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Original Article

Contrasting effects of mangroves and armoured shorelines on fish assemblages in tropical estuarine seascapes

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Coastal seascapes are composed of a diversity of habitats that are linked in space and time by the movement of organisms. The context and configuration of coastal ecosystems shapes many important properties of animal assemblages, but potential seascape effects of natural and artificial habitats on nearby habitats are typically considered in isolation. We test whether, and how, the seascape context of natural and urban habitats modified fish assemblages across estuaries. Fish were sampled with underwater videos in five habitat types (mangroves, rock bars, log snags, unvegetated sediments, armoured shorelines) in 17 estuaries in eastern Australia. Different habitats supported distinct fish assemblages, but the spatial context of mangroves and armoured shorelines had pervasive ecological effects that extended across entire estuaries. In most estuarine habitats, fish diversity and abundance was greatest when they were in close proximity of mangroves, and decreased due to the proximity of armoured shorelines. Many cities are centred on estuaries, and urban expansion is often associated with the fragmentation of mangrove forests. Our findings emphasize that these transformations of urban estuarine landscapes are likely to propagate to broader ecological impacts detectable in multiple habitats beyond mangrove forests.

Keywords: biodiversity, fish community, seascape, tropical estuaries, urbanization

Introduction

The spatial context of ecosystems can shape the composition of animal assemblages, the distribution of ecological functions, and the structure of food webs in landscapes and seascapes (Turner and Gardner, 2015; Pittman, 2017). Coastal seascapes form a mosaic of different ecosystems, which provide habitat for fish and other mobile marine organisms that move between habitat patches to feed, seek refuge from predators, spawn, and disperse (Sheaves, 2009; Nagelkerken *et al.*, 2015). The abundance and diversity of fish in many seascapes is, therefore, frequently determined by the complexity, composition, and spatial context of coastal ecosystems (Grober-Dunsmore *et al.*, 2009; Boström *et al.*, 2011; Olds *et al.*, 2018b). Consequently, maximizing seascape connectivity and minimizing the fragmentation and loss of fish habitats are key considerations for both the management of fish populations and the conservation and restoration of fish habitats (Gilby *et al.*, 2018; Young *et al.*, 2018).

Estuaries support a suite of habitats that provide foraging and resting sites for adult fishes, and nursery habitats for the juveniles of many species that move offshore as adults (Beck *et al.*, 2001;

Whitfield, 2017). Fish migrate among estuarine habitats with tidal, diel, and seasonal changes that govern either their accessibility, or suitability, as fish habitat, or with ontogenetic changes in resource requirements (Gillanders *et al.*, 2003; Sheaves, 2005; Krumme, 2009). Thus, the spatial properties of estuarine habitats (i.e. size, isolation, position, configuration) can shape both the level of larval recruitment, and the frequency of visitation by juvenile and adult fishes (Beck *et al.*, 2001; Litvin *et al.*, 2018). It is widely appreciated that variation in habitat extent, isolation, and connectivity can modify the composition of fish assemblages in estuaries (see reviews by Sheaves, 2009; Boström *et al.*, 2011; Nagelkerken *et al.*, 2015). For example, fish diversity and abundance is often greatest in structurally complex ecosystems that provide habitats for fish, particularly when those habitat patches are both large and located close to either saltmarshes, mangrove forests, seagrass meadows, oyster reefs, or rocky reefs (e.g. Irlandi and Crawford, 1997; Micheli and Peterson, 1999; Pittman *et al.*, 2007; Olds *et al.*, 2012; Henderson *et al.*, 2017a). These effects of seascape context can also modify the composition of fish assemblages over unvegetated soft sediments in both relatively natural estuaries (Clynick and Chapman, 2002), and in urban waterways (Gilby *et al.*, 2017a; Olds *et al.*, 2018a).

Fish movements might link habitats across seascapes, but different habitats are typically considered in isolation by studies that test for possible effects of seascape connectivity on fish assemblages (Pittman, 2017; Gilby *et al.*, 2018). Previously, research has shown that the ecological footprint of seagrass extends beyond the boundaries of individual meadows, with pervasive effects on fish assemblages and food webs in numerous other marine habitats (Connolly and Waltham, 2015; Gilby *et al.*, 2018). There are many estuaries, however, that cannot support seagrass, such as large tropical systems and highly modified urban waterways, because of high turbidity, large tidal ranges or unsuitable substrates (Waycott *et al.*, 2009; Unsworth *et al.*, 2015). These urban estuaries can contain artificial structures (e.g. rock walls, bridges, jetties, pontoons) that provide a suite of foraging and sheltering opportunities for fish and add structural complexity to estuaries that have been dredged, or modified, to enhance ship passage (Hindell, 2007; Waltham and Connolly, 2011). However, due to the negative effects of poor water quality and habitat loss, urbanization can have negative impacts that permeate throughout estuaries and reduce linkages between critical fish habitats (Bishop *et al.*, 2017; Munsch *et al.*, 2017). These types of estuaries dominate the coastlines of many countries (Waltham and Connolly, 2011; Dafforn *et al.*, 2015), and can support diverse habitats and fish in high abundance (Chapman and Blockley, 2009; Sheaves *et al.*, 2015; Bishop *et al.*, 2017). It is not clear, however, whether other structurally complex habitats (e.g. mangroves or rocky reefs) exert widespread ecological effects, which transcend habitat boundaries across estuarine seascapes which do not contain seagrass meadows.

We used tropical and subtropical estuaries in eastern Australia as model systems to test whether the effects of seascape context on fish assemblages were consistent across multiple estuarine habitats. Tropical and subtropical estuarine seascapes in our study area support a heterogeneous mix of natural habitats, including mangrove forests, rock bars, log snags, unvegetated sediments, and a variety of armoured shorelines and urban structures (Abrantes and Sheaves, 2009; Martin *et al.*, 2018). These estuaries are therefore ideal for examining whether, and how, seascape context alters the composition of fish assemblages in different estuarine habitats. We expected positive effects on fish abundance and diversity from natural structurally complex habitats like mangroves and rock bars (Olds *et al.*, 2012; Bradley *et al.*, 2017), negative effects from armoured shorelines in urban estuaries (Waltham and Connolly, 2011; Gilby *et al.*, 2017a) and for these effects to proliferate across the estuarine seascape.

Methods

Study area

We surveyed fish assemblages in the lower reaches of 17 estuaries along the east coast of Queensland, Australia, from Water Park Creek in the north (−22.94°S) to the Mary River in the south (−25.41°S) (Figure 1). All surveys were conducted during daylight hours in the austral winter, and within 2 h of high tide, to minimize potential confounding effects from tidal, diel and seasonal variation, and to maximize water clarity for visual surveys (Gilby *et al.*, 2017a). Salinity can play a major role in structuring the composition of estuarine fish assemblages (Whitfield, 1999), so we standardized salinity by restricting surveys to the marine reaches (30–36 psu) of each estuary.

Surveying fish assemblages

Fish assemblages were surveyed in five estuarine habitats: mangrove forests, log snags, rock bars, unvegetated sediments, and armoured shorelines. The estuaries across this range do not contain seagrass meadows, so we could not sample this habitat. We aimed to sample five replicates in each habitat type in each estuary, but this was not always possible because some habitats were not present in all estuaries. In total, we surveyed fish assemblages from 365 sites, which were distributed across 5 habitats in 17 estuaries. Sites were separated by a minimum of 50 m to limit the potential for counting the same fish twice (Gilby *et al.*, 2018). Fish assemblages were surveyed with remote underwater video stations (RUVS), which were deployed for a period of 30 min at each site. RUVS consisted of a high definition GoPro camera that was mounted on a 5-kg weight. We did, however, not use stereo-RUVS during fish sampling and are therefore unable to determine the size of individual fish that are recorded during the surveys. RUVS are an effective technique for surveying fish from a variety of estuarine habitats, and are preferred over baited camera systems for this purpose because they do not use bait to attract fish from other fish habitats (Watson *et al.*, 2005; Harvey *et al.*, 2007; Bradley *et al.*, 2017). RUVS deployments in structurally complex habitats were positioned so that the field of view of cameras was aligned with the edge of the focal habitat patch; this approach minimized the potential for dense habitat to obscure the view of the camera and allowed us to identify individuals moving in and out of habitats. Fish abundance, diversity, and assemblage composition were extracted from video footage using the standard MaxN statistic (Henderson *et al.*, 2017b). When individuals were unable to be identified to species level, they were identified to the lowest taxonomic level, with this then being considered as one species group in all analysis on diversity and community composition.

Measuring environmental attributes

Data on the spatial distribution of estuarine habitats was acquired from existing benthic habitat maps (source: Queensland Government). Quantum GIS was used to measure the area of, and relative proximity, of all estuarine habitats (i.e. including mangrove forests, log snags, rock bars, unvegetated sand and mud, armoured shorelines) in the immediate vicinity of each site (following Olds

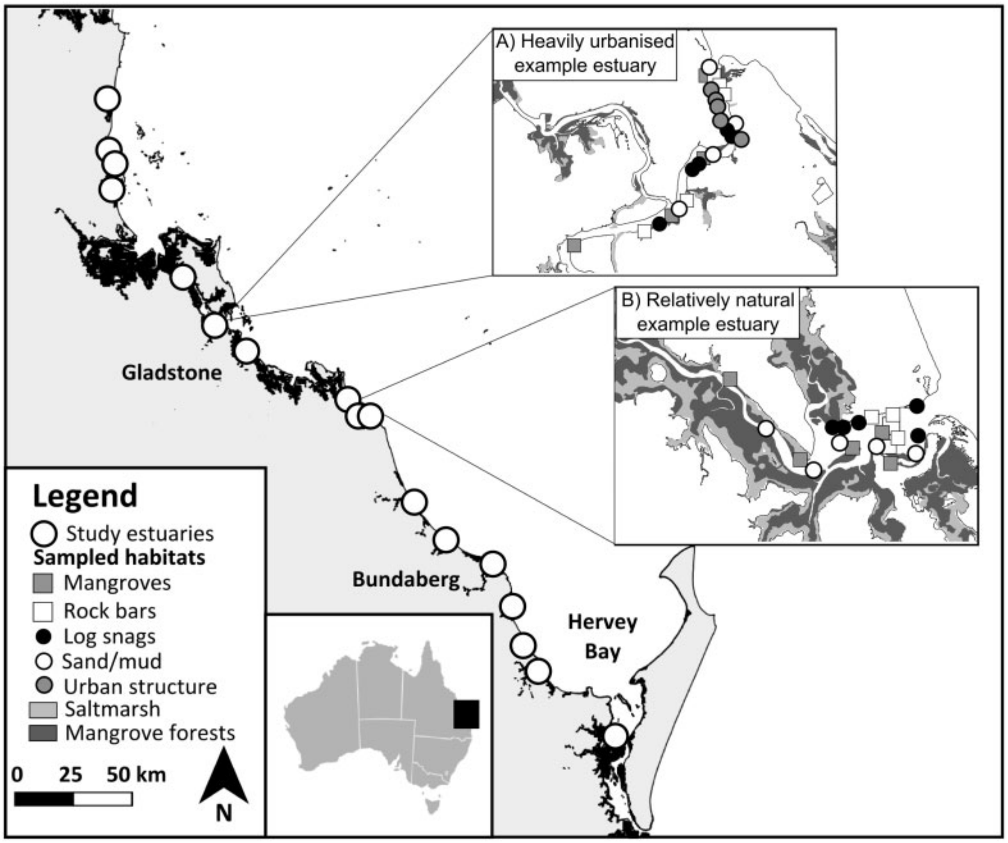

Figure 1. Location of study estuaries in central Queensland, Australia. Insets illustrate examples sampling different habitats along: (a) an urban estuary with abundant armoured shorelines; and (b) a relatively natural estuary with abundant mangroves.

et al., 2012; Gilby *et al.*, 2017a; Henderson *et al.*, 2017a). All mangrove forests were at least 20 m wide, log snags, and rock bars were a minimum of 4 m^2 in extent and armoured shorelines were made of up jetties, bridge pylons, and artificially hardened shorelines (Gilby *et al.*, 2018). We did not, however, measure the proximity of habitat patches to the nearest habitat patch of the same type. The area of habitats in the surrounding seascape was measured within a 500-m buffer around each site; this buffer size was chosen because it encompasses the daily home ranges of many estuarine fish species in the study area (Olds *et al.*, 2012). We also recorded water depth, water clarity and salinity, and measured the distance of each site from the mouth of each estuary to account for possible effects of these physico-chemical variables on fish assemblages (Gilby *et al.*, 2017b; Henderson *et al.*, 2017b).

Data analysis

We used multiple approaches to determine the effects that seascape context have on the composition of fish assemblages in estuaries. First, we used a distance-based linear model (DistLM) approach to determine the factors the drive changes in fish assemblages across multiple habitats. Second, we identify the key drivers of fish community assemblages occurring in each individual habitat using a LINKTREE analysis. Finally, we used generalized additive models (GAMs) to test for the effects that significant seascape variables have on the abundance and species richness of fish in each habitat.

We used a DistLM to test for correlations between the composition of estuarine fish assemblages (square-root transformation, Bray–Curtis similarity matrix), and the type, area, and spatial context of fish habitats in estuarine seascapes (McArdle and Anderson, 2001) in PRIMER-E with PERMANOVA (Anderson *et al.*, 2008). Models were fitted using stepwise selection, and the best-fit model was chosen using Akaike information criterion (AICc) corrected for small sample sizes. DistLM results were then visualized using distance-based redundancy analysis (dbRDA) (Anderson *et al.*, 2008). Significant factors from the DistLM are displayed on the dbRDA as vectors to detail the direction of an individual factors effect. We used univariate PERMANOVA to identify differences in fish abundance and species richness between each estuarine habitat type. Factors included in the DistLM best-fit model were then examined in LINKTREE analyses on each habitat separately to test whether, and how, seascape features modify the composition of fish assemblages (Anderson, 2004; Clarke *et al.*, 2008). Groupings within LINKTREEs were characterized using similarity profile (SIMPROF) tests at a significance level of 0.01 (999 permutations). The composition of species at each terminal node within LINKTREES were broken up into three groups, mangrove associated, structure associated, and sand/mud associated, in order to show how spatial features influenced the composition of fish. These groupings were based on previous studies in the region (Olds *et al.*, 2012; Gilby *et al.*, 2018). The relative importance of seascape metrics for fish assemblages across all habitats was then quantified as the sum of

Table 1. Results of DistLM sequential test that tested for correlations between fish assemblages (Bray–Curtis similarity matrix) and the type and spatial context of estuarine fish habitats (Normalized data).

Variable	AICc	Pseudo-F	*p*	Prop. of variance explained
+Habitat type	4659.6	19.912	0.001	0.04
+Armoured shoreline area	4652.8	8.834	0.001	0.02
+Mangrove distance	4648.6	6.237	0.001	0.01
+Rock bar area	4643.8	5.113	0.001	0.01
+Mangrove area	4644.5	3.067	0.008	0.01
+Armoured shoreline distance	4643.8	2.672	0.020	0.01
+Mouth distance	4643.7	2.174	0.043	0.01

Models were fitted using the stepwise selection process and evaluated with AICc.

variance explained (B%) by each variable in all LINKTREE analyses (Gilby *et al.*, 2018). GAMs were then used to test for possible effects of significant seascape metrics on the species richness and abundance of fish in each habitat. We used GAMs over other approaches as they allow for non-linear relationships between variables. Analyses were conducted using the *mgcv* package of R (Bartoń, 2013). Model overfitting was minimized by restricting individual models to four or fewer knots (i.e. individual polynomial functions that combine to smooth GAMs) (Zuur *et al.*, 2009).

Results

Influence of habitat type on estuarine fish assemblages

DistLM identified differences between habitats was the most important determinant of estuarine fish assemblages, followed by the spatial context and configuration of habitat patches relative to other ecosystems that provide complex habitat structures for fish (Table 1, Figure 2a). Here, fish assemblages were most correlated with habitat type, the area of mangroves, rock bars and armoured shorelines, and the distance to mangroves, armoured shorelines, and the mouths of estuaries (Table 1). LINKTREEs identified that the spatial context of mangrove forests and armoured shorelines were the most significant predictors of variation in the composition of fish assemblages across most estuarine habitats (Figures 3 and 4). Mangrove and sand/mud-associated fish species were more abundant in most habitats when they were in close proximity to mangroves and further away from armoured shorelines (Figure 4). Pairwise univariate PERMANOVA results indicated fish diversity and abundance was highest in the four structurally complex habitats (Figure 2b and c). In contrast, fish diversity and abundance were lowest over unvegetated sediments, which are characterized by limited habitat heterogeneity (Figure 2b and c).

Effects of seascape context modify fish assemblages across estuaries

GAMs on fish abundance and diversity in mangroves were negatively correlated with the proximity of armoured shorelines, with both fish abundance and diversity in mangroves increasing with increased distance from urban structures (Figures 5 and 6). In contrast, both the abundance and diversity of fish on armoured shorelines were positively correlated with the proximity of mangrove forests (Figures 5 and 6). GAMs on the abundance and diversity of fish over rock bars, log snags, and unvegetated sediments were also correlated with the spatial context of mangrove forests and armoured shorelines (Figures 5 and 6). The effects of mangroves on fish abundance and diversity were positive for log snags and unvegetated sediments, and negative for rock bars (Figures 5 and 6). In contrast, the effects of armoured shorelines on fish abundance and diversity were negative for unvegetated sediments, and non-linear for log snag and rock bar habitats (Figures 5 and 6).

Discussion

The spatial context and arrangement of habitats in estuarine seascapes shapes the distribution, diversity, and abundance of fish assemblages (Grober-Dunsmore *et al.*, 2009; Nagelkerken *et al.*, 2015; Olds *et al.*, 2018b). Many fish species aggregate around habitats of high structural complexity, and fish diversity and abundance is often greatest when these habitats are linked to other habitats which provide complementary resources for fish assemblages (Sheaves, 2009; Boström *et al.*, 2011; Pittman, 2017). Our findings show that the effects of habitat and seascape context combine to structure fish assemblages in estuarine seascapes (sensu Gilby *et al.*, 2018). Fish diversity and abundance were typically highest in structurally complex habitats, such as mangrove forests, rock bars, log snags, and armoured shorelines, which provide diverse feeding and sheltering opportunities for fish assemblages. The spatial context of mangrove forests and armoured shorelines were, however, also significant predictors of fish assemblages, with armoured shorelines having consistently negative ecological effects that were pervasive in estuarine seascapes. Fish diversity and abundance in most habitats were linked positively to the proximity of mangroves, and negatively to the proximity of armoured shorelines. These findings indicate that mangroves and armoured shorelines can have widespread, and contrasting, ecological effects in estuarine seascapes, and show that the functional effects of mangrove loss might transcend habitat boundaries in urban estuaries (Waltham and Connolly, 2011; Sheaves *et al.*, 2014; Brook *et al.*, 2018).

Mangroves are important habitat for a diversity of fish species that use these inundated forests as feeding areas, refuges from predators and juvenile nurseries (Sheaves, 2005; Nagelkerken *et al.*, 2008). The habitat function of mangroves for fish vary with the size and species composition of forests, the frequency of tidal inundation, and their spatial context relative to other marine ecosystems (Faunce and Serafy, 2006; Igulu *et al.*, 2014; Sheaves *et al.*, 2016). Due to the ebb and flow of tides, many mangrove forests only provide habitat for marine organisms for short periods each day, and fish must retreat to subtidal habitats with tidal egress (Baker *et al.*, 2015; Whitfield, 2017). The proximity of subtidal refuges can, therefore, be pivotal in shaping fish assemblages in mangrove forests and in turn, the assemblages in subtidal habitats at low tide (Pittman *et al.*, 2007; Jones *et al.*, 2010). The spatial context of adjacent mangrove forests can also modify the diversity and abundance of fish in other subtidal habitats, including mud flats, seagrass meadows, coral, and rocky reefs (Olds *et al.*, 2012; Gilby *et al.*, 2018). Our results show that the habitat values of mangroves for fish can extend across entire estuarine seascapes, and into a range of both natural and artificial fish habitats. However, the area of mangroves was not as significant as mangrove proximity in structuring the composition of fish assemblages across estuaries, the differing areas of habitats (i.e. mangrove forests vs. rock bars or log snags) would be expected to have an impact on the overall biomass

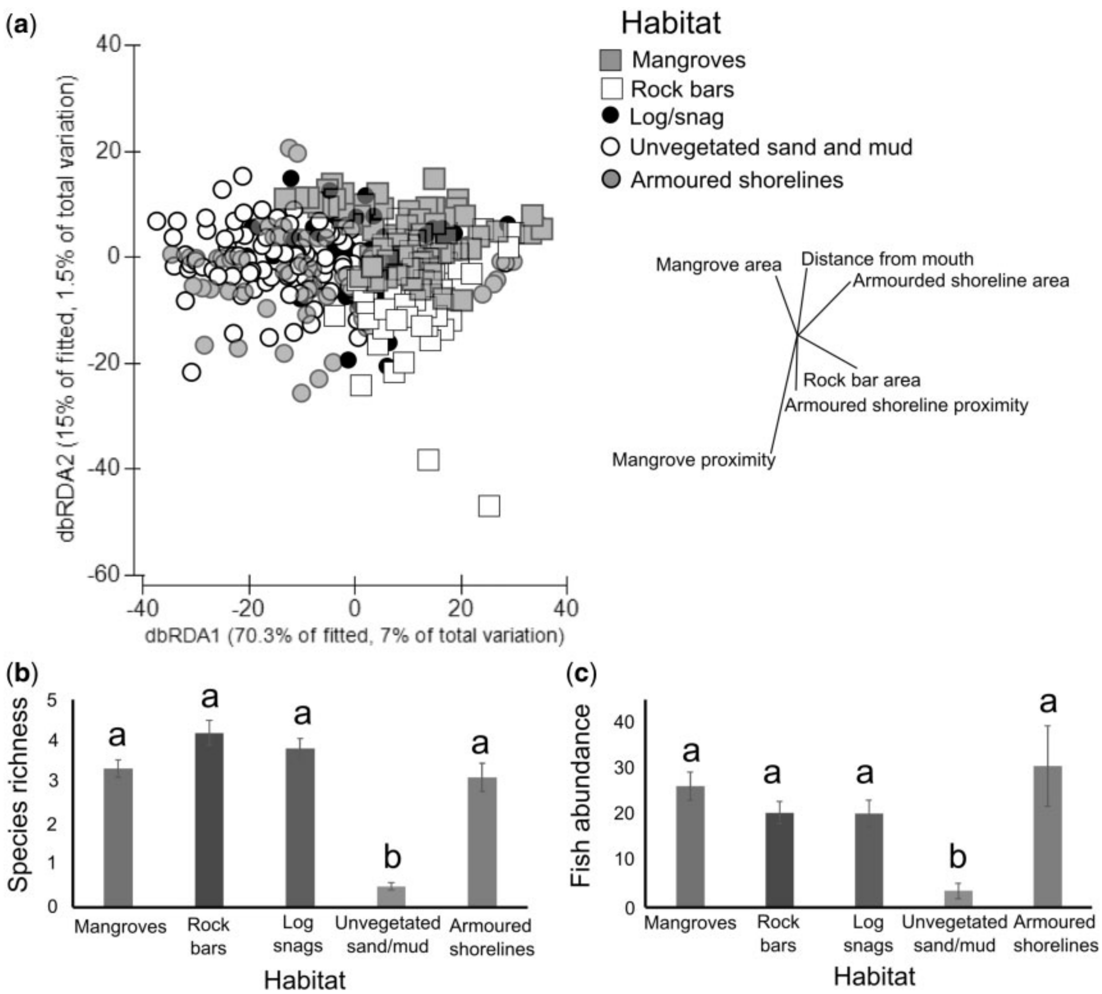

Figure 2. Different estuarine habitats supported distinct fish assemblages. (a) dbRDA ordination showing how fish assemblages from each habitat are correlated with important habitat and seascape metrics; these effects are illustrated with vectors. (b) Species richness and (c) total fish abundance (± SE) in each estuarine habitat. Letters depict significant differences identified by pairwise tests following permutational multivariate analysis of variance (PERMANOVA).

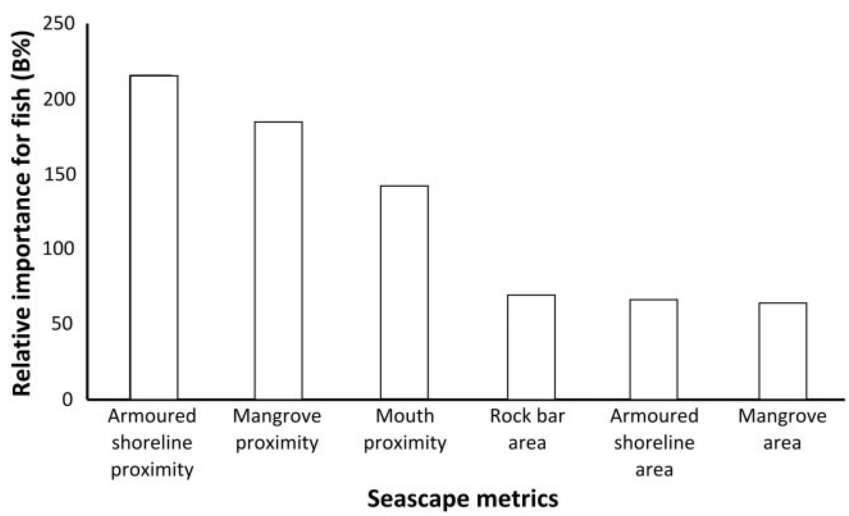

Figure 3. Relative importance of seascape metrics for fish assemblages across all habitats. The importance of metrics was quantified as the sum of variance explained (B%) in all LINKTREE analyses (see Figure 4).

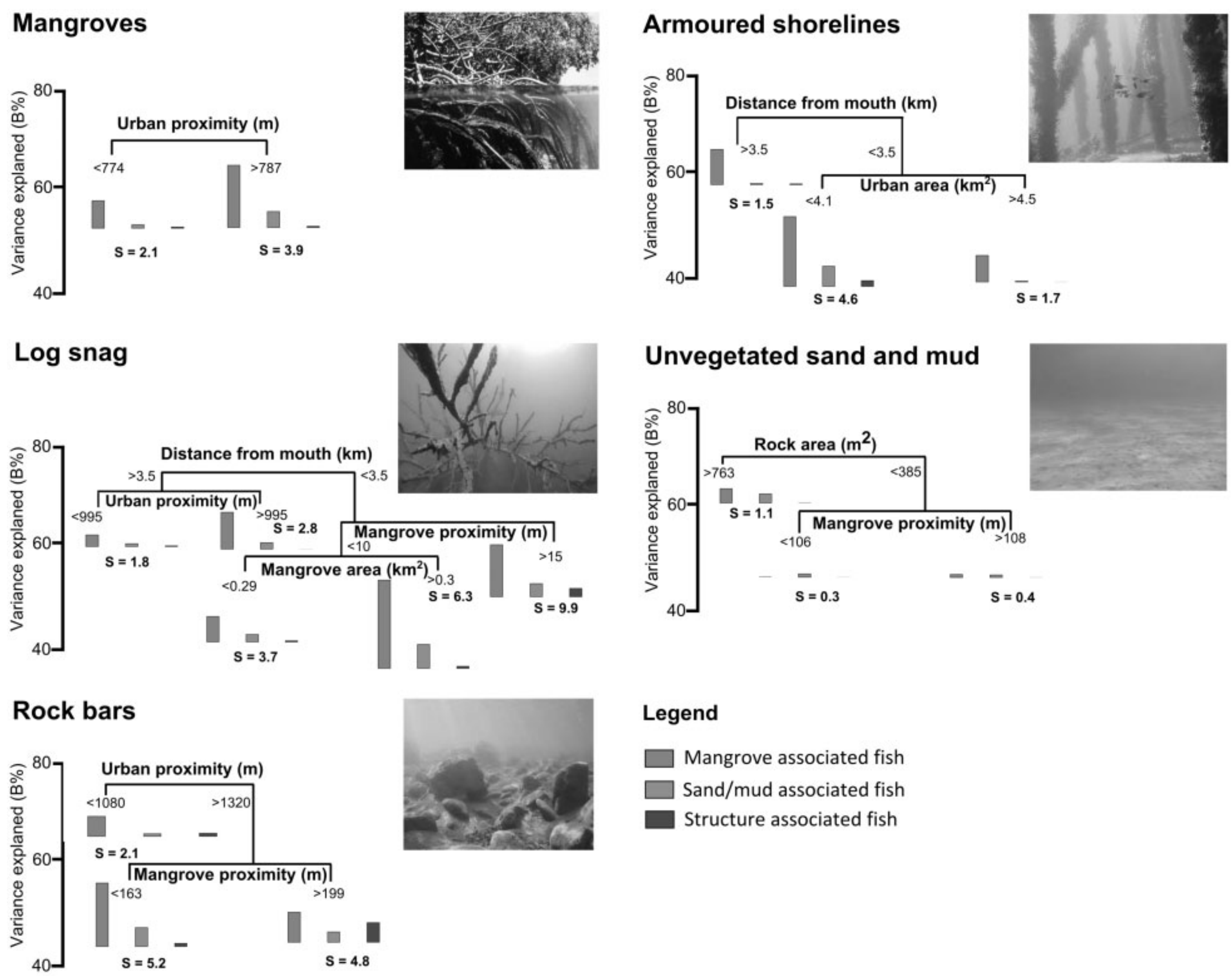

Figure 4. Summary of linkage tree (LINKTREE) results illustrating how fish assemblages in each habitat relate to significant seascape metrics. Variables located higher in each LINKTREE explain a greater proportion of variation in the composition of fish assemblages. Numbers below terminal nodes show the mean species richness and bar plots indicate the total abundance of fish that are associated with each habitat type (in order of mangrove, sand/mud, and structure associated). All bar plots have the same axis.

of fish assemblages occurring in different estuarine habitats. Seagrass meadows can alter the composition of fish assemblages across multiple habitats in sub-tropical seascapes (Gilby *et al.*, 2018). Our results suggest that mangroves might have similar pervasive effects in estuaries that cannot support seagrass, such as those with large tidal ranges or high turbidity. Mangrove forests are, however, under threat in many countries from the effects of urbanization and fragmentation (Halpern *et al.*, 2009; Jennerjahn *et al.*, 2017). To maintain diverse and abundant fish assemblages in urban estuaries, it will therefore be critical to retain and conserve interconnected patches of high-quality mangrove habitat (Brook *et al.*, 2018; Olds *et al.*, 2018a).

The diversity and abundance of fish in most estuarine habitats were negatively correlated with the proximity of adjacent armoured shorelines and urban structures. The effects of urbanization are widespread, and are frequently centred on estuaries, which provide a focal point for intense coastal development (Kennish, 2002; Halpern *et al.*, 2009; Fang *et al.*, 2018). Urban estuaries can support an abundance of fish, but these assemblages are typically characterized by both low diversity and high dominance, due to the combined negative effects of water quality degradation, habitat loss and pollution that typically accompany urbanization (Munsch *et al.*, 2017; Pereira *et al.*, 2017). Most research has described how fish diversity and abundance change in the immediate vicinity of particular types of urban structures, or documented how fish assemblages and food webs differ between urban estuaries and relatively natural seascapes (Chapman and Blockley, 2009; Bishop *et al.*, 2017). Our results show that the ecological effects of urbanization can, however, extend across estuarine seascapes to modify the composition of fish assemblages in most natural habitats (Brook *et al.*, 2018; Olds *et al.*, 2018a). Given that the spatial context of urban structures can shape patterns in diversity and abundance across entire estuaries, it might therefore be sensible to manage urban estuaries as landscapes comprised of spatially connected patches of both natural and artificial habitat.

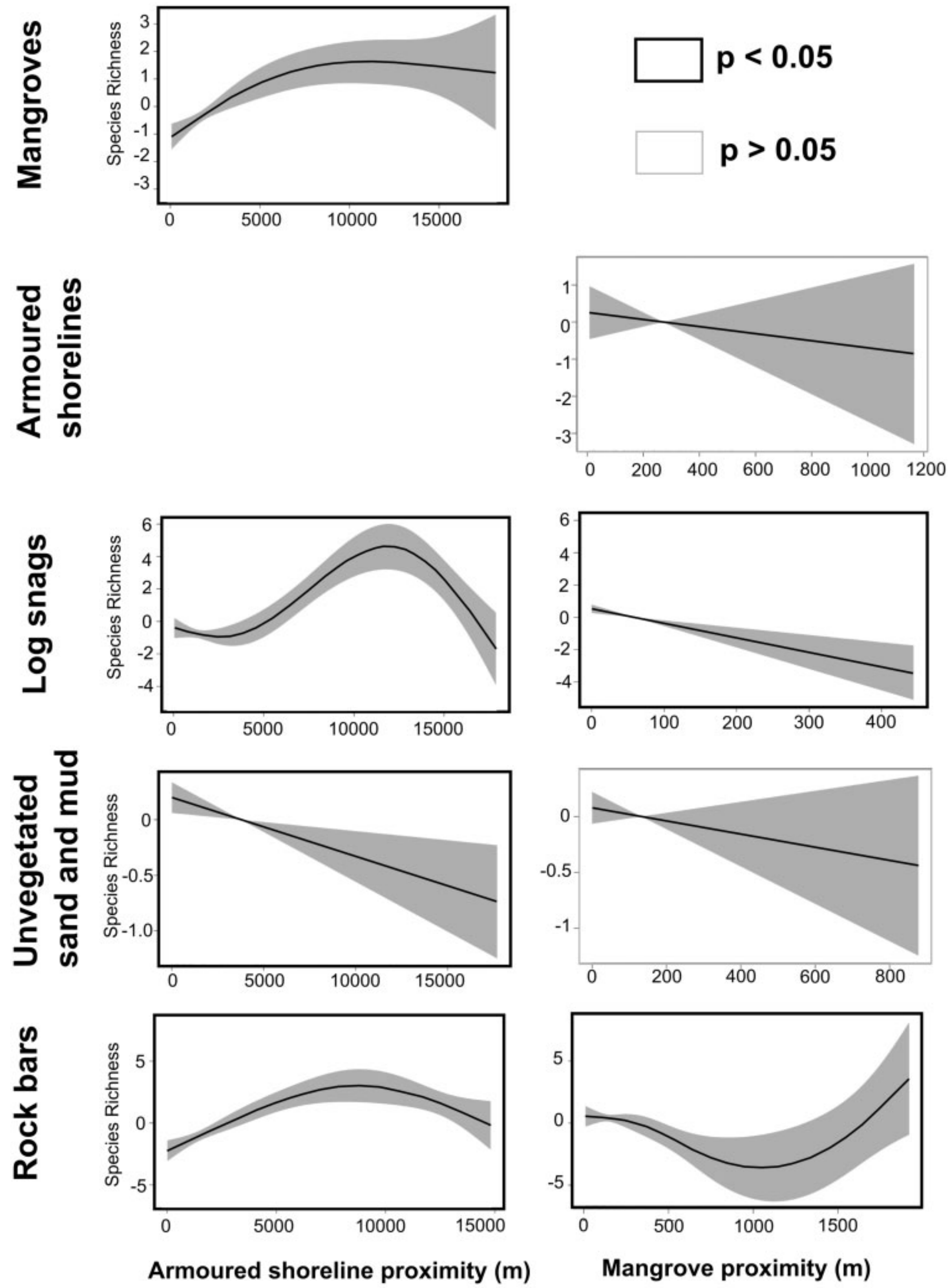

Figure 5. GAMs plots showing how the species richness of fish in each habitat was correlated with spatial proximity of armoured shorelines and mangroves (i.e. the two most important seascape metrics).

In addition to the consistent spatial effects of mangroves and urban structures on fish assemblages in estuarine seascapes, we determined that the proximity of habitat patches to the mouth of estuaries was a significant factor in determining the composition of estuarine fish assemblages. In this study, both fish abundance and diversity were greater over armoured shorelines and log snag habitats that were closer to the open ocean. Many fish move between estuaries and the open sea to spawn, disperse, or with ontogenetic changes in resource requirements (Beck *et al*., 2001; Gillanders *et al*., 2003; Boström *et al*., 2011). The ocean is also the principle source of larval recruits for fish assemblages in many estuarine habitats (Sheaves, 2009; Pittman, 2017; Whitfield, 2017), however, as we were unable to measure the size of individuals, future studies should aim to assess the size range of fish for which seascape context effects occur. When considered together with the widespread effects of mangroves and armoured shorelines on fish assemblages, these findings demonstrate that the spatial context of fish habitats can structure patterns in diversity and abundance across entire estuaries, and support the management of estuaries as functionally connected seascapes (Nagelkerken *et al*., 2015; Litvin *et al*., 2018; Olds *et al*., 2018b).

We show that the ecological footprint of mangrove forests and urban structures extends beyond the boundaries of these habitats,

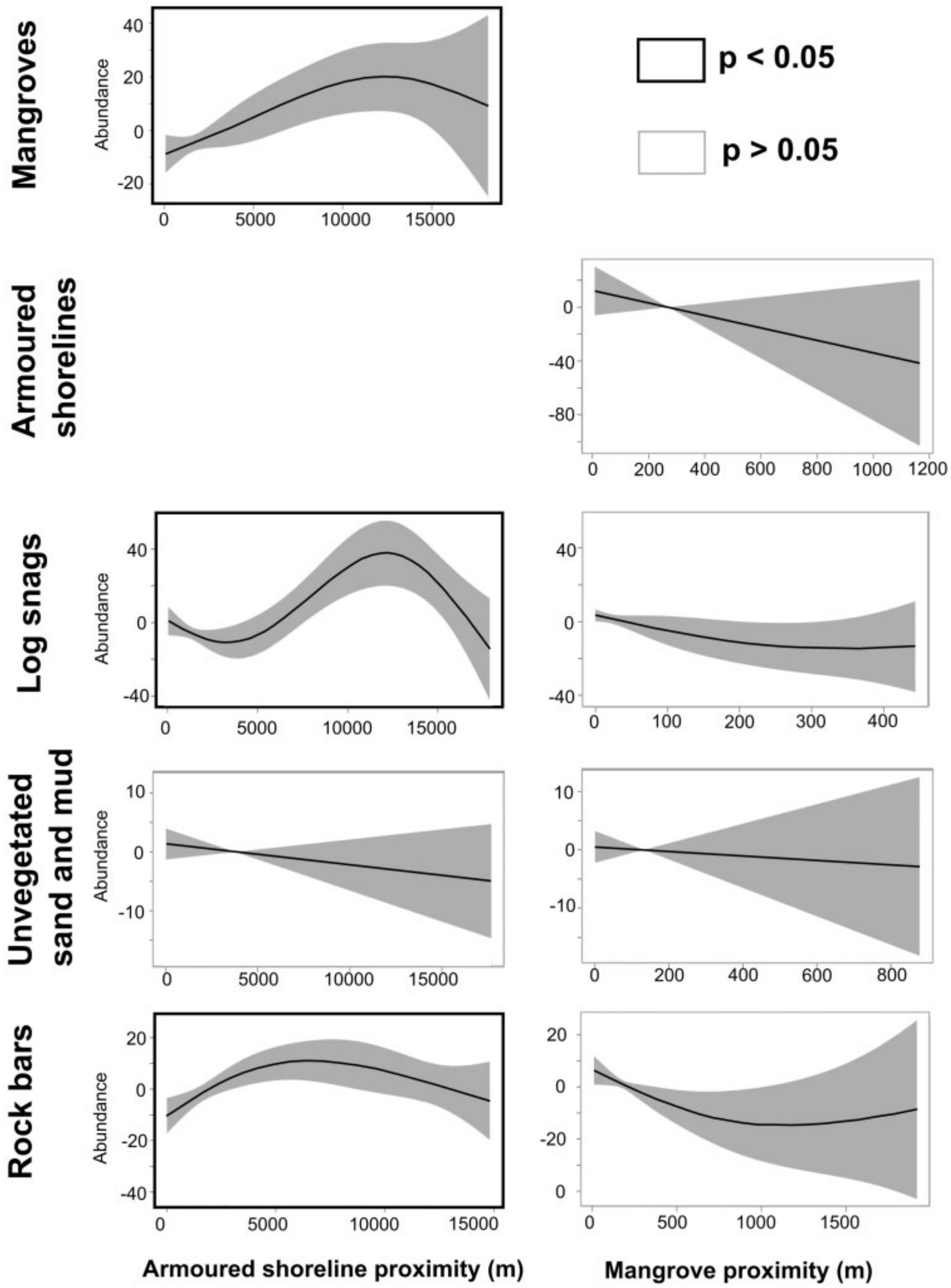

Figure 6. GAMs plots showing how the abundance of fish in each habitat were correlated with spatial proximity of armoured shorelines and mangroves (i.e. the two most important seascape metrics).

with contrasting and pervasive effects on fish assemblages and food webs in numerous marine habitats. Many cities are centred on estuaries, and their expansion is often associated with the installation of urban structures in estuaries, a hardening of estuarine shores, and the fragmentation of mangrove forests. Our findings suggest that when mangroves are replaced by armoured shorelines, the ecological effects of this habitat transformation extend to fish assemblages in most estuarine habitats. Many estuarine seascapes are comprised of spatially linked fragments of natural and artificial habitat, and we suggest that conserving patches of high-quality mangrove habitat that are functionally connected across coastal seascapes, both to each other and to other ecosystems, will be critical for maintaining diverse and abundant fish assemblages in urban estuaries.

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