wetted cradle for surgery. Transmitters were inserted through a 1cm incision in the ventral surface of the fish toward the rear of the peritoneal cavity. The incision was closed with two dissolvable stitches tied with a double surgeon's knot. All surgical equipment and acoustic transmitters were submerged in povidone-iodine antiseptic (Betadine) prior to insertion to prevent infection. Post-surgery, fish were transferred to an oxygenated holding tank with 50 L of fresh seawater. Ram ventilation was also used to increase water flow over the gills and assist in recovery. Fish were then monitored until recovery (~30 minutes) before release. All fish recovered from surgery and were released at their point of capture.

5.2.3 Data analysis

Tagged fish were passively tracked from August 2018 through to March 2020 (~19 months; Table A3.1). Fish 1 and 2 had a limited number of detections (< 20) and were excluded from subsequent analyses (Table 5.1; Fig. 5.2). The residency of the tagged luderick was estimated using a residency index (I_R) (Afonso et al. 2008; Ferguson et al. 2013). This was calculated for each individual as the total number of days a fish was detected divided by the total possible number of days the fish could be detected (i.e. period between the release date and the last day detected for each individual) multiplied by 100. I_R was determined for (a) the whole array (hereafter referred to as I_R – array), and (b) each receiver station to identify medium and small-scale residency patterns. Low I_R values represented fish being detected on very few days whereas absolute residency ($I_R = 100$) meant fish were detected on every possible day. The number of stations that individuals visited per week and per month was quantified to describe the movement patterns and site fidelity of luderick between reefs. We also determined the Minimum Linear Dispersal (MLD) for each fish as the distance between the release location and the furthest station visited.

Generalised linear mixed models (GLMMs) were applied to test for relationships between the movements of luderick and environmental variables. The movement metrics used in the analyses were the daily presence/absence of fish in the array, the weekly number of stations visited and the weekly MLD for each fish. Five environmental variables were included in the analyses and included wave height, wave direction, wave period, sea temperature and tidal range. Swell variables were collected from the Batemans Bay wave buoy and tidal data was collected from a gauge in Batemans Bay, both operated by the Manly hydraulics laboratory (https://www.mhl.nsw.gov.au). Swell and tide variables were collected hourly and averaged to obtain daily and weekly means. Preliminary data exploration was performed using the methods outlined in Zuur et al. (2009). Collinearity was evident between swell period and direction, with southerly swells having higher periods. We therefore excluded swell period from the subsequent analyses. All continuous predictor variables were standardised to allow them to be compared on the same scale by subtracting the sample mean and dividing by the standard deviation. GLMMs for the daily presence/absence of luderick were conducted using a binomial distribution and the weekly number of stations visited was modelled with a Poisson distribution. A zero-inflated negative binomial distribution was used to model the MLD travelled by fish per week to account for apparent overdispersion and zero-inflation in these data (Brooks et al. 2017). Model fitting was conducted using the 'lme4' (Bates et al. 2007) and 'glmmTMB' (Magnusson et al. 2017) package in R version 3.6.3 (R Core Development Team, 2018). We used Akaike's information criterion corrected for small sample sizes (AICc) and differences in AICc (ΔAICc) to evaluate support among all possible candidate models (Burnham and Anderson, 2002). The best model was the one with the lowest AICc and models within ±2 ΔAICc were considered to have reasonable support (Burnham and Anderson, 2002). The proportion of variance explained was calculated for the fixed effects (marginal R^2) and the combined fixed and random effects (conditional R^2) (Nakagawa, 2014).

The home range of each fish was estimated using the Brownian bridge movement model (BBMM) to calculate utilization distributions (UD). The BBMM was selected in preference to other methods that quantify space-use (e.g. fixed kernels) as it considers the time-ordered characteristic of telemetry data by modelling the probability of an animal being located in an area based on its start and end locations, the time elapsed between detections and the speed of movements (Bullard, 1991; Horne et al. 2007). The location of individuals for the BBMM were estimated using a mean position algorithm to ascertain centres of activity (COA) following Simpfendorfer et al. (2002).

BBMM estimation required two smoothing parameters to be calculated. Firstly, the Brownian motion variance parameter (σ^2_m) which describes the mobility of the animal and the distance it can travel from the line between two successive points. The ‘liker’ function was employed to estimate σ^2_m using the maximum likelihood approach as per Horne et al. (2007). The second smoothing parameter related to the location error (δ) was based on the receiver detection range estimated at 300 m. Fish home ranges were calculated as 50% UDs (core home range) and 95% UDs (extent of home range) using the ‘kernelbb’ function in the R package ‘adehabitatHR’ (Calenge, 2006). UDs were not calculated for Fish 1 and Fish 2 due to their limited number of detections (Table 5.1). Spearman rank correlations were used to test for relationships between the length of fish and I_R-array, the number of stations visited (per week, month and total), the MLD and the 50% and 95% UDs. Differences in the movement pattern of fish between day and night were investigated using a Rayleigh’s Z test, which determined if there was a non-random pattern in the number of detections over diel periods (i.e. 24 hours).

5.3 Results

5.3.1 General detection patterns

All tagged fish were detected within the array for at least a month (Table A3.1; Fig. 5.2). A total of 22,387 acoustic detections of luderick were recorded, with the number of detections for fish ranging from 2 (Fish 2) to 15 948 (Fish 5) (Table 5.1). Five fish (50%) were detected within the array for the entire study period (i.e. 589 days) (Table A3.1; Fig. 5.1). It was assumed that Fish 3 remained within the array, despite long periods of absence as this fish likely frequented areas with poor receiver coverage (Fig. 5.2). Fish with early absences from the array had their final detections between October 2018 and February 2019 which equates to 43 - 190 days post tagging (Table A3.1; Fig. 5.2). Five fish were not detected within the array for periods greater than one month before reappearing (Fig. 5.2). No fish with early absences from the array were detected to leave the study area (i.e. movement north or south out of the array) or on any receivers along the NSW coastline forming the AATAMS network.

Table 5.1 Summary data for the 10 tagged luderick (*Girella tricuspidata*) monitored in the Bendalong array including the movements between reefs, residency to the array and the activity spaces for each fish. I_R – array: residency index to the array, MLD: Minimum linear distance between release point and the farthest receiver an individual was detected, 95% and 50% UD: utilisation distributions (UDs) using Brownian bridge movement models.

										Mean no. stations visited	
Fish #	**Days detected**	**Station nearest release**	**Total no. detections**	**No. stations visited**	**Furthest station visited**	**I_R - array**	**MLD (km)**	**95% UD (km^2)**	**50% UD (km^2)**	**Per week**	**Per month**
1	4	B8	13	2	B7	2.1	0.513	-	-	-	-
2	2	B8	2	1	B8	2.25	0.25	-	-	-	-
3	30	B8	139	3	B6	5	0.85	1.62	0.37	1.2	1.62
4	42	B7	158	4	B5	36.19	1.1	2.11	0.42	1.13	2.75
5	433	B7	15948	1	B7	77.6	0.17	1.15	0.25	1	1
6	223	B7	3557	1	B6	39.86	0.47	1.18	0.25	1	1.17
7	198	B7	741	3	B5	31.3	1.1	2.21	0.59	1.3	2.67
8	17	B7	315	1	B7	39.54	0.17	1.15	0.25	1	1
9	33	B7	1136	1	B7	71.74	0.17	1.15	0.25	1	1
10	98	B7	378	3	B5	16.937	1.1	2.09	0.52	1.1	2.25

5.3.2 Residency and Site fidelity

Luderick detections occurred across four stations in the centre of the array (B5-B8) which covered a ~3 km stretch of coastline (Fig. 5.2). Residency to the array was variable between individuals and I_R-array ranged from 2.1 to 77.6% (Table 5.1). Fish generally exhibited the greatest residency (I_R) to the receiver nearest to their point of release (Fig. 5.3). The exceptions were Fish 3, which had a slightly greater residency at B7 compared to B8, and Fish 10 which had its greatest residency at both B7 and B5 (Fig. 5.3). It was notable, however, that the residency indices for these fish were low at each station (i.e. $I_R < 7\%$) (Fig. 5.3). Three fish (5, 8 and 9) were only detected on stations closest to their point of release, being detected on up to 77.6% of days they were tracked (Fig. 5.2, 5.3).

Half of the tagged luderick moved to adjacent stations before returning to release reefs (Table 5.1; Fig. 5.2). On average, individuals visited less than 1.5 stations per week and only four fish visited over 2 stations per month (Table 5.1). The average Minimum Linear Dispersal (MLD) was 0.59 km (± 0.41 km SD) and ranged from 0.17 to 1.1 km (Table 5.1). Most movements between stations occurred around Bendalong point (i.e. B6 to B8) which is connected by sections of continuous reef. Three individuals, however, performed movements across ~ 500 m of a mosaic of reef and sand patches to B5 before moving back to their release reef. The I_R, number of stations visited and MLD were not found to be significantly correlated to the fork length of the tagged luderick (Spearman correlation: rho = 0.05 – 0.47, $P > 0.05$).

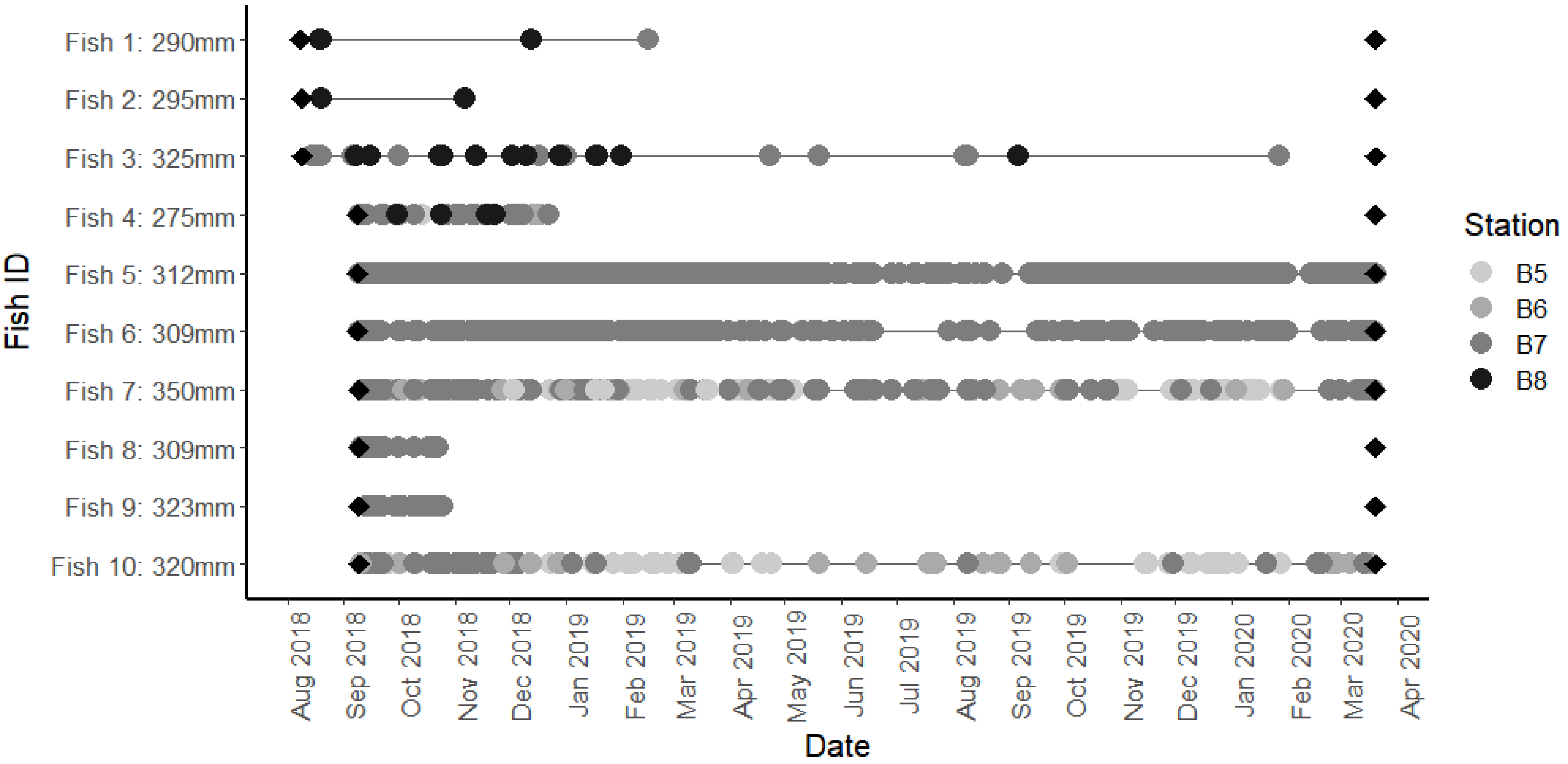

Figure 5.2 Timing and location of detections for the 10 tagged luderick (*Girella tricuspidata*). Black diamonds denote the date fish were tagged (August and September 2018) and the final download of the acoustic receivers (March 2020). Please see Figure 5.1 for the spatial location of each station.

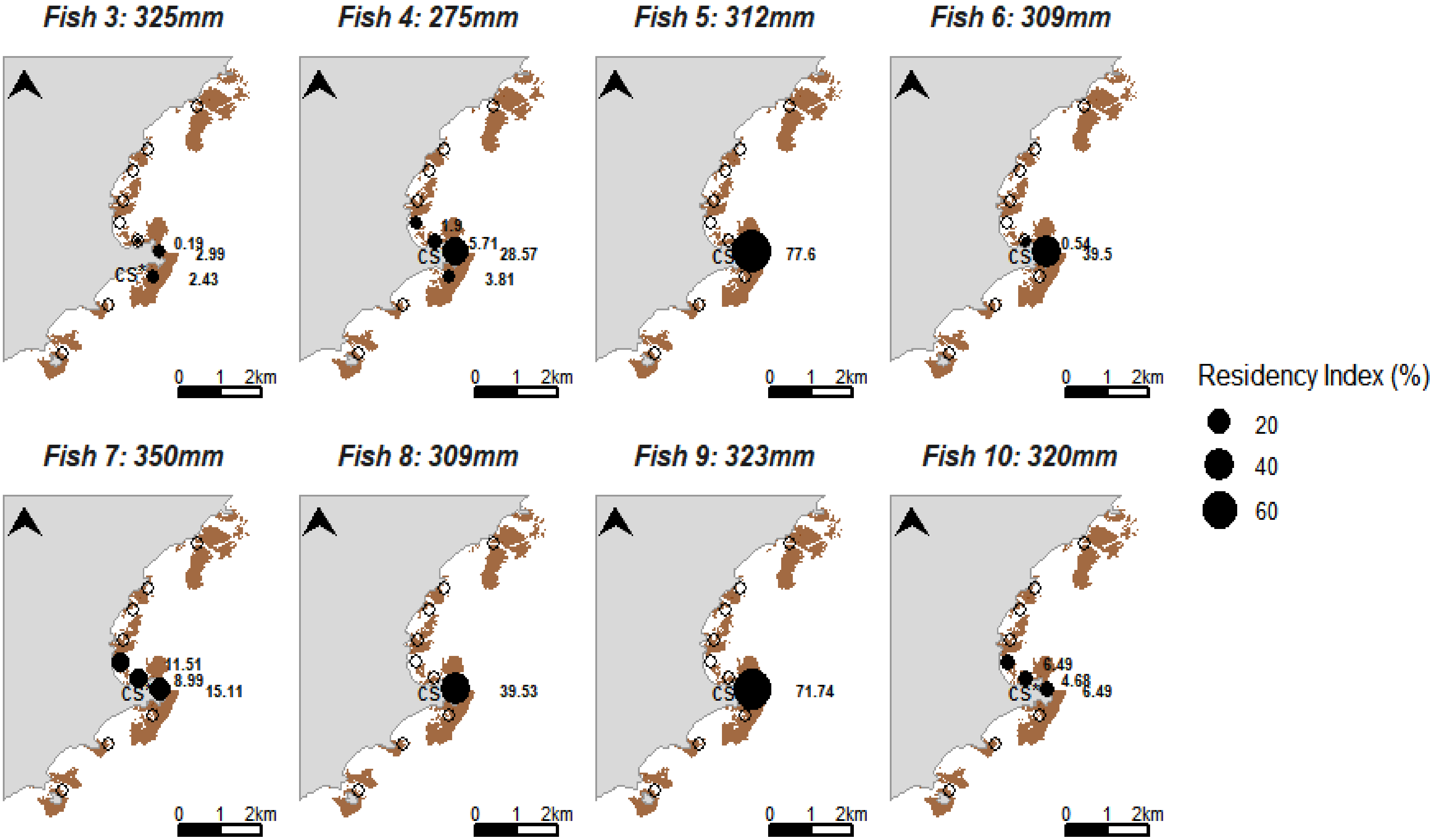

Figure 5.3 Residency index by station for 8 luderick (*Girella tricuspidata*) passively tracked in the Bendalong receiver array. The size of the filled circles and numbers illustrate the I_R values at each station. Reef patches are coloured in brown. Empty circles depict the location of acoustic receiver stations and CS* represents where each fish was captured and released.

5.3.3 Space-use

Luderick were estimated to have relatively small home ranges, with core areas (50% UD) varying between 0.25-0.59 km^2 (mean = 0.36 km^2) and extent home ranges (95% UD) from 1.15-2.21 km^2 (mean = 1.5 km^2) (Table 5.2; Fig. 5.4). Core areas were centered over the station nearest to release for half of the fish (n = 5). Fish 7 and 10 had the largest core areas that covered three stations (i.e. B5-B7) (Fig. 5.4). It was notable that while Fish 4 had a relatively small core area, it had the largest home range extent which encompassed four stations (B5-B8) (Fig. 5.4). No significant correlations were found between the 50% and 95% UDs and the length of the fish (Spearman correlation: rho = 0.4 and 0.22, $P > 0.05$)

5.3.4 Environmental variables and diel patterns

We found clear influences of environmental variables on the daily presence/absence of tagged luderick within the array, with model selection showing the greatest support (i.e. no other models within ±2 AICc) for the full model containing all fixed effects (Table 5.2). Swell variables were the most important predictors for the daily occurrence of luderick, with fish having a significantly greater chance of being absent within the array on days with higher swell heights (estimate = -0.448, SE = 0.054, $z = -8.241$, $P < 0.0001$) and swell coming from a southerly direction (estimate = -0.215, SE = 0.049, $z = -4.381$, $P < 0.0001$). Fish were also significantly more likely to be absent on days with higher tide heights (estimate = -0.139, SE = 0.05, $z = -2.739$, $P < 0.005$). Further, fish had a significantly greater chance of being present within the array in warmer sea temperatures (estimate = 0.194, SE = 0.05, $z = 3.864$, P <0.0005). However, these fixed effects only explained a small portion of the variation in the data ($R^2m = 0.07$) whereas the random effect of Fish ID accounted for 33% of the variation (i.e. $R^2c - R^2m = 0.33$; Table 5.2). Environmental variables were not found to affect the number of stations visited per week or the MLD, as the null models had the lowest AICc for these movement metrics (Table 5.2).

There was a strong non-random pattern in the detections of luderick over diel cycles (Rayleigh's z-test: $P < 0.05$), with greater detections recorded during the day than compared to night (Fig. 5.5). The initial and final detections were associated with sunrise (0600 h) and sunset (1800 h) for most fish (Fig. 5.5). Only one fish (Fish 7) was detected consistently across all hours of the day (Rayleigh's z-test: $P = 0.94$; Fig. 5.5).

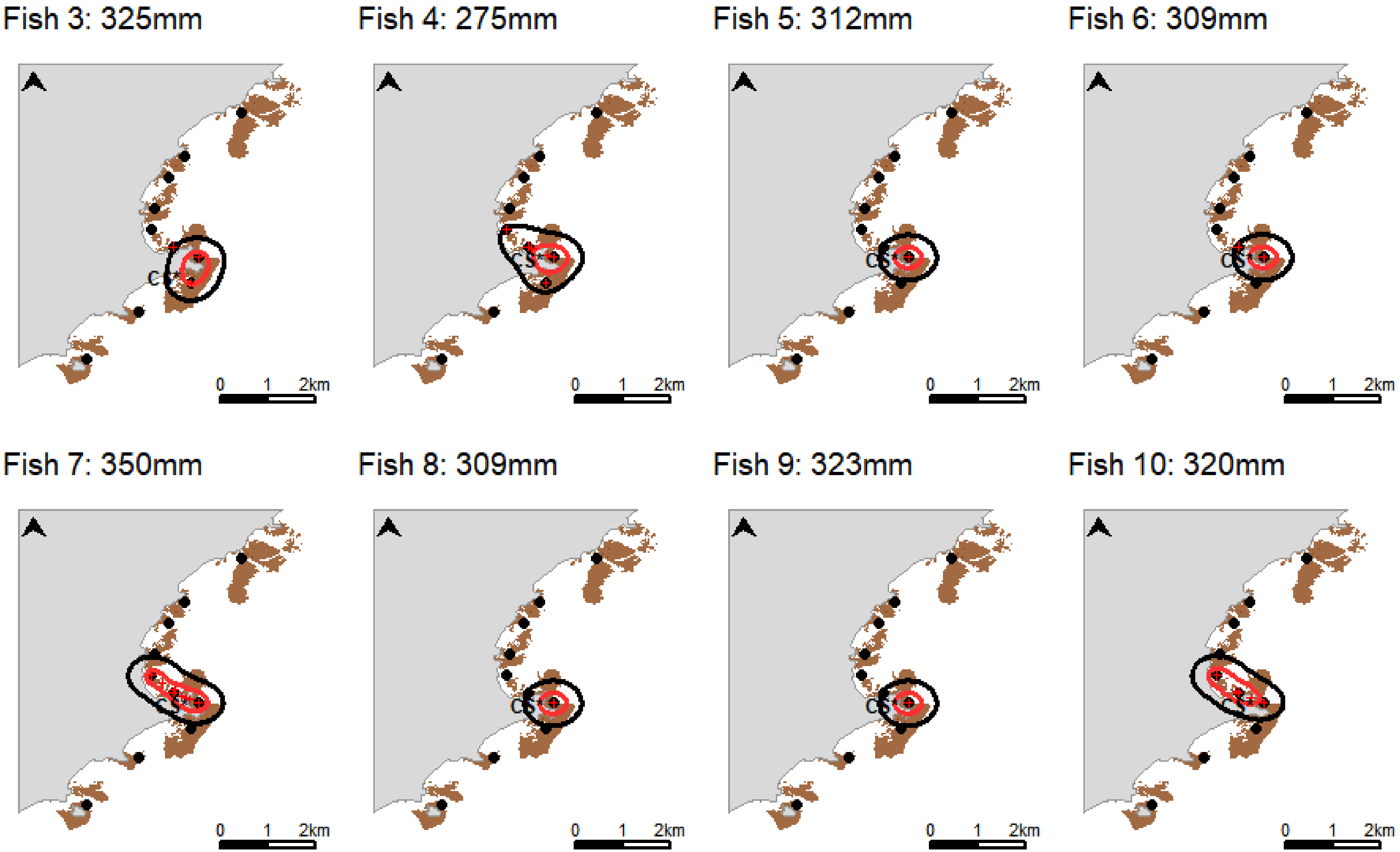

Figure 5.4 Spatial representation of the 50% and 95% utilisation distributions (UD) for 8 luderick (*Girella tricuspidata*) calculated using Brownian bridge movement models. ○ 95% UD (extent of home range); ○ 50% UD (core home range); + Centres of activity (COA) estimates, CS* capture site, ● station locations.

Table 5.2 Top three candidate models based on AICc for the Generalized Linear Mixed Models (GLMMs) exploring relationships between the daily presence/absence of fish, weekly number of stations visited and minimum linear dispersal. * denotes model with a zero-inflated negative binomial distribution. R^2m represents the marginal R^2 and R^2c is the conditional R^2. All models include fish ID as a random effect.

Response	Model(s)	AICc	ΔAICc	R^2m	R^2c
Daily presence/absence	**~ Swell height + Swell direction + Sea temperature + Tide**	**2855.2**	**0**	**0.07**	**0.40**
	~ Swell height + Swell direction + Sea temperature	2861.3	6.08	0.06	0.40
	~ Swell height + Swell direction + Tide	2867.7	12.55	0.06	0.38
Number of stations visited per week	**Null model**	**780.6**	**0**	**-**	**0.02**
	~ Swell height	782.6	2	0	0.02
	~ Swell direction	782.6	2	0	0.02
Minimum Linear Dispersal *	**Null model**	**1132.6**	**0**	**-**	**0.69**
	~ Tide	1133.6	1	0	0.69
	~ Swell direction	1133.9	1.3	0	0.69

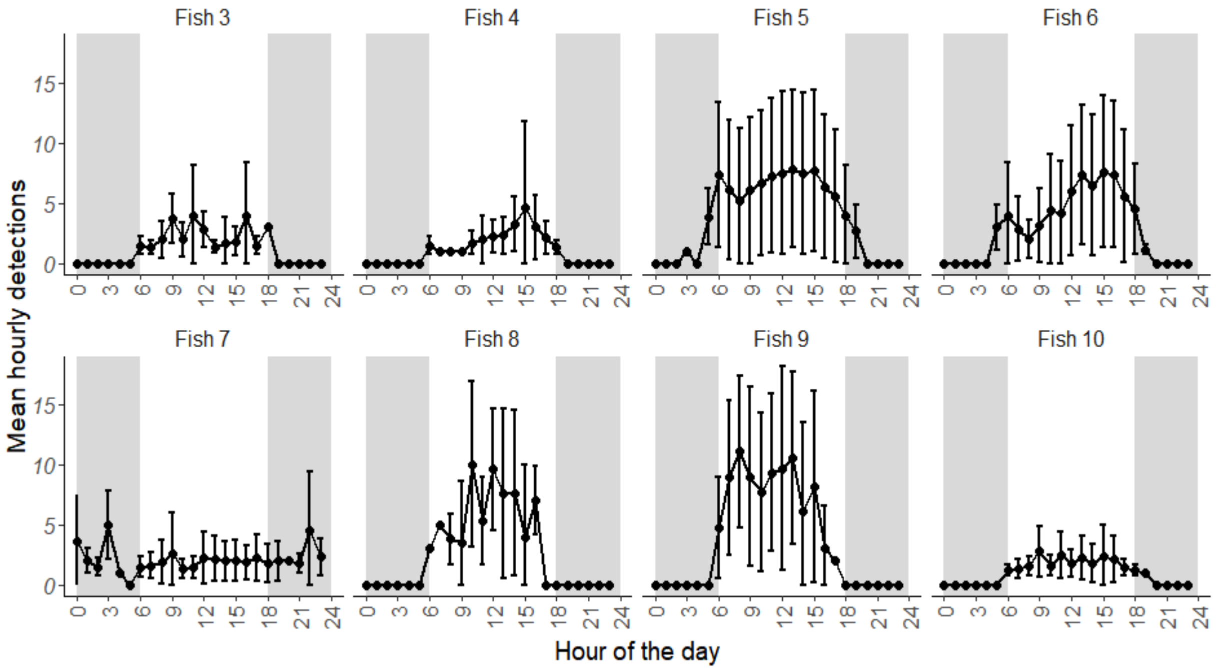

Figure 5.5 The mean number of detections for each hour of the day for 8 tagged luderick (*Girella tricuspidata*) within the Bendalong array. Solid dots represent the mean hourly value and error bars are ± standard deviation. Shading illustrates nocturnal hours between 18:00 and 06:00.

5.4 Discussion

5.4.1 Generalities in luderick movement

As predicted, the site-attachment, residency and diurnal activity patterns observed in this study are strikingly similar to the movements reported for luderick within a coastal embayment (Ferguson et al. 2013; Ferguson et al. 2016) yet differ from the highly mobile fish acoustically tracked in estuaries (Cadiou, 2016). For instance, Ferguson et al. (2016) reported similar movements for luderick across several locations in Jervis Bay with individuals having small home ranges and remaining on capture reefs between 43 to 96% of days over an eleven-month period. Luderick in Jervis Bay also commonly moved to adjacent reefs before returning to release locations, however, these inter-reef movements were more frequent and occurred across broader scales (i.e. up to 10 km) than those observed in the current study. In contrast, previous research tracking luderick in

NSW estuaries reported that individuals were highly mobile, performing large downstream migrations (up to 30 km) or egressing from the estuaries to move along the open coast (Cadiou, 2016). These large-scale movements in estuaries were in response to high flow conditions and low salinity associated with periods of heavy rainfall. We therefore contend that there are generalities in the movement behaviour of luderick on reefs in coastal systems, where fish exhibit higher residency and site-attachment in comparison to estuaries due to greater oceanic inputs and much more stable physico-chemical conditions.

The high residency and small home ranges observed for luderick on coastal reefs are also comparable to those of other temperate reef-associated fishes (Afonso et al. 2008; Harasti et al. 2015; Lee et al. 2015; Stocks et al. 2015; Aspillaga et al. 2016; Lowry et al. 2017). These restricted movements across a small area suggest that small sections of reef provide sufficient resources and that individuals have a degree of habitat familiarity. Such habitat familiarity would correspond with fitness advantages by increasing the success of predator evasion and foraging efficiency (Brown, 2001; Warburton, 2003; Forrester and Steele, 2004). Furthermore, it is also possible that fish exhibited residency to capture reefs because they contained a greater amount of food. For example, luderick have been reported to preferentially select reefs that contain a high coverage of *Ulva* spp. (Ferguson et al. 2015), however more research is required to determine whether the home ranges of luderick correlate to algal coverage and grazing rates on the open coast.

5.4.2 Relationships between movement and environmental conditions

During large swells, which are predominantly caused by storms and come from a southerly direction in NSW, luderick were more likely to appear absent from the array. Contrary to predictions, there was no evidence of fish in the current study moving to adjacent reefs that were on more sheltered areas of coastline in large swells. While this could be due to waves reducing the detection range of receivers (Kessel et al. 2014; Stocks et al. 2014), reef-associated fish have also been reported to move to deeper waters or sheltered sections of reef in periods of high swell (Stocks et al. 2015; Aspillaga et al. 2016; Bacheler et al. 2019; Matley et al. 2019). For example, *Girella elevata*, a closely related species to luderick that also inhabit shallow temperate rocky reefs in NSW have been reported to move to deeper reefs to shelter from stochastic periods of high swell and wind (Stocks et al. 2015). We therefore suggest that individuals may have sought refuge in deeper waters or sections of reef that offered less turbulent conditions as this would minimise the energetic costs associated with swimming in high energy flows (Roche et al. 2014). While Ferguson et al. (2013) did not examine the influence of environmental conditions on luderick movements, reefs in a sheltered coastal embayment are rarely exposed to large swells. This may be one reason why the residency indices from the coastal embayment were higher than those observed in the high-energy reef patches from the current study.

Several other environmental factors also correlated to the presence of luderick within the array. Fish were absent during periods of higher tides, which is likely due to increased access to the intertidal zone where luderick feed on algae such as *Ulva* spp. (Ralston and Horn, 1986; Kingsford, 2002). Furthermore, tagged fish were found to have a greater likelihood of being present within the array (and assumed to be more active) on days with warmer sea temperatures. While luderick can remain active across a range of temperatures, the optimal temperature for the species activity has been estimated at 19.3°C (±1.3 SE) (Payne et al. 2016). Previous tracking research has reported that luderick in estuaries were more active in warmer conditions (up to 23.1°C) (Cadiou, 2016). In the current study, there was little daily variation in sea temperature as the study area is dominated by oceanic conditions. However, sea temperature varied considerably between seasons, ranging from ~14°C in cooler months (Aug-Sept) to ~25°C in warmer months (Jan-March). Therefore, the relationship between activity and temperature likely reflects seasonal changes to luderick movement patterns, rather than daily changes.

Luderick were detected far more frequently during the daytime than at night, which may be associated with diurnal activity patterns where fish seek food and shelter. This is under the assumption that greater detections in the daytime are associated with increased activity, not decreased detection ranges of receivers that are commonly observed at night in some systems (Kessel et al. 2014; Swadling et al. 2020). Similar diel patterns in movements have been reported in luderick (Ferguson et al. 2013) and other Girellids (Stocks et al. 2015). For instance, Ferguson et al. (2013) observed that luderick have smaller home ranges at night and seek refuge behind the edges of reefs which would block acoustic signals reaching receivers positioned on reefs. While it was beyond the scope of this study to quantify the fine-scale movement patterns of tagged fish (using active tracking or a positioning system), our findings suggest luderick on coastal reefs exhibit this nocturnal behaviour and it is a common predator avoidance strategy employed by many reef-associated fish worldwide (Jorgensen et al. 2006; Claisse et al. 2011; Harasti et al. 2015; Honda et al. 2016). Higher activity of herbivorous fish during daylight hours may also be associated with it being easier to visually locate algae (Ralston and Horn, 1986). Furthermore, diel feeding may be an optimal foraging strategy as the nutritional content of algae is greatest in the daytime, particularly the afternoon (Taborsky and Limberger, 1980; Zemke-White et al. 2002; Raubenheimer et al. 2005).

5.4.3 Technical considerations

There are several possible reasons why many fish had extended or permanent absences from the array before the end of the study period. Firstly, luderick have been suggested to exhibit partial migration with a proportion of the population migrating large distances northward to spawn (Gray et al. 2012; Curley et al. 2013; Cadiou, 2016). It is possible that some departures from the array were associated with fish spawning, as the final detections occurred during the predicted spawning period of the species in the study area (i.e. October to February; Gray et al. 2012). However, there was no evidence of fish leaving the study area (no detections on the northern or southern receivers) and no detections on other coastal or estuarine arrays along the NSW coastline. While the receiver array was designed to cover most rocky reefs in the study area, this was not always possible as many reefs had rocky outcrops or shallow sections which would impede acoustic signals. It is possible that fish used these shallow reefs or even deeper offshore areas when migrating out of the array and were not detected. Moreover, it is likely that luderick regularly used sections of reef with poor receiver coverage as this explains why many fish were absent for periods of days to months before suddenly reappearing again. In this circumstance, our residency indices would have been underestimated and this may have also resulted in the lower residency observed in this study when compared to Ferguson et al. (2013). Natural mortality or fishing related mortality may have led to the deaths of fish during the study and therefore early absences (Klinard and Matley, 2020). The study area is a popular fishing destination, and some of our tagged fish may have been captured. Although the fate of some of the tagged fish remains unclear, this study represents only 589-days of the 900-day battery life of the transmitters (i.e. 65%) so they may be detected on receivers in the future.

5.4.4 Management Implications

The movement of fish is central to the design of effective conservation and management strategies (Kramer and Chapman, 1999; Grüss et al. 2011; Crossin et al. 2017). For example, the protection afforded by Marine Protected Areas (MPAs) to fish populations is dependent on the scale of individuals daily movements and the amount of time they spend outside of reserves (Kramer and

Chapman, 1999). If reserves are not sufficiently large enough to encompass the home range of fish, then they can be susceptible to fishing pressure when moving in areas outside of the reserves (Kramer and Chapman, 1999; Pittman et al. 2014; Green et al. 2015). It remains challenging to design MPAs that are effective for multiple species with varying home-range sizes, particularly given the limited data on fish movements. Therefore, it is important to improve our understanding on the movement patterns of many targeted fish species and form generalities. Information on the movement of luderick is particularly important for MPA design as the species is harvested in fisheries and may be vulnerable to local depletion due to restricted movement patterns, the species longevity (> 26 years) and late maturation (> 4 years) (Gray et al. 2012). Given the general high residency and site-attachment on reefs and the fact that restricted movements would mean only a small proportion of fish would cross reserve boundaries, we suggest that appropriately sized and positioned spatial management units could be a useful tool to conserve luderick populations in both coastal embayment's and reefs along the open coast. Indeed, this notion is supported by observations of the species being larger and more abundant within no-take zones in comparison to fished areas in a Marine Park within a coastal embayment (Ferguson et al. 2016). Overall, these findings highlight the importance of considering the spatial context of fish when developing generalities in movement patterns. Gaining such generalities will greatly assist designing effective conservation strategies across a range of environmental systems. The challenge for future research, however, will be to explore the movement patterns for numerous species in different environmental contexts. This information is essential to better inform resource managers and allow them to confidently design management strategies aimed at conserving multiple species.

5.5 References

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Chapter 6: General Discussion

Seascape ecology is an emerging field investigating the ecological consequences of spatial heterogeneity in the marine environment (Grober-Dunsmore et al. 2009, Boström et al. 2011, Pittman 2018). A preeminent concept in seascape ecology is that patch types are not independent from one another and are connected by the movement of organisms and matter. The connectivity of marine fishes across the seascape operates over multiple spatiotemporal scales and is thought to be a key process underpinning the structure of assemblages. For example, numerous reef-associated fish worldwide recruit to inshore vegetated patch types (e.g. seagrasses or mangroves) and once a certain age or size class is reached, disperse to adult populations on coastal reefs (Pittman and McAlpine 2003, Sambrook et al. 2019). However, the movements of reef-associated fish connecting habitats at various life-stages remains poorly quantified, with current understanding being largely conceptual and inferred from observational studies. This is particularly true for the movement of juvenile fish within nursery areas and the spatial scale of ontogenetic habitat shifts. Detailed evaluation of seascape connectivity at various life-stages will improve scientific understanding on species-habitat relationships, the drivers of species distributions and the structure and dynamics of populations. This information is vital to the design of effective management strategies that ensure the maintenance of biological diversity and ecosystem services.

I sought to address several key knowledge gaps on seascape connectivity and fish movements by adopting various contemporary techniques in the temperate seascapes of south-eastern Australia. First, I used an observational approach to investigate the spatial scale of connectivity between estuarine nursery areas and coastal rocky reefs, and the implications of this connectivity on the effect of "no-take" marine reserves. I did this by comparing changes in the abundance and size-structure of three targeted reef-associated fish species with varying life-history traits (*Chrysophrys auratus*, *Pseudocaranx georgianus* and *Nemadatylus douglasii*) using Baited Remote Underwater Video Systems (BRUVS) deployed on reefs across > 400 km of coastline and two Marine Parks (**Chapter 2**). As such an observational approach infers movement, I then use acoustic telemetry to track both juvenile and adult fish to provide a more detailed and direct understanding on their movement patterns and seascape connectivity. Before doing so, I undertook a novel acoustic range test in seagrass patches where the detection range of receivers and the performance of a Vemco Positioning System was compared when acoustic tags were positioned within and above the seagrass canopy (**Chapter 3**). This information was collected to inform the analyses and interpretation of data in **Chapter 4**, where I acoustically tracked juveniles of two targeted species (*Acanthopagrus australis* and *Girella tricuspidata*) within nursery areas and attempted to quantify the spatiotemporal scales over which they move to reef habitats. Finally, I explored the movement of adult *G. tricuspidata* on wave dominated reefs along the open coastline to assess whether the species show any generalities in movement patterns between seascapes with differing environmental conditions (**Chapter 5**).

6.1 Seascape connectivity of temperate fishes

A key finding of my research was the consistent movement of fish from nursery areas to rocky reefs habitats across small spatial scales (100’s m to km’s), with these movements occurring in greater numbers to nearby reefs compared to those further afield. I demonstrated this through inference by assessing changes in size and abundance patterns, or directly using acoustic telemetry. Size and abundance data collected using BRUVS across a temperate bioregion (Batemans Marine Bioregion) indicated that one of the most important species for fisheries in Australia and New Zealand, *C. auratus* (pink snapper), was smaller and more abundant on coastal reefs close to estuaries (**Chapter 2**). Given that *C. auratus* is known to use estuaries as juveniles (Ferrell and Sumpton 1997, Gillanders 2002), these findings were consistent with an ontogenetic habitat shift and suggested juveniles are supplied to coastal reefs across a spatial scale of 8.5 kilometres. Previous studies have reported strong linkages between estuaries and coastal reefs for *C. auratus* (Gillanders 2002, Fowler et al. 2005, Hamer et al. 2005, Hamer et al. 2011, Rees et al. 2021), however they have been unable to quantify the scales that juveniles disperse. For instance, Rees et al. (2021) recently found that juvenile *C. auratus* were more likely to be present on patch reefs near large estuaries in the Sydney Region. However, Rees et al. (2021) explored the presence-absence of categorical size-classes (i.e. juvenile < 25 cm or adult > 32 cm) and did not provide estimates on the scale of connectivity between estuaries and reefs. Through utilising body length data and estuarine proximity as continuous variables, I was able to model the spatial distribution of size-classes along the open coast in relation to estuaries and determine the spatial scale that the species perform ontogenetic habitat shifts. Such an approach has rarely been done to quantify connectivity (but see Galaiduk et al. 2017), with most research simply binning size-class data for fishes. My findings highlight that using size data as a continuous variable may provide a more realistic representation of ecological processes and a better understanding on the scales of connectivity (Galaiduk et al. 2017). Small-scale connectivity was also revealed using the more detailed approach of acoustic telemetry in **Chapter 4**, where juveniles of two harvested fishes, *G. tricuspidata* (luderick) and *A. australis* (yellowfin bream) were found to move more frequently between seagrass and directly adjacent reefs. Overall, my findings align with previous literature reporting that numerous species around the globe disperse from nursery areas to reefs over small spatial scales (100's m to km's), and that this connectivity can influence the distribution of fishes (Mumby et al. 2004, Dorenbosch et al. 2005, Grober-Dunsmore et al. 2007, Berkström et al. 2012, Olds et al. 2012b, Olds et al. 2013, Nagelkerken et al. 2017, Rees et al. 2018, Swadling et al. 2019, Berkström et al. 2020).

Not only did my research demonstrate the distance over which fish connect habitats across temperate seascapes, but it also provided evidence on the temporal scale of ontogenetic habitat shifts. Unexpectedly, the movement of both juvenile *G. tricuspidata* and *A. australis* from seagrass to rocky reefs did not represent permanent dispersal (**Chapter 4**). Tagged individuals instead regularly visited reef habitats for short time periods before returning to the area of seagrass where they were released. Although these movements may simply indicate that fewer individuals of these species permanently disperse to reef populations than expected, past research has also reported similar phenomena. For instance, juveniles from a range of systems have been observed to either gradually disperse, or undertake repeated excursions, from inshore nursery areas to coastal adult habitats (Childs et al. 2008, Appeldoorn et al. 2009, Huijbers et al. 2015, Murray et al. 2018, Stamp et al. 2021). These visits outside of individuals home-ranges within nursery areas have been associated with area expansion prior to a permanent ontogenetic habitat shift (Childs et al. 2008, Murray et al. 2018). While it was not possible to determine if juvenile *C. auratus* moved in and out of estuaries using BRUVS in **Chapter 2**, it was interesting that mature adults (< 300 mm FL) were distributed evenly on reefs along the coastline, irrespective of estuarine proximity. Considering this finding, I proposed that the dispersal of the species occurs as a stepwise process, where individuals move to reefs adjacent (< 8.5 km) estuaries at 1 to 2 years of age (180-220 mm FL) and then a proportion of these animals move to reefs along the coastline as they grow. These findings from both observational data and acoustic telemetry suggest that ontogenetic habitat shifts do not happen suddenly across large spatial scales, rather they may be a gradual process where fish slowly emigrate from nursery areas to adult populations.

Assessing habitat-use and connectivity as fish move across the seascape is essential to develop a deeper understanding of fish-habitat relationships (Hitt et al. 2011, Nagelkerken et al. 2015, Pittman 2018). I observed that juvenile fish can connect multiple patch types during their routine movements, with both juvenile *G. tricuspidata* and *A. australis* moving between seagrass, creeks (containing seagrass and mangroves) and rocky reefs (**Chapter 4**). Typically, nursery areas have been defined as discrete or homogenous patch types based on whether they; i) have high densities of juveniles, ii) provide increased juvenile growth rates or survival, and iii) contribute a disproportionate number of recruits to adult populations when compared to other patch types (Beck et al. 2001, Adams et al. 2006, Dahlgren et al. 2006). There is a growing body of literature proposing that such definitions may be too simplistic, as they overlook the mobility of many fish species at juvenile life-stages and their capacity to move between patches (Sheaves et al. 2006, Nagelkerken et al. 2015, Sheaves et al. 2015, Litvin et al. 2018). The movements of juvenile fish linking multiple patch types in **Chapter 4** provides some of the first direct movement data to support the claims that the nursery role of habitats need to be refined. Specifically, these data indicate that nurseries should be defined using the "seascape nursery" approach coined by Nagelkerken et al. (2015), where the nursery areas of species are perceived as a spatially explicit seascape containing a mosaic of connected patch types. While defining discrete patches as nurseries may work for species with high juvenile abundances in one or two patch types, the seascape nursery approach is more realistic and will improve the identification and management of fish populations and critical fish habitats (Nagelkerken et al. 2015, Litvin et al. 2018, Bradley et al. 2019, Olson et al. 2019).

Both juvenile (*G. tricuspidata* and *A. australis*) and adult (*G. tricuspidata*) fish were found to exhibit site-attachment, small home-ranges and connect habitats over small spatial scales (**Chapters 4 and 5**). Adults of both species have previously been reported to demonstrate similar movement patterns (Ferguson et al. 2013, Ferguson et al. 2016, Lowry et al. 2017, Taylor et al. 2018), but this may be dependent on their environmental context. For example, adult *G. tricuspidata* tracked on reefs along the open coast (**Chapter 5**) and within a coastal embayment (Ferguson et al. 2013, Ferguson et al. 2016) both had high residency and site-attachment to reefs. However, *G. tricuspidata* tagged in several estuaries in NSW were found to move large distances downstream (up to 30 km) or leave the system entirely (Cadiou 2016).

The large-scale movements of the species in estuaries are postulated to be caused by weather events with high rainfall that cause strong flows and low salinity, forcing fish to move (Cadiou 2016). I therefore propose that the higher residency and site-attachment of *G. tricuspidata* in coastal reefs compared to estuaries is due to coastal seascapes experiencing oceanic inputs and much more stable physico-chemical conditions. These findings illustrate that seascape connectivity and fish movements may be nuanced and dependent on environmental context, highlighting the need to perform repeated studies in various systems to gain a general, predictive understanding of ecological processes.

6.2 Applying acoustic telemetry to quantify seascape connectivity

Acoustic telemetry is a valuable tool to monitor the movement of fish connecting patch types and provide novel insights for spatial ecology (Donaldson et al. 2014, Hussey et al. 2015). For instance, studies often use acoustic tracking to investigate movements linking patches for foraging, shelter, and spawning (Luo et al. 2009, Hitt et al. 2011, Marshell et al. 2011, Ferguson et al. 2013, Pittman et al. 2014, Matley et al. 2015, Taylor et al. 2018, Ebrahim et al. 2020). From a seascape ecology perspective, acoustic tracking can be adopted to explore how fish move in response to seascape patterning across multiple scales and different life-stages (Hitt et al. 2011, Pittman 2018). The application of acoustic telemetry, however, has generally been limited to adult fish or those species with large juvenile body sizes (e.g. > 30 cm; Childs et al. 2015, Taylor et al. 2017b, Murray et al. 2018, Staveley et al. 2019, Kendall et al. 2021, Stamp et al. 2021). Therefore, the movement of small juvenile fish and the scale of ontogenetic habitat shifts remains unclear, with current understanding coming mainly from observational studies inferring movement between patch types (Grober-Dunsmore et al. 2007, Appeldoorn et al. 2009, Olds et al. 2012b, Rees et al. 2018, Swadling et al. 2019). The lack of studies tracking small-bodied juvenile fishes is undoubtedly due to issues surrounding tag size, with high tag to body mass ratios (e.g. the 2% rule) reported to create adverse health and behavioural effects

(Jepsen et al. 2005, Thorstad et al. 2009). Technological advances in acoustic telemetry have led to the creation of smaller and longer lasting tags, meaning that tracking small juvenile fish (15-20 cm) is now possible and I demonstrated this in **Chapter 4**. Furthermore, there are now a suite of innovative analytical techniques to model telemetry data (e.g. network analyses) that quantify the linkages between patches (Jacoby et al. 2012, Finn et al. 2014, Jacoby and Freeman 2016, Staveley et al. 2019, Whoriskey et al. 2019). Such techniques deliver a standardised method to explore connectivity patterns with telemetry data and provide information that traditional analyses (e.g. Utilisation distributions) cannot, like identifying corridors of movements between patches (Jacoby et al. 2012, Lédée et al. 2015, Becker et al. 2016).

Although it is now possible to track the movement and connectivity of small fishes, it remains a challenge to match the size, power and battery life of tags with the configuration of acoustic receiver arrays and the cryptic behaviour of juveniles. Currently, studies wanting to quantify the movement patterns of small-bodied fish are restricted to using small tags, which inherently have lower power, shorter battery life and reduced detection ranges compared to larger tag models. For instance, I found the detection range of V7 tags to be ~ 85 m in seagrass, whereas higher powered tags (equivalent to V16 tags) were detected 250 m away (**Chapter 3**). Further difficulties may be experienced when tracking juvenile fish with cryptic behaviours, as I observed for the first time that the detection range of receivers decreased to 40 m when V7 tags were amongst seagrass fronds, and this diminished the performance of a Vemco Positioning System. Large reductions in the efficacy of acoustic telemetry due to macrophytes have since been reported in freshwater systems (Stott et al. 2021, Weinz et al. 2021). These findings highlight the importance of conducting *in situ* acoustic range tests before undertaking telemetry studies and the need to account for fish behaviour. This information will have important ramifications for configuring receiver arrays and interpreting collected data, as it is difficult to determine if the absence of detections represent the absence of fish or the poor detection range of receivers (Kessel et al. 2014).

6.3 Implications of connectivity for marine management and conservation

Marine Protected Areas (MPAs) are a spatial management strategy employed worldwide, generally aiming to conserve biodiversity and manage fisheries (Halpern 2003, Lester et al. 2009, Gaines et al. 2010, Hernandez et al. 2021). The conservation value of MPAs to fish is often questioned by various stakeholders, as there is a general belief that many species move over scales larger than the areas afforded protection by marine reserves (Kramer and Chapman 1999, Martin et al. 2016, Hilborn 2017). I provide evidence that both juveniles and adults of targeted fish species can show residency and site-attachment over a substantial time, suggesting that MPAs would provide significant protection to these fishes (**Chapter 4 and 5**). Indeed, the restricted movements of juvenile *G. tricuspidata* and *A. australis* released in a no-take marine reserve in Jervis Bay Marine Park meant that few fish (5 of 33 tagged individuals) were detected crossing into fished areas (**Chapter 4**). Furthermore, I observed a key targeted species, *C. auratus*, to be larger and more abundant inside marine reserves across two marine parks spanning a temperate bioregion (**Chapter 2**). It was notable, however, that the proximity of marine reserves to estuarine nurseries did not influence reserve effects for this species. This contradicts findings from previous literature in the tropics demonstrating that seascape connectivity can lead to increased abundances of species within reserves because these areas experience a greater inflow of recruits (Huntington et al. 2010, Olds et al. 2012a, Olds et al. 2013, Martin et al. 2015, Ortodossi et al. 2018). I propose that the limited effect between estuarine connectivity and the abundance of *C. auratus* within reserves found in **Chapter 2** was likely due to the species dispersing to adult reef patches before they reach the minimum length (i.e. 300 mm TL) required to be taken in fisheries at the study site. Overall, my findings provide support to the growing number of studies reporting the efficacy of MPAs in south-eastern Australia and around the world, either through increased fish abundance, body size or biomass (Anderson et al. 2014, Edgar et al. 2014, Kelaher et al. 2014, Friedlander et al. 2017, Harasti et al. 2018, Malcolm et al. 2018, Goetze et al. 2021, Knott et al. 2021), or the residency of fish within reserve boundaries (Lowe et al. 2003, Ferguson et al. 2013, Harasti et al. 2015, Lee et al. 2015, Aspillaga et al. 2016, Ferguson et al. 2016, Fetterplace et al. 2016, Honda et al. 2016, Lea et al. 2016).

For MPAs to effectively conserve fish populations, they must be located, sized and spaced to adequately cover the areas used by species during their daily and life-cycle movements (Kramer and Chapman 1999, Grüss et al. 2011, Crossin et al. 2017). A general "rule of thumb" when designing MPAs is to represent a portion of the different patch types in a bioregion within reserve boundaries, under the assumption that these patches contain distinct biological assemblages and act as surrogates for biodiversity (Roberts et al. 2003, Gaines et al. 2010, Saarman et al. 2013, Rees et al. 2018). However, habitat representation is a crude approach that does not consider seascape connectivity, so MPAs may not be reaching their conservation potential. Considering the post-settlement movement of fishes and how they link patches should lead to the incorporation of critical fish habitats within MPA design and improved conservation outcomes (Carr et al. 2017, Weeks 2017, Weeks et al. 2017). The lack of consideration for connectivity in MPA design (Balbar et al.2019) is almost certainly a result of the limited information on fish movements linking patches over multiple spatial and temporal scales. In this thesis, I demonstrate that targeted reef-associated fish connect patches across small-spatial scales (100's m to km's) and that this can influence the abundance and size structure of populations (**Chapter 2 and 4**). These findings highlight the need to incorporate seascape connectivity into MPA design, as simply representing patch types within reserves would likely fail to include these linkages and therefore not protect fish throughout their life-histories. Instead of MPA design focussing on habitat representation, it may be more appropriate to focus on areas where key fish habitats are close to one another, such as nursery and adult habitats. This should ensure that MPAs are designed adequately so they maintain ecological processes and ensure the ecological viability and integrity of fish populations (TFMPA 1999).

While it is valuable to recognise the importance of incorporating connectivity in management strategies, it is equally valuable to know how to practically apply this information (Carr et al. 2017, Rees, 2017). There have been a limited number of studies integrating seascape connectivity into MPA design, and these have introduced three main approaches that include; i) using algorithms derived from observational data that create a connectivity matrix and identify movements between critical habitats (Mumby 2006), ii) using network analyses to infer connectivity across the seascape for species moving over different spatial scales and identify hotspots for MPA planning and assessment (Engelhard et al. 2016, Friesen et al. 2019), and iii) incorporating important components of the seascape (e.g. areas where nursery and adult habitats are in close proximity) into spatial prioritisation using decision-support software (e.g. Marxan; Weeks, 2017). Not only are these approaches logical and transparent, but they represent cost and time effective methods to identify optimal subsets of patches that guide the design of MPAs. Adopting these approaches has been hindered by the lack of information on seascape connectivity, particularly in temperate seascapes, so MPAs worldwide continue to focus on representing a certain percentage of patch types within their boundaries. I would argue, however, that the risks of unfavourable conservation outcomes from ignoring connectivity outweigh those associated with attempting to include it, even with limited quantitative information.

The productivity and sustainability of coastal fisheries is dependent on habitats (Hayes et al. 1996, Brown et al. 2019), yet many nearshore macrophytes are under immense pressure from anthropogenic stressors and are experiencing global declines (Waycott et al. 2009, Li et al.

2018, Dunic et al. 2021). The small-scale connectivity observed in this thesis for *C. auratus* between estuaries and coastal reefs (**Chapter 2**), and juvenile *G. tricuspidata* and *A. australis* within seascape nurseries (**Chapter 4**), highlight the strong contribution of nurseries to coastal fisheries and allude to the potential consequences of this habitat loss. Specifically, the loss or degradation of nearshore macrophytes may reduce their nursery function and disrupt connectivity patterns between patches, leading to fewer recruits entering coastal fisheries and potential localised population depletion (Jordan et al. 2009, Sundblad et al. 2013, Brown et al. 2019). This is particularly concerning given that south-eastern Australia is a climate change hotspot (Hobday and Lough 2011, Hobday and Pecl 2014, Scanes et al. 2020). Predictions suggest that the region will become warmer and drier, resulting in changes to environmental flows, physico-chemical conditions, and the loss of patch types (Gillanders et al. 2011, Smale et al. 2019, Scanes et al. 2020), which could impact connectivity patterns across the seascape. This is best exemplified by the predicted changes to the morphology of estuaries, with reduced rainfall expected to cause a build-up of sand bars that close estuary mouths and prevent any fish (e.g. *C. auratus*) performing ontogenetic habitat shifts to the marine environment (Gillanders et al. 2011). Overall, my findings highlight the importance of conserving vegetated habitats, managing seascapes to maintain connectivity (e.g. artificially opening estuary mouths in future climatic scenarios) and mitigating anthropogenic stressors on habitats as this will ensure adequate recruitment and the sustainability of fisheries.

Habitat restoration is being increasingly used by management to intervene or offset human modification of seascapes, and to augment ecosystem services such as fisheries (Gilby et al. 2018a, Duarte et al. 2020). Most coastal restoration strategies have been directed at single patch types including seagrass (Paling et al. 2009, Tan et al. 2020, Ferretto et al. 2021), saltmarsh (Warren et al. 2002), mangroves (Ellison 2000, Worthington and Spalding 2018, Su et al. 2021), oyster reefs (Humphries and La Peyre 2015, Gilby et al. 2018b) or artificial reefs

(Becker et al. 2018, Folpp et al. 2020). There is a need when restoring habitats to consider their context within the seascape, as their connectivity to adjacent patches can enhance their conservation benefits (Gilby et al. 2018a, Duncan et al. 2019, Gilby et al. 2019, Pittman et al. 2021). For example, Gilby et al. (2018a) reported that of 89 coastal marine restoration projects only 13% incorporated seascape context in their design, but over half of these resulted in more diverse and larger animal populations than natural control sites. Indeed, the results of this thesis suggest that habitat restoration should consider the context and seascape connectivity, and that they could be incorporated within seascapes to build effective fish nurseries and promote ecosystem services such as fisheries production.

6.4 Future Directions

In this thesis, I have improved current understanding of seascape connectivity to better inform management practices, and I wish to highlight several promising directions for future research. Firstly, there is a disparity in the global distribution of studies examining the importance of seascape patterning for fish distributions and ecological processes, with most research originating from tropical biomes (Dorenbosch et al. 2005, Dorenbosch et al. 2006, Grober-Dunsmore et al. 2007, Berkström et al. 2012, Olds et al. 2012b, Nagelkerken et al. 2017, Martin et al. 2018, Berkström et al. 2020). My research revealed similar patterns to those reported within tropical seascapes, with connectivity occurring over small spatial scales (100’s m to km’s) and influencing fish populations. This adds to the growing body of literature suggesting that there are generalities in the response of fish to seascape patterns between tropical and temperate marine systems (Staveley et al. 2016, Perry et al. 2018, Rees et al. 2018, Swadling et al. 2019). Furthermore, I build on this previous research by using contemporary techniques to explore seascape connectivity, such as acoustic telemetry or stereo-BRUVs to collect continuous body length data. Future research should adopt these techniques to gain a more quantitative understanding of connectivity and test for generalities in the patterns I observed within other temperate seascapes.

Another valuable avenue for future work is to investigate the role of connectivity in more remote seascapes, such as deep-water patch types. I demonstrate the scale of connectivity and its importance for the distribution of *C. auratus* on reefs at similar depth contours (15-36 m) along the coastline, but this does not consider the dispersal of the species to populations on deeper reefs (e.g. > 100 m depth). The paucity of data on the seascape ecology of deep-water fishes is caused by the difficulty of sampling these assemblages and the limited maps of deep patch types. Recent developments in sampling techniques (e.g. stereo-BRUVs, ROVs) that can be used at great depths and an increased availability of high-resolution maps of deep-water seascapes (e.g. swath acoustic surveys), has resulted in recent assessments of the spatial distribution of deep-water fishes (Sih et al. 2017, Williams et al. 2019, Wellington et al. 2021). The need to understand the seascape connectivity of deep-water fish assemblages is heightened by the fact that they may have previously acted as natural refuges from fishing or other disturbances (Morato et al. 2006), yet they are now experiencing greater fishing pressure due to improved equipment (e.g. sounders or electric fishing reels) and many species are vulnerable to depletion as they have late maturation, slow growth and low fecundity (Devine et al. 2006).

There have been calls to consider seascape connectivity when defining nursery areas, but this is largely founded from observational studies inferring juvenile fish movements across a mosaic of patch types (Sheaves et al. 2006, Nagelkerken et al. 2015, Litvin et al. 2018). Using acoustic telemetry, I provided some of the first data that directly demonstrates small-bodied juvenile fish regularly connect patch types within seascapes during their routine movements. These findings provide considerable support for the nursery-role concept to shift its focus from defining nursery areas as discrete patch types and move towards them being perceived as "seascape nurseries" that contain an interconnected mosaic of patches (Nagelkerken et al.

2015). Quantifying the movements of juvenile fish within seascape nurseries in both tropical and temperate systems is worthy of greater research as this will help inform resource managers to identify key fish habitats and their contribution to fisheries (Nagelkerken et al. 2015, Litvin et al. 2018). Furthermore, it is notable that I did not observe individuals permanently dispersing to reefs. Future research using acoustic telemetry to track juvenile fish is therefore necessary to better elucidate the spatial and temporal scales of ontogenetic habitat shifts.

I encourage future research that acoustically track fish movements to use tags with sensors and consider the limitations of the technology. Acoustic tags can now be equipped with various sensors that measure parameters such as acceleration, temperature, predation and depth (Hussey et al. 2015, Lennox et al. 2017, Taylor et al. 2017a, Brownscombe et al. 2019, Weinz et al. 2020). Combining the location of individuals with these parameters provides remarkable insights into both the behavioural and spatial ecology of fishes. For instance, behavioural states (e.g. foraging, chasing or predator avoidance) can be determined using triaxial accelerometers and overlayed on seascape maps to produce “activity seascapes”, which illustrate the locations/times where different activities occur and how energy expenditure varies across the seascape (Brownscombe et al. 2017, Pittman 2018, Papastamatiou et al. 2018, Meese and Lowe 2020). Whilst tags with sensors provide additional data on fish movements, they do come at increased financial costs and were outside of the scope of this thesis. I also demonstrate that studies must consider the efficacy of acoustic telemetry in their study system and how it is affected by fish behaviour, as I observed dramatic decreases in the detection range of receivers when tags were ensconced amongst seagrass fronds (**Chapter 3**). Considering the importance of this information for the interpretation and analyses of movement data, future research should explore possible ways to overcome reduced detections ranges when fish are amongst seagrass fronds. Furthermore, the effects of fish behaviour in other patch types on the performance of acoustic telemetry should be quantified, such as fish sheltering under reef ledges or burying themselves in soft sediments. Finally, it is envisaged that if advances in technology progress at the current rate, small tags possessing high power and long battery life will soon be available (Lennox et al. 2017). When this occurs, I highly recommend future studies adopt this technology to provide a more sophisticated understanding on juvenile fish movements and their dispersal across the seascape.

Research determining whether connectivity improves the efficacy of management practices and the ecological consequences of seascape change (e.g. habitat loss or fragmentation) have recently been highlighted as key research priorities in seascape ecology (Pittman et al. 2021). Previous studies in tropical seascapes suggest incorporating connected patches into no-take marine reserves can enhance conservation outcomes (Nagelkerken et al. 2012, Olds et al. 2012a, Olds et al. 2013, Martin et al. 2015, Olds et al. 2016). It was unexpected that I did not find any evidence in **Chapter 2** of the connectivity between estuaries and reefs improving reserve effects along the open coast. Future research is required to better understand the importance of connectivity for the performance of marine reserves in temperate seascapes. Furthermore, seascapes containing degraded or lost habitats are associated with decreased fish abundance and biomass (Hughes et al. 2002, Deegan and Buchsbaum 2005, Brown et al. 2019). However, many questions remain about the effects of this habitat loss on connectivity and fish assemblages in adjacent patch types, such as "does the loss of nursery habitat correlate with decreased fish abundances in surrounding waters" or "are there thresholds in the amount of habitat degradation or loss that must be exceeded to disrupt connectivity patterns?". Questions such as these are challenging to answer, but future research should endeavour to explore them given the large losses of coastal habitats occurring globally and the predicted human impacts on biodiversity in the future (Waycott et al. 2009, Hobday and Lough 2011, Li et al. 2018, Smale et al. 2019, Dunic et al. 2021).

6.5 Concluding remarks

My research represents an important step in improving current understanding on connectivity in temperate seascapes and its implications for marine management. I demonstrate the spatial scale that juvenile fish disperse from estuarine nursery areas to coastal reefs across a temperate marine bioregion and how this influences the abundance and size structure of fish populations. I provide the first evidence on the performance of acoustic telemetry in seagrass and decreased detection ranges of receivers and VPS efficacy when tags are amongst seagrass fronds; a pattern that has since been shown to occur in freshwater systems containing macrophytes (Stott et al. 2021, Weinz et al. 2021). I also used acoustic telemetry to gain more detailed information on the movement and connectivity patterns of both juvenile and adult fishes which provided important insights for the definition of nursery areas, the potential spatiotemporal scale of ontogenetic habitat shifts, the generality of movements in varying environmental contexts and the efficacy of MPAs. In a global context, this thesis represents a valuable contribution to the field of seascape ecology, by improving current understanding on seascape connectivity in temperate seascapes and how it can be integrated into management and conservation strategies to ensure the maintenance of biodiversity and ecosystem services into the future.

6.6 References

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Appendix 1

Supporting Information for

Chapter 2: Seascape connectivity of temperate fishes between estuarine nursery areas and open coastal reefs

This includes:

Table A1.1

Figures A1.1 – A1.6

Table A1.1. All models within ±2 AICc values of the top model for all fish variables. The most parsimonious (i.e. “best” models) are in bold

Response		**edf**	**wAICc**	**AICc**	**R^2**	**Best model (s)**
Species abundance	***Chrysophrys auratus***	**38.06**	**1**	**3690.23**	**0.28**	**Distance to estuary + Status*Year**
	Nemadactylus douglasii	**25.93**	**0.23**	**608.84**	**0.16**	**Distance to estuary + Estuary area (20 km)**
		25.89	**0.2**	**609.12**	**0.16**	**Distance to estuary + Status**
		26.88	0.1	610.49	0.16	Distance to estuary + Status + Depth
		26.88	0.1	610.53	0.16	Distance to estuary + Estuary area (20 km) + Depth
		26.88	0.1	610.53	0.16	Distance to estuary + Estuary area (20 km) + Status
	Pseudocaranx georgianus	**33.78**	**0.21**	**2445.61**	**0.11**	**Estuary area (10 km) + Year**
		34.54	0.121	2446.71	0.11	Estuary area (10 km) + Year + Status
		34.76	0.079	2447.55	0.11	Estuary area (10 km) + Year + Depth
Species lengths	***Chrysophrys auratus***	**8**	**0.75**	**3867.85**	**0.14**	**Distance to estuary + Status*Year**
	Nemadactylus douglasii	**8**	**0.45**	**3466.7**	**0.06**	**Distance to estuary + Status*Year**
		8	**0.26**	**3467.81**	**0.05**	**Estuary area (10 km) + Status*Year**
	Pseudocaranx georgianus	**8**	**0.3**	**3178.35**	**0.0001**	**Depth + Status*Year**
		8	**0.27**	**3178.56**	**0.002**	**Distance to estuary + Status*Year**
		8	**0.23**	**3178.83**	**0.0001**	**Estuary area (10 km) + Status*Year**

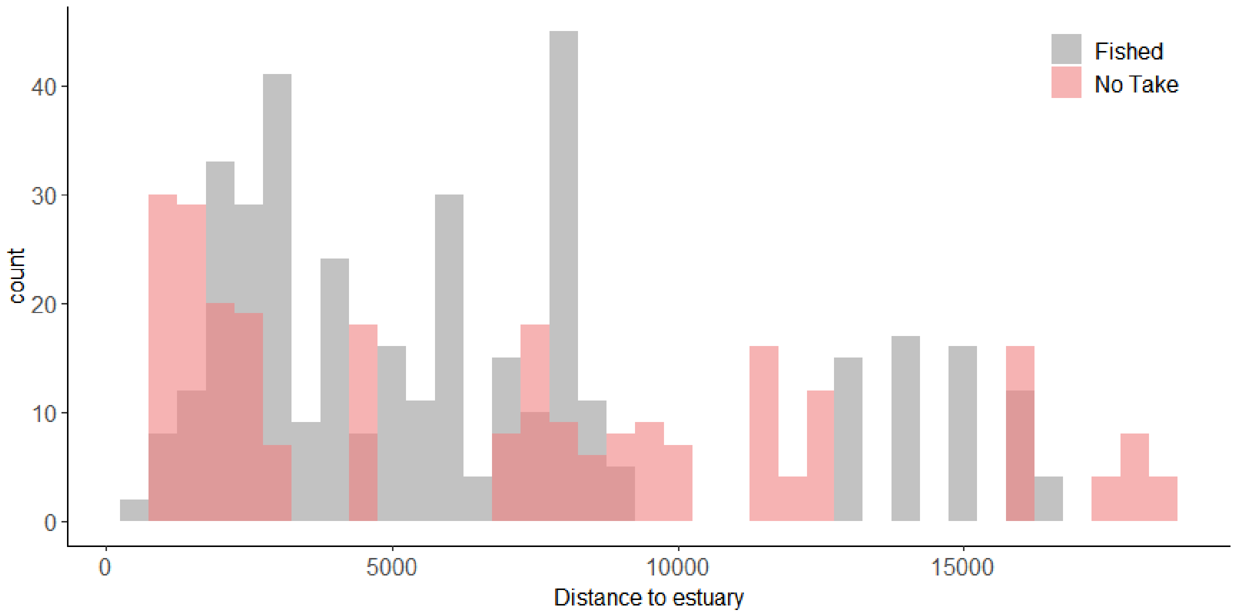


Figure A1.1. Frequency distributions of sites located in fished areas (grey bars) and no-take marine reserves (red bars) with distance to the nearest estuary (m).

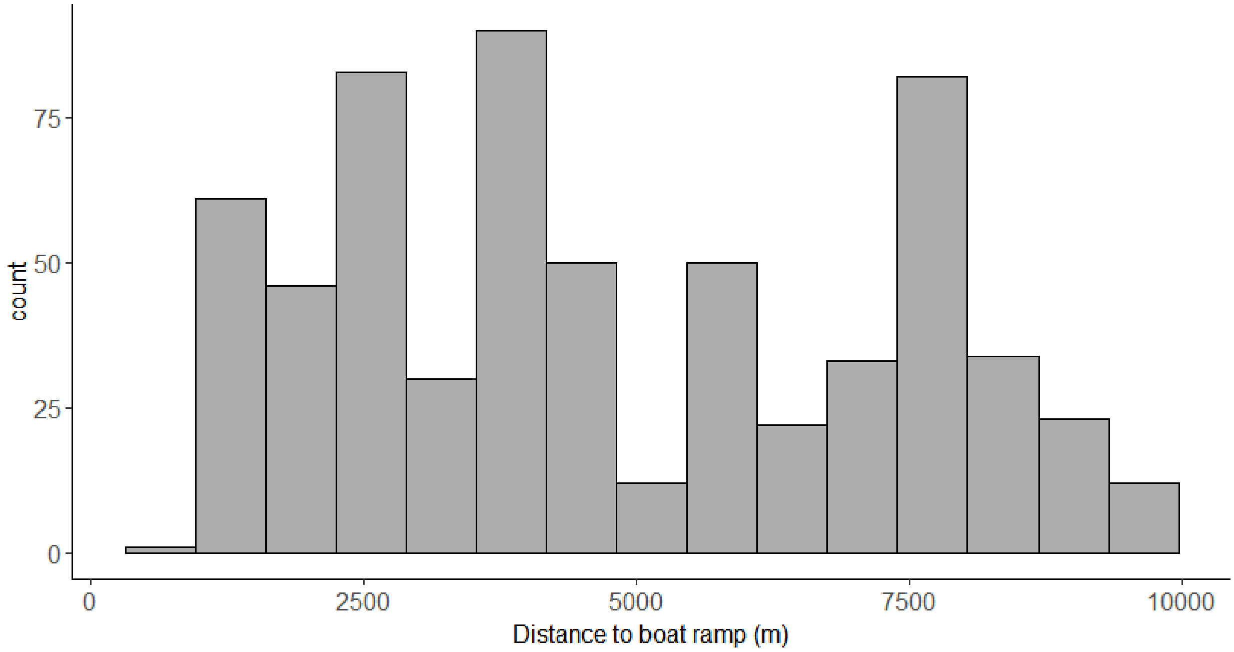


Figure A1.2: The frequency of sample sites at various distances from boat ramps (m). The location of boat ramps was accessed from transport NSW (https://opendata.transport.nsw.gov.au/dataset/nsw-boating-ramps). We only included ramps that were in "fair" or "good" condition and those located in open estuaries classified by Roy et al. (2001).

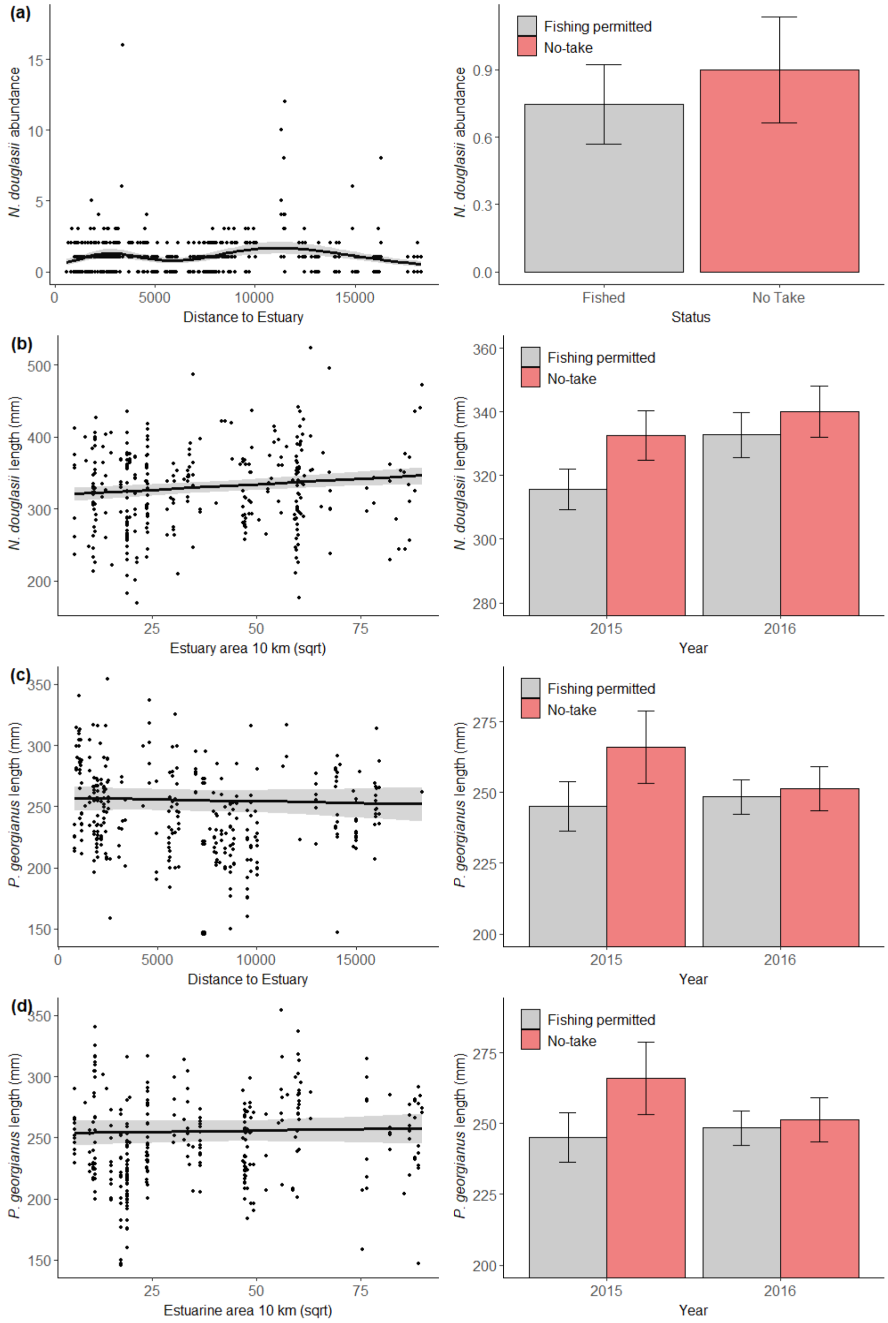


Figure A1.3. Relationships for the alternate parsimonious model(s) (Table 2.1) between explanatory variables and (a) *Nemadactylus douglasii* (grey morwong) abundance, (b) *Nemadactylus douglasii* length (mm), and (c) – (d) *Pseudocaranx georgianus* (silver trevally) length (mm). Fitted GAMM prediction curves (solid line) are included. Ribbons and error bars represent ± standard error. Grey bars = fished areas and red bars = ‘no-take’ marine reserves (i.e. NTMR).

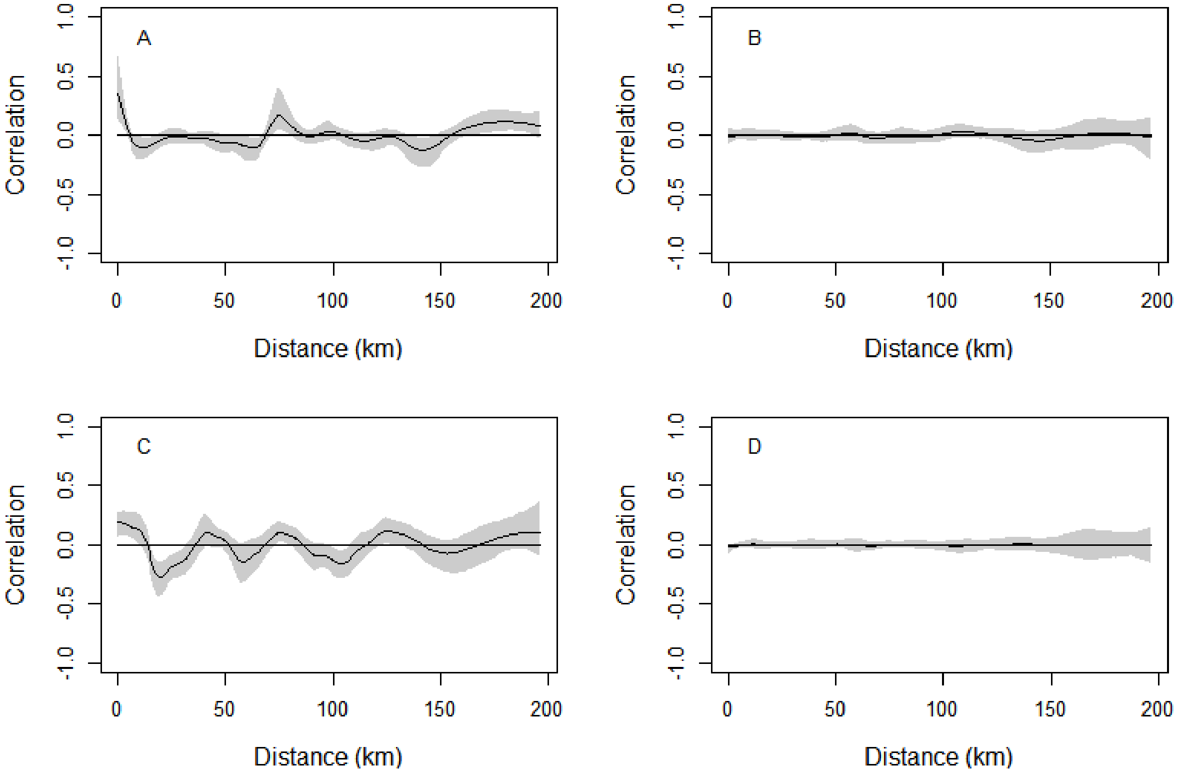


Figure A1.4. Spline correlograms examining spatial autocorrelation for analyses of the abundance and length of *Chrysophrys auratus* (pink snapper). Shaded areas depict 95% pointwise bootstrap confidence intervals in (A) raw *C. auratus* abundance data, (B) GAMM residuals for the model containing *C. auratus* abundance and the distance to estuary, status*year and site (C) raw *C. auratus* length data, and (D) GAMM residuals for the model containing *C. auratus* length and the distance to estuary, status*year and site.

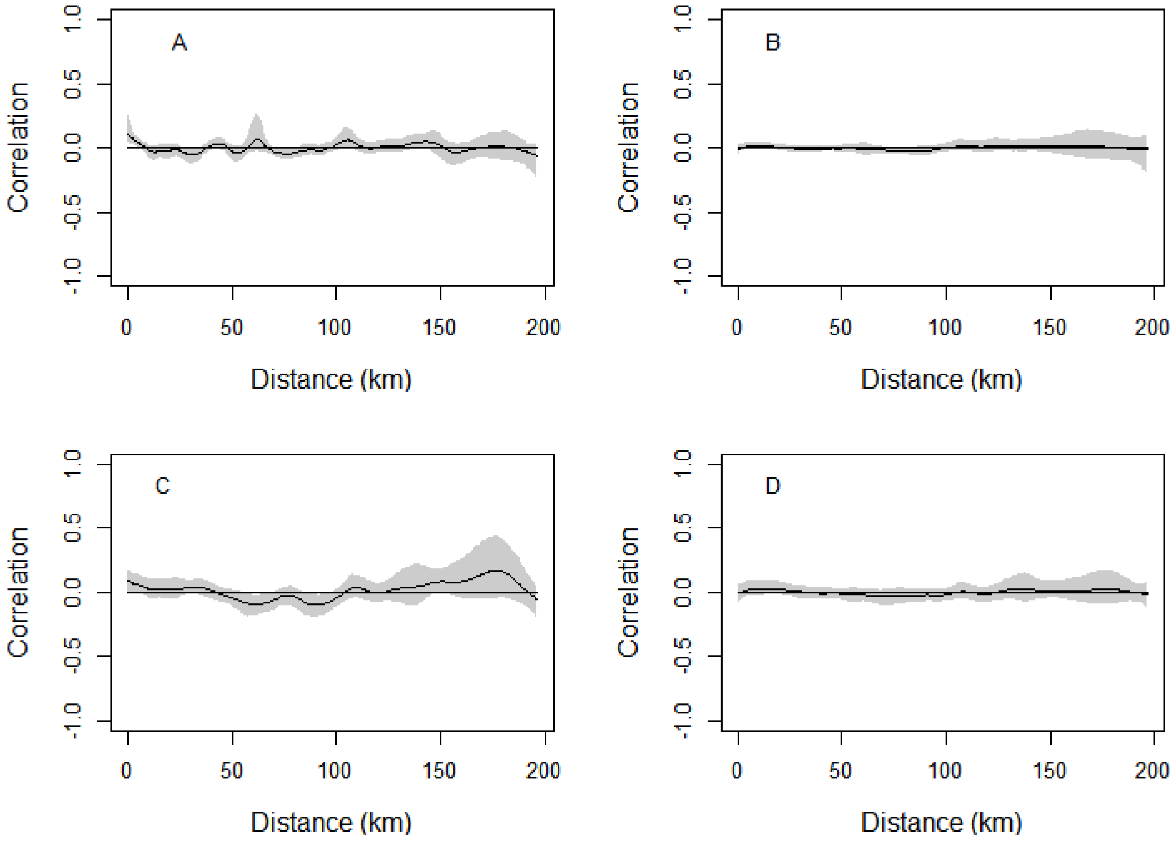


Figure A1.5. Spline correlograms examining spatial autocorrelation for analyses of the abundance and length of *Nemadactylus douglasii* (grey morwong). Shaded areas depict 95% pointwise bootstrap confidence intervals in (A) raw *N. douglasii* abundance data, (B) GAMM residuals for the model containing *N. douglasii* abundance and the distance to open estuary, estuary area 20 km and site, (C) raw *N. douglasii* length data, and (D) GAMM residuals for the model containing *N. douglasii* length and the distance to estuary, status*year and site.

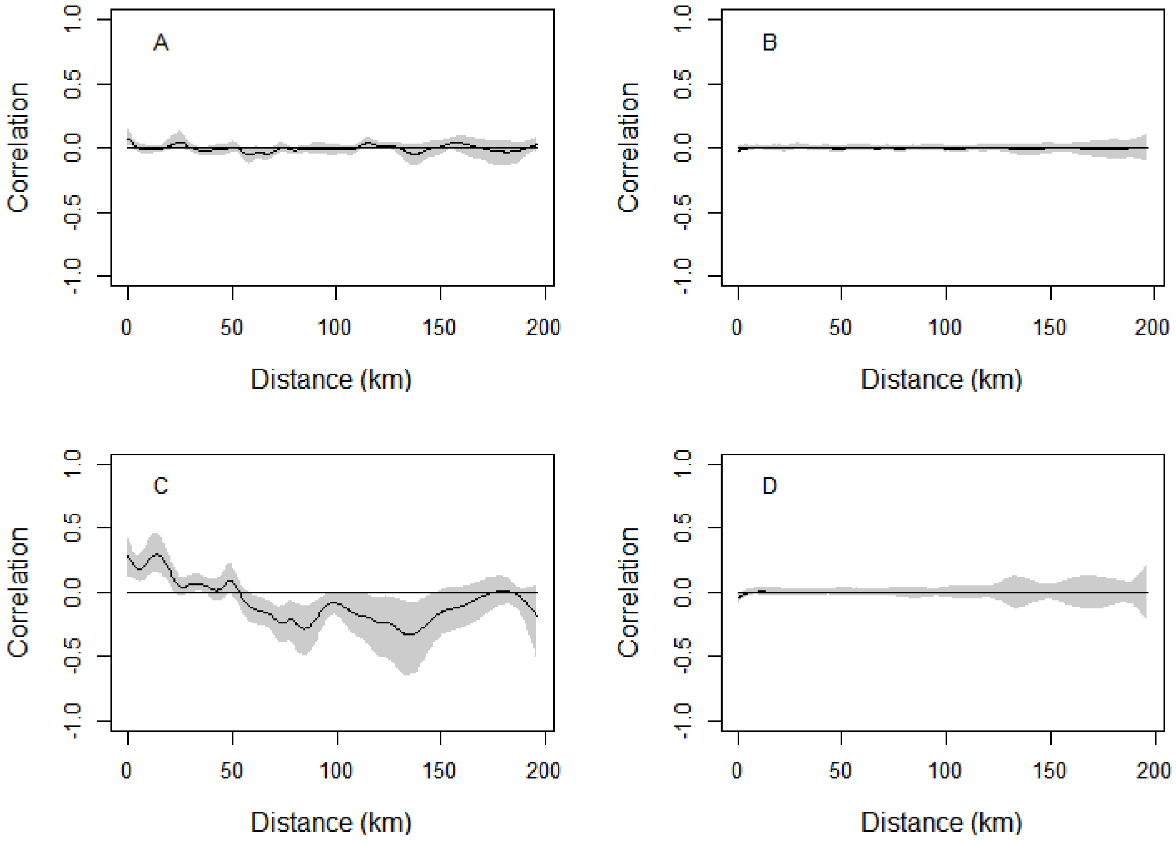


Figure A1.6. Spline correlograms examining spatial autocorrelation for analyses of the abundance and length of *Pseudocaranx georgianus* (silver trevally). Shaded areas depict 95% pointwise bootstrap confidence intervals in (A) raw *P. georgianus* abundance data, (B) GAMM residuals for the model containing *P. georgianus* abundance and mangrove area 20km and site, (C) raw *P. georgianus* length data, and (D) GAMM residuals for the model containing *P. georgianus* length and depth, status*year and site.

Appendix 2

Supporting Information for

Chapter 4: Consequences of juvenile fish movement and seascape connectivity: Does the concept of nursery habitats need a rethink?

This includes:

Table A2.1

Figures A2.1 – A2.5

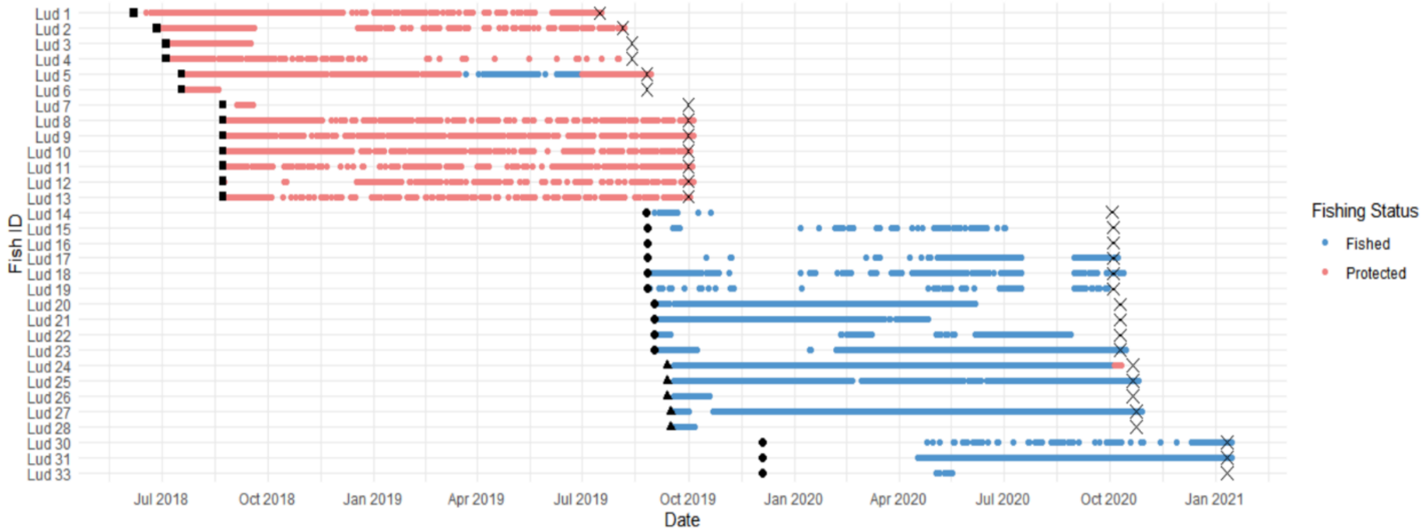
Table A2.1: Summary information for tagged luderick (*Girella tricuspidata*) and yellowfin bream (*Acanthopagrus australis*) tracked in Jervis Bay Marine Park. Please refer to Fig. 4.1 for a map of release locations.

Fish ID	**Species**	**Release location**	**Date Released**	**Fork Length (mm)**	**Days Detected**	**Days at Liberty**	**Total no. Detections**	**No. stations visited**	**50% UD (km^2)**	**95% UD (km^2)**
Lud 1	Luderick	Hare Bay	07-06-18	199	252	406	3182	8	0.072543	0.926207
Lud 2	Luderick	Hare Bay	27-06-18	146	184	407	1363	8	0.07181	1.28306
Lud 3	Luderick	Hare Bay	05-07-18	150	66	73	762	3	0.035905	0.367845
Lud 4	Luderick	Hare Bay	05-07-18	186	113	393	954	5	0.036638	0.398621
Lud 5	Luderick	Hare Bay	18-07-18	194	323	409	4975	10	0.05056	1.011207
Lud 6	Luderick	Hare Bay	18-07-18	216	33	32	1608	6	0.105517	0.415474
Lud 7	Luderick	Hare Bay	23-08-18	172	13	26	193	3	0.020517	0.094526
Lud 8	Luderick	Hare Bay	23-08-18	184	223	408	1674	5	0.023448	0.153879
Lud 9	Luderick	Hare Bay	23-08-18	184	298	408	2183	10	0.108448	1.027327
Lud 10	Luderick	Hare Bay	23-08-18	193	254	406	2462	7	0.030776	0.36125
Lud 11	Luderick	Hare Bay	23-08-18	171	207	408	1218	8	0.047629	0.759138
Lud 12	Luderick	Hare Bay	23-08-18	179	138	408	756	6	0.258664	1.206853
Lud 13	Luderick	Hare Bay	23-08-18	182	182	406	1299	6	0.039569	0.363448
Lud 14	Luderick	Woollamia	26-08-19	145	15	55	115	1	0.018655	0.090168
Lud 15	Luderick	Woollamia	27-08-19	181	52	311	331	3	0.018655	0.096386
Lud 16	Luderick	Woollamia	27-08-19	172	1	1	1	-	NA	NA
Lud 17	Luderick	Woollamia	27-08-19	152	105	409	1243	1	0.018655	0.093277
Lud 18	Luderick	Woollamia	27-08-19	192	163	413	2956	3	0.021765	0.12126
Lud 19	Luderick	Woollamia	27-08-19	162	72	400	750	1	0.018655	0.093277
Lud 20	Luderick	Myola	02-09-19	170	270	278	21689	3	0.018655	0.096386
Lud 21	Luderick	Myola	02-09-19	173	230	238	36302	3	0.024874	0.214538
Lud 22	Luderick	Myola	02-09-19	171	131	361	18587	3	0.055966	0.292269
Lud 23	Luderick	Myola	02-09-19	200	292	409	39363	3	0.04042	0.261176
Lud 24	Luderick	Moona Crk	13-09-19	185	130	395	86906	9	0.043529	0.37
Lud 25	Luderick	Moona Crk	13-09-19	160	386	409	113998	2	0.04042	0.183445
Lud 26	Luderick	Moona Crk	13-09-19	162	30	6	5994	1	0.018655	0.090168
Lud 27	Luderick	Moona Crk	16-09-19	164	387	409	145700	1	0.018655	0.090168
Lud 28	Luderick	Moona Crk	16-09-19	175	17	20	5723	1	0.018655	0.090168
Lud 29	Luderick	Myola	04-12-19	212	NA	NA	NA	-	NA	NA
Lud 30	Luderick	Myola	04-12-19	213	86	409	246	1	0.018655	0.090168

Lud 31	Luderick	Myola	04-12-19	231	275	409	86496	1	0.018655	0.090168
Lud 32	Luderick	Myola	04-12-19	199	NA	NA	NA	-	NA	NA
Lud 33	Luderick	Myola	04-12-19	162	11	165	718	1	0.018655	0.090168
Bream 1	Yellowfin Bream	Carama nlet	13-09-19	155	130	407	1790	5	0.841527	5.626273
Bream 2	Yellowfin Bream	Carama Inlet	13-09-19	145	8	7	719		NA	NA
Bream 3	Yellowfin Bream	Carama Inlet	25-10-19	210	171	407	1963	9	0.379377	2.638393
Bream 4	Yellowfin Bream	Carama Inlet	25-10-19	195	83	367	622	6	0.142554	3.398297
Bream 5	Yellowfin Bream	Carama Inlet	25-10-19	168	160	401	3768	4	0.587459	7.620876
Bream 6	Yellowfin Bream	Hare Bay	13-11-19	225	210	260	3358	6	0.072426	1.924475
Bream 7	Yellowfin Bream	Hare Bay	13-11-18	213	291	409	2892	7	0.157499	1.532453
Bream 8	Yellowfin Bream	Hare Bay	14-11-19	166	366	409	5078	3	0.028741	0.147152
Bream 9	Yellowfin Bream	Hare Bay	27-11-19	217	405	409	24050	5	0.022993	0.112663
Bream 10	Yellowfin Bream	Carama Inlet	11-12-19	284	264	409	7880	10	0.266713	3.927125
Bream 11	Yellowfin Bream	Hare Bay	17-12-19	240	389	409	10699	3	0.034489	0.198885
Bream 12	Yellowfin Bream	Hare Bay	17-12-19	281	146	408	1827	9	0.105766	4.393874
Bream 13	Yellowfin Bream	Hare Bay	17-12-19	298	191	403	4307	4	0.135656	2.331443
Bream 14	Yellowfin Bream	Hare Bay	17-12-19	280	399	409	35711	5	0.02989	0.541474
Bream 15	Yellowfin Bream	Hare Bay	17-12-19	284	52	155	420	4	0.304651	1.72559
Bream 16	Yellowfin Bream	Carama Inlet	11-02-20	221	130	282	1716	1	0.044835	0.551821
Bream 17	Yellowfin Bream	Carama Inlet	11-02-20	161	135	243	2595	3	0.117262	1.135831
Bream 18	Yellowfin Bream	Carama Inlet	11-02-20	158	250	407	7752	6	0.097718	1.377253
Bream 19	Yellowfin Bream	Carama Inlet	11-02-20	239	234	409	2147	7	0.078175	2.03369
Bream 20	Yellowfin Bream	Carama Inlet	11-02-20	189	209	408	3511	3	0.173594	1.870443

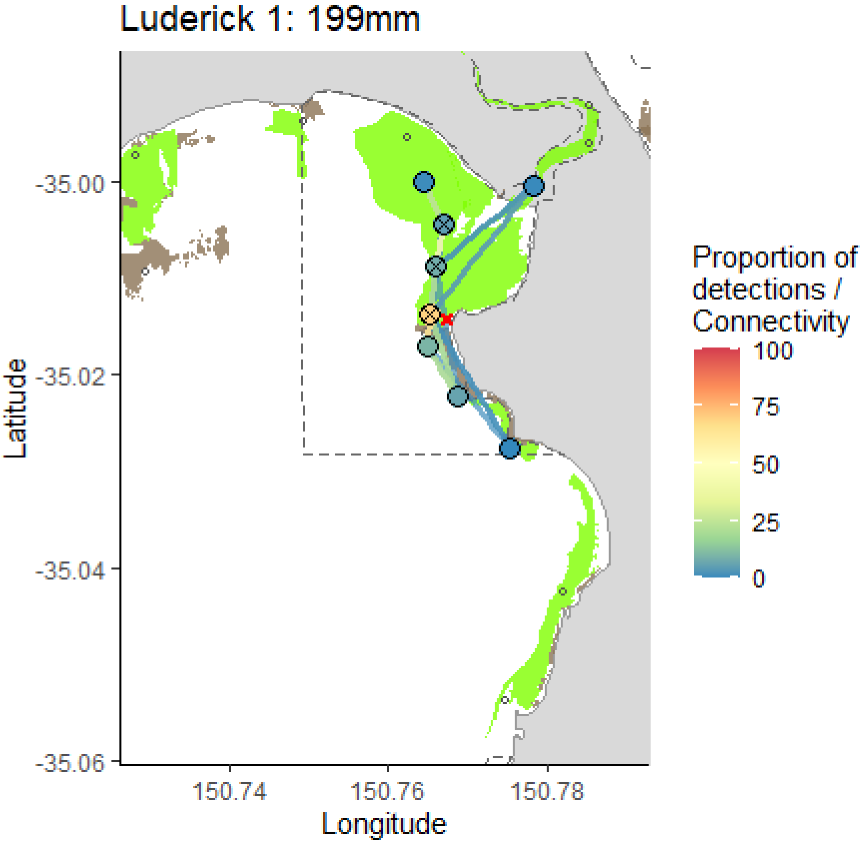
Figure A2.1: Detection history over the study period for tagged a) luderick and b) yellowfin bream at receivers in NTMR (i.e. protected – pink) or fished areas (blue). Tag deployment is represented by the black dots, with shape referring to release locations; black squares = Hare Bay, black circles = Curramebene Creek, black triangles = Moona Moona Creek, black diamonds = Carama Inlet. Crosses indicate the anticipated date which battery failure occurred.

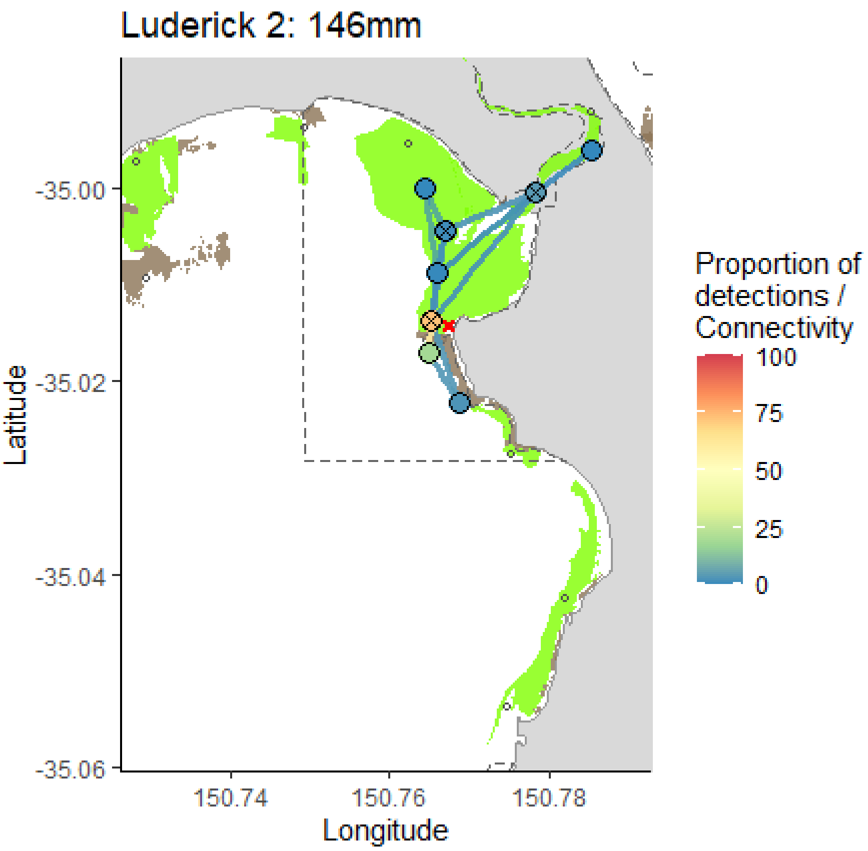
(a) Luderick



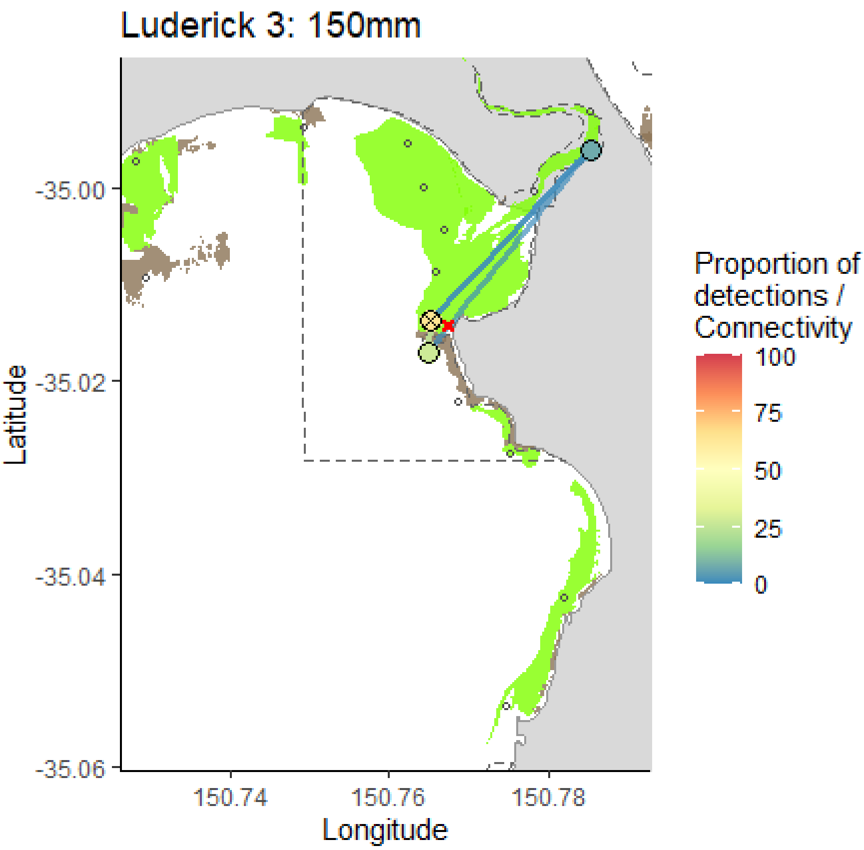
(b) Yellowfin Bream

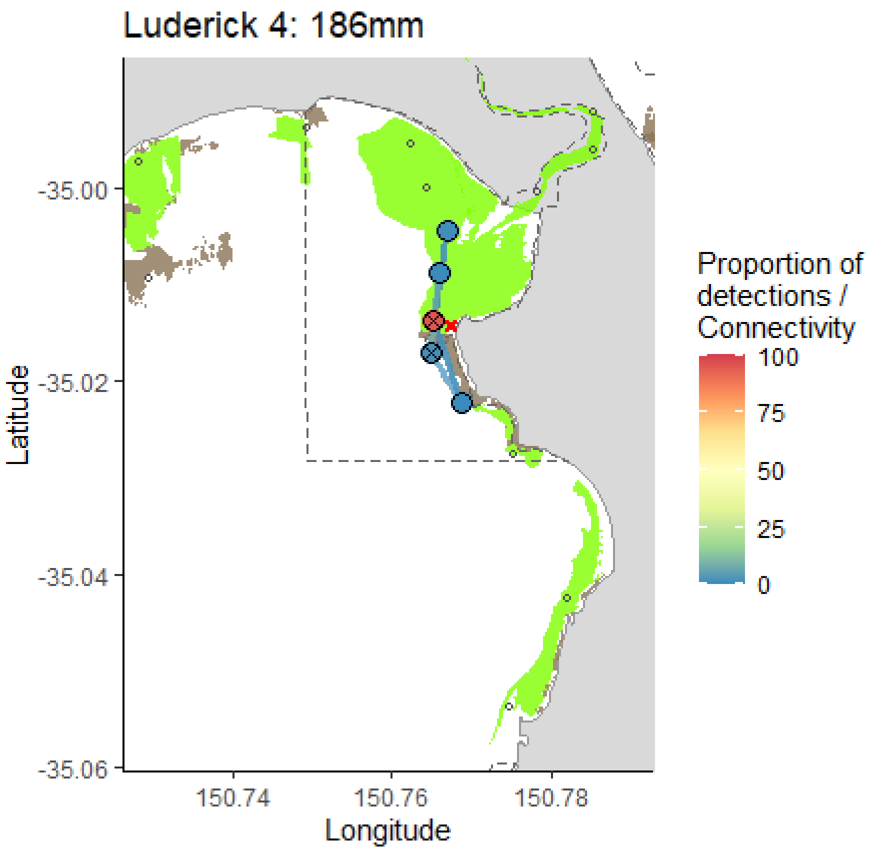
Figure A2.2: Individual movement networks for all thirteen luderick released in Hare Bay. The colour of nodes illustrates the proportion of detections at a given receiver and edge colour shows the number of movements between receivers. Empty black circles show the non-visited receivers. The red 'x's are the release location of fish and black crosses on receivers represent core-use receivers. Dashed areas illustrate no-take marine reserves.

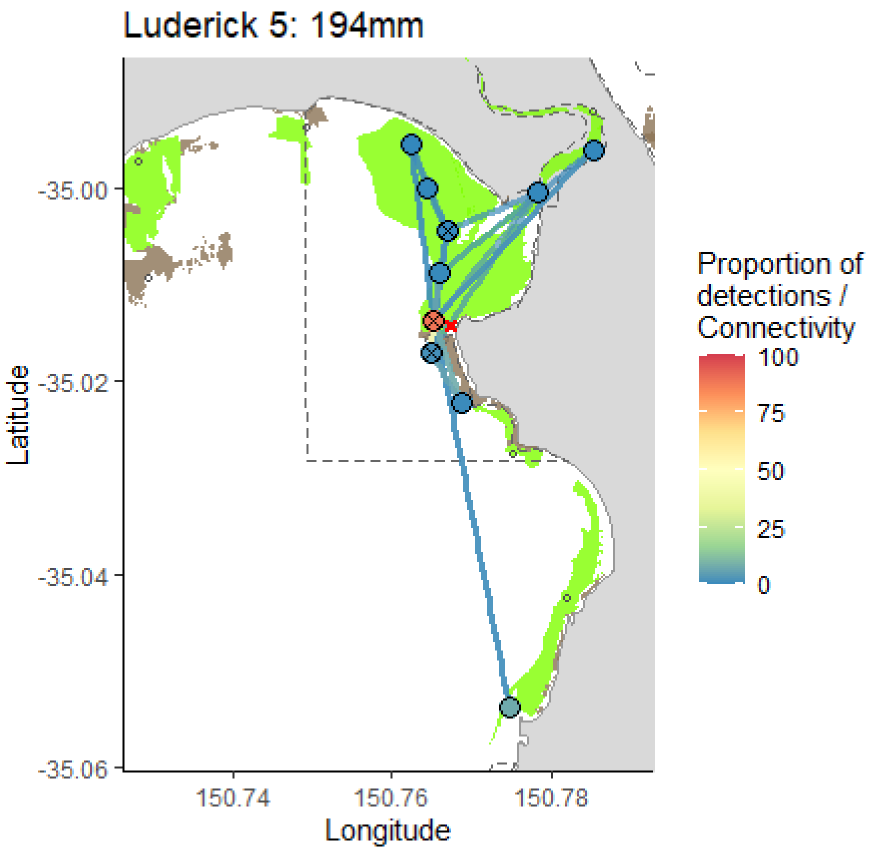


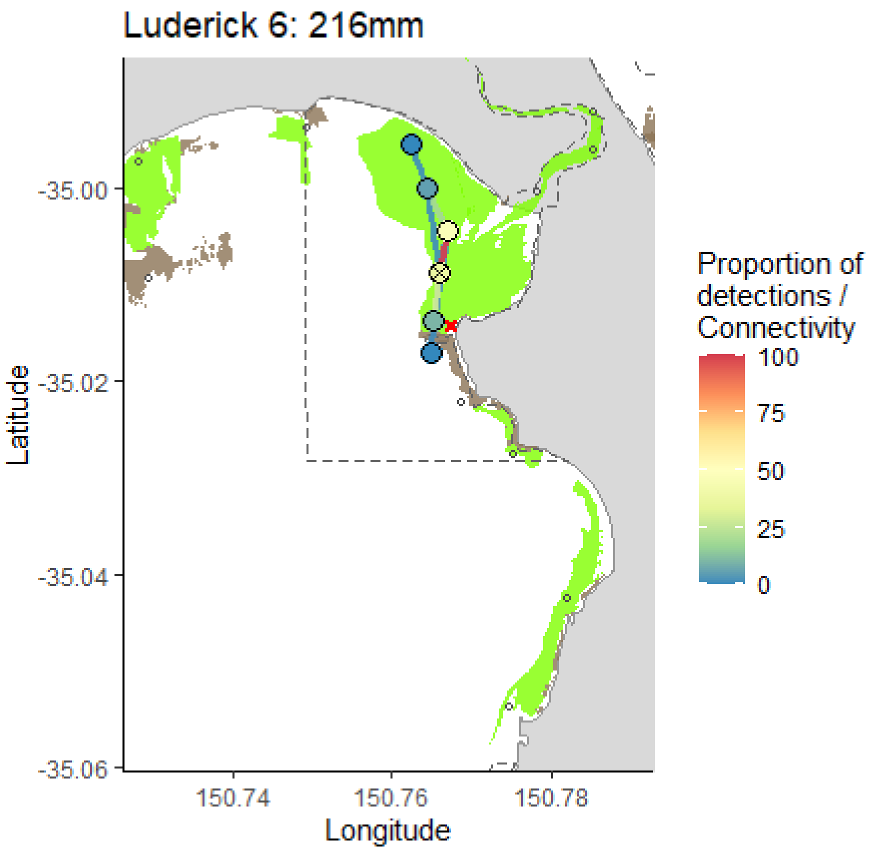

Luderick 2: 146mm
Latitude
-35.00
-35.02
-35.04
-35.06
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0

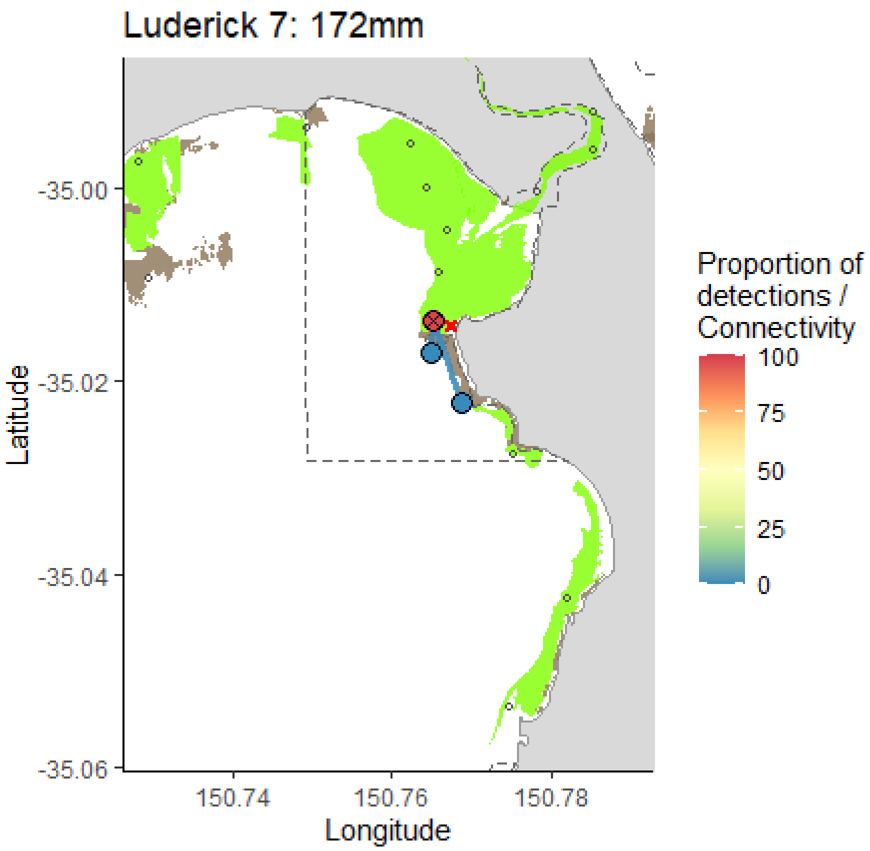
Luderick 3: 150mm

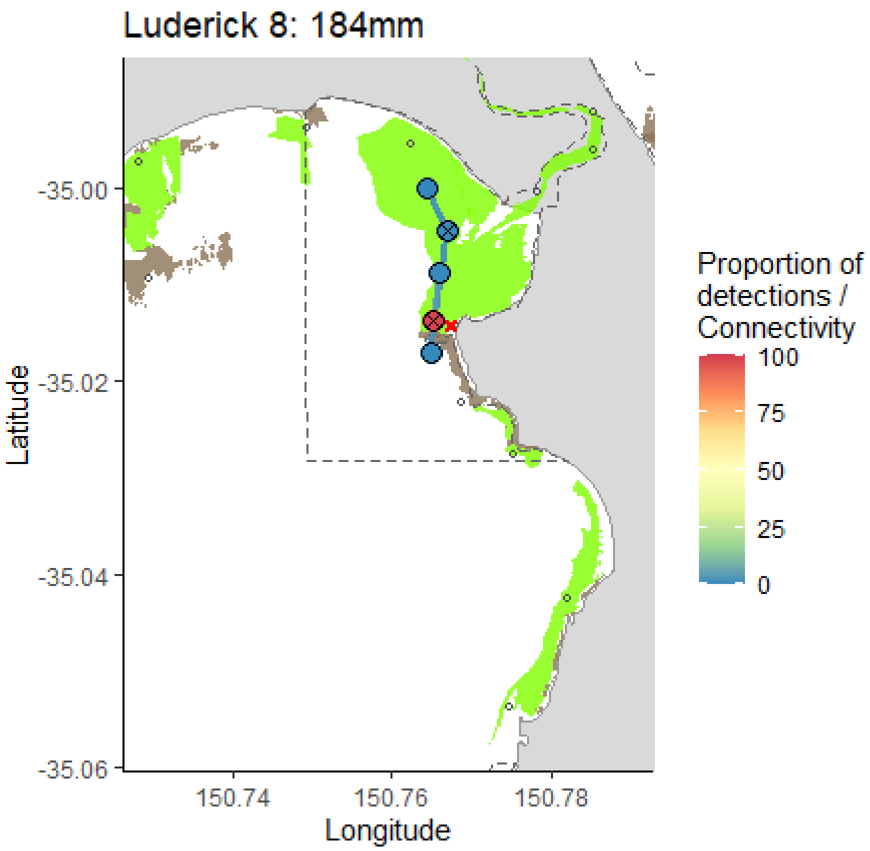


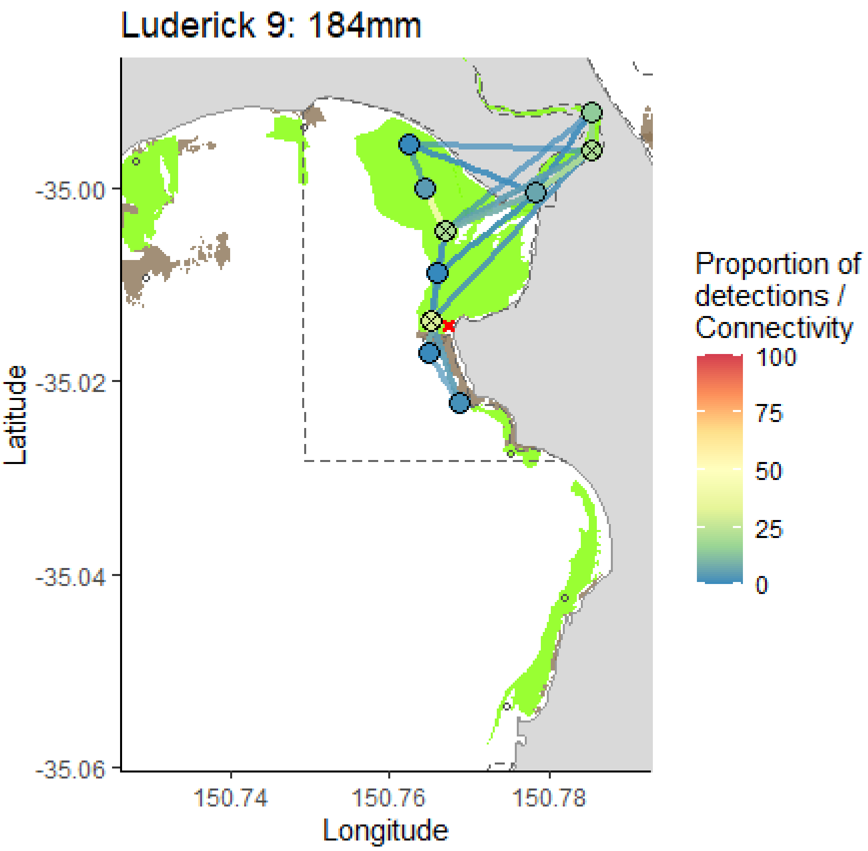

Luderick 4: 186mm
Latitude
-35.00
-35.02
-35.04
-35.06
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0

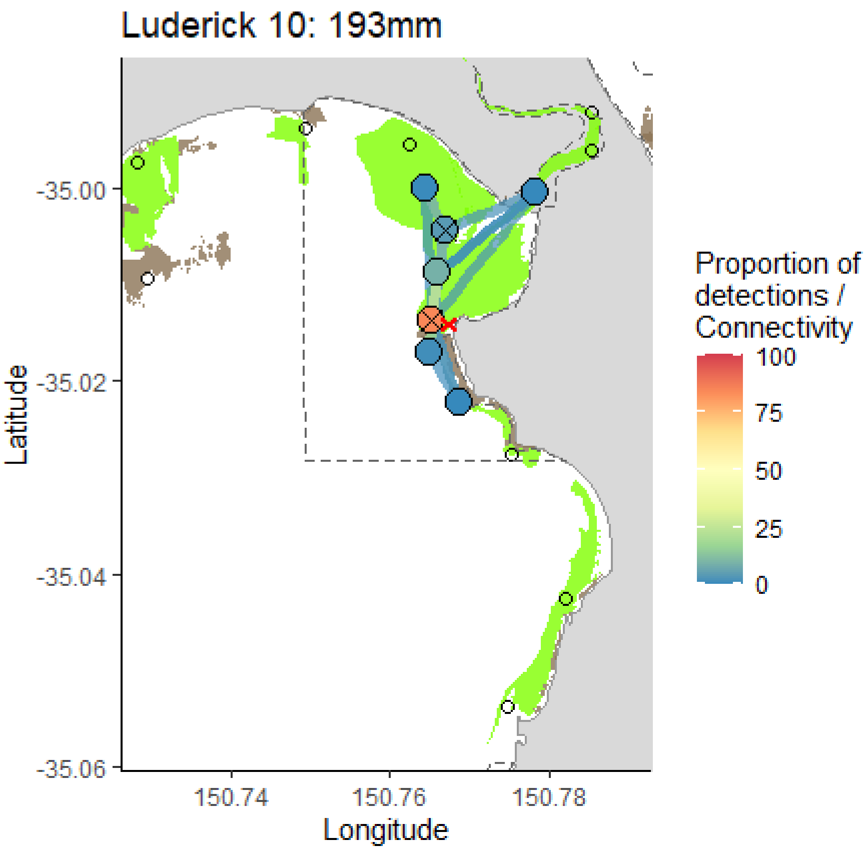

Luderick 5: 194mm
-35.00
-35.02
-35.04
-35.06
Latitude
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0

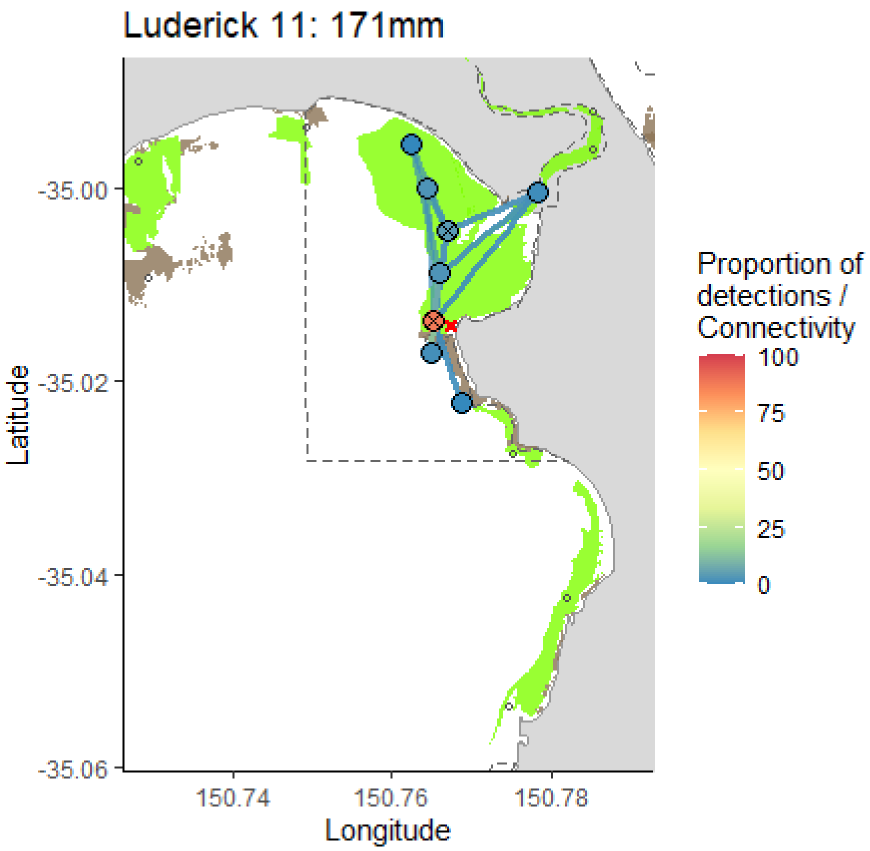

Luderick 6: 216mm
-35.00
-35.02
-35.04
-35.06
Latitude
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0


Luderick 7: 172mm
Latitude
-35.00
-35.02
-35.04
-35.06
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0

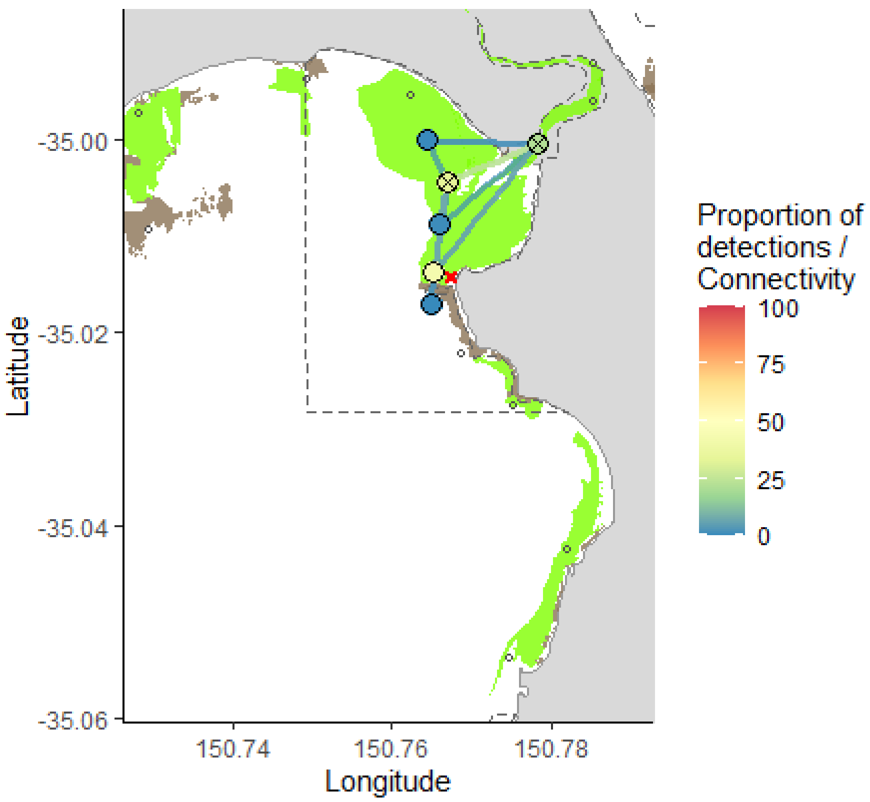

Luderick 8: 184mm
-35.00
-35.02
-35.04
-35.06
Latitude
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0


Luderick 9: 184mm
Latitude
-35.00
-35.02
-35.04
-35.06
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0


Luderick 10: 193mm
-35.00
-35.02
-35.04
-35.06
Latitude
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0


Luderick 11: 171mm
Latitude
-35.00
-35.02
-35.04
-35.06
Longitude
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0

Luderick 12: 179mm



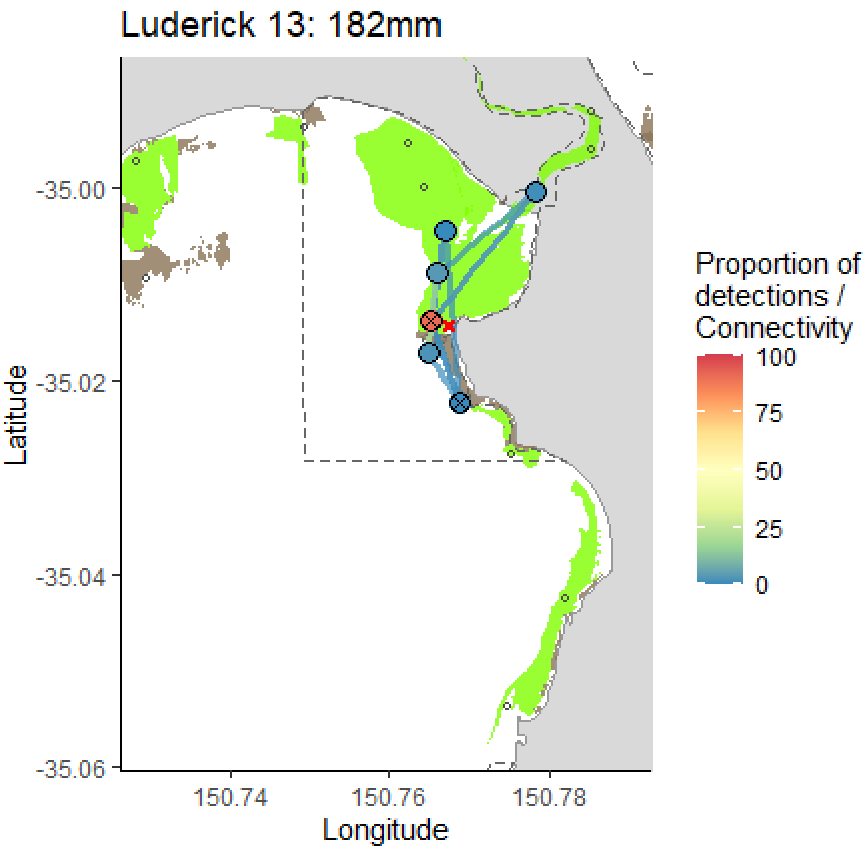
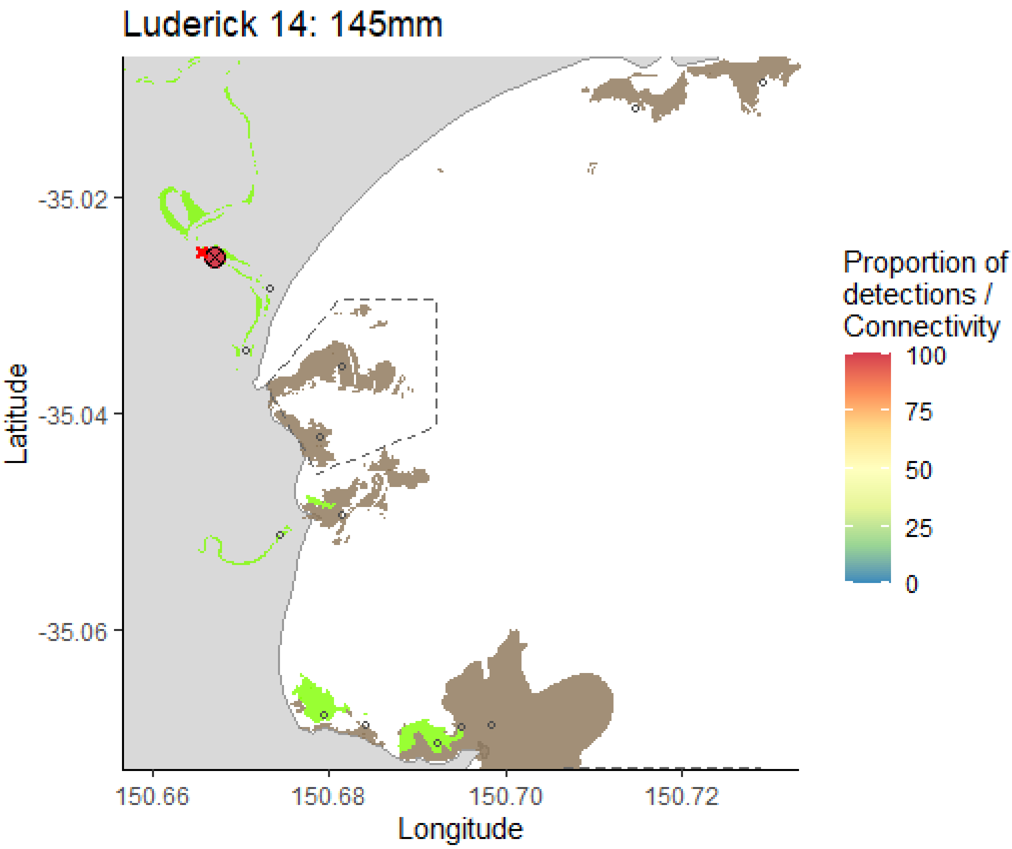
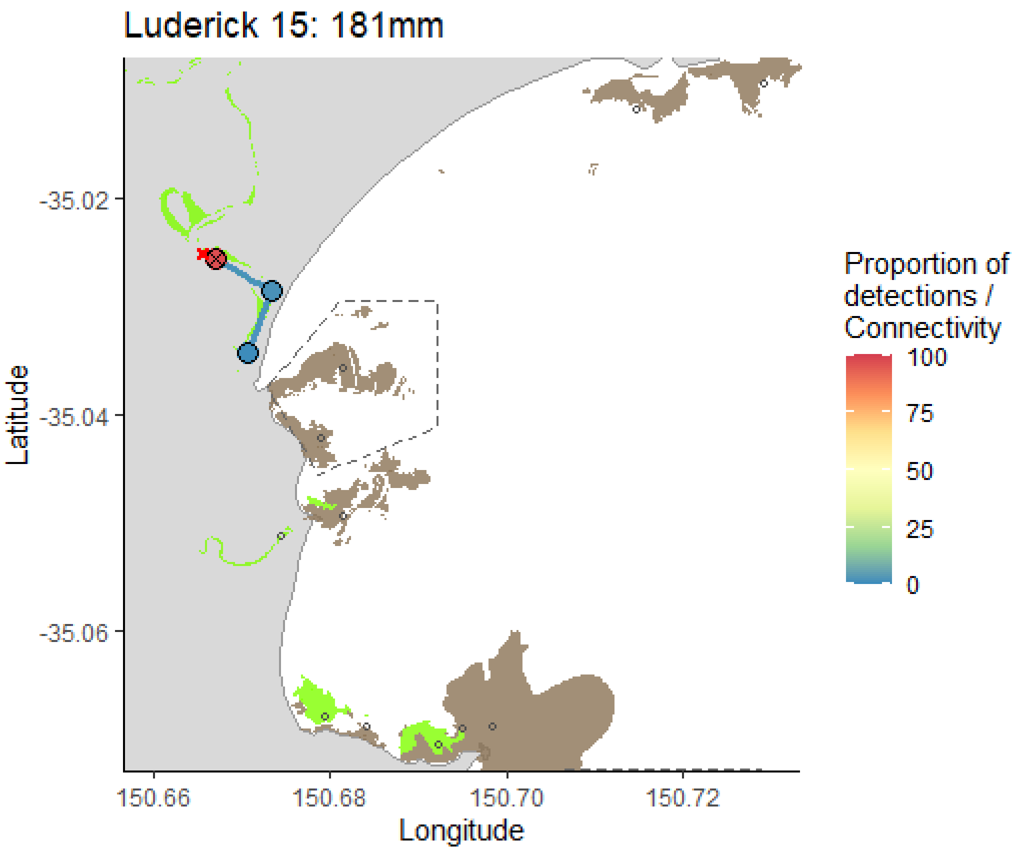
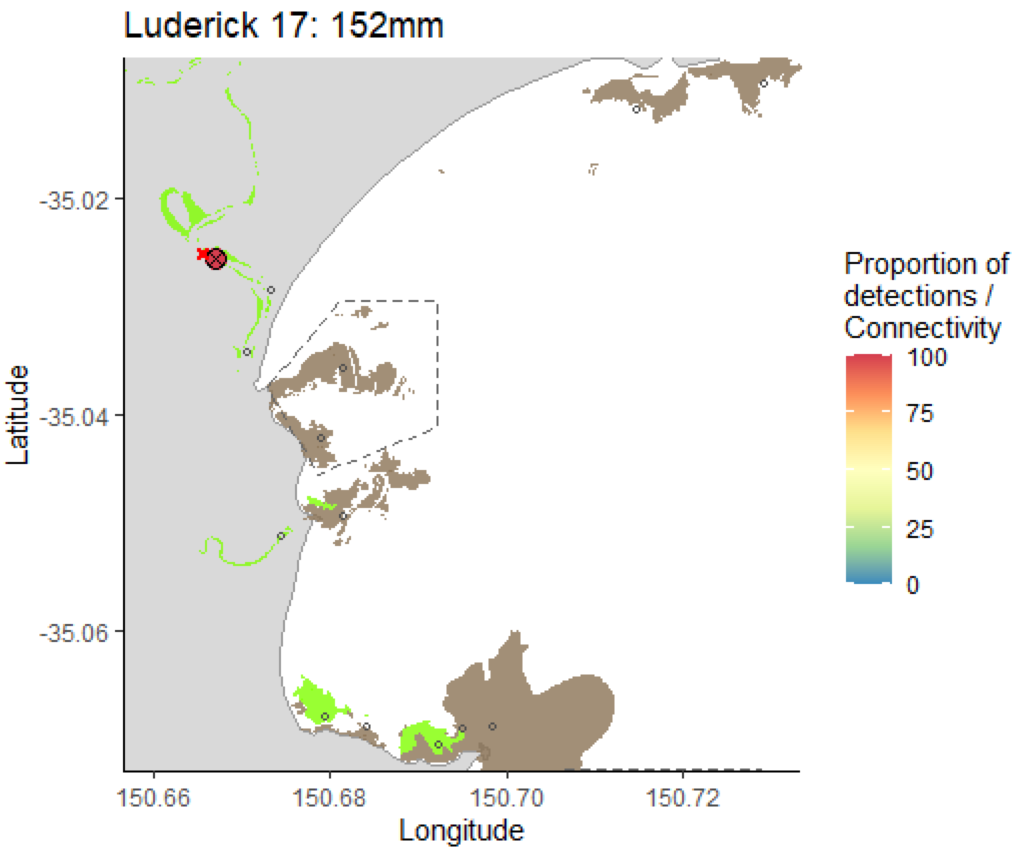
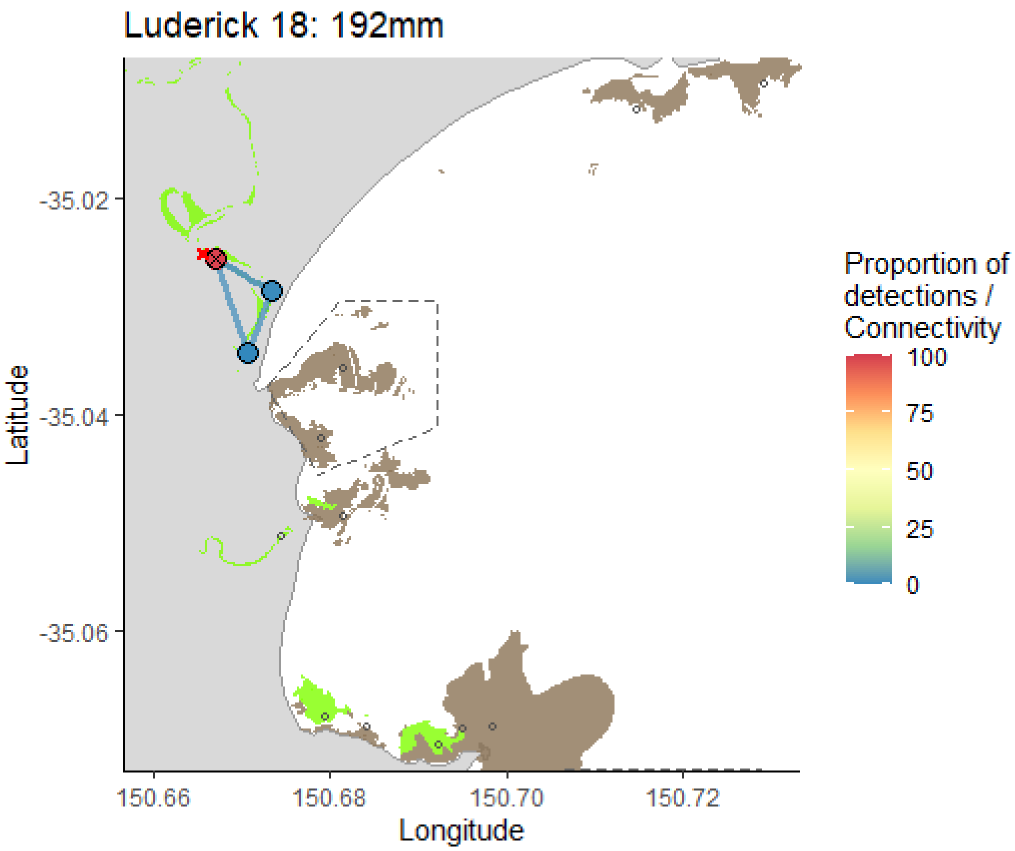

Luderick 13: 182mm
Latitude
-35.00
-35.02
-35.04
-35.06
Longitude
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0

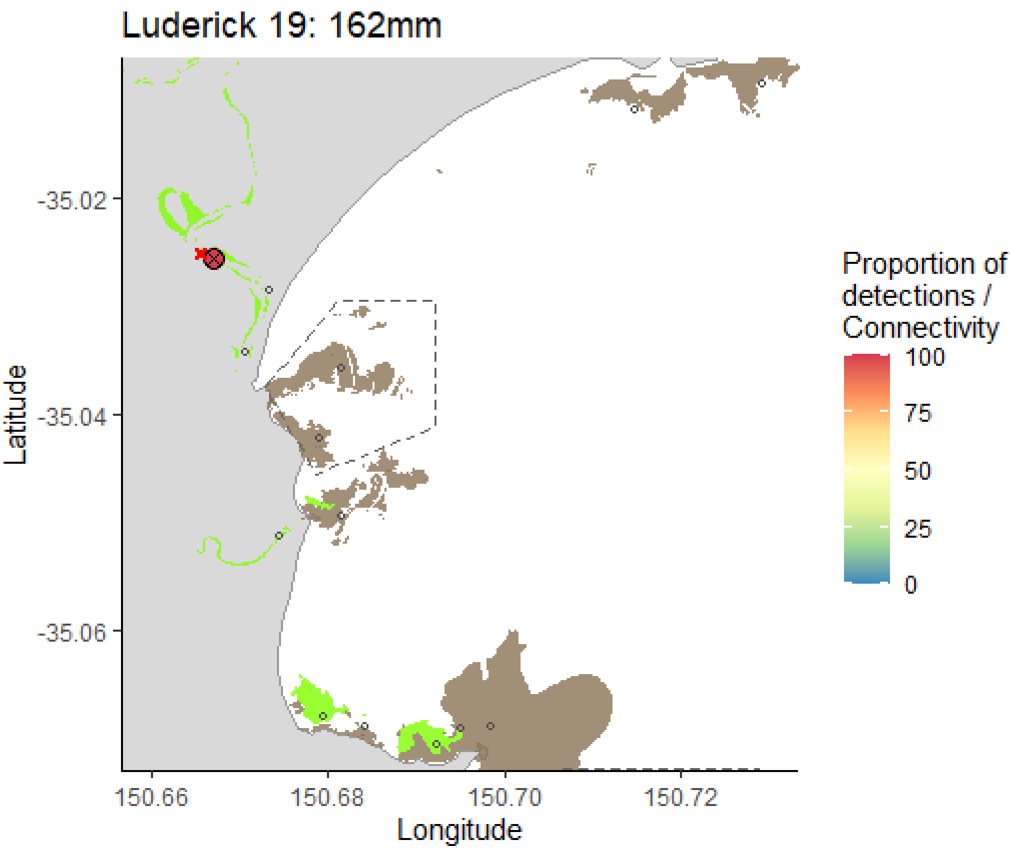
Figure A2.3: Individual movement graphs for the twelve luderick used in analyses released in Curramebene Creek. The colour of nodes illustrates the proportion of detections at a given receiver and edge colour shows the number of movements between receivers. Empty black circles show the non-visited receivers. The red ‘x’s are the release location of fish and black crosses on receivers represent core-use receivers. Dashed areas illustrate no-take marine reserves. Please note three fish did not have sufficient detections and were not included.



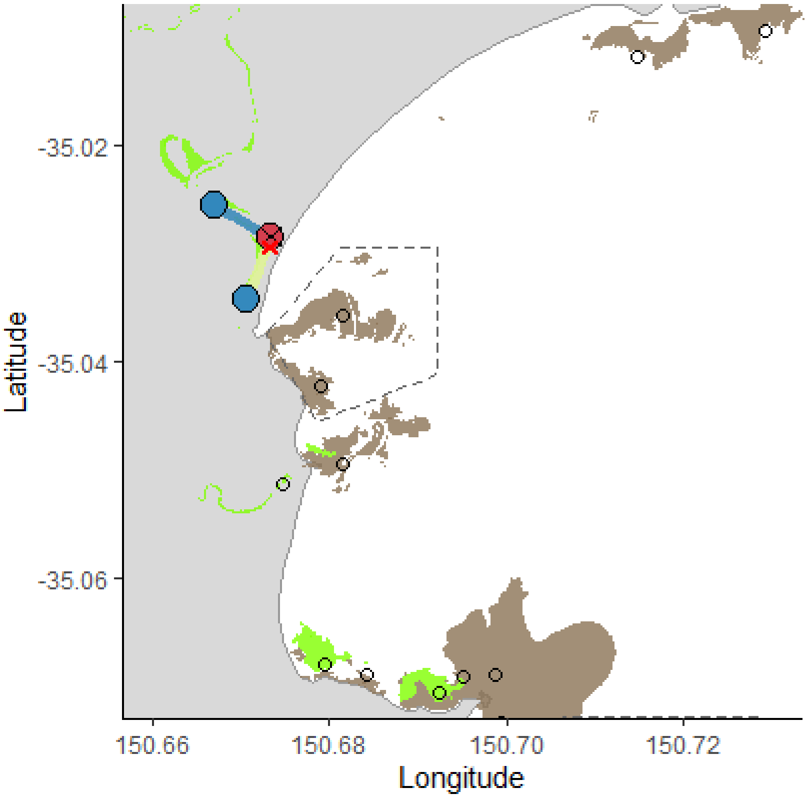

Luderick 15: 181mm
Latitude
-35.02
-35.04
-35.06
Longitude
150.66
150.68
150.70
150.72
Proportion of detections / Connectivity
100
75
50
25
0

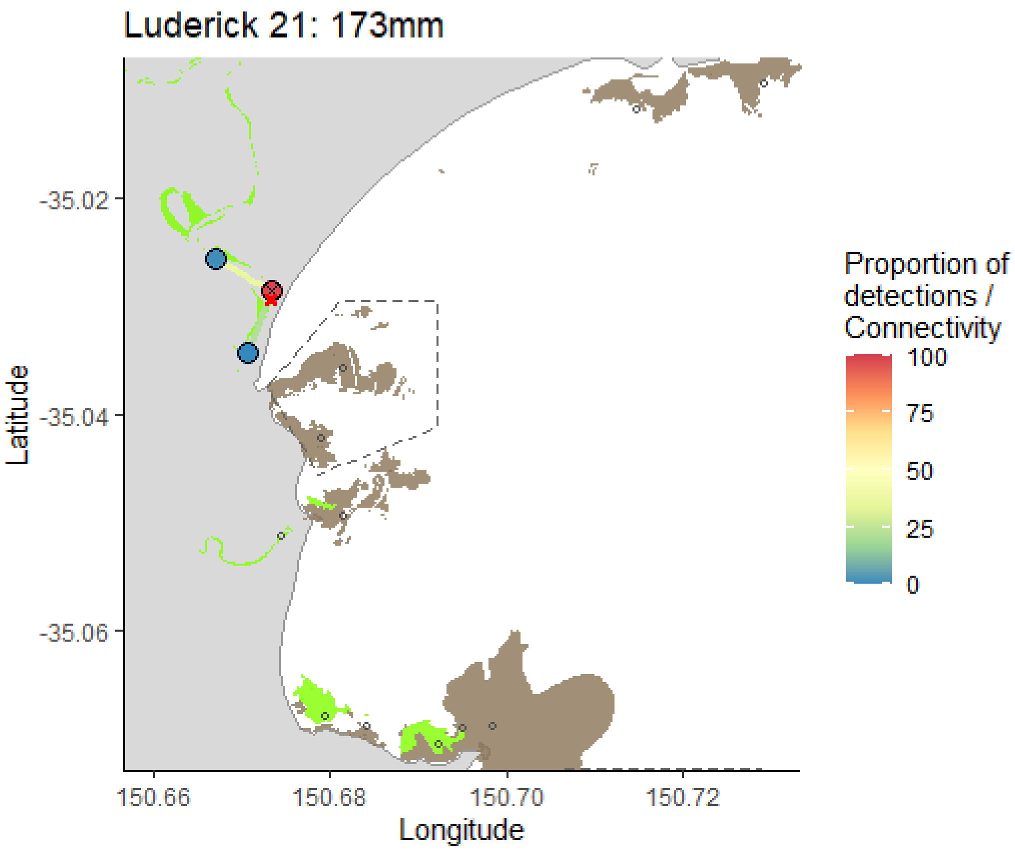

Luderick 17: 152mm
-35.02
-35.04
-35.06
Latitude
150.66
150.68
150.70
150.72
Longitude
Proportion of detections / Connectivity
100
75
50
25
0

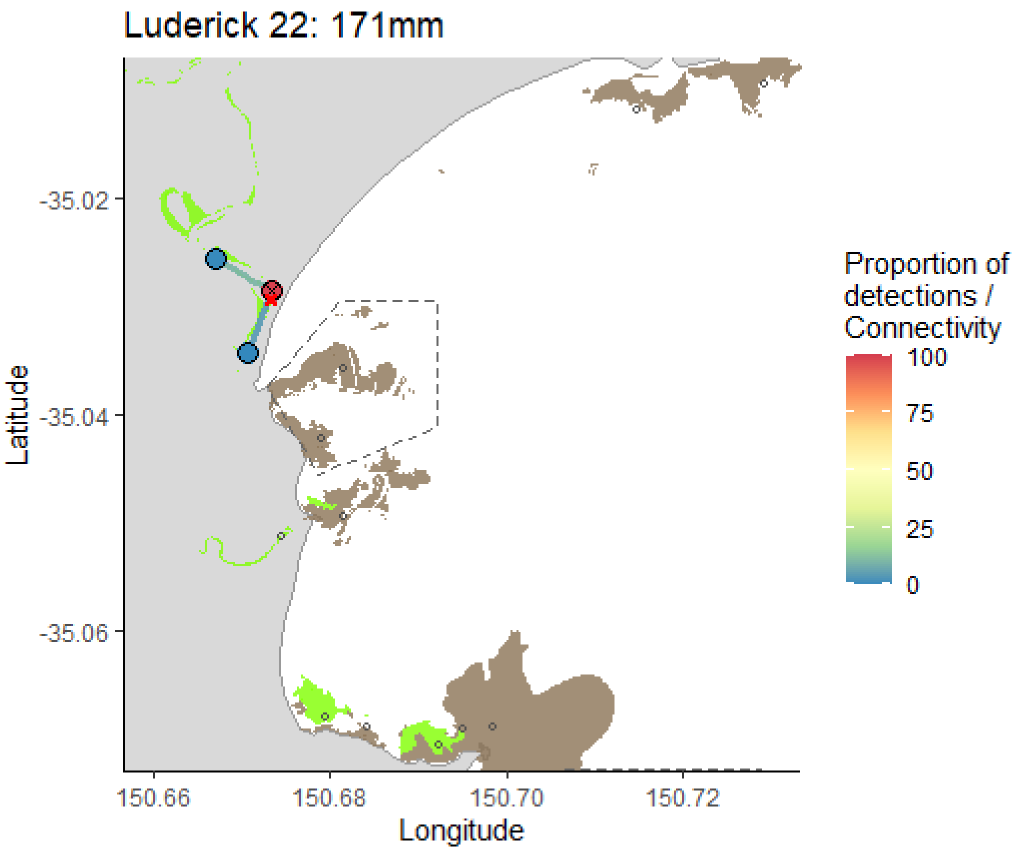

Luderick 18: 192mm
-35.02
-35.04
-35.06
Latitude
150.66
150.68
150.70
150.72
Longitude
Proportion of detections / Connectivity
100
75
50
25
0

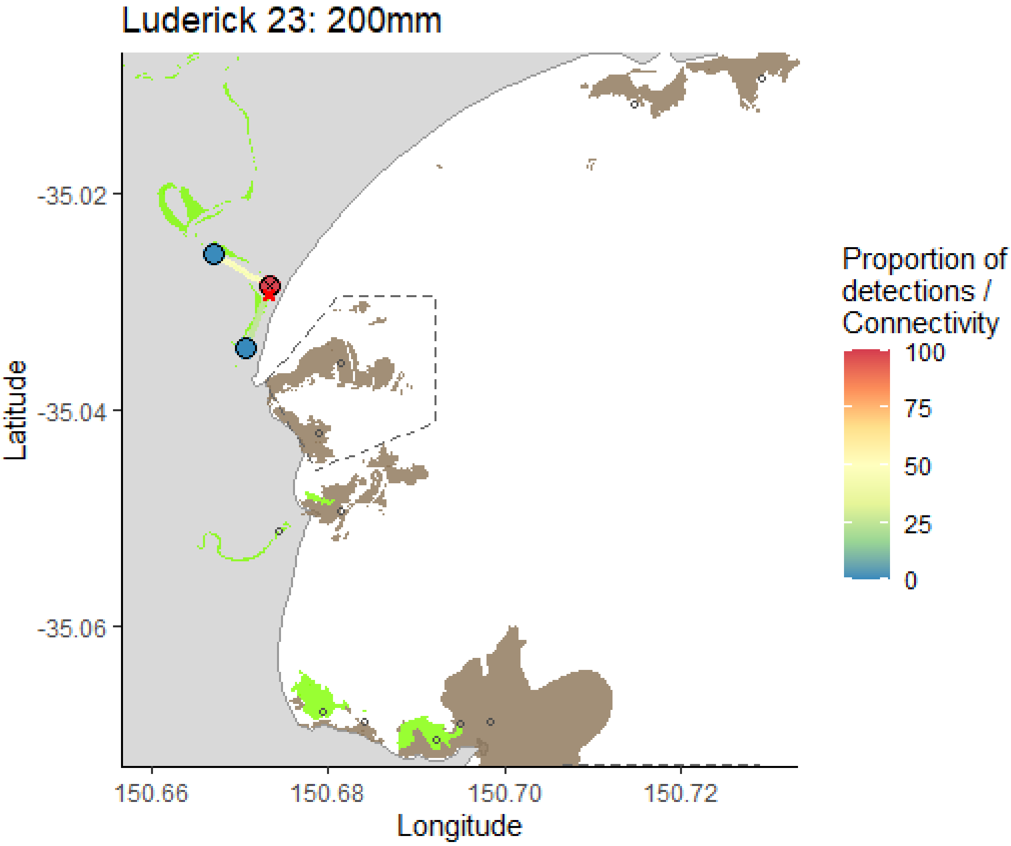

Luderick 19: 162mm
Latitude
-35.02
-35.04
-35.06
Longitude
150.66
150.68
150.70
150.72
Proportion of detections / Connectivity
100
75
50
25
0

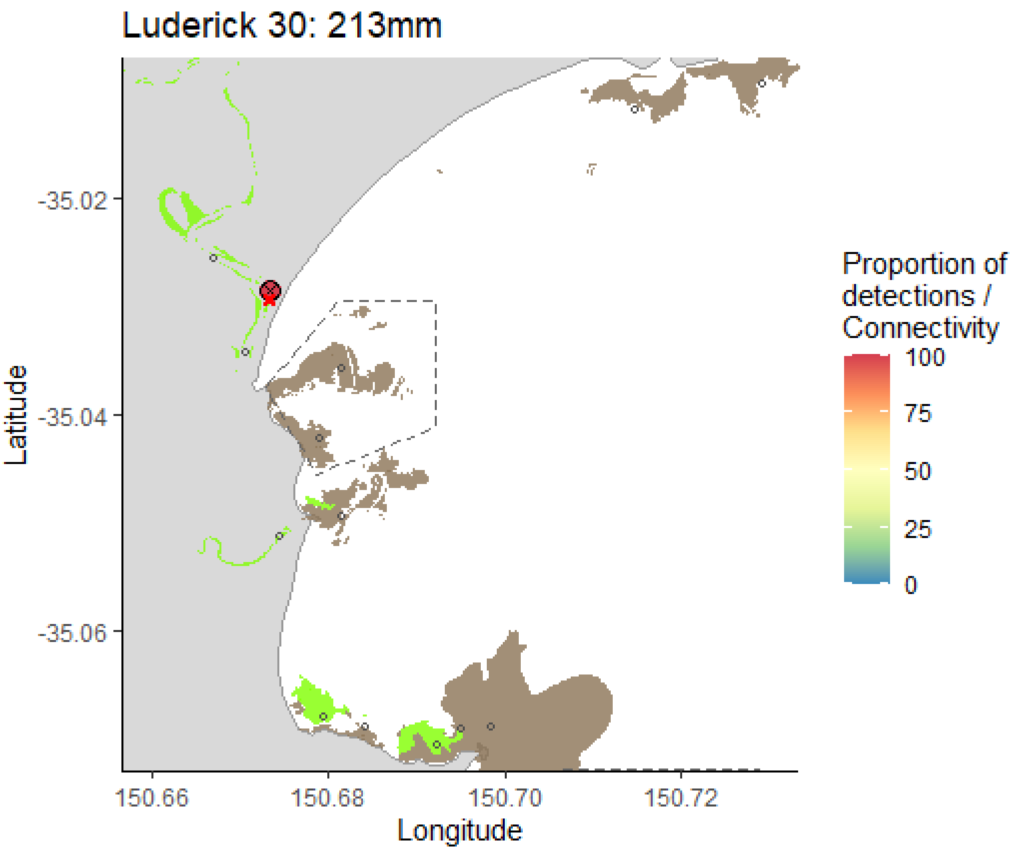
Luderick 20: 170mm

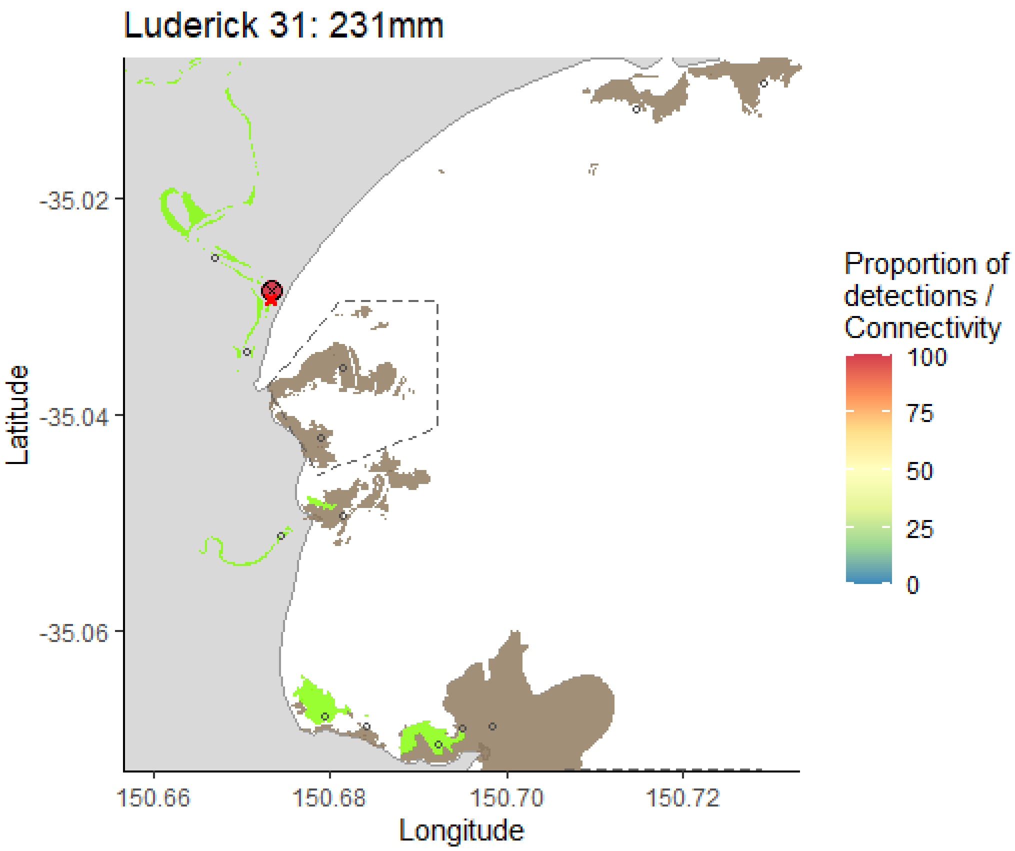



Luderick 21: 173mm
Latitude
-35.02
-35.04
-35.06
150.66
150.68
150.70
150.72
Longitude
Proportion of detections / Connectivity
100
75
50
25
0


Luderick 22: 171mm
-35.02
-35.04
-35.06
Latitude
150.66
150.68
150.70
150.72
Longitude
Proportion of
detections /
Connectivity
100
75
50
25
0


Luderick 23: 200mm
Latitude
-35.02
-35.04
-35.06
Longitude
150.66
150.68
150.70
150.72
Proportion of detections / Connectivity
100
75
50
25
0


Luderick 30: 213mm
Latitude
-35.02
-35.04
-35.06
Longitude
150.66
150.68
150.70
150.72
Proportion of detections / Connectivity
100
75
50
25
0


Luderick 31: 231mm
Latitude
-35.02
-35.04
-35.06
Longitude
150.66
150.68
150.70
150.72
Proportion of detections / Connectivity
100
75
50
25
0

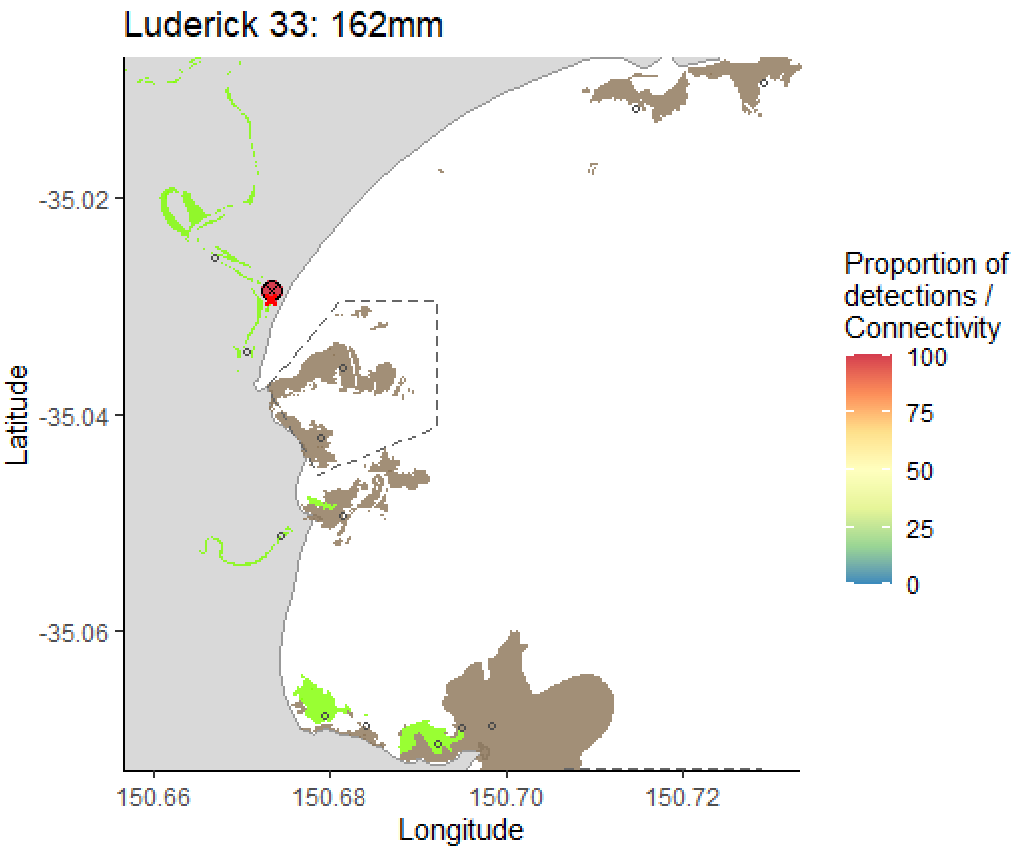
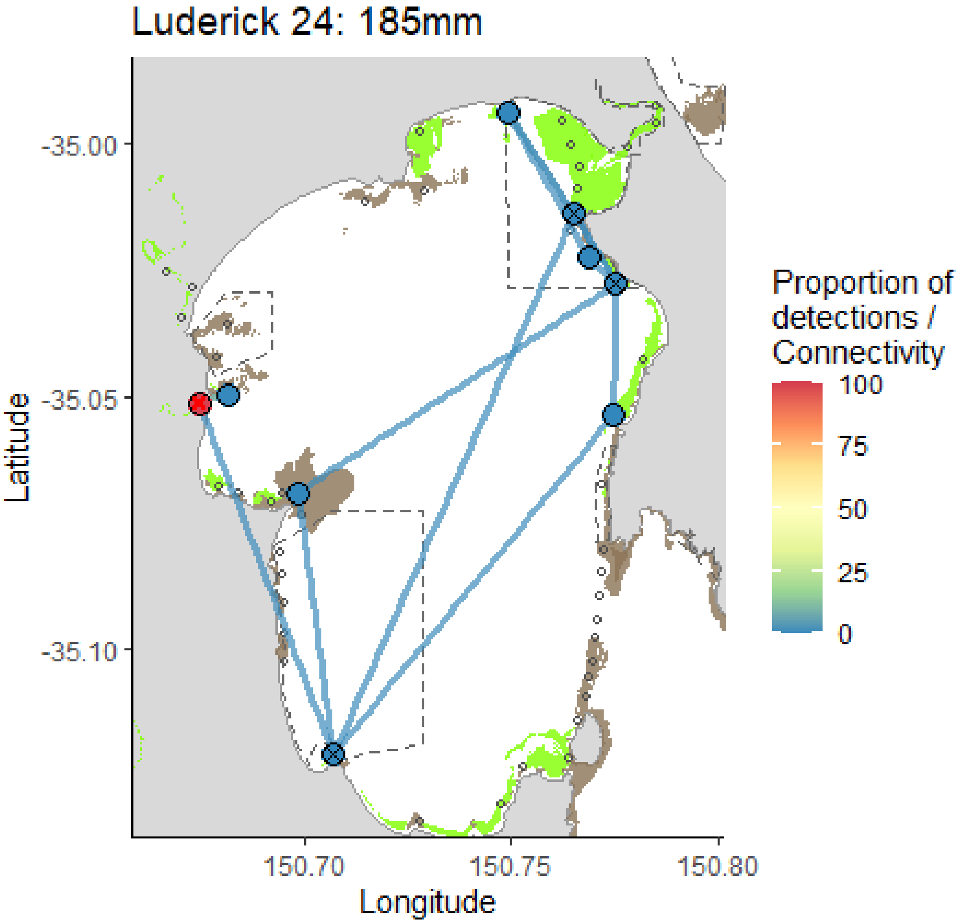
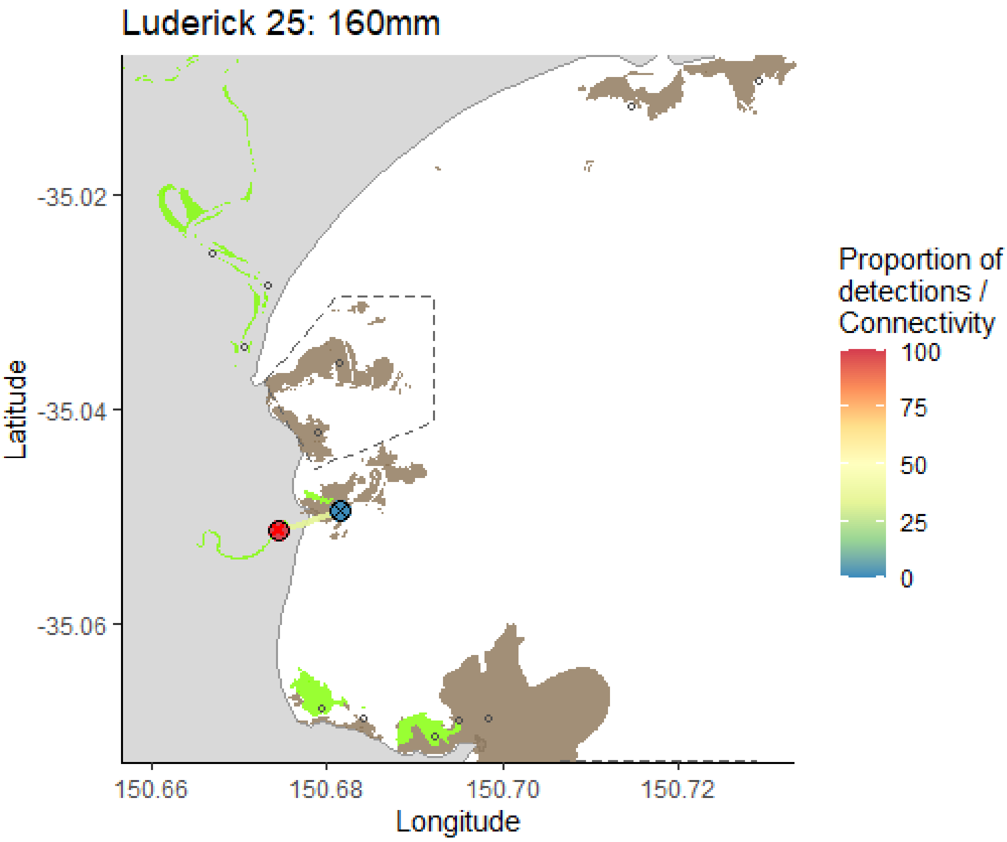
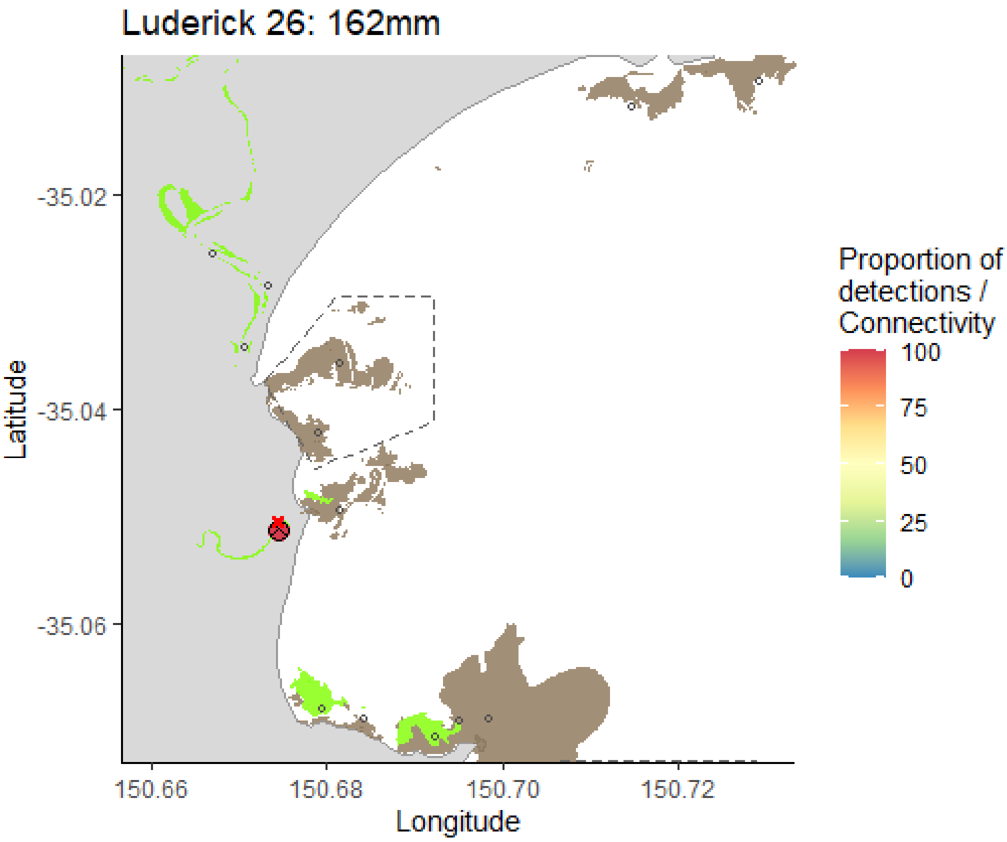
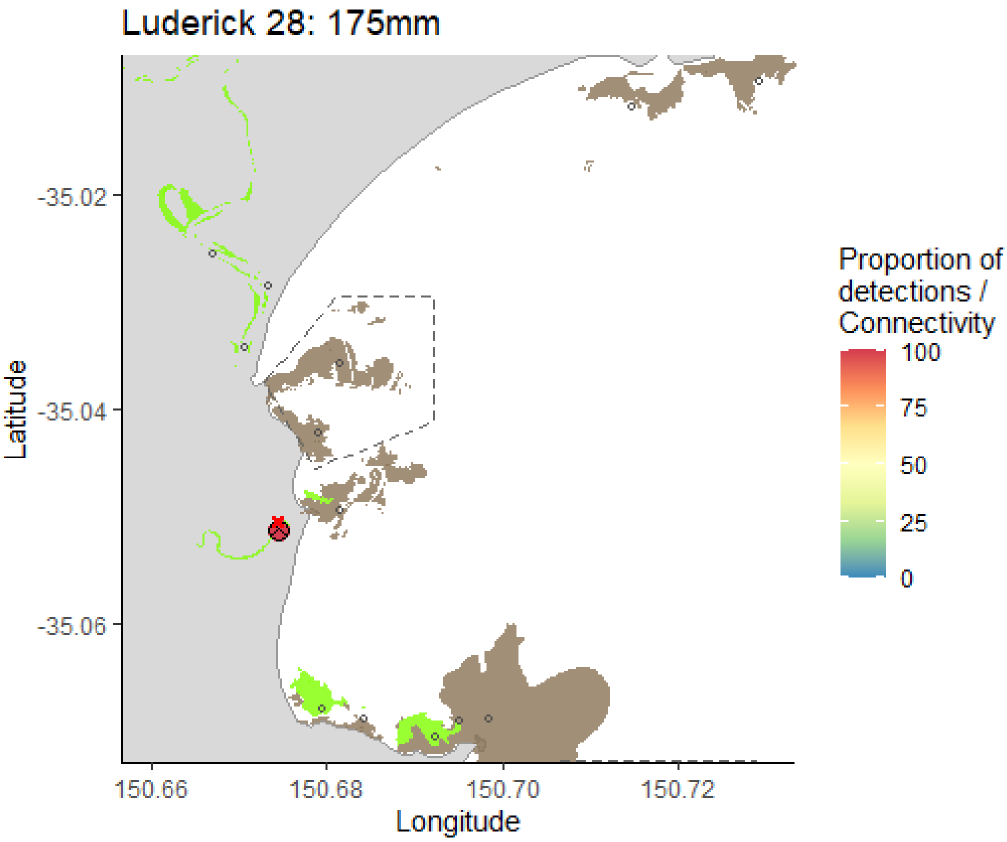

Luderick 33: 162mm
Latitude
-35.02
-35.04
-35.06
Longitude
150.66
150.68
150.70
150.72
Proportion of detections / Connectivity
100
75
50
25
0

Figure A2.4: Individual movement graphs for the five luderick used in analyses released in Moona Moona Creek. The colour of nodes illustrates the proportion of detections at a given receiver and edge colour shows the number of movements between receivers. Empty black circles show the non-visited receivers. The red ‘x’s are the release location of fish and black crosses on receivers represent core-use receivers. Dashed areas illustrate no-take marine reserves.




Luderick 25: 160mm
Latitude
-35.02
-35.04
-35.06
Longitude
150.66
150.68
150.70
150.72
Proportion of detections / Connectivity
100
75
50
25
0


Luderick 26: 162mm
Latitude
-35.02
-35.04
-35.06
Longitude
150.66
150.68
150.70
150.72
Proportion of detections / Connectivity
100
75
50
25
0


Luderick 28: 175mm
Latitude
-35.02
-35.04
-35.06
Longitude
150.66
150.68
150.70
150.72
Proportion of detections / Connectivity
100
75
50
25
0

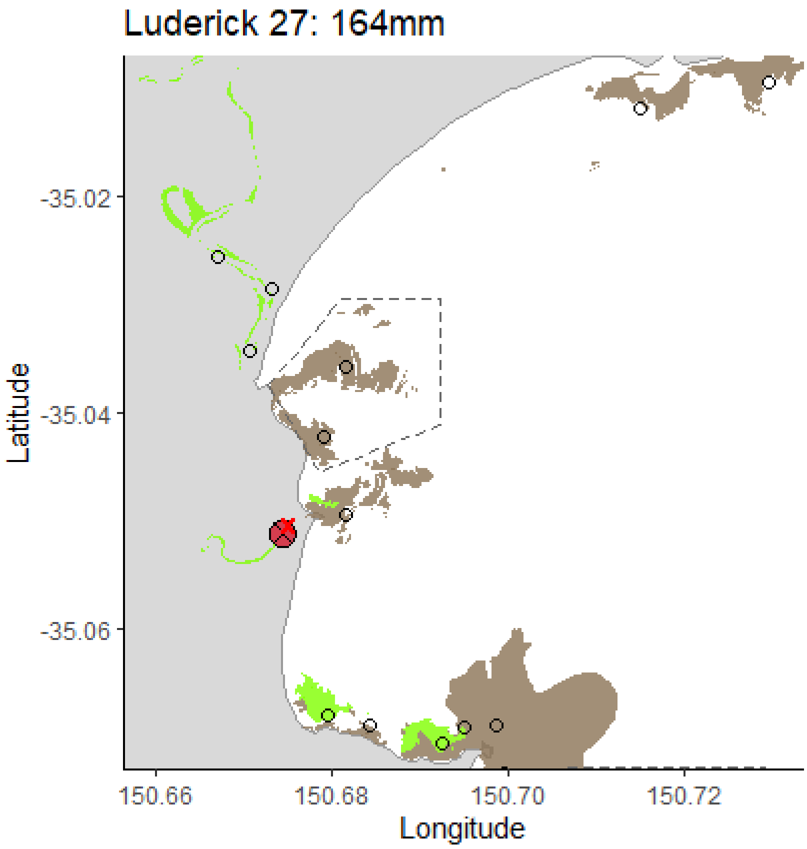
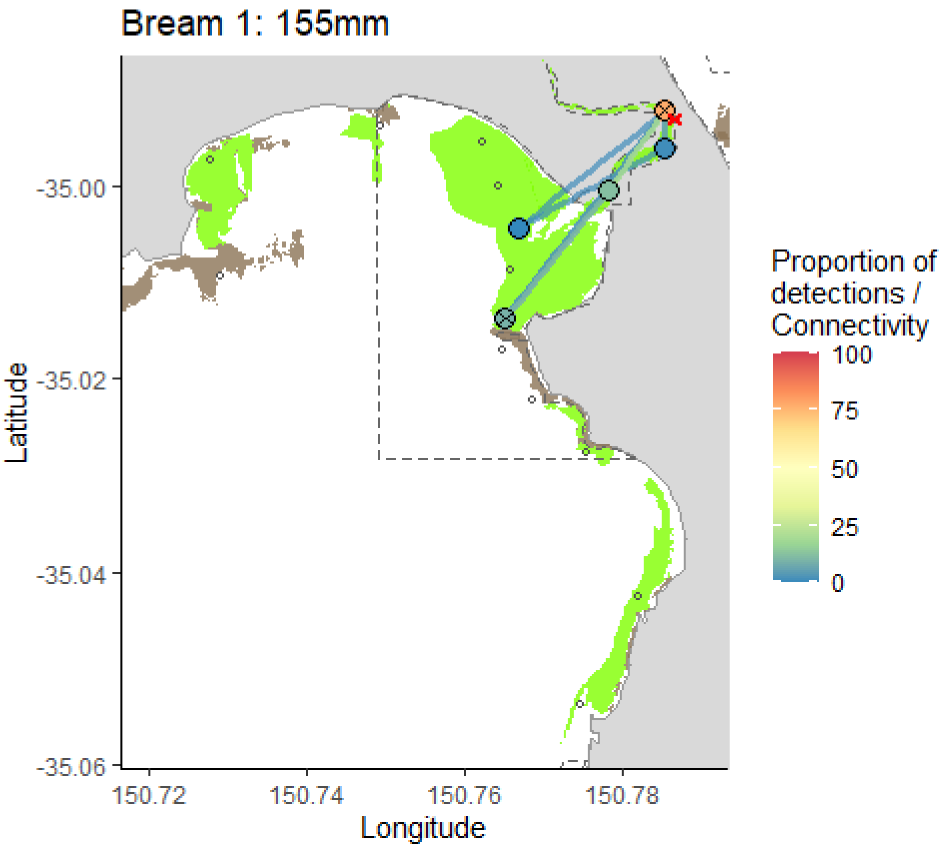
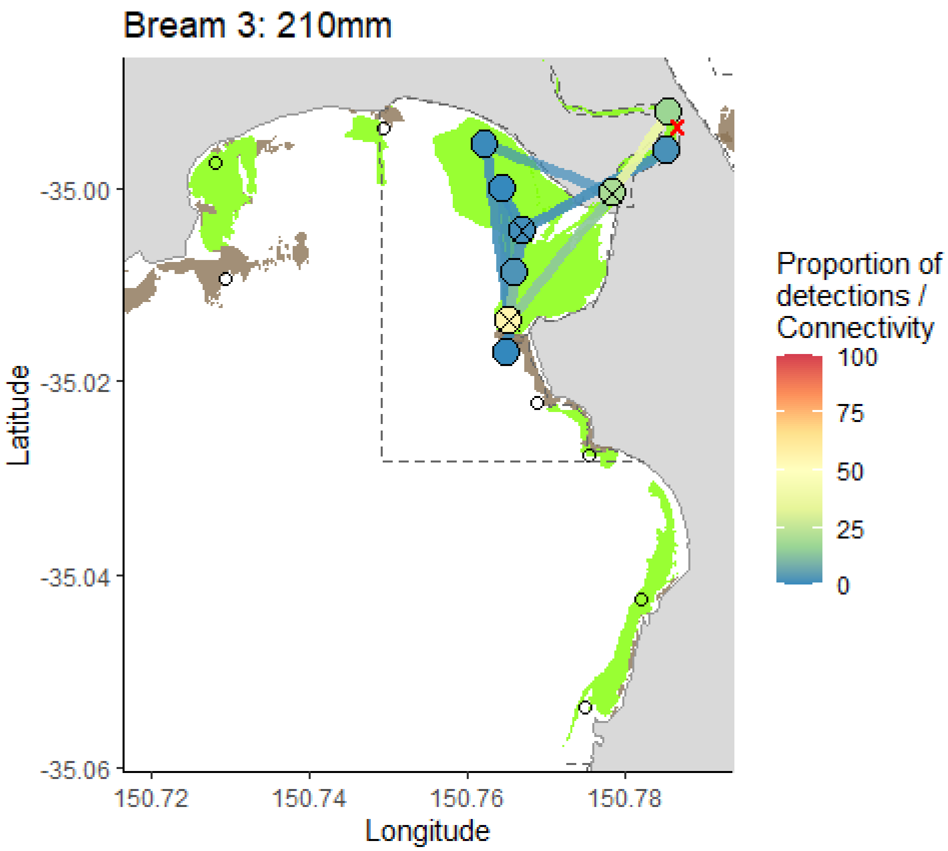
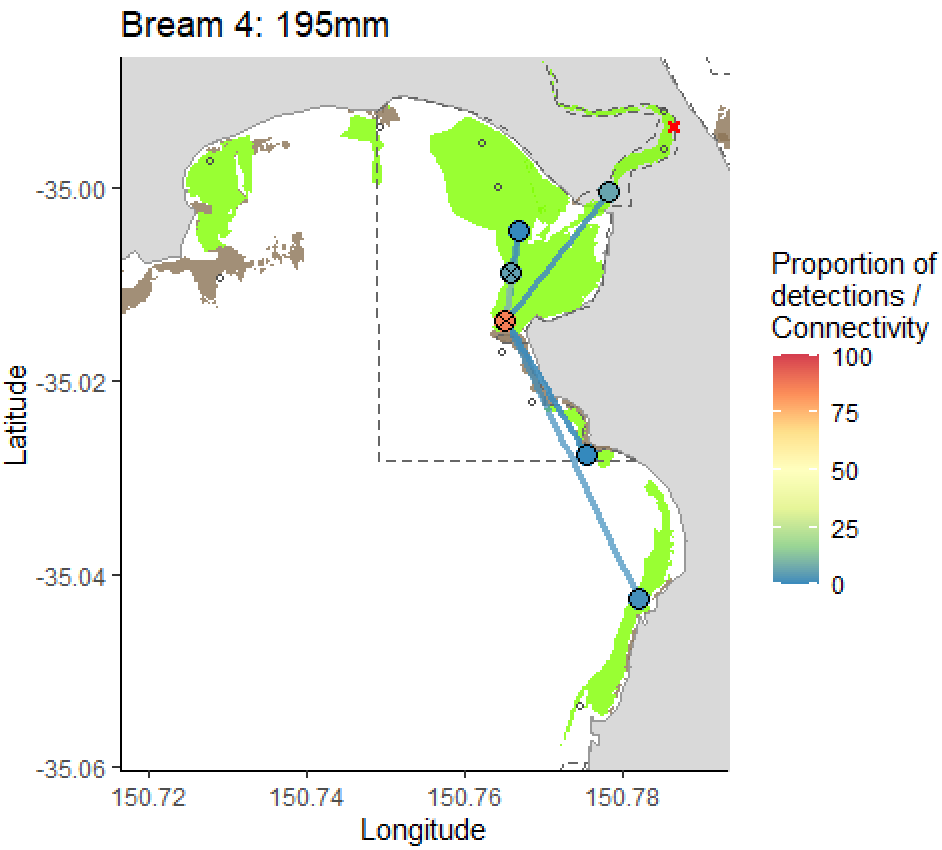
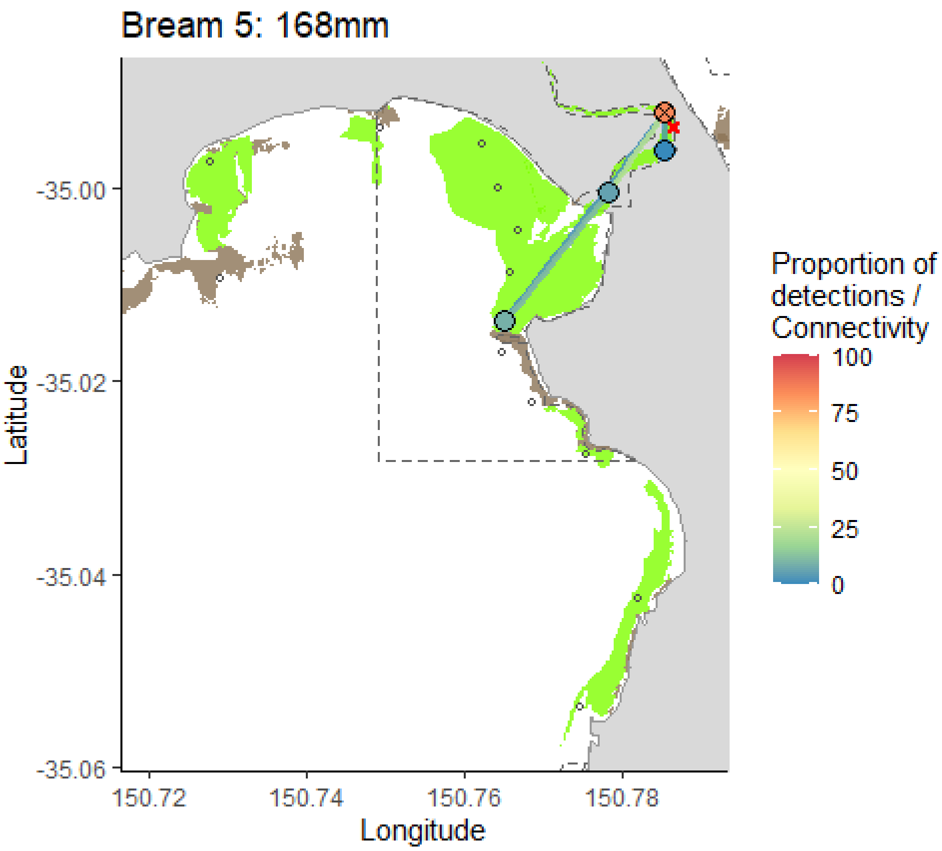

Luderick 27: 164mm
-35.02
-35.04
-35.06
Latitude
150.66
150.68
150.70
150.72
Longitude

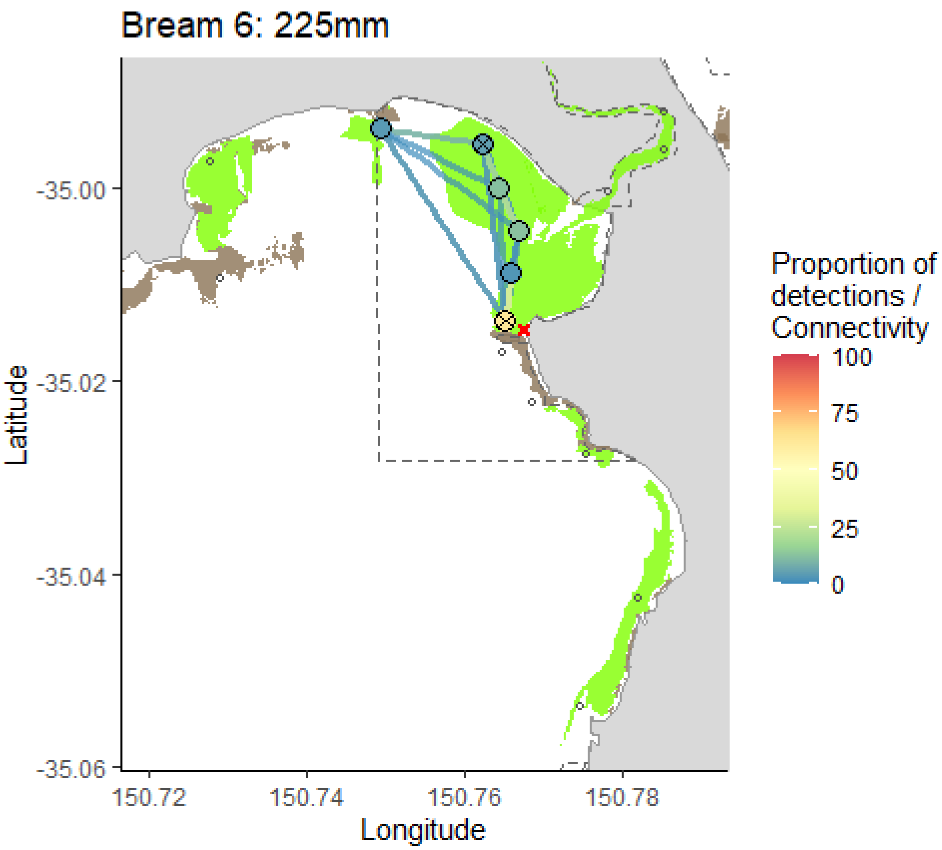
Figure A2.5: Individual movement graphs for the nineteen yellowfin bream used in analyses that were released in Hare Bay and Carama Inlet. The colour of nodes illustrates the proportion of detections at a given receiver and edge colour shows the number of movements between receivers. Empty black circles show the non-visited receivers. The red 'x's are the release location of fish and black crosses on receivers represent core-use receivers. Dashed areas illustrate no-take marine reserves. Please note one fish did not have sufficeint detecttions and was not included.

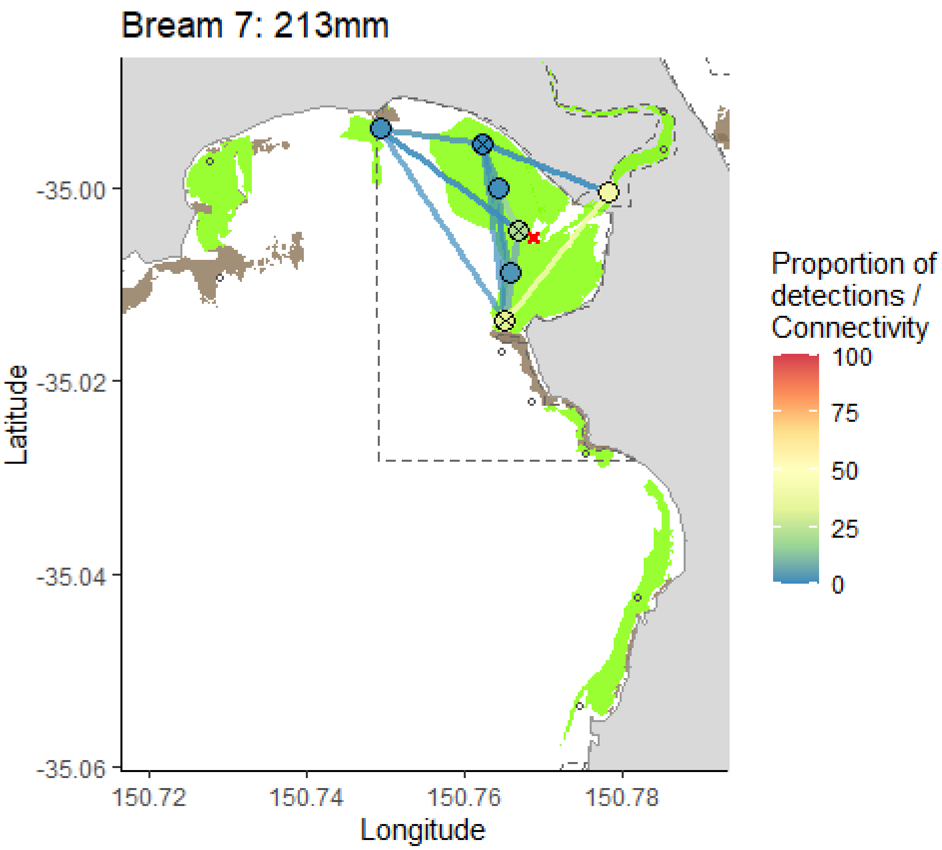


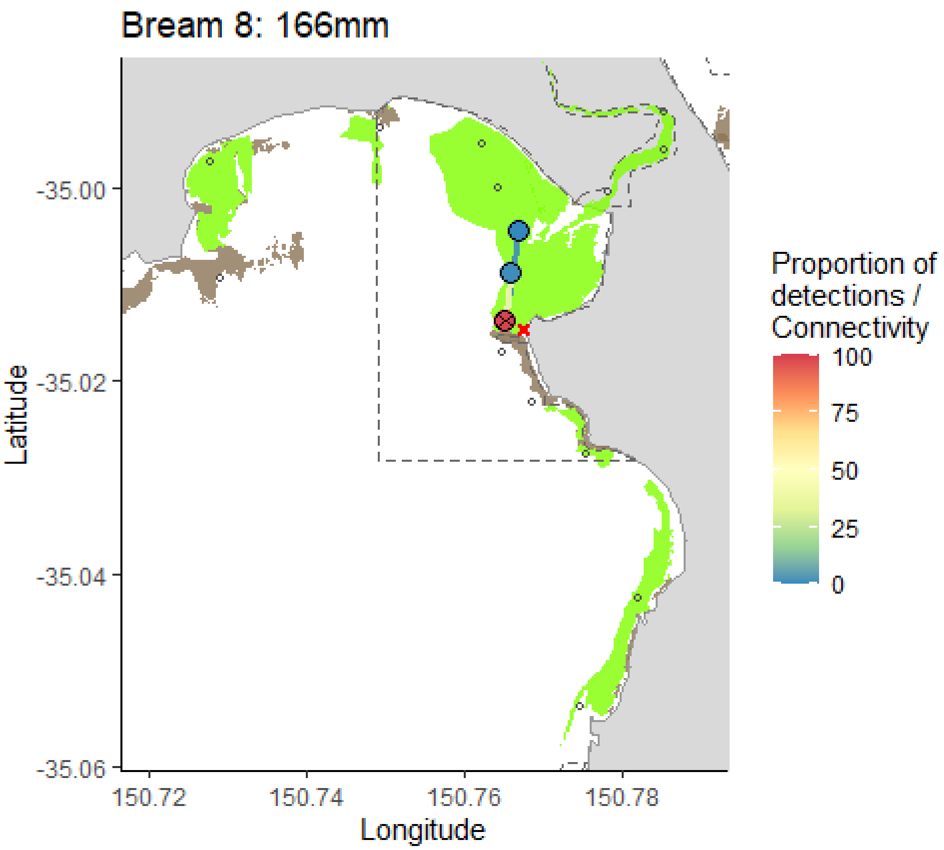

Bream 3: 210mm
Latitude
-35.00
-35.02
-35.04
-35.06
Longitude
150.72
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0

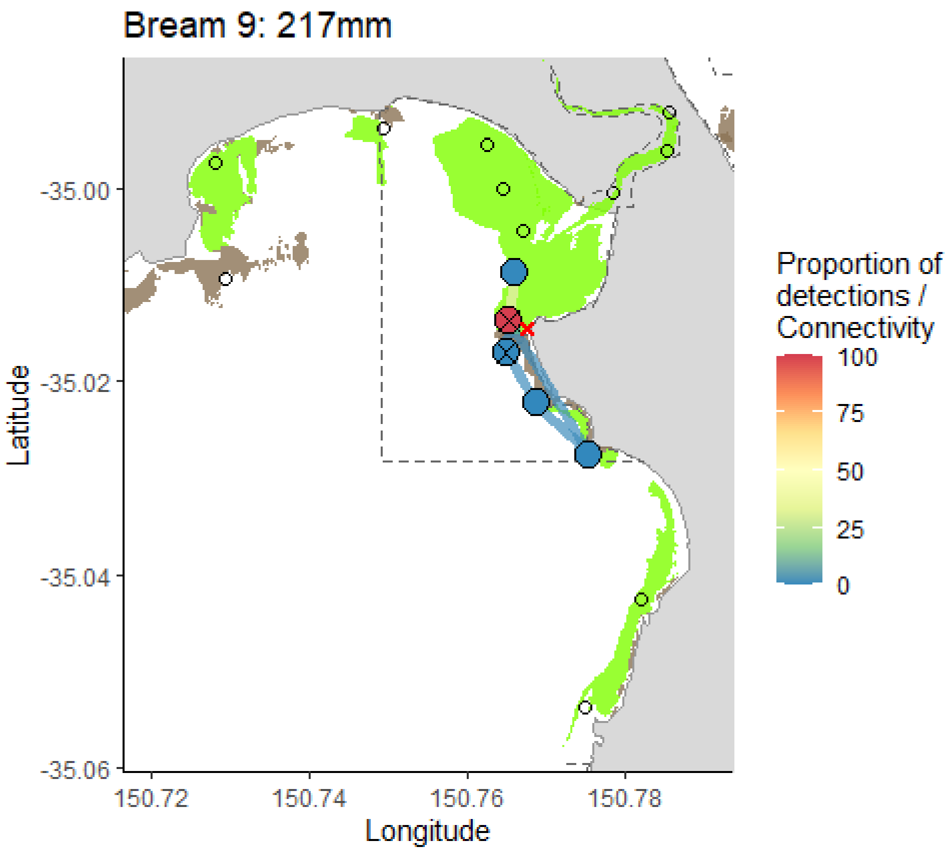

Bream 4: 195mm
Latitude
-35.00
-35.02
-35.04
-35.06
Longitude
150.72
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0

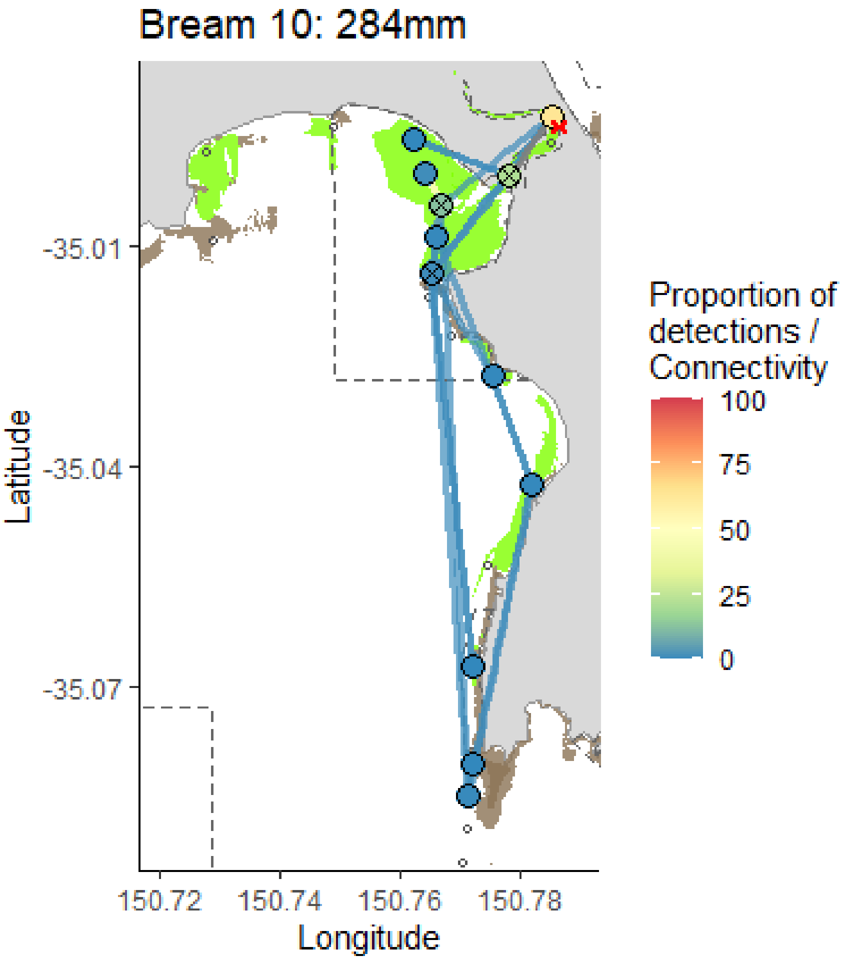

Bream 5: 168mm
Latitude
-35.00
-35.02
-35.04
-35.06
150.72
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0

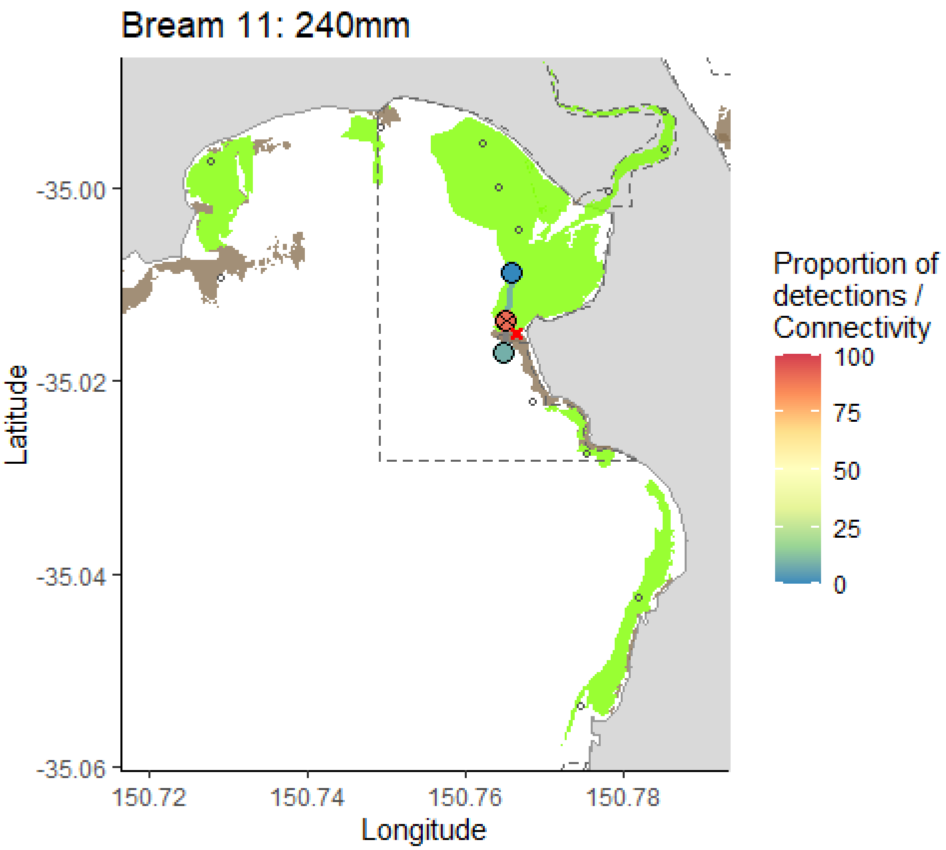

Bream 6: 225mm
Latitude
Longitude
-35.00
-35.02
-35.04
-35.06
150.72
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0

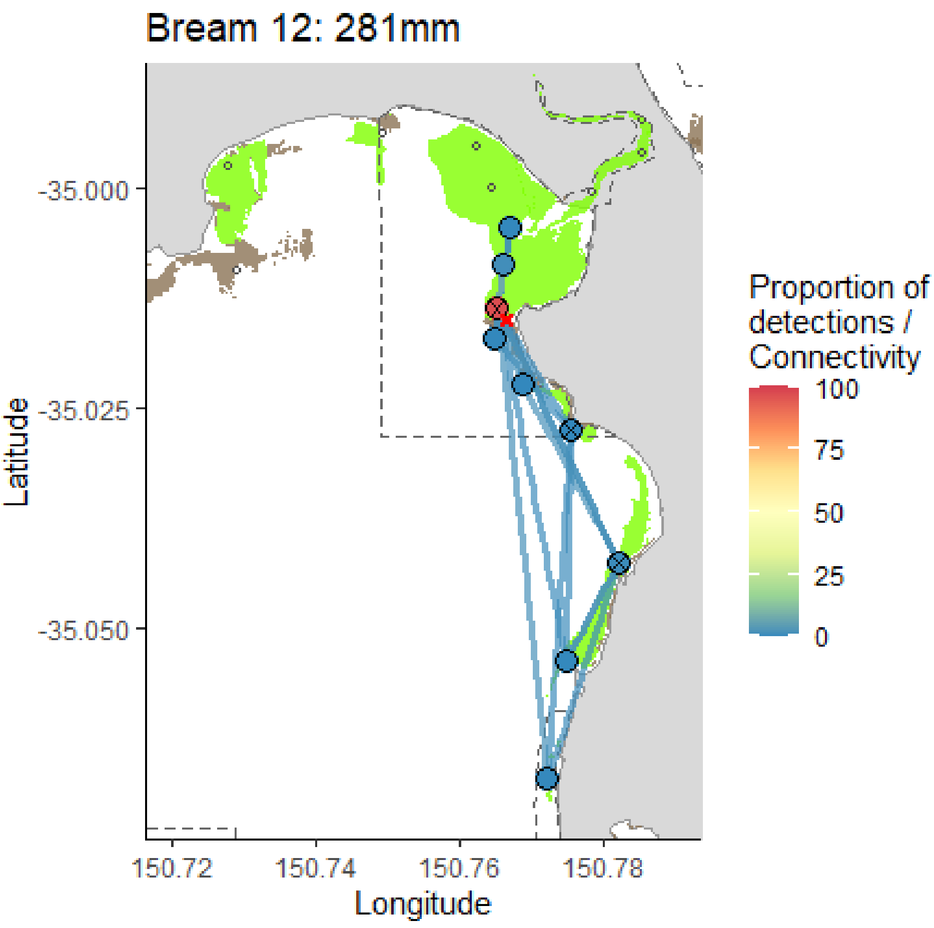

Bream 7: 213mm
Latitude
-35.00
-35.02
-35.04
-35.06
150.72
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0

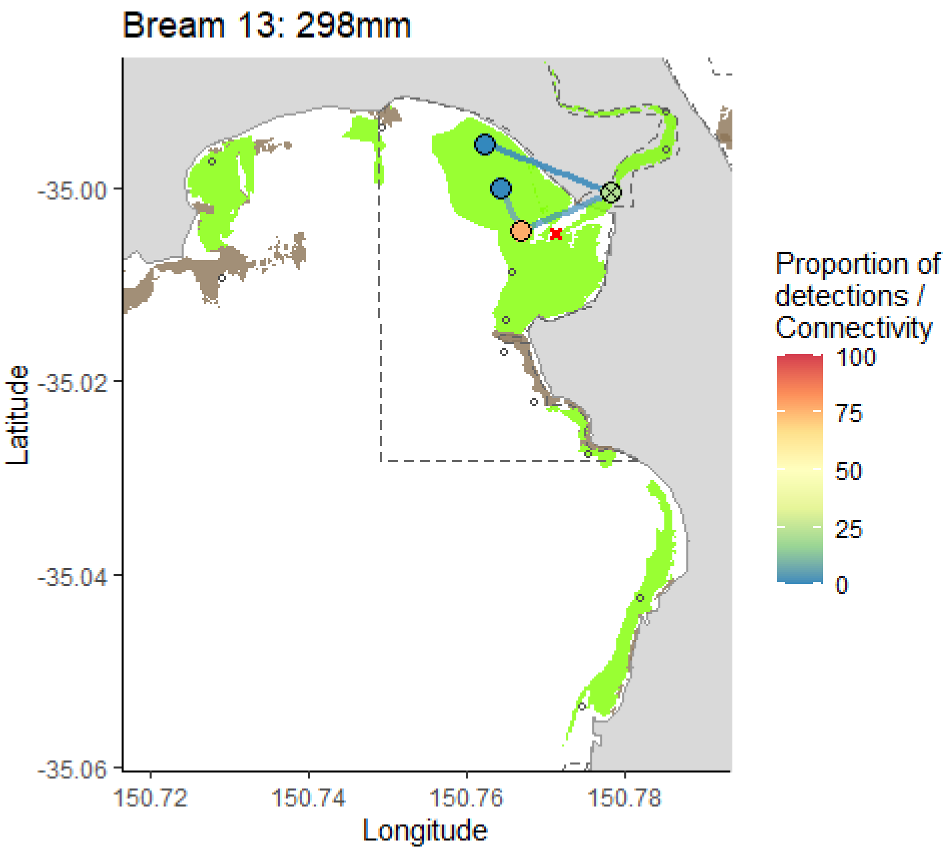

Bream 8: 166mm
Latitude
-35.00
-35.02
-35.04
-35.06
Longitude
150.72
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0

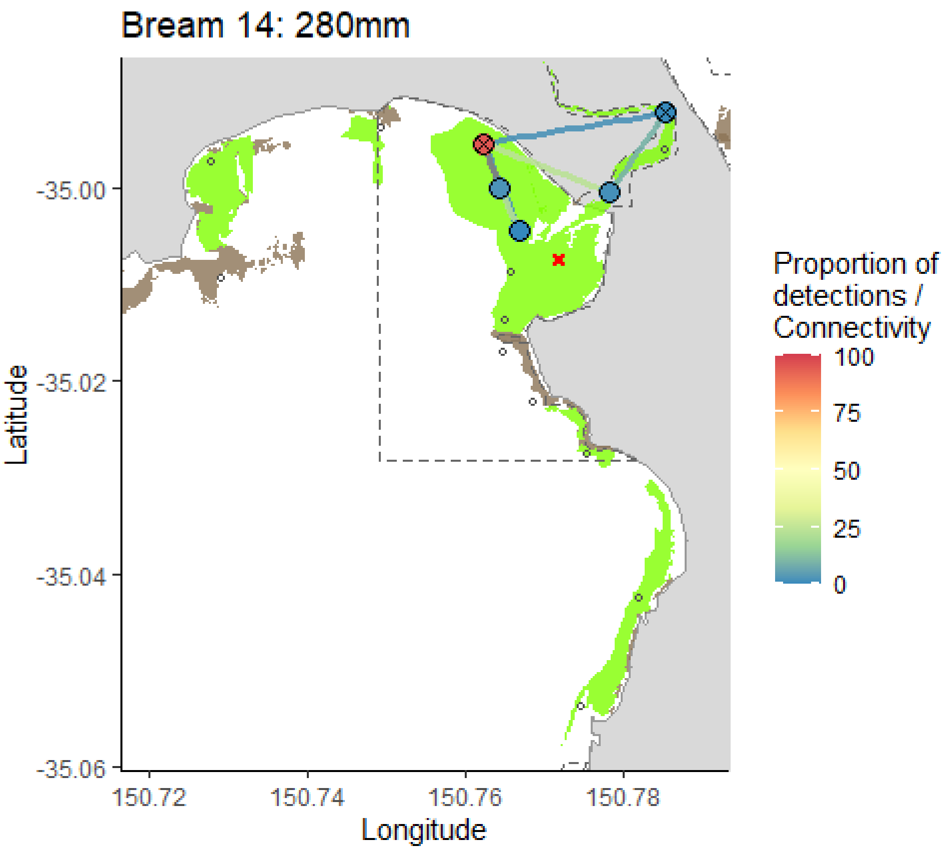

Bream 9: 217mm
-35.00
-35.02
-35.04
-35.06
Latitude
150.72
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0


Bream 10: 284mm
-35.01
-35.04
-35.07
Latitude
150.72
150.74
150.76
150.78
Longitude
Proportion of
detections /
Connectivity
100
75
50
25
0


Bream 11: 240mm
Latitude
-35.00
-35.02
-35.04
-35.06
Longitude
150.72
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0


Bream 12: 281mm
Latitude
-35.000
-35.025
-35.050
Longitude
150.72
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0


Bream 13: 298mm
Latitude
-35.00
-35.02
-35.04
-35.06
150.72
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0


Bream 14: 280mm
Latitude
-35.00
-35.02
-35.04
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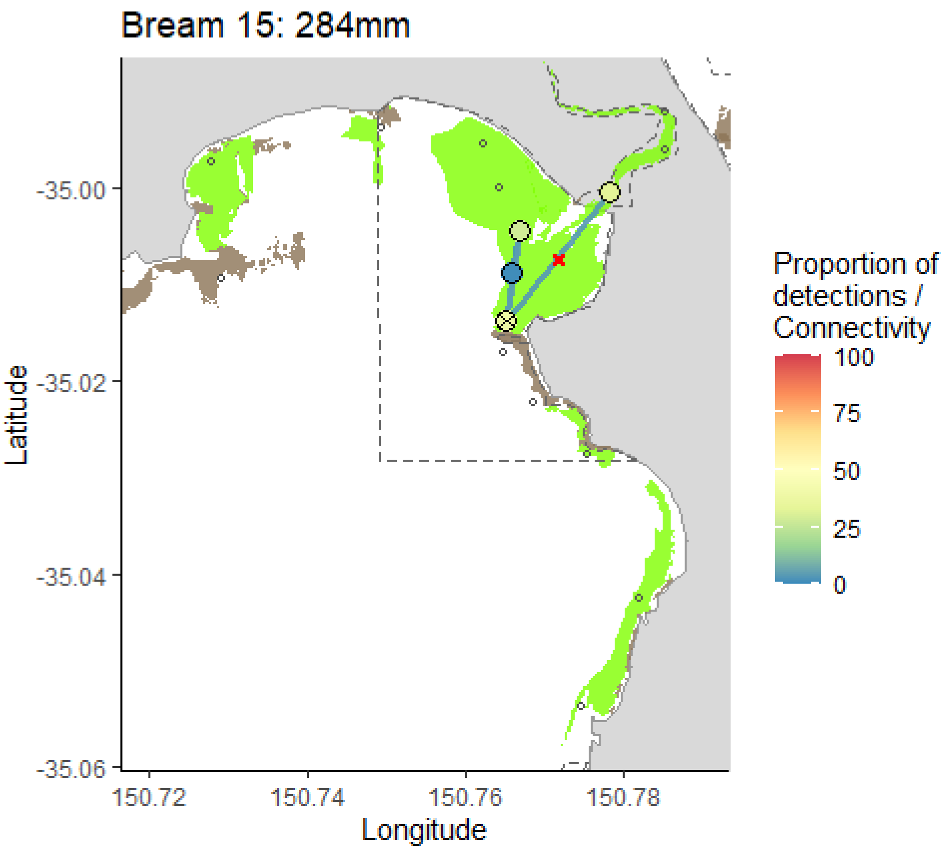
150.72
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0


Bream 15: 284mm
Proportion of detections / Connectivity
100
75
50
25
0
Latitude
-35.00
-35.02
-35.04
-35.06
150.72
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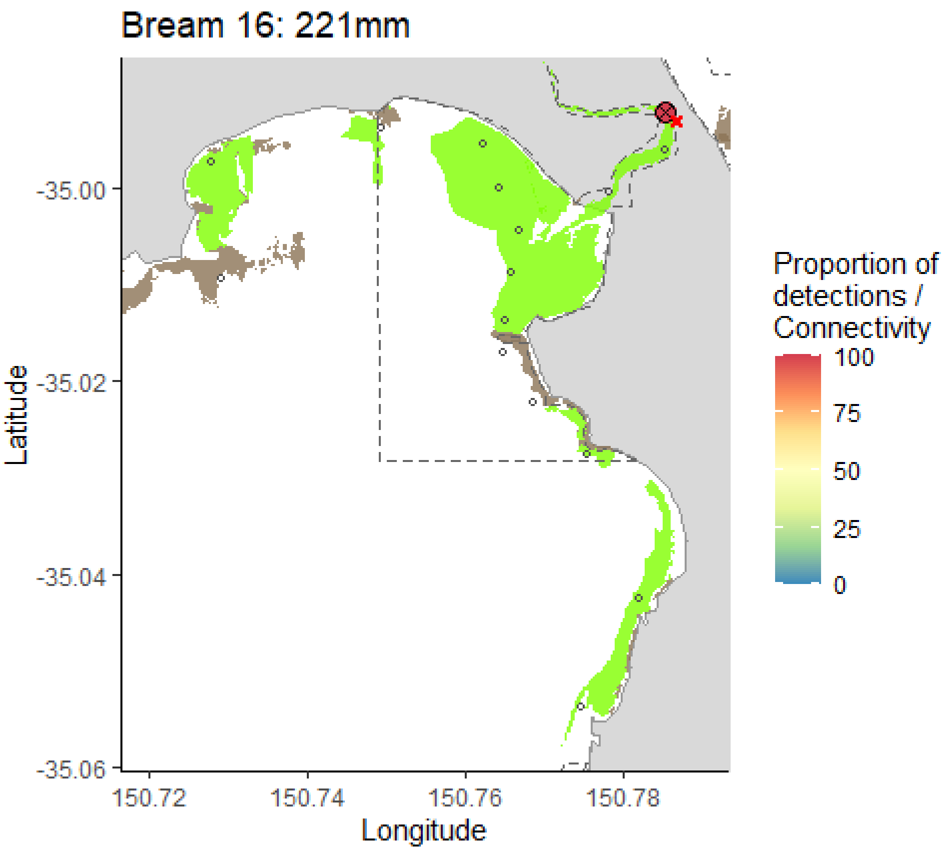
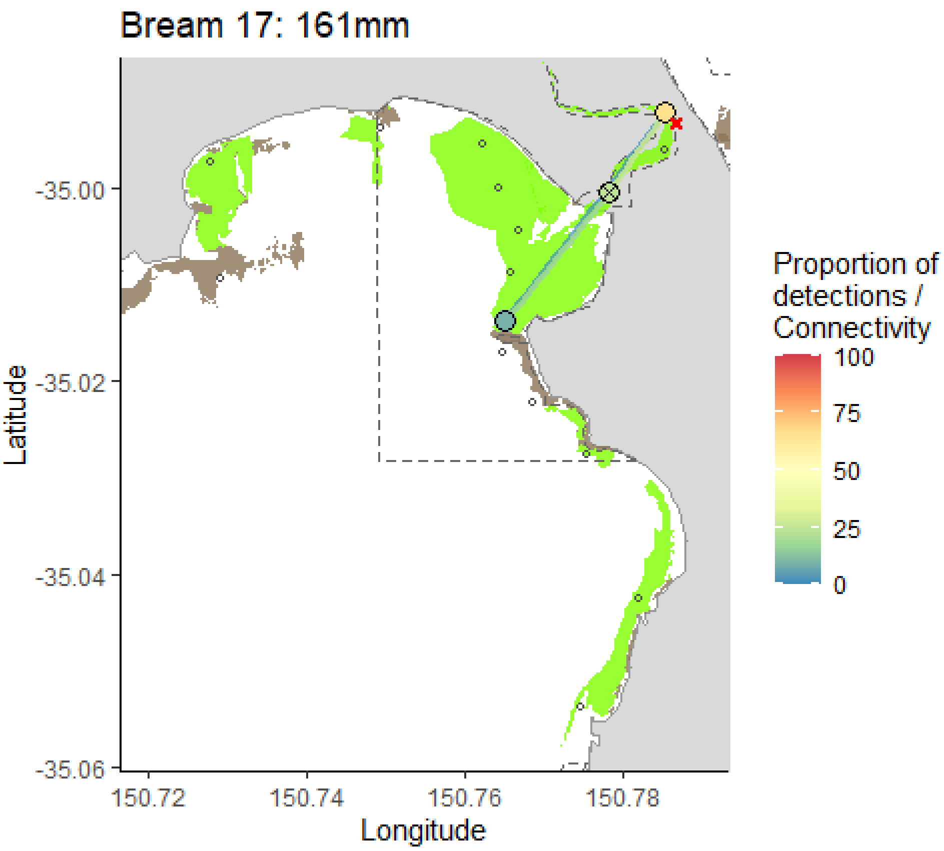
150.76
150.78
Longitude


Bream 16: 221mm
Latitude
-35.00
-35.02
-35.04
-35.06
Longitude
150.72
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0


Bream 17: 161mm
Latitude
-35.00
-35.02
-35.04
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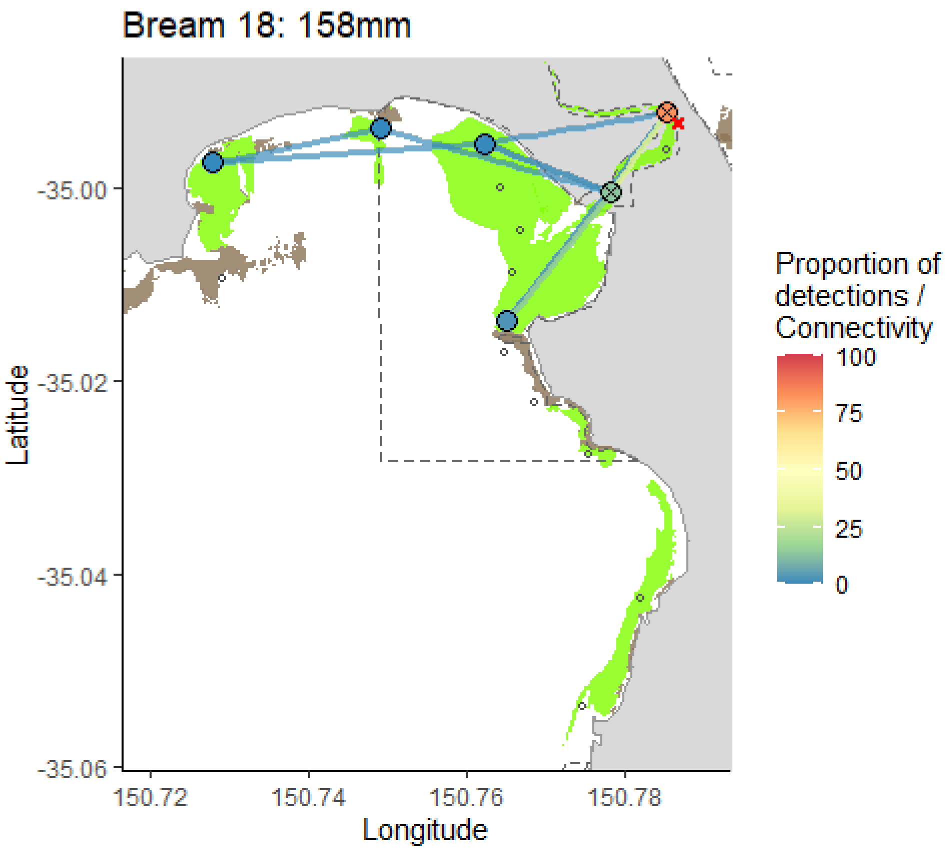
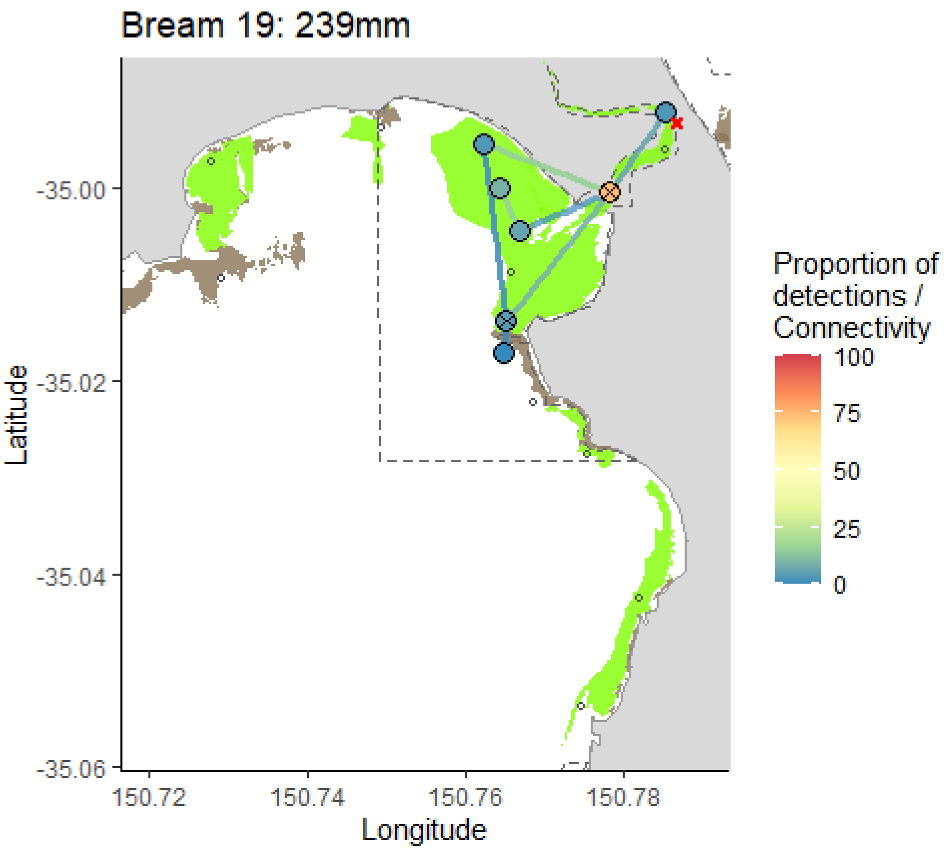
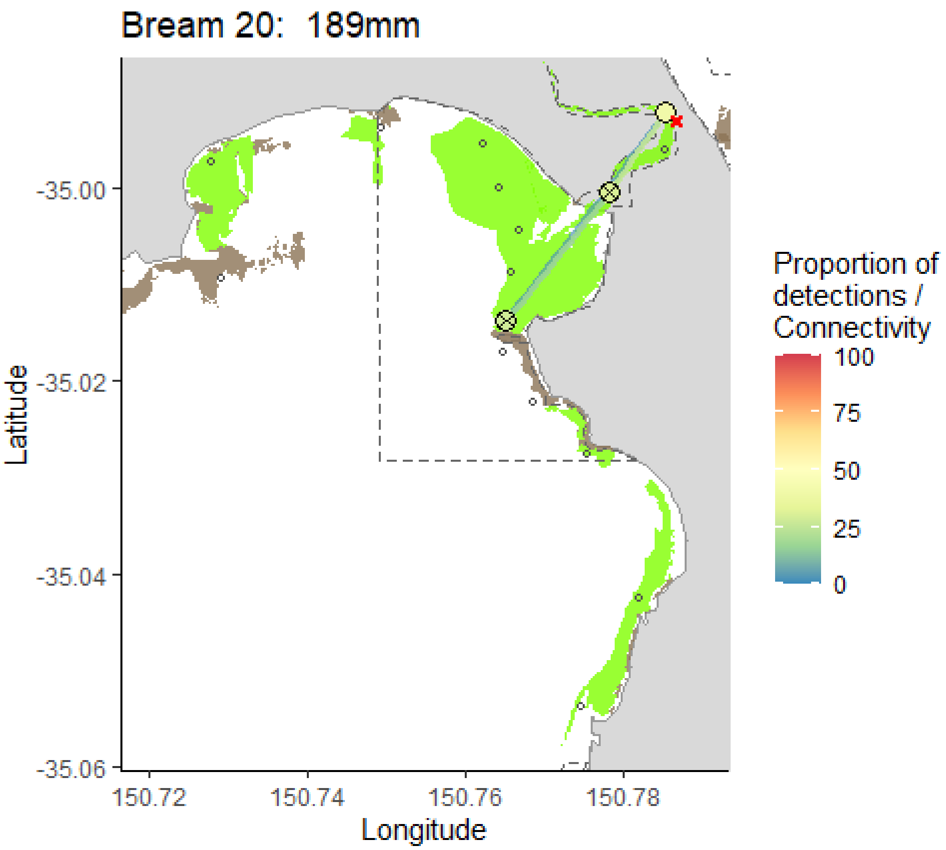
150.72
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0



Bream 18: 158mm
-35.00
-35.02
-35.04
-35.06
Latitude
150.72
150.74
150.76
150.78
Longitude
Proportion of detections / Connectivity
100
75
50
25
0


Bream 19: 239mm
Latitude
-35.00
-35.02
-35.04
-35.06
Longitude
150.72
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0


Bream 20: 189mm
Latitude
-35.00
-35.02
-35.04
-35.06
Longitude
150.72
150.74
150.76
150.78
Proportion of detections / Connectivity
100
75
50
25
0

Appendix 3

Supporting Information for

Chapter 5: Assessing generality in patterns of movement for a targeted fish: home range and residency of Luderick (Girella tricuspidata) on open coastal reefs

This includes:

Table A3.1

Table A3.1: Summary of the tagging, biological and detection data for the 10 acoustically tagged luderick (*Girella tricuspidata*) passively tracked in this study.

Fish #	Fork length (mm)	Release date	Station nearest release	Last date detected
1	290	08-08-2018	B8	14-02-2019
2	295	09-08-2018	B8	06-11-2018
3	325	09-08-2018	B8	26-01-2020
4	275	08-09-2018	B7	22-12-2018
5	312	08-09-2018	B7	19-03-2020
6	309	08-09-2018	B7	18-03-2020
7	350	09-09-2018	B7	18-03-2020
8	309	09-09-2018	B7	22-10-2018
9	323	09-09-2018	B7	25-10-2018
10	320	09-09-2018	B7	17-03-2020