The effects of habitat connectivity and complexity on the distribution of inshore reef fish communities

Alexander Jarrett

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Abstract

Coastal seascapes are valuable habitat for animals and humans alike, providing numerous ecosystem services. Within coastal seascapes, habitats that are better connected and contain highly complex structures (e.g. inshore rocky and coral reefs), often contain a greater diversity and abundance of species. Reef systems, particularly those situated near the coast, are however, under constant threat from anthropogenic disturbances and exposure to sediments, pollutants and nutrients that are discharged from the land. In this study I surveyed fish communities using two sampling methods, baited and unbaited remote underwater video systems to determine the spatial and habitat drivers of fish community structure, diversity and abundance on inshore rocky reefs. I found that species richness, harvested and total fish abundance were modified by reef complexity and connectivity to headlands, urbanistation and neighbouring reef patches. All fish functional groups, herbivores, omnivores, piscivores and zoobenthivores increased in abundance on reefs that were of moderate extent, highly complex and further urbanistation. Finally, I found that baited remote underwater video systems identified a greater diversity and overall abundance of fish compared to those on unbaited cameras. I highlight the importance of understanding the different features that influence fish assemblages in coastal seascapes, with fish communities here typically modified by reef quality and position within the broader seascape, however, these effects are modified by urbanistation. I suggest that in order to maximise benefits for fish communities, conservation and management must focus on conserving inshore rocky reefs that are located within a complex seascape and had the greatest complexity.

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Statement of Originality

I certify that the work presented in the thesis, to the best of my knowledge and belief, is original, except as acknowledged in the text, and that the material has not been submitted, either in whole or part, for a degree at this or any other university. I acknowledge that I have read and understood the university's rules and requirements relating to the awarding of my honours degree and to my thesis. I certify that I have complied with these.

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Alexander Jarrett

General Prelude

In this thesis, I examine the effects of habitat connectivity and complexity on the distribution of inshore reef fish communities.

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The effects of habitat connectivity and complexity on the distribution of inshore reef fish communities

Alexander D. Jarrett[1]*, Jesse D. Mosman[2], Ben L. Gilby[1], Andrew D. Olds[2], Christopher J. Henderson[2]

1. School of Science, Technology and Engineering, University of the Sunshine Coast, Petrie, Queensland 4502, Australia
2. School of Science, Technology and Engineering, University of the Sunshine Coast, Queensland 4558, Australia

*Corresponding author – adj012@student.usc.edu.au

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Introduction

Globally, coastal ecosystems are facing significant threat due to their heavy use from human activities (Lotze et al. 2006, Worm et al. 2006), however many of these activities are essential for trade, energy, and resource gathering (Halpern et al. 2008). Due to extensive human disturbance throughout coastal ecosystems, habitat degradation and biodiversity loss have been accelerated, undermining the ecological resilience of coastal ecosystems (Jackson et al. 2001, Syvitski et al. 2005, Barbier et al. 2011). In particular, many coastal ecosystems have been under constant threat from increased urban development, climate change and overfishing (Stuart-Smith et al. 2008), and globally, are declining in species abundance, richness and productivity (Willis et al. 2003, Mora et al. 2011). Due to the impacts of urbanisation, the health and resilience of critical fish populations and habitat have diminished, as well as the important ecological functions that they provide (e.g. herbivory, predation and carrion consumption) (Olds et al. 2018a). Coastal seascapes are composed of a mosaic of different ecosystems, including intertidal mangroves forests, saltmarsh, seagrass meadows, shellfish reefs, and coral and rocky inshore reefs (Burke et al. 2001), which are strongly influenced by the condition of the broader landscape, ultimately modifying the composition of fish communities (Mellin et al. 2016, Hölting et al. 2019, Gaines et al. 2020). For example, marine reserves located within a complex seascape,which generally have reduced human disturbance and better habitat condition (e.g. connected and complex structures), have been shown to have a greater abundance and richness of harvested and functionally important fish species than those areas impacted by humans (Gaines et al. 2020). Similarly, high quality mangrove forests and seagrass meadows that have greater complexity (e.g. increased shoot length or pneumatophore counts) can offer increased protection and refuge for juvenile fish species from predators (Primavera 1997, Nanjo et al. 2011, Nanjo et al. 2014, Mosman et al. 2023). Maintaining coastal ecosystems in a good condition and well connected with other ecosystems offers an ideal approach to support a greater abundance and diversity of coastal fish (Olds et al. 2012b).

Habitat connectivity, which is the linkage between ecosystems, modifies the movement of organisms for feeding, reproduction, and dispersal, shapes food webs and promotes diversity in ecosystems (Boström et al. 2011, Hyndes et al. 2014, Olds et al. 2018b). Habitats that are better connected often contain a greater diversity and abundance of species, and can maintain a greater level of overall ecological functioning (Olds et al. 2012b). For example, reef fish rely on connected habitats to regulate their population through predation and reproduction, with energy transferred through the ecological functions supported by species (e.g. herbivory on coral reefs) (Sheaves 2009). The magnitude and direction of connections within coastal seascapes are dictated by the spatial arrangement of ecosystems (Cowen et al. 2007, Olds et al. 2018b, Borland et al. 2021). Many marine organisms rely on high connectivity between ecosystems throughout their lives, such as the movement of coastal fish between habitats (Nagelkerken et al. 2015), migration of whales from breeding areas to feeding areas (Rosenbaum et al. 2014) and dispersal of propagules in the oceans currents (Lee et al. 2014). Human disturbance has, however, drastically impacted connectivity between ecosystems globally with land-use changes, habitat destruction and fragmentation from urbanisation pressures posing significant challenges to biodiversity and conservation worldwide (Sala et al. 2000). Improving connectivity, and reducing habitat fragmentation and loss are crucial factors for both the conservation and restoration of fish habitat as well as the management of fish communities (Gilby et al. 2018b, Young et al. 2018). Consequently, in recent years conservation, restoration and management practices that focus on improving the connectivity between complex, high quality habitats have been prioritized (Weeks 2017, Gilby et al. 2018a, Perry et al. 2023).

Complex habitats provide increased resources, refugia, and reproductive opportunities for species (Beyer et al. 2010, Doherty & Driscoll 2018), often leading to the abundance and diversity of species in an ecosystem being greater within complex ecosystems (Graham &

Nash 2013). This structural complexity creates microhabitats for animals within the ecosystem, increasing diversity and abundance due to the additional niche space that is created in these complex ecosystems (Crowder & Cooper 1982). Structural complexity can vary in degree between different marine habitats, like coral reefs or rocky reefs, which generally exhibit higher levels of complexity when contrasted with unstructured habitats such as macroalgae beds or sand/rubble beds (Hall & Kingsford 2021). Furthermore, coral reefs are some of the world's most diverse ecosystems due to the large variety of available feeding niches created by this heterogenous structural complexity (Boaden & Kingsford 2015). These complex habitats also mediate the growth and mortality rates in juvenille fish species (Bradley et al. 2019) and are often the main driver of population regulation (Chambers & Trippel 2012). Within these complex habitats, large bodied species (e.g. Lutjanidae, Haemulidae and Serranidae) rely on boulders, caves and tabulate corals found in structurally complex reefs for enhanced predation opportunities (Kerry & Bellwood 2012), while small bodied species occupy the microhabitats provided by small rocks, branching corals and seagrasses which provide shelter from predators (Wilson et al. 2008, Boström-Einarsson et al. 2013). Subsequently, this varied complexity of benthic habitats within coastal seascapes mediates predator-prey interactions (Garpe & Öhman 2003), particularly within the shelter-rich substrate of reef communities (Jones et al. 2004, Boaden & Kingsford 2015).

Globally, inshore rocky reef systems (<1.4km from shore (Vanderklift et al. 2009) typically contain a greater diversity of fish species, at higher abundance, and with a greater number of juvenile fish compared to nearby bare substrate (Guidetti 2000). Inshore reefs can be found amongst other complex non-reef habitats within heterogenous seascapes (Pittman & Brown 2011), such as surf zones (Olds et al. 2018c), estuaries (Olds et al. 2012b, Mosman et al. 2020) and headlands (Quaas et al. 2019). The highly complex structures of inshore reefs benefit fish assemblages through the shelter and resources they provide, leading to greater fish abundance and richness (García-Charton & Pérez-Ruzafa 2001, Friedlander et al. 2003, Emslie et al. 2008). Rocky and coral reef systems, particularly those situated near the coast, are under constant threat from exposure to sediments, pollutants and nutrients that are discharged from the land (McCulloch et al. 2003, Bainbridge et al. 2018) and physical pressures such as waves and currents (Jackson-Bué et al. 2022). With high wave activity, sediment may bury or expose the rocky structure increasing stress on the inshore reef, modifying both benthic and mobile marine organisms (Ricardo et al. 2016, Latrille et al. 2019). As inshore rocky reef patches are dynamic and constantly shifting, this modifies their connectivity to other habitats and the size of the reef, which ultimately will influence the distribution of coastal fish communities (Acosta & Robertson 2002, McManamay et al. 2014, Stier et al. 2014).

Coastal ecosystems are well understood in many settings (Olds et al. 2012b, Gilby et al. 2018, Mosman et al. 2020), however, quantifying the environmental drivers of inshore rocky reef fish communities within the broader coastal seascape is one area that remains understudied, particularly in subtropical seascapes. Here, we assess how habitat connectivity, context and condition variables modify the structure of fish communities on inshore rocky reefs. These ecosystems provide a crucial link for fish species in the coastal seascape mosaic, where species move between estuaries, headlands, surf zones and offshore reefs. Therefore, the aims of this study are to: 1) determine how differing habitat complexity and connectivity influence fish community structure, species richness and fish abundance on inshore rocky reefs and 2) identify how two complementary survey methods modify the outcomes of these findings. I expect that 1) higher abundance and species diversity will occur at complex and well-connected reefs due to the increased availability of resources, and foraging opportunities, and 2) that a greater abundance and diversity will occur on large reef patches that are well connected and 3) that a baited sampling approach will identify more fish species at higher abundances, due to the attraction of the bait.

Methods

Study area

Fish assemblages were recorded at a total of 13 inshore reefs across a ~35km stretch of coastline in southeast Queensland, Australia (Fig. 1), with the northern most reef being Point Arkwright (-26.54°S, 153.10°E), spanning down to the southernmost reef, Caloundra headland (-26.80°S, 153.15°E). This coastline supports a wide array of ecosystems including inshore reefs, offshore reefs and estuaries, and landscape features such as headlands and exposed beaches. This region does, however, include stretches of coastline that have been modified with moderate to high levels of urbanisation (e.g. modified shorelines, habitat removal and replaced with urban structures). To maximise variation, the 13 inshore reefs in this study were selected across a gradient of distances to (1) an estuary mouth (2) urban land (3) headlands and (4) nearest neighbouring reef patch. We sampled during the austral winter season and during daylight hours and when the tide was high (Borland et al. 2017). To minimise the effects of wave activity on sampling, I only surveyed inshore reefs when swell height was less than 1 m and swell period was below 10 seconds (Mosman et al. 2020).

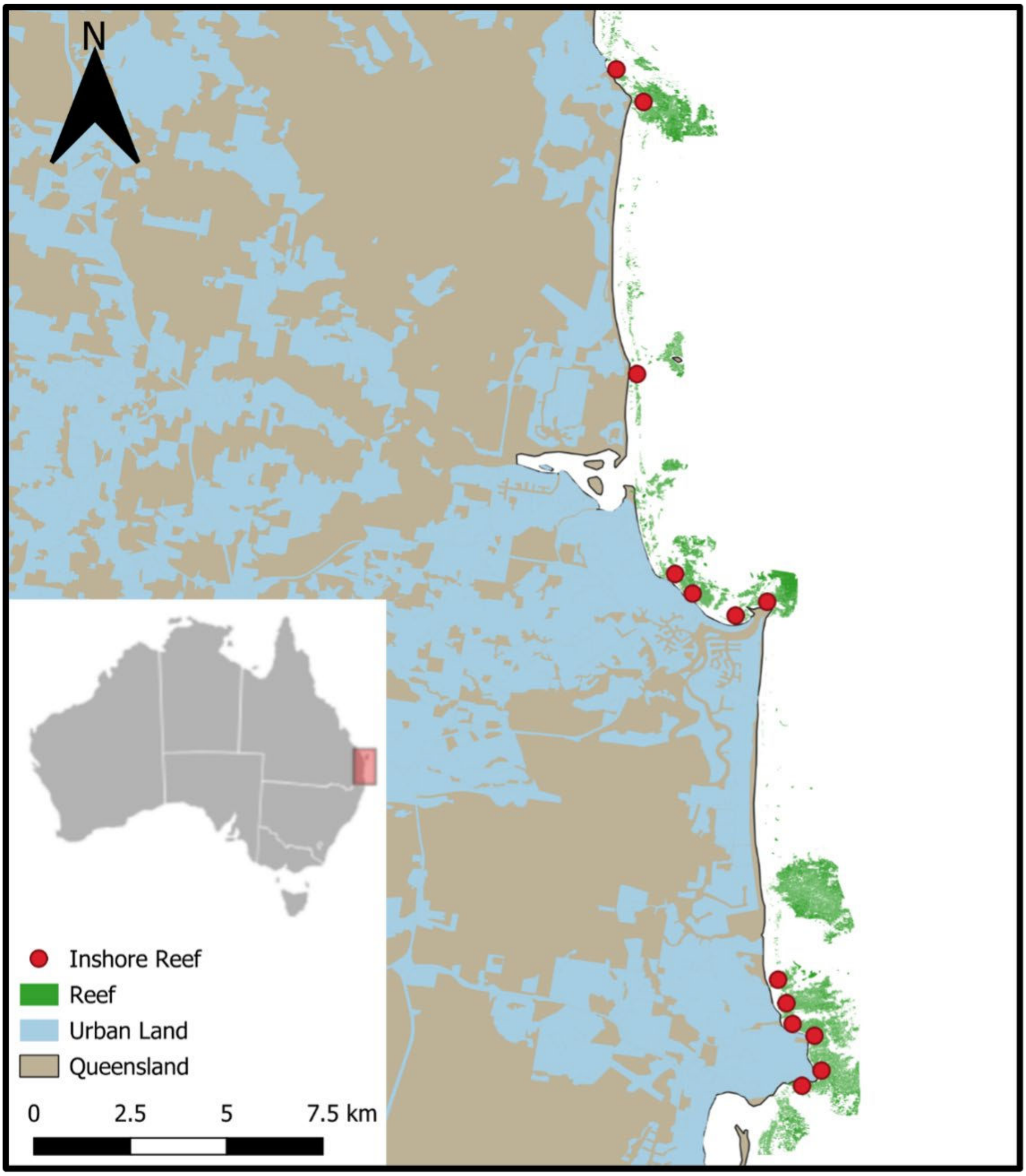

Figure 1 Fish assemblages we surveyed along a 35km stretch of coastline on the Sunshine Coast, Queensland. Locations were selected by their connectivity and variation of nearby habitats and features. To survey fish species, RUVS and BRUVS were deployed at 13 inshore reef sites, indicated by the red spots.

Fish assemblages

Fish assemblages were surveyed using unbaited and baited remote underwater video systems (RUVS and BRUVS) (Henderson et al. 2017). These devices consist of a GoPro camera mounted on a 15kg disc to ensure low movement when submerged. Each BRUVS and RUVS had a 1m PVC pipe pointing away from the camera (Ortodossi et al. 2019). For the BRUVS, a bait bag (20cm x 30cm) was filled with approximately 500g of pilchards (*Sardinops sagax*) and then attached to the end of the pipe. Pilchards were used as they are the standard bait for BRUVS in this region of the world (Wraith et al. 2013). At each site, five replicate RUVS were deployed for 30 minutes and at minimum, 200m apart to avoid the confounding effects of one individual being observed on multiple cameras (Dorman et al. 2012). Each deployment was optimally dropped in a depth of 3-4 m and made to ensure they were facing rocky reef structure (Henderson et al. 2019) . Every replicate was deployed behind the breaking waves to limit the possibility of swell moving the camera (Mosman et al. 2020). BRUVS were deployed for one hour due to the bait bags attracting more individuals subsequently maximising possible assemblage variation, with the same sites sampled as the RUVS. This yielded 32.5 hours of RUVS footage and 65 hours of BRUVS footage, a combined total of 97.5 hours. Species richness, total fish abundance, harvested fish abundance and the abundance of fish in each functional group (e.g. herbivore, omnivore, piscivore, zoobenthivore, zooplanktivore, based on Elliott et al. (2007) were calculated using the *MaxN* statistic, wherein the maximum number of individuals of the same species can be seen on a single frame at a time, a standard method when sampling with BRUVS and RUVS (Harvey et al. 2007).

Classifying seascape variables

To determine which different seascape features described the variation in coastal fish assemblage compositions I measured multiple seascape factors that are known to influence coastal fish assemblages in this region (Olds et al. 2018a, Mosman et al. 2020). I used the aerial imagery program NearMap (NearMap 2022) to measure: (1) distance to nearest estuary mouth, (2) distance to nearest headland, (3) distance to nearest reef patch, (4) distance to urbanisation, (5) distance to shoreline, and we used QGIS (QGIS Development Team 2022) to calculate (6) the area of headland within a 500m and 4km buffer, (7) the area of urban land within 500m and 4km buffer and (8) the area of reef structure within a 500m and 4km buffer of each deployment (Table 1). I decided to use these two spatial buffers to reflect both small- and large-scale impacts and habitat availability (Henderson et al. 2022). I analysed RUVS footage to categorize the complexity levels of the reef at each deployment on a rating of zero to five. Complexity ratings of zero to one were characterised by a lack of three-dimensional structure, typically bare sediment with sandy substrate. Two to three were structurally simple communities, with scattered small rocks or coral structures. Four to five contained highly complex three dimensional structures, with high vertical relief, typically many large rocks or coral growth providing refuge and shelter (Fabricius et al. 2014). In the R statistical framework (R Core Team 2022), the environmental metrics were tested for co-linearity by using the Pearson's correlation coefficient, in which it was found that distance to urban and distance to shoreline correlated ($r^2 = 0.811$) and urban area 500m buffer correlated with urban area 4km buffer ($r^2 = 1.00$), therefore the distance to shoreline and urban area 4km buffer variables were removed from any further analyses.

Data Analysis

To test which environmental factors (Table 1) influenced the variation in fish assemblages and distributions, multivariate generalised linear models (manyGLMs) were created in the *mvabund* package in R (Wang et al. 2012). Both RUVS and BRUVS analyses were conducted under the same format. Due to manyGLM models not being able to account for random factors, I included site as a fixed effect to represent the effects of within-site similarities. The manyGLM employed a negative binomial family, and the process of selecting the best-fit models involved a reverse stepwise simplification approach based on the Akaike Information Criterion (AIC), in which the best-fit model was that which contained environmental factors with the lowest AIC values. To visualize the effects of these significant factors on fish assemblages identified in the manyGLM, I used non-metric multidimensional scaling ordination (nMDS) based on a Bray-Curtis dissimilarity matrix. Vectors in the nMDS relate to significant variables in the manyGLM, with vectors pointing in the direction of sites relating to higher values of that variable, with the length of the line relating to the strength of the correlation.

Using the *glmmTMB* package in R I was then able to construct generalised linear mixed models (GLMMs) to explore the effects of our environmental variables on species richness, total fish abundance, harvested fish abundance, and the abundance of each fish functional group (Elliott et al. 2007, Brooks et al. 2017). The site variable was included in each GLMM as a random factor. Natural splines were fitted to the GLMMs with no more than three polynomial functions, to capture possible nonlinear effects using the *splines* package in R (Brooks et al. 2017). To select the best fit models for our GLMMs, we used the dredge function in the *MuMIn* package which created models by using every possible combination of factors. Here I limited our best fit models to only include up to three significant factors. I used the Anova function in the *car* package to calculate the p-value and chi-squared values (χ^2) for each variable in the GLMMs (Fox et al. 2007). The distribution of the residuals, outliers and dispersal of variance was checked at the beginning of each GLMM to identify which distribution family to use. RUVS GLMMs utilized a poisson distribution while the over dispersed BRUVS models were distributed using the negative binominal family (Wang et al. 2012).

Table 1 Definition and measurement methods of environmental variables.

Variable	Definition	Predictive Hypothesis	Units	Method
Distance to estuary	The gap between a deployment and the nearest estuarine inlet	Estuaries often release nutrients into nearby marine ecosystems in the form of plumes (Hyndes et al. 2014). This boost in nutritional support to the ecosystem may promote species diversity and richness at closer deployments.	Meters	Nearmap
Distance to headland	The gap between a deployment and the nearest headland	Typically headlands are complex coastal habitats which increase biodiversity, functional diversity, and abundance (Ortodossi et al. 2019). I predict that deployments within proximity of a headland will support more fish species with high levels of functional diversity.	Meters	Nearmap
Distance to reef	The gap between separated reef structures	Neighbouring reef rocky reef structure adds habitat heterogeneity, promoting an increase in species richness, abundance, and functional diversity (Ortodossi et al. 2019). Here I predict that reef patches close together will support greater fish species and functional diversity than more isolated patches.	Meters	Nearmap
Distance to Urbanisation	The gap between a deployment and the nearest urban structure	The effects of urbanisation have been found to extract resources, spread pollution and alter species compositions (Halpern et al. 2008). Therefore it is predicted that species richness, abundance and functional diversity will be highest further form urban disturbances.	Meters	Nearmap
Distance to shoreline	The gap between a deployment and the shoreline	It is predicted that species will prefer further distance from the shoreline due to deeper waters, and further distance from human disturbances.	Meters	Nearmap
Area of headland	The area of headland within a 500m^2 or 4km^2 buffer of each deployment	Higher headland area would suggest larger headlands, indicating more complex habitat. I predict higher abundance and richness when area of headland increases across both metrics.	Meters squared	QGIS
Area of urban land	The area of urbanisation within a 500m^2 or 4km^2 buffer of each deployment	I predict that urbanisation within 500m^2 of a deployment will negatively impact fish communities, however urbanisation within 4km^2 is too far from a deployment to have much of an impact.	Meters squared	QGIS
Area of reef	The area of reef within a 500m^2 or 4km buffer of each deployment	Here I predict as the area of reef increases, so will abundance, richness and functional diversity due to the high levels of habitat heterogeneity that is found in reef habitats.	Meters squared	QGIS

Results

I found 97 species on inshore reefs over 96 hours of camera footage from the BRUVS and RUVS. I found 71 species and 2328 individuals with the RUVS footage, and 81 species and 2924 individuals from the BRUVS. Black rabbitfish (*Siganus fuscescens*) was the most frequently occurring species across both BRUVS and RUVS occurring 663 and 605 times respectively. Additionally noted was the high abundance of eastern Sea garfish (*Hyporhamphus australis)* which occurred 223 times on the BRUVS and 179 times on the RUVS, and yellowtail scad with 228 individuals observed on the RUVS and 223 individuals on the BRUVS.

Habitat context and connectivity modifies fish communities

Habitat context and connectivity significantly influenced the variation in fish assemblage compositions (Fig. 2, Table 2). I found that RUVS fish assemblages were most impacted by distance to estuary and area of reef within 500m buffer (Fig. 2a), however, assemblages analysed on the BRUVS indicated they were most influenced by headland area within a 500m buffer (Fig. 2, Table 2). Different metrics describing the fish community (e.g. species richness, harvested fish abundance and total fish abundance) observed on the RUVS were best explained by reef area within a 500m^2 buffer, reef complexity, urban area within a 500m^2 buffer, distance to urbanisation and distance to headland (Fig. 3). Similarly, the best fit models for BRUVS deployments indicated that reef area, urban area and headland area within 500m^2 buffers, reef complexity, distance to nearest reef patch and distance to urbanisation explained the variation in fish metrics (Fig. 4). On the RUVS analyses, species richness was highest when reef area had a moderate extent (χ^2 = 9.331, p = 0.009, Fig. 3a), and when reefs were complex (χ^2 = 28.111, p <0.001, Fig. 3b). Harvested fish abundance was found to increase as reef complexity increased (χ^2 = 53.264, p <0.001, Fig. 3e). Total fish abundance on RUVS increased when either in immediate proximity or very far away from a headland (χ^2 = 64.347, p <0.001, Fig. 3g) and when the reef was complex (χ^2= 137.882, p <0.001, Fig. 3h). BRUVS footage revealed that species richness increased with reef complexity (χ^2 = 11.359, p = 0.003, Fig. 4a) and reef area (χ^2 = 12.644, p = 0.002, Fig. 4b). Harvested fish abundance on the BRUVS was highest when close to neighbouring reef patches (χ^2 = 15.132, p <0.001, Fig. 4d) and when nearby headland area was small (χ^2 = 8.179, p = 0.017, Fig. 4e). Total fish abundance on BRUVS was highest when neighbouring reef patches were far away (χ^2 = 171.046, p = <0.001, Fig. 4g) and when reef area was reduced (χ2 = 102.033, p = <0.001, Fig. 4i).

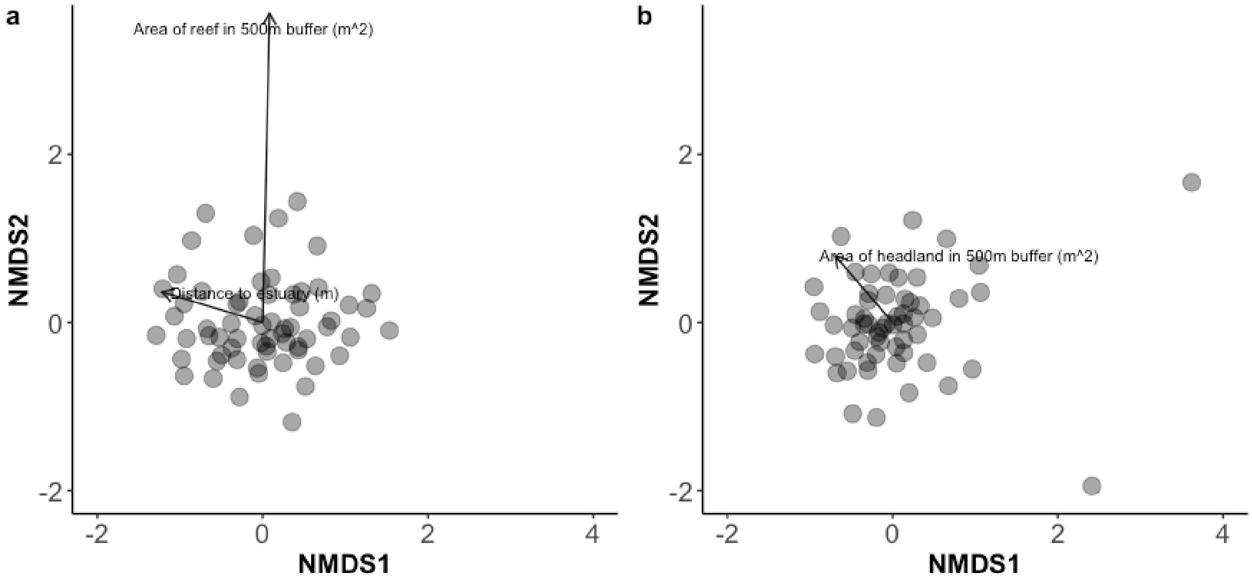

Figure 2 Non-metric multi-dimensional scaling ordinations (nMDS) highlighting the effects of environmental factors across the entire fish assemblages. For the RUVS deployment, a) displays the relationship between area of reef in a 500m^2 buffer with distance to estuary and the one indicator species identified in our manyGLM. The BRUVS (b) illustrates the correlation of area of headland in a 500m^2 buffer on the assemblage. The black line indicates the correlation of the environmental factor on the fish assemblages.

Table 2 Summary of “p uni” results, indicating the most significant habitat type for fish assemblages observed across both sampling methods

Factor	χ^2	p
Remote Underwater Video Stations	141.9	0.005
Distance to estuary	129.3	0.018
Reef area 500m buffer (m^2)		
Baited Remote Underwater Video Stations		
Headland area 500m buffer (m^2)	142.5	0.008

Urbanisation negatively impacts fish communities

All fish metrics (e.g. species richness, harvested fish abundance and total fish abundance) recorded on RUVS and BRUVS included at least one urban area within a $500m^2$ buffer and distance to urban measurement in the best fit model (Fig. 3 & 4). Species richness observed on the RUVS was highest when the area of nearby urbanisation was lowest (χ^2 = 11.848, p = 0.003, Fig. 3c). Harvested fish abundance increased when in proximity to urbanisation (χ^2 = 34.561, p <0.001, Fig. 3d), and was highest when sites had a low extent of urbanisation (χ^2 = 187.124, p <0.001, Fig. 3f). RUVS recorded a greater total fish abundance when urban area was at a moderate extent (χ^2 = 212.535, p <0.001, Fig. 3i). The BRUVS deployments highlighted that species richness was impacted by urban area within a $500m^2$ buffer, with species richness at its highest at a moderate extent of urban area (χ^2 = 8.721, p = 0.013, Fig. 4c). Harvested fish abundance also was at its highest when urban area within a $500m^2$ buffer had moderate extent (χ^2 = 24.242, p <0.001, Fig. 4f). Total fish abundance on BRUVS was highest when at a moderate distance away from urbanisation (χ^2 = 95.203, p = <0.001, Fig. 4h).

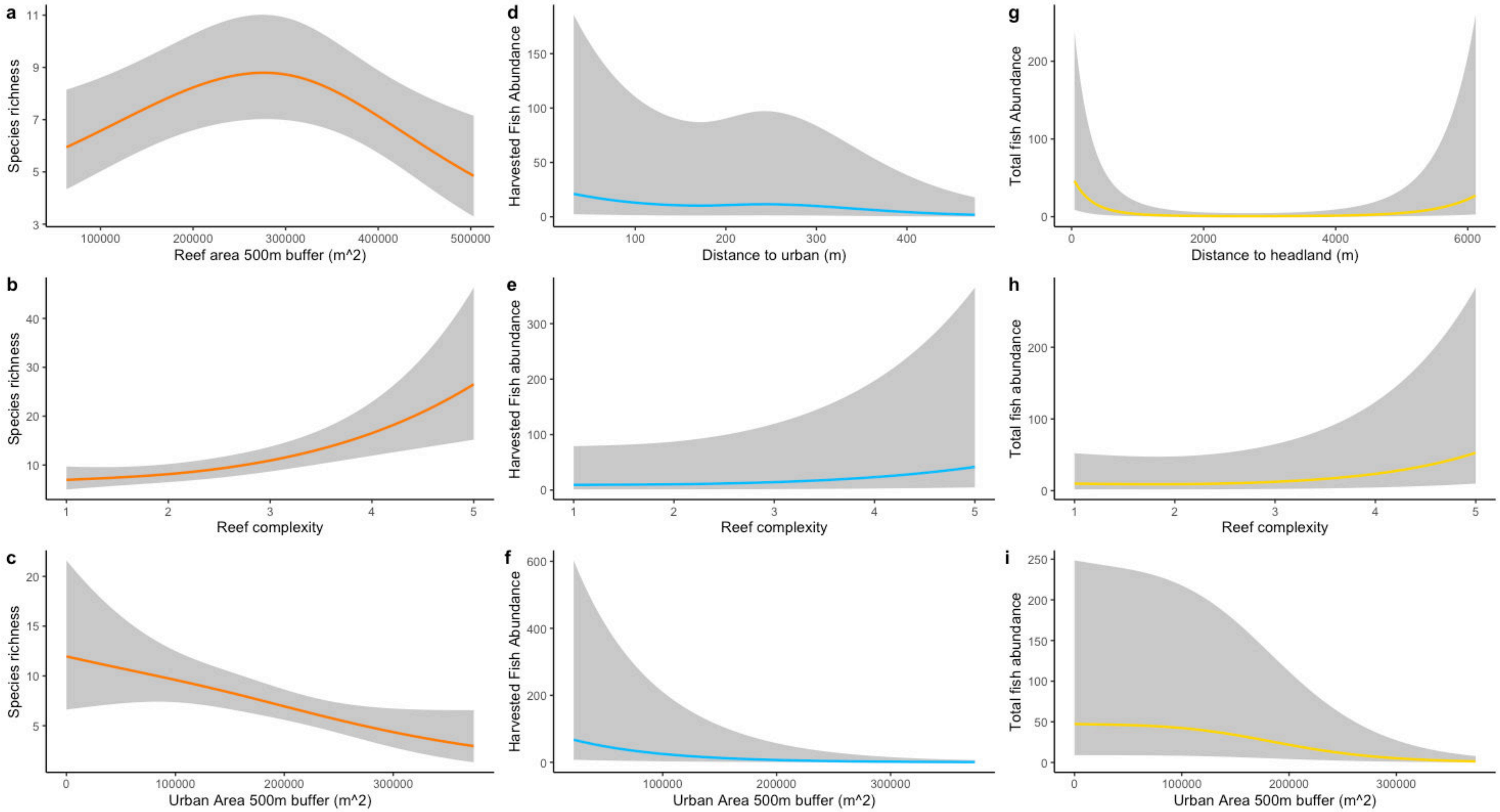

Figure 3 Generalised linear mixed models highlighting the effects between different environmental and urban factors on the RUVS analysis. (a-c) illustrates the variation of species richness, (d-f) illustrates harvested fish abundance, and (g-i) highlights total fish abundance variation. Grey shaded area illustrates the 95% confidence intervals.

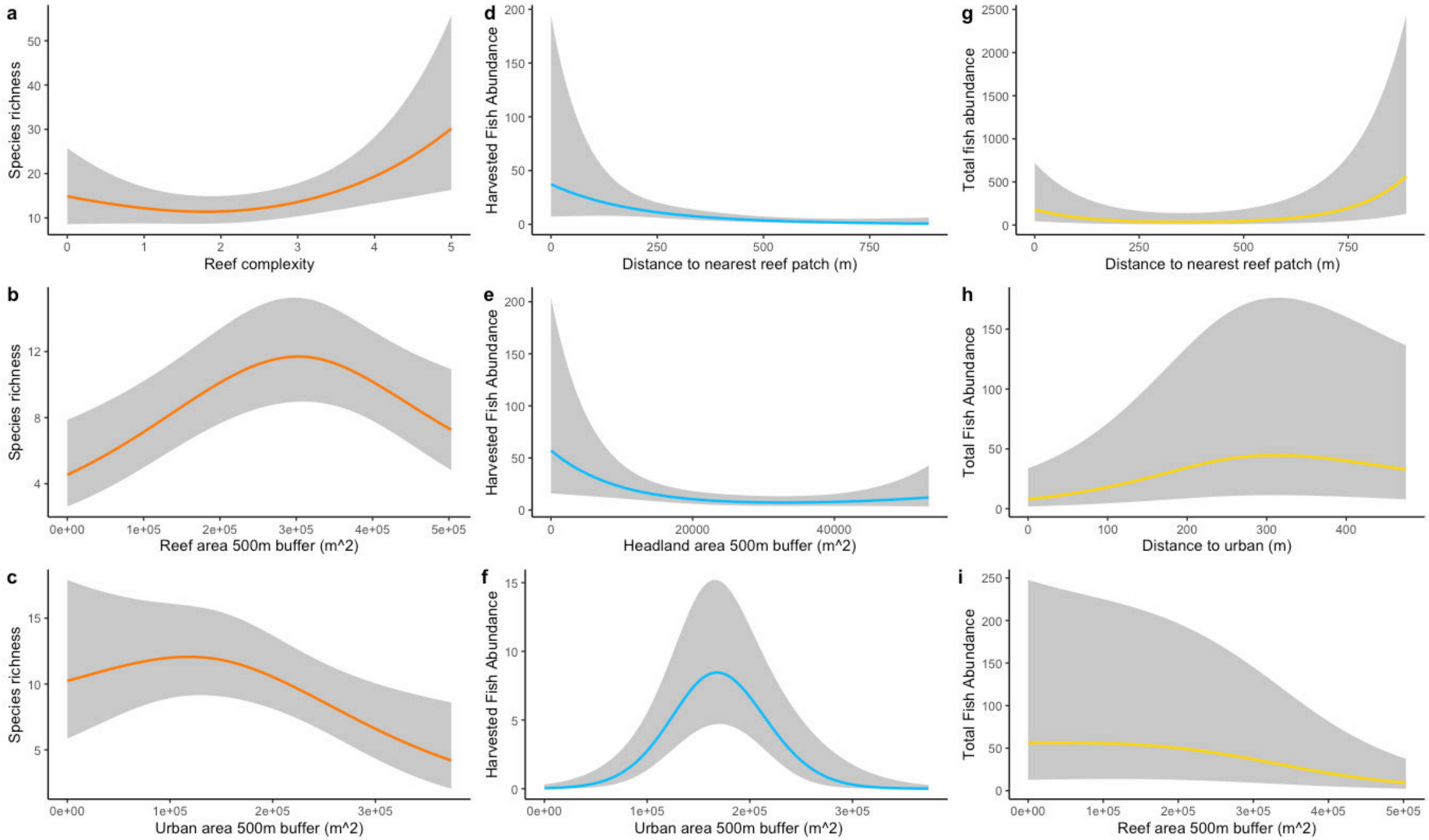

Figure 4 Generalised linear mixed models highlighting the effects of different environmental and urban factors on the BRUVS analysis. (a-c) shows the variation in species richness, (d-f) highlights harvested fish abundance variation and (g-i) indicates the variation in total fish abundance. Grey shaded area illustrates the 95% confidence intervals.

Functional group distributions

Zoobenthivores were the most dominant functional group across both deployment methods with 53 species identified. I found 13 species of herbivores, 7 species of omnivores, 23 species of piscivores and only 1 zooplanktivore. Due to only observing one zooplanktivore (southern herring, *Herklotsichthyes castelnaui*) on BRUVS footage, the GLMM was modelled on southern herring abundance alone as the representative for the functional group. The most abundant species were black rabbitfish (*Siganus fuscescens*), yellowtail scad (*Atule mate*), eastern sea garfish (*Hyporhamphus australis*), eastern pomfred (*Schuettea scalaripinnis*) and Gunthers wrasse (*Pseudolabrus guentheri*). The top harvested species were black rabbitfish, yellowtail scad, southern herring and stripped barracuda (*Sphyraena obtusata)*.

Herbivores

The most abundant herbivore that occurred across all sites was the black rabbitfish which we observed 1268 individuals. For the RUVS analysis, herbivores were typically found occupying sites that had low urban area within a 500m^2 buffer ($\chi 2$ = 5.729, p = 0.057, Fig. 5a), with a gradual decrease in individuals as urban area increased. However on the BRUVS, herbivore abundance was higher when distance to headland was at a moderate extent (χ^2 = 8.962, p = 0.012, Fig. 6a), when the headland area within 500m^2 was lowest (χ^2 = 29.829, p <0.001, Fig. 6b), and when the urban area within a 500m^2 buffer was at a moderate extent (χ^2 = 10.319, p = 0.006, Fig. 6c).

Omnivores

The omnivore that was most abundant was the eastern sea garfish occurring a total of 369 times. Omnivore variation was explained on the RUVS by distance to estuary with higher abundance when near the estuary mouth (χ^2 = 12.195, p = 0.006, Fig. 5b). Reef complexity modified omnivore abundance with this being highest when the complexity rating was a four or higher (χ^2 = 6.315, p= 0.042, Fig. 5c). Lastly, on the BRUVS observations we found that omnivore abundance is highest when either near or very far from nearby reef patches (χ^2 = 17.703, p = 0.021, Fig. 6d). Complexity impacted omnivores with a higher abundance occurring when the complexity rating was 3 or higher (χ^2 = 16.304, p <0.001, Fig. 6e). Omnivore abundance was highest when reef area within a 500m buffer was at a moderate extent (χ^2 = 10.309, p = 0.006, Fig. 6f).

Piscivores

The most frequently occurring piscivore species was the yellowtail scad with 451 individuals observed. The RUVS analysis found that piscivore variation was best explained by the urban area within a $500m^2$ buffer with piscivore abundance being highest when urban area was lowest (χ^2 = 6.5519, p= 0.038, Fig. 5d). The BRUVS analysis found that piscivores were most abundant when close to the estuary mouth (χ^2 = 13.227, p = 0.001, Fig. 6g). Piscivores were most abundant when reef area within a $4km^2$ buffer was large (χ^2 = 19.760, p <0.001, Fig. 6h). Piscivores were modified by urban area within a $500m^2$ buffer, with a higher abundance when urban area was lowest (χ^2 = 9.554, p = 0.008, Fig. 6i).

Zoobenthivores

The most abundant zoobenthivore observed was the eastern pomfred with 349 total individuals noted. There were no environmental factors that best explained the variation of zoobenthivores on the RUVS analysis. Zoobenthivore abundance on BRUVS was found to be highest at an intermediate distance away from headlands (χ^2 = 8.593, p = 0.013, Fig. 6j). Zoobenthivore abundance was highest when close to a nearby reef or when further away (χ^2

= 6.857, p = 0.032, Fig. 6k). Zoobenthivores were most abundant at a moderate extent of reef area (χ^2 = 7.682, p = 0.021, Fig. 6l).

Zooplanktivores

I only observed one zooplanktivore species, the southern herring which had an abundance of 95 individuals, but this was only recorded on one BRUVS deployment. There were no environmental factors that significantly modified the abundance of southern herring (Table 3).

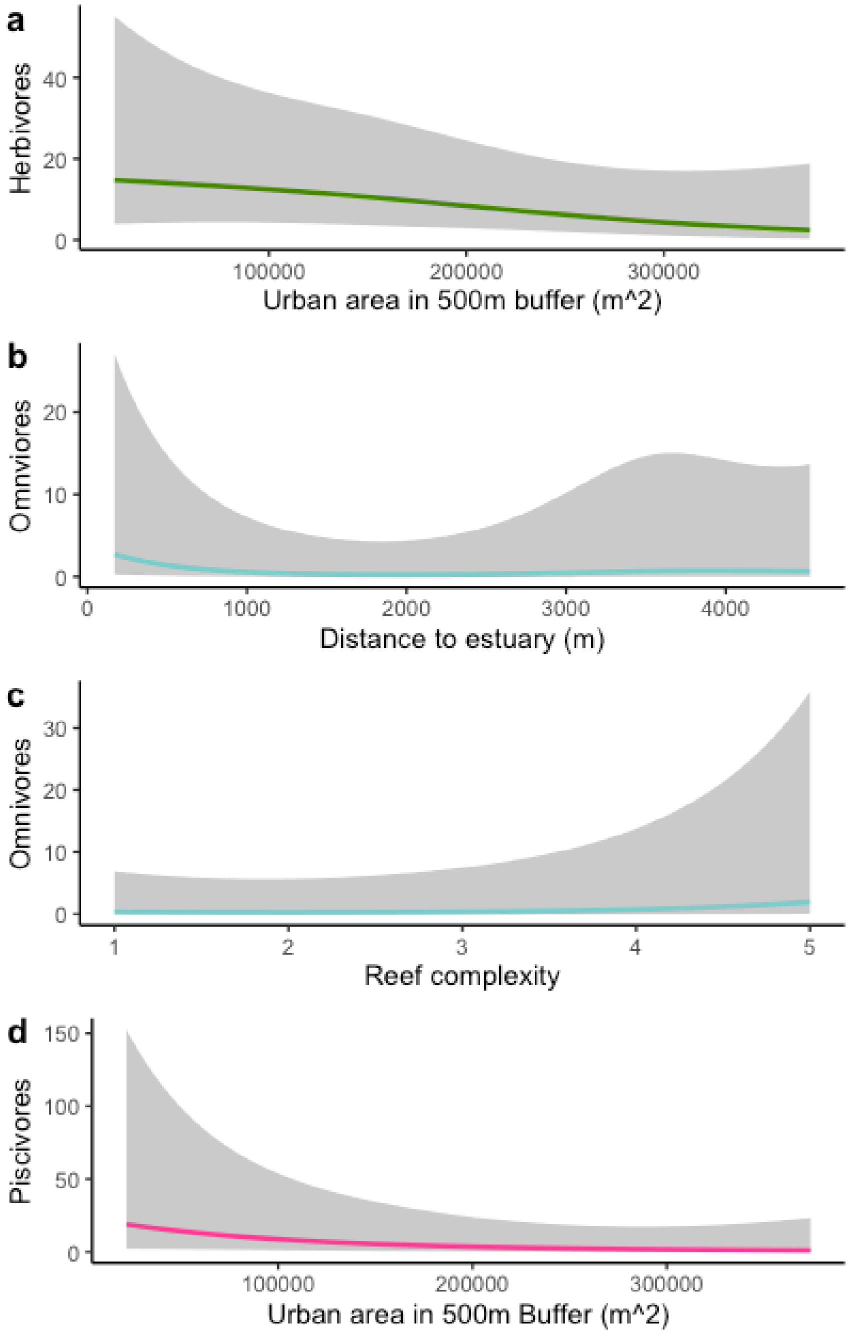

Figure 5 Generalised linear mixed models illustrating the effects of different factors describing the variation of the functional groups on the RUVS analysis. Grey shaded area illustrates the 95% confidence intervals.

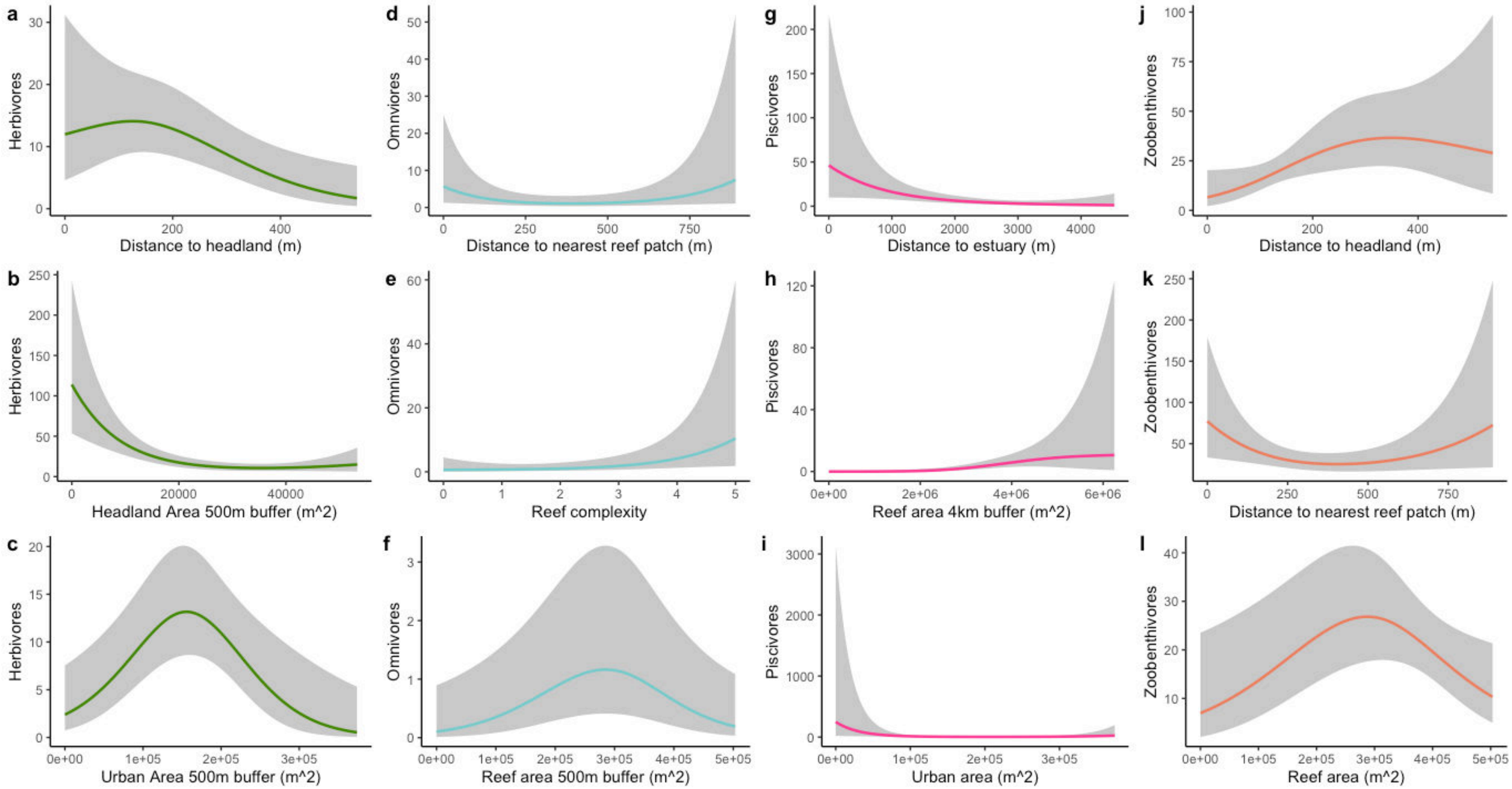

Figure 6 **Generalised linear mixed models illustrating the effects of environmental and urban factors on the (a-c) herbivores, (d-f) omnivores, (g-i) piscivores and (j-l) zoobenthivores on the BRUVS analysis. Grey shaded area illustrates the 95% confidence intervals.**

Table 3 The best fit models and their significant values for each response variable on RUVS and BRUVS

Response variables	**Best fit model**
RUVS	
Species richness	Reef area 500m buffer (χ^2 = 9.331, p = 0.009) + Reef complexity (χ^2 = 28.111, p <0.001) + Urban area 500m buffer (χ^2 = 11.848, p = 0.003)
Harvested fish abundance	Distance to urban (χ^2 = 34.561, p <0.001) + Reef complexity (χ^2 = 53.264, p <0.001) + Urban area 500m buffer (χ^2 = 187.124, p <0.001)
Total fish abundance	Distance to headland (χ^2 = 64.347, p <0.001) + Reef complexity (χ^2 = 137.882, p <0.001) + Urban area 500m buffer (χ^2 = 212.535, p <0.001)
Herbivores	Urban area (χ^2 = 5.729, p = 0.057)
Omnivores	Distance to estuary (χ^2 = 12.195, p = 0.006) + Reef complexity (χ^2 = 6.315, p= 0.042) + Distance to headland (χ^2 = 5.597, p = 0.061)
Piscivores	Urban area 500m buffer (χ^2 = 6.5519, p= 0.038)
Zoobenthivores	Distance to estuary (χ^2 = 45.853, p <0.001) + Distance to urban (χ^2 = 65.907, p <0.001) + Headland area 500m buffer (χ^2 = 45.329, p <0.001)
BRUVS	
Species richness	Urban area 500m buffer (χ^2 = 8.721, p = 0.013) + Reef area 500m buffer (χ^2 = 12.644, p = 0.002) + Reef complexity (χ^2 = 11.359, p = 0.003)
Harvested fish abundance	Distance to nearest reef patch (χ^2 = 15.132, p <0.001) + Headland area 500m buffer (χ^2 = 8.179, p = 0.017) + Urban area 500m buffer (χ^2 = 24.242, p <0.001)
Total fish abundance	Distance to nearest reef patch (χ^2 = 171.046, p = <0.001) + Distance to urban (χ^2 = 95.203, p = <0.001) + Reef area 500m buffer (χ^2 = 102.033, p = <0.001)
Herbivores	Distance to headland (χ^2 = 8.962, p = 0.012) + Headland area 500m buffer (χ^2 = 29.829, p <0.001) + Urban area 500m buffer (χ^2 = 10.319, p = 0.006)
Omnivores	Distance to nearest reef patch (χ^2 = 17.703, p = 0.021) + Reef area 500m buffer (χ^2 = 10.309, p = 0.006) + Reef complexity (χ^2 = 16.304, p <0.001)
Piscivores	Distance to estuary (χ^2 = 13.227, p = 0.001) + Reef area 4km buffer (χ^2 = 19.760, p <0.001) + Urban area 500m buffer (χ^2 = 9.554, p = 0.008)
Zoobenthivores	Distance to nearest headland (χ^2 = 8.593, p = 0.013) + Distance to nearest reef patch (χ^2 = 6.857, p = 0.032) + Reef area 500m buffer (χ^2 = 7.682, p = 0.021)
Zooplanktivores	NULL

Discussion

Habitat complexity, and connectivity impact fish communities and are essential to determining the distribution of fish species and to design critical conservation and management strategies (Airoldi et al. 2005). Additionally, the condition, availability, and context of habitats, which are influenced by the physical and biological aspects of seascapes, can further dictate the composition of fish assemblages in marine ecosystems (Sheaves 2009, Nagelkerken et al. 2015, Borland et al. 2017). In this study I found that fish richness was influenced by the area of reef and urbanisation nearby and the complexity of that reef. Harvested fish abundance was highest when nearby headland area and urban area was low and when close to neighbouring, highly complex reef systems. Similarly total fish abundance was influenced by connectivity and the area of nearby headlands, urbanisation and neighbouring reef patches and reef complexity. I found that herbivores and piscivores on both RUVS and BRUVS sites were more common when nearby urban area was minimised. Similarly, herbivores and zoobenthivores, both had an increase in abundance when headland area was at a moderate extent. Omnivores and zoobenthivores were more abundant when the area of reef nearby had a moderate extent. Lastly, omnivores and piscivores were more common when near an estuary. I highlight the need to prioritise the management of complex inshore reef habitats within diverse seascapes that have reduced urbanisation nearby in order to maximise fish abundance, diversity and a diversity of fish functional groups.

Inshore rocky reef systems typically provide benefits for fish communities through the added shelter and resources they provide, leading to greater fish abundance and diversity (García-Charton & Pérez-Ruzafa 2001, Friedlander et al. 2003, Emslie et al. 2008). Although many coastal ecosystems are well studied (Olds et al. 2012b, Gilby et al. 2018, Mosman et al. 2020), little is known about the environmental factors that influence inshore rocky reef fish communities, particularly within sub-tropical seascapes. Here, I found that complexity, the area of reef and connectivity to natural ecosystems strongly influenced species richness, total fish abundance, harvested fish abundance and the abundance of the multiple fish functional groups, highlighting the importance of complex seascapes in structuring coastal fish communities. For example, I found the herbivores, with the most common being the black rabbitfish, were more abundant in rocky headlands that consist of subtidal rocky reef. This reef is ideal habitat for algae growth due to clearer water, promoting herbivore abundance (Witman & Dayton 2001, Thibaut et al. 2017). Similarly, omnivore abundance increased on mid-sized complex reef systems, which provide a broad variety of algae and benthic organisms to feed on (Thompson et al. 2007), and when nearby estuaries, which are highly productive ecosystems with a wide availability of prey items such as juvenile fish and invertebrates (Schlacher & Connolly 2009). Lastly, I identified that the complexity and area of the reef system and proximity to headland was a significant factor influencing the total abundance of fish, the abundance of harvested fish and the abundance of zoobenthivores (Borland et al. 2022). Our findings support the maintenance of diverse and complex seascapes as a key feature of coastal seascape as they modify the distribution and abundances of key components of the fish community (e.g. diversity, abundance and the abundance of key functional groups), however the impacts of urbanisation are likely to be detrimental to these effects on inshore reefs.

Human disturbance such as increased urban development, climate change and overfishing can reduce connectivity, condition and extent of coastal ecosystems (Stuart-Smith et al. 2008, Bishop et al. 2017). These impacts of urbanisation, reduce the health and resilience of critical fish populations and their habitat, as well as the important ecological functions that they provide (e.g. herbivory, predation and carrion consumption) (Olds et al. 2018a). In this study, species richness, total fish abundance and harvested fish abundance recorded on unbaited camera were found to decline as urban area increased or when close to nearby urbanisation, contrasting to the baited cameras where we found that species richness and harvested fish abundance both benefited from a moderate extent of urbanisation. This result suggests that some species may be able to cope with moderate levels of disturbance, with some impacted ecosystems containing a greater abundance of food or refuge (Aronson et al. 2014, Dafforn et al. 2015, Olds et al. 2018a) For example, I found that herbivores were more abundant in ecosystems near a moderate extent of urbanisation, which commonly contain in-water structures (e.g. jetties, pontoons and artificial seawalls) and increased nutrients that promote algal growth (Bishop et al. 2017). Conversely, I found piscivores to be negatively impacted by human disturbance. In this study, the most commonly occurring piscivores observed were yellowtail scad, thick lip trevally (*Ferdauia orthogrammus)* and *Sphyraena* species which are the targets of commercial and recreational fishers (Defeo et al. 2009, Vargas-Fonseca et al. 2016). I show that human disturbance has contrasting effects on coastal fish assemblages. Herbivores may benefit from urban structures promoting specific shelter and feeding opportunities, while piscivores may actively avoid areas impacted by humans due to increased recreational fishing. I suggest that urban development strategies concentrated in coastal regions be approached with caution, aiming to minimize potential adverse impacts on the coastal fish populations.

Identifying the habitat context, connectivity and condition of ecosystems that are optimal for maintaining increased biodiversity, productivity and ecosystem functioning is essential for the conservation of coastal environments (Nagelkerken et al. 2015, Olds et al. 2016). Furthermore, the levels of nearby urbanisation, the complexity of habitats and their configuration should be considered when determining suitable locations for management and conservation (Crowder et al. 2000, Olds et al. 2012a). Here, I highlight that coastal fish communities typically benefit from an increased diversity of natural ecosystems within the seascape and are negatively impacted by anthropogenic disturbances. I suggest that conservation and management strategies moving forward, should be focused around moderate to large sized reefs with high levels of complexity. The natural features of coastal seascapes were consistently beneficial for species richness, total fish abundance and the array of functional groups. In our study region, complex inshore reef systems are typically established around natural headlands, which should be the focus for conservation efforts, particularly when those headlands are in close proximity to estuaries. These identified rocky reef ecosystems are pivotal for the promotion of biodiversity (Beger et al. 2010), the maintenance of ecological functions (e.g. predation, herbivory, carrion consumption) (Manning et al. 2018), and facilitate the provisioning of ecosystem services (fisheries) (Ferreira et al. 2019) that the fish communities provide. Of the 97 species observed in this study, approximately 20 are targeted by recreational and commercial fisheries. Following the suggested strategies will benefit the coastal fish communities by providing essential habitat required for shelter, feeding and reproduction, promoting fish populations and subsequently benefiting recreational and commercial fisheries (Olds et al. 2012a, Edgar et al. 2020). Ultimately, due to the unique and essential roles of the functional groups found in these marine ecosystems it is of paramount importance to recognise and address the different conservation strategies required to benefit all functional groups to maintain a healthy and sustainable ecosystem (Sheaves 2009, Hall & Kingsford 2021).

This study highlights how complex natural ecosystems, their connectivity to other ecosystems, their context within the broader seascape and the level of nearby human disturbance can modify the distribution and abundance of coastal fish species found within nearshore rocky reef ecosystems. I identified that increased complexity and connectivity of the rocky reefs to other ecosystems were the main factors that positively modified the species richness, total fish abundance, harvested fish abundance and functional group composition, and suggest that maintaining these features should be a key focus for conservation and management. However, I did find that in some contexts a moderate amount of urbanisation provided benefits for some coastal species and therefore when designing conservation strategies should not be viewed as a reason to not implement conservation or management. Understanding how human disturbances and the composition of the coastal seascape interact to modify fish communities is key to maintaining diverse and abundant coastal fish assemblages now and in the future.

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