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The effects of shoreline armouring on estuarine fish are contingent upon the broader urbanisation context

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ABSTRACT: Natural ecosystems in estuaries are modified by the effects of runoff from disturbed watersheds and are frequently replaced by armoured estuarine shorelines. Whilst the effects of these 2 stressors are widely recognised, they are typically studied in isolation, and it is not clear how these contrasting types of urbanisation interact to shape faunal assemblages. In this study, fish assemblages were surveyed with underwater videos arranged in a 200 m grid throughout the lower reaches of 3 estuaries in eastern Australia (resulting in ≥63 sites per estuary and 277 sites in total) which differed in their extent of shoreline and watershed urbanisation. Overall, the least urbanised estuary supported more than twice the number of fish species and a significantly greater abundance of fish. The spatial patterns of fish diversity and abundance within estuaries were related to the proximity of urbanised shorelines, with most fish groups aggregating near armoured shorelines. These effects of distance from urbanised shorelines were, however, modified by the degree to which the entire estuary had been modified. We show that the ecological effects of urbanisation can extend across estuaries and suggest that coastal landscapes should therefore be managed as interlinked mosaics of both natural and artificial habitats.

KEY WORDS: Habitat · Mangroves · Spatial ecology · Urbanisation · Watershed

INTRODUCTION

Human modifications of landscapes are increasing in extent and severity globally (Lotze et al. 2006, Clausen & York 2008). In urban settings, common ecological consequences of anthropogenic changes include lower habitat quality (Cardinale et al. 2012, Aronson et al. 2014), fewer species at lower abundance (Chapin et al. 2000), lessened ecological functions (such as predation; Barbier et al. 2011), and alterations to the movement of organisms and energy across system boundaries (Massol et al. 2011, Qviström 2017). Whilst urbanisation is generally considered to be ecologically detrimental (McKinney 2002), some species are either not strongly impacted or can even prosper in urban areas (Connell & Glasby 1999, Beninde et al. 2015, Dafforn et al. 2015). Furthermore, because organisms, matter, and energy move among ecosystems, the effects of urbanisation can have wide-reaching consequences that extend across landscapes (Massol et al. 2011, Qviström 2017).

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Urbanisation is largely a coastal phenomenon, and more than half of the global human population now lives at or near the seashore (Neumann et al. 2015). Impacts of coastal urbanisation can be diverse, including heavy fishing pressure near large coastal cities (Jackson et al. 2001), inputs of sediments, nutrients, and pollutants (Kennish 2002, Pan & Wang 2012, Liu et al. 2018), and the replacement of natural habitats (e.g. mangroves, wetlands) with armoured shorelines (i.e. shorelines modified by the placement of hard engineering structures such as revetments, concrete walls, rip raps, jetties, and piers) (Bulleri & Chapman 2010, Munsch et al. 2017). Whilst our understanding of the ecological effects of urbanisation is increasing (Elliott et al. 2014), the degree to which these different stressors interact to modify coastal ecosystems and faunal communities, and the scales over which such changes occur, remain poorly understood (Teichert et al. 2016, Heery et al. 2017).

Estuaries are habitat for many fish species that support commercial and recreational fisheries (Sheaves et al. 2013, Nagelkerken et al. 2015). The replacement of estuarine habitats with armoured shorelines can, therefore, have significant social, cultural, economic, and environmental consequences (Kennish 2002, Lotze et al. 2006, Berendse et al. 2015, Munsch et al. 2017). Armoured shorelines create different feeding and refuge conditions for fish (Barbier et al. 2011) and can therefore modify fish assemblages over multiple spatial scales (Luck 2007, McKinney 2008, Bulleri & Chapman 2010, Layman et al. 2014, Beninde et al. 2015). As a consequence, the abundance of some fish groups or species might be higher adjacent to armoured shorelines (Hindell 2007, Werry et al. 2012, Rodemann & Brandl 2017). Alternatively, some fish groups might be particularly sensitive to the removal of natural habitats because their food items are also closely associated with natural habitats (Gittman et al. 2016, Munsch et al. 2016, Kornis et al. 2018). For example, zooplanktivores are most abundant in, or near, mangroves and saltmarshes where their prey, fish and crustacean larvae, are most abundant (Giarrizzo et al. 2011, Davis et al. 2014, Saintilan & Mazumder 2017). Because most fish species use a number of different ecosystems as habitat (Pittman et al. 2004, Boström et al. 2011, Pittman et al. 2014), it is likely that the impacts of shoreline armouring propagate across seascapes that are functionally linked by fish movement (Sheaves 2009, Rodemann & Brandl 2017).

Some fish school around structurally complex habitats in coastal seascapes, whether they be natural or artificial, for several key reasons. Structurally complex habitats provide areas of calmer waters in their lee, where fish aggregate to save energy (Breitburg et al. 1995, Lenihan 1999), and can be positively related to fish biomass (Gratwicke & Speight 2005). Structurally complex habitats in estuaries also provide alternate opportunities for feeding because they often support a different assemblage of encrusting and sessile invertebrates than soft coastal substrates. Because of their high structural complexity, these areas also provide small fish with protection from larger predators (Orth et al. 1984, Micheli & Peterson 1999). For these reasons, fish diversity and abundance are often centralised around structurally complex estuarine habitats, with their assemblages declining in diversity, abundance, and size in the adjacent sandy matrix (Bradley et al. 2017).

Direct modifications to instream estuarine habitat extent and quality, caused by the placement of infrastructure and engineered shore stabilisation, are in many cases supplemented by broader changes to water quality and land use on the estuarine floodplain. In particular, urbanised watersheds can create large loads of sediments, nutrients, and toxicants that lower habitat quality for fish (Halpern et al. 2008), causing local extirpation of species most sensitive to water quality changes (Whitfield & Elliott 2002, Kornis et al. 2017) and poorer health of fish in urban estuaries (Schlacher et al. 2005, 2007).

Whilst the direct effects of habitat replacement by armoured shorelines are documented at local scales (Bulleri & Chapman 2010), and the broader effects of environmental quality are described at watershed scales (Elliott et al. 2014), it is not clear how these contrasting stressors combine to affect the distribution of estuarine fish assemblages (but see Breitburg & Riedel 2005, Bilkovic & Roggero 2008, Kornis et al. 2017). In this study, we examine how the extent of shoreline armouring and area of remaining verge vegetation (in this case, mangroves) in an estuary interact with how tightly fish are associated with the armoured shorelines. We hypothesised that we would identify more fish and a greater number of fish species at sites closer to armoured shorelines in estuaries with more extensive mangrove forests because the less urbanized ecosystem would support a higher abundance of more sensitive species and has an overall higher carrying capacity. Conversely, we expect fewer fish and lower diversity around armoured shorelines in an estuary with more extensively armoured shorelines and fewer mangroves because of the combined negative impacts from poor habitat quality and extent and reduced environmental heterogeneity.

MATERIALS AND METHODS

Study estuaries

We studied fish responses to urbanisation in 3 subtropical estuaries located in southeast Queensland, Australia (Fig. 1). These estuaries were chosen because they have broadly similar catchment geomorphologies and drain from the same mountain range (Withnall & Cranfield 2013), have similar bathymetry and river flow rates (see Gilby et al. 2017b), and a similar range of habitats available to fish (see Gilby et al. 2018). The key difference between them, however, is with respect to the area of mangroves and the degree of shoreline armouring in the lower estuary (i.e. areas modified by the placement of hard engineering structures such as revetments, concrete walls, rip raps, jetties, and piers), and the extent of urbanisation across the watershed (Table 1) (Gilby et al. 2017b). Consequently, we henceforth label the Noosa River as 'low urbanisation', the Maroochy River as 'moderate urbanisation', and the Mooloolah River as 'high urbanisation' for the purpose of this study (Fig. 1, Table 1). For further information on and justification of these categories, see Text S1 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m605p195_supp.pdf.

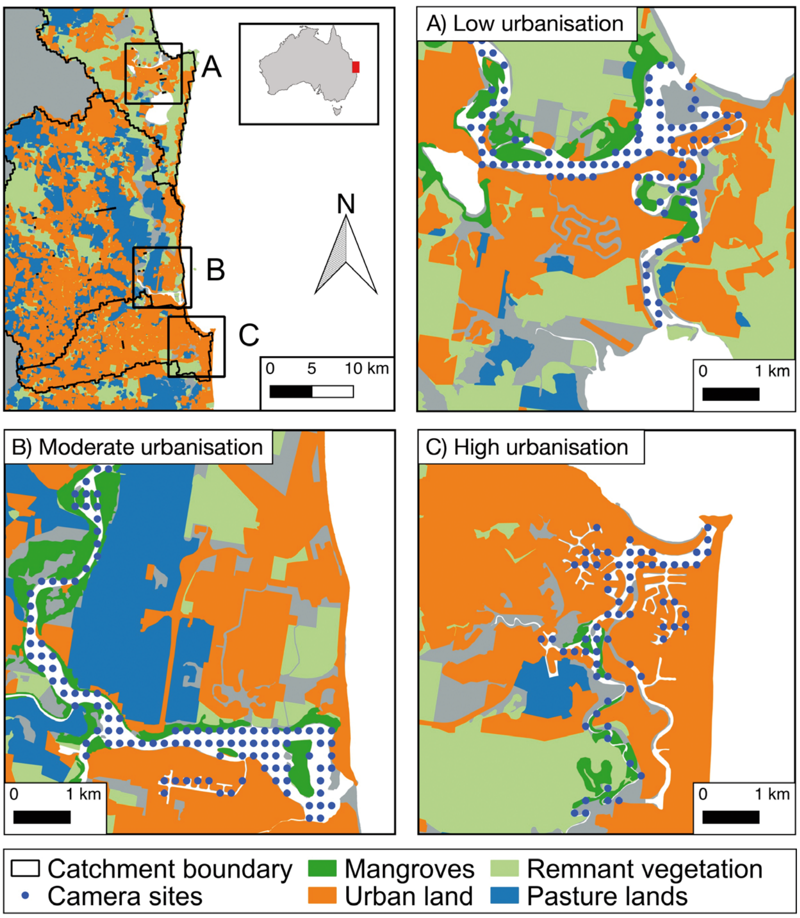

Fig. 1. Location of the 3 study systems in Queensland, Australia, with insets showing the location of fish camera sites within each estuary. (A) Noosa River (N = 100) is characterised by low urbanisation levels and a high cover of remnant mangroves. (B) Maroochy River (N = 110) has moderate urbanisation levels and (C) Mooloolah River (N = 63) has high urbanisation levels, and very low remnant vegetation

Fish surveys

Because salinity is a principal determinant of the distribution of fish in estuaries (Barletta et al. 2005), the extent of surveys in each estuary were standardised to encompass the estuarine reaches from the inlet to the point upstream at which salinity averaged 27 psu over the previous 10 yr (HLWMP 2017). This approach has been used by other studies to standardise the extent of surveys in estuaries across the study area (Gilby et al. 2017b).

Sampling sites were spread evenly across this extent in each estuary in a 200 m grid, resulting in 100, 110 and 63 sites for the low, moderately and highly urbanised estuaries, respectively (Fig. 1). The grid was not anchored to any specific place in the estuary and was randomly overlaid using GIS. This design was chosen for 2 reasons: (1) a 200 m spacing between sites lowered the probability of non-independence of observations as individual fish are unlikely to be encountered at more than 1 site during our 30 min sampling periods (Harvey et al. 2004, Gilby et al. 2016), and (2) it maximised the number of sites and therefore the degree to which we could survey the full extent of seascape heterogeneity in the lower reaches of each estuary (Gilby et al. 2017b).

Fish were sampled with remote underwater video stations (RUVs). RUVs consisted of a camera mounted on a weight (2 kg concrete block), which was raised above the seafloor on a 10 cm high bracket to expand the field of view. High definition videos were recorded for 30 min with GoPro Hero 4 cameras (1960 × 1080 pixels at

Table 1. List of included environmental variables, the ecological hypothesis associated with the variables, the method of data acquisition, the source of data, and mean values for each estuary. 'Estuary-scale measures' refer to factors measured at the scale of the watershed, or the entire sampled stretch of the estuary, whereas 'site-scale measures' are attributes of individual sites measured at small spatial scales (<500 m)

Variable	Definition	Data layer source	Urbanisation Low	Urbanisation Moderate	Urbanisation High
Estuary-scale measures					
Extent of armoured shorelines in the lower estuary	The percentage of the shoreline of the sampled stretch of the estuary that is urbanised. Armoured shorelines are defined as areas modified by the placement of hard engineering structures such as revetments, concrete walls, rip raps, jetties, piers, etc	Queensland Government (2014)	10%	10%	51%
Percentage of watershed urbanisation	The percentage of the watershed that is urbanised land. The watershed is defined as all land which drains through each estuary. Urban areas included all areas of residential (be they high, or low density), industrial, transport and communication (including roads), waste treatment and disposal, and other service land use. The extent of watershed urbanization also correlates highly with the extent of agricultural lands (R^2 = 0.97) and remnant vegetation (R^2 = 0.86) in the catchment	Queensland Government (2014)	8%	41%	40%
Area of mangroves in sampled stretch (m^2 m^{-1})	The area of mangroves in the sampled stretch of the estuary, divided by the largest 'Distance of site to estuary mouth' value (see below) for that estuary	Queensland Government (2015)	47.7	28.9	6.2
Site-scale measures					
Urban land near site (m^2)	Area of urban land within 500 m of a site	Queensland Government (2014)	206 964	187 599	367 649
Mangroves near site (m^2)	Area of mangroves within 500 m of a sit	Queensland Government (2015)	106 030	138 803	36 160
Distance of site to estuary mouth (m)	Distance from the site to the centre of the estuary mouth	Measured in QGIS (QGIS Development Team 2017)	3244	4593	3621
Distance of site to armoured estuarine shoreline (m)	Distance from the site to the nearest armoured estuarine shoreline	Queensland Government (2014)	185	455	386
Distance of site to mangroves (m)	Distance from the site to the nearest mangroves	Queensland Government (2015)	332	213	1213

60 frames s^{-1}). To maximise water depth and underwater visibility, all RUV deployments were done within 2 h either side of high tide. Sampling was completed over 4 consecutive days in each estuary, with all 3 estuaries being sampled during 2 wk in May 2017 (late austral autumn) and between the 10:00 and 16:00 h to avoid any crepuscular effects. RUVs were never placed directly in the highly structurally complex ecosystems (i.e. amongst the prop roots of the mangroves). Where they were placed near mangroves or jetty pylons, etc., the video field of view was directed along the edge of the habitat to enable a clear view of fish around the habitat. All sites within each estuary were completed over 3 consecutive days for a total of 9 d consecutive field time. All estuaries are relatively shallow throughout the sampled stretch (Gilby et al. 2018), so all deployments were made in water depths of less than 6 m.

MaxN, the maximum number of individuals of each fish species visible in video frames at any one time, was used to quantify fish assemblages at each site (to at least genus level in all cases). MaxN is the most widely accepted metric for quantifying fish numbers from underwater footage as it provides a conservative estimate of relative fish abundance (Cappo et al. 2003, Dorman et al. 2012).

Quantification of habitat and environmental variables

We tested for effects of 3 classes of environmental variables that are known to influence the distribution and abundance of fish in estuaries: (1) the area of natural and urban habitats around our sites (in 500 m buffers) and in the watershed (Gilby et al. 2017a); (2) the distance of sampling sites to mangroves, armoured shorelines, and the estuary mouth (Connolly & Hindell 2006); and (3) light penetration (secchi disc) and salinity (refractometer) measured on the day of survey at each site (Table 1). We found no significant differences in light or salinity values between our 3 estuaries ($p > 0.06$), and there is little evidence to suggest that these water quality metrics reach levels that either vary too greatly or reach extremes that influence the distribution of fish in the region (Gilby et al. 2016, 2018, Olds et al. 2018), so these were not included as variables in statistical models. The areas of habitats, as well as distances between habitats, were calculated in QGIS (v.2.18.11; QGIS Development Team 2017).

Statistical analyses

Correlations between the structure of fish assemblages at every RUVS site (i.e. the fish assemblage dataset; a multivariate matrix of the type and number of each species) and the suite of site-scale environmental variables plus the broader categorical factor 'estuary' (i.e. the explanatory variables to which the fish are responding directly) were examined with distance-based linear models (DistLM) in PrimerE (Anderson 2004). Estuary encompasses the multiple differences in estuary-scale environmental measures (especially with respect to the broader levels of urbanisation and remaining mangroves, i.e. low, moderate, and high urbanisation), the interactive nature of these measures, and better reflects environmental measures that fish are responding directly to within coastal ecosystems. We acknowledge that this analysis corresponds to only 1 estuary at each of our 'impact levels' (i.e. $n = 1$). The level of intense sampling used in this study precludes any meaningful replication at each impact level. This shortfall is, however, offset by our high level of replication within individual estuaries ($n \geq 63$). Models were calculated on Modified Gower Log10 dissimilarity measures for the fish assemblage (Anderson et al. 2006) and normalised Euclidean distance for environmental variables. 'Important' environmental variables which are used in subsequent univariate analyses were determined by the outcomes of the sequential tests (i.e. the 'best fit' model) of the DistLM analysis.

Generalised linear models were then used to test for correlations between a suite of descriptive univariate metrics of the fish assemblage and important environmental variables that were identified in DistLM models. All GLMs were fitted with Poisson distributions and conducted in R (R Core Team 2017). We tested 3 types of fish metrics: (1) 'diversity and abundance' (species richness, harvestable fish abundance), which represented descriptors that are often used by environmental managers and in monitoring programs (Whitfield & Elliott 2002) (Table S1 in the Supplement), (2) 'habitat associations' (mangrove- or structure-associated), which represented typical occurrence patterns of fish in regional estuaries as determined by recent studies in estuaries of the region (Olds et al. 2012, Henderson et al. 2017, Gilby et al. 2018) (Table S1), and (3) 'trophic groups' (abundance of piscivores and zooplanktivores) (per Elliott et al. 2007), which represented the typical prey intake and feeding behaviour (Table S1). We selected piscivores because they are more likely to be affected by declines in water clarity (Lunt & Smee 2015) and are often tightly associated with structured habitats in this region (Gilby et al. 2016, 2018). Conversely, zooplanktivores are often tightly associated with mangroves because mangroves provide their preferred zooplankton prey in great abundance. Zooplanktivores are also particularly sensitive to changes in water quality because these have immediate consequences for planktonic food webs and therefore zooplankton prey (Giarrizzo et al. 2011, Davis et al. 2014, Saintilan & Mazumder 2017).

RESULTS

Differences in fish assemblages

Estuarine fish assemblages were shaped by the combined effects of distance from armoured shorelines and the estuary in which the site was positioned (explaining 4.3% of total variation; Table 2, Fig. S2 in

Table 2. Distance-based linear model output showing associations between environmental metrics and variation in fish assemblage structure. For full descriptions and data sources of all factors, see Table 1. AIC_c: corrected Akaike's information criterion; SS: sum of squares

Test/variable	AIC_c	SS	Pseudo-*F*	p	Variance explained	Cumulative variance explained
Marginal tests						
Estuary	5.92	4.90	0.001	0.035		
Distance of site to armoured estuarine shoreline	2.66	4.35	0.008	0.016		
Distance of site to estuary mouth	2.03	3.30	0.028	0.012		
Distance of site to mangroves	0.99	1.60	0.127	0.006		
Mangroves near site	0.98	1.59	0.164	0.006		
Urban land near site	0.37	0.60	0.68	0.002		
Sequential tests						
+Estuary	−136.84	5.9	4.9	0.001	0.035	0.035
+Distance of site to armoured estuarine shoreline	−137.31	1.5	2.5	0.046	0.009	0.043

the Supplement). A total of 62 fish species was recorded. Urbanisation was associated with sizeable variation in species richness between estuaries. The highly and moderately urbanised estuary each supported 19 species, whilst the least urbanised estuary had 53 species. Species accumulation curves support this large difference in fish diversity, with the moderately and highly urbanised estuaries approaching an asymptote, but the least urbanised estuary did not reach an asymptote up to the 100 samples taken (Fig. 2). Species assemblages differed significantly between estuaries (Fig. S2). The most abundant species in the highly-urbanised estuary were yellowfin bream *Acanthopagrus australis* (an omnivore) and yellowtail scad *Trachurus novaezelandiae* (a zooplanktivore), each comprising 29% of total fish abundance (Table S1). In the moderately urbanised estuary, the most abundant species were estuary perchlet

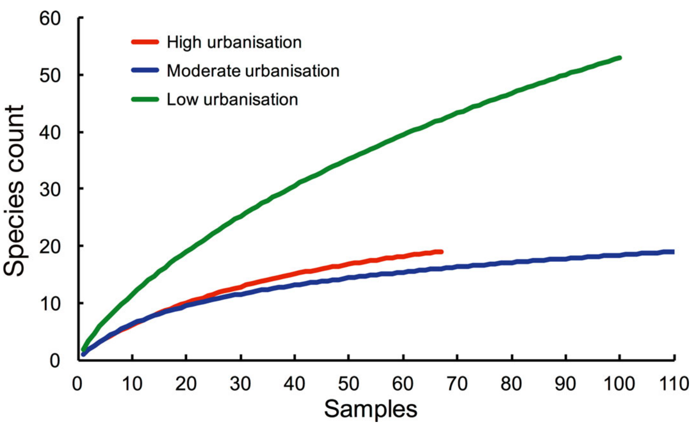

Fig. 2. Species accumulation curves for fish species in 3 estuaries with varying degrees of urbanisation in Queensland, Australia

Ambassis marianus (a zooplanktivore) (30% of total abundance), yellowfin bream (12%), and sea mullet *Mugil cephalus* (a detritivore) (10%). Similarly, the most abundant species in the least urbanised estuary were also estuary perchlet (28%), yellowfin bream (18%), and sea mullet (12%) (Table S1).

Effects of urbanisation on fish assemblages

The extent of catchment and estuarine shoreline armouring strongly modified the spatial response of estuarine fish to armoured shorelines (Fig. 3, Table 3). There were either no clear or very weak distance effects in the most urbanised estuary (Fig. 3). By contrast, we observed distinct clines for several metrics in the 2 estuaries with low or moderate degrees of urbanisation, particularly in terms of species richness and the abundance of harvestable fish species, which generally declined with increasing distance from armoured shorelines (Fig. 3A,B). The strongest distance effects in relation to armoured shorelines were observed for the abundance of piscivores and structure-associated fish: significantly more individuals occurred close to armoured shores and numbers declined sharply farther away (Fig. 3D,E). Similarly, the abundance of mangrove-associated fish declined with increasing distance from armoured shorelines, but only in the moderately and highly urbanised estuaries (Fig. 3C). Zooplanktivores were most abundant in the least urbanised estuary, where their numbers were positively correlated with distance from armoured shorelines (Fig. 3F). By contrast, the abundance of zooplanktivores in moderately and highly urbanised estuaries declined with increasing distance from armoured shorelines (Fig. 3F).

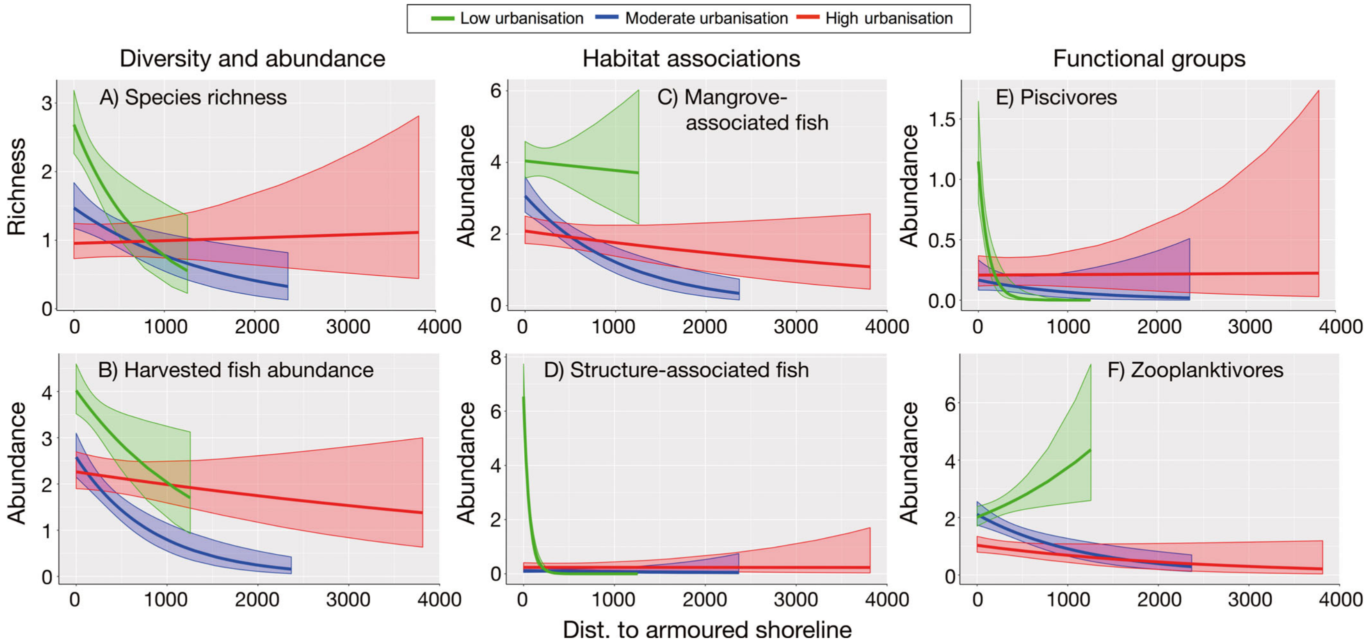

Fig. 3. Generalised linear models illustrating variation in the effects of proximity to armoured shorelines on fish assemblages from estuaries that differ in their extent of urban modification for the abundance of (A,B) indicator groups: (A) species richness and (B) harvested fish abundance; (C,D) habitat-association groups: (C) mangrove-associated fish and (D) structure-associated fish, and (E,F) functional groups: (E) piscivores and (F) zooplanktivores. Shaded areas are 95% confidence intervals

Table 3. Summary of generalised linear models testing for relationships between fish metrics (response) and 2 predictors: distance of site to armoured estuarine shoreline (DA) and estuary (Es)

Targets/source	df	χ^2	p
Management targets			
Species richness			
DA	1	13.86	<0.001
Es	2	54.02	<0.001
DA × Es	2	6.23	0.04
Harvestable fish abundance			
DA	1	35.31	<0.001
Es	2	70.02	<0.001
DA × Es	2	13.33	<0.002
Habitat associations			
Mangroves			
DA	1	16.89	<0.001
Es	2	79.41	<0.001
DA × Es	2	17.86	<0.001
Structure			
DA	1	146.64	<0.001
Es	2	327.55	<0.001
DA × Es	2	69.22	<0.001
Functional groups			
Piscivores			
DA	1	19.29	<0.001
Es	2	27.15	<0.001
DA × Es	2	18.03	<0.001
Zooplanktivores			
DA	1	2.22	0.14
Es	2	49.21	<0.001
DA × Es	2	26.38	<0.001

DISCUSSION

The consequences of removing natural vegetation from watersheds and the impacts of armouring of estuarine shorelines on coastal fishes are widely recognised, but these effects have typically been studied in isolation (Bulleri & Chapman 2010, Bishop et al. 2017, Heery et al. 2017; but see Breitburg & Riedel 2005, Bilkovic & Roggero 2008, Kornis et al. 2017). Consequently, it is not clear whether, and to what extent, these different effects of urbanisation interact to shape fish assemblages (Clynick et al. 2008, Bulleri & Chapman 2010, Sheaves et al. 2010). In this study, fish diversity and abundance typically decreased with increasing distance from armoured shorelines, irrespective of the broader levels of shoreline armouring in the estuary. In this sense, it is possible that armoured shorelines provide some value for some species of fish in these estuaries. On top of this, we found that the number and type of fish that congregated near urban structure were higher in the least urbanised estuary and scaled to the lowest values in the most urbanised estuary. This finding suggests that whilst armoured shorelines can provide some value for some species of fish, the number of fish that congregate around them is likely contingent on the broader urbanization context of the rest of the estuary (principally mangrove extent, but also total shoreline armouring and watershed urbanization). Alternatively, this finding could suggest that the abundance of urban structure-associated fish might not be modified by landscape-scale urbanization; a hypothesis that would support our finding of strong habitat associations in even the lowest urbanized estuary. Any human modification to estuarine ecosystems will be likely to have negative consequences for some species (e.g. there may have been species already lost from our systems due to this level of urbanization). However, it might be possible to maintain the broader values of the estuaries if natural vegetation is maintained. These findings have significant consequences for the management of natural ecosystems in urban estuaries because they suggest that maintaining natural ecosystems, like mangroves, across coastal seascapes is essential for maximising both fish diversity in estuaries and the habitat values of armoured shorelines for many fishes.

Coastal vegetation loss, especially of mangroves, is one of the most significant impacts on coastal ecosystems (Barbier et al. 2011, Gibbes et al. 2014, Sheaves et al. 2015). In this study, the richness and abundance of most components of the fish assemblage were highest in the least urbanised estuary — the estuary with the largest extent of mangroves. This result concurs with the hypothesis that estuaries with highly urbanised abutting land and catchments contain fewer fish and lower biodiversity overall (Browne & Chapman 2014). These findings are likely a result of 2 key stressors on estuarine biota. Firstly, poorer water quality in more urbanised estuaries due to greater sediment (Sheaves et al. 2014), pollutant (Waltham & Connolly 2007), and nutrient runoff (Barbier et al. 2011) from altered catchments filters out sensitive species that are vulnerable to fluctuations in these physico-chemical attributes of estuarine waters (Whitfield & Elliott 2002). Secondly, replacement of natural habitat throughout estuaries with armoured shorelines (as has occurred in our highly urbanised estuary) reduces habitat heterogeneity (Waltham & Connolly 2011), removes critical nursery and spawning habitats (Nagelkerken et al. 2015), and limits the abundance of fish groups that are particularly vulnerable to these sorts of impacts (in this instance, zooplanktivores, for example; Sheaves et al. 2015). Combined, the outcome is reduced biodiversity and fish abundance within highly urbanised estuaries (Sheaves et al. 2010, Heery et al. 2017) and a homogenisation of assemblages across seascapes (McKinney & Lockwood 1999, McKinney 2006).

The movement of organisms, matter, and energy across seascapes means that the effects of urbanisation are rarely confined to the armoured shorelines themselves (Lee et al. 2006). In this study, we found that fish abundance or richness was consistently higher at sites nearer to armoured shorelines. Fish abundance and richness metrics typically declined with increasing distance from armoured shorelines, irrespective of the level of watershed urbanisation. Overall, the ecological effects of urbanisation in highly urbanised estuaries resulted in the lowest fish diversity and abundance, and these impacts did not decline as with increasing distance from armoured shorelines. The key exceptions include structure-associated fish, which decline very rapidly with increasing distance from armoured shorelines in the least urbanised estuary. The structure-associated species recorded in this study are mostly reef-associated species sensitive to poor water quality (such as butterflyfishes and wrasses; see Table S1) and are therefore usually absent from moderately and highly urbanised estuaries (Gilby et al. 2017a). The remaining fish fauna are a group of highly resilient, mostly generalist species which roam across seascapes and are less associated with structured habitats (i.e. biotic homogenisation) (McKinney 2006, Gilby et al. 2016), resulting in no clear spatial patterns in relation to urban shorelines in the moderately and highly urbanised estuaries.

Determining how key monitoring and biodiversity targets respond to urbanisation is important in optimising monitoring and modifying management actions in the future (Beck et al. 2001). In this study, species richness and harvestable fish abundance, factors often targeted for monitoring and management (Whitfield & Elliott 2002, Gilby et al. 2017a), were higher in the least urbanised estuary and higher closer to armoured shorelines in all estuaries regardless of the level of urbanisation. Whilst strong trends were found for structure-associated fish, the opposite was true for mangrove-associated fish. The abundance of mangrove-associated fish increased with increasing distance from armoured shorelines in the least urbanised estuary, which might reflect the extensive area of remnant mangroves that provide valuable habitat for mangrove-associated fish throughout this estuary (Peters et al. 2015, Whitfield 2017). By contrast, the abundance of mangrove-associated fish declined with increasing distance from armoured shorelines in both the moderately and highly urbanised estuaries, which support only small patches of mangroves. These findings suggest that remnant mangroves might enhance the habitat value of armoured shorelines for fish and show how the loss of mangroves from highly urbanised estuaries can substantially alter estuarine fish assemblages (Peters et al. 2015).

The abundance of fish functional groups can act as indicators of environmental change and disturbance in coastal ecosystems (Whitfield & Elliott 2002, Sheaves et al. 2010). In this study, piscivorous fish were positively associated with urbanisation at all levels, with piscivore abundance also declining sharply with distance from armoured shorelines in the least urbanised estuary. Piscivores might use armoured shorelines as refuges, taking shelter in calmer waters in the lee of structures between foraging excursions to other habitats or feeding areas because they support an abundance of small fishes from other functional groups. Armoured shorelines might, therefore, partially replace the habitat roles that some natural ecosystems provide for fish, provided that sufficient remnant vegetation remains to maintain the ecological condition of the estuary.

Previous studies have demonstrated zooplanktivores to be highly sensitive to urbanisation at multiple levels (Whitfield 1985). Firstly, the abundance of zooplanktivores is reduced in urbanised estuaries because they are closely associated with natural spawning habitats (especially mangroves; Allen et al. 1995). Secondly, their preferred zooplankton prey items in estuaries, principally crab and fish larvae, are always in higher abundance in natural habitats, especially mangroves and saltmarsh (Morgan 1990). Zooplanktivores are also particularly sensitive to any changes in hydrology and water quality, which modify planktonic food webs, and therefore alter their food resources (Kornis et al. 2017). Finally, zooplanktivores are negatively associated with armoured shorelines, but piscivores, the key predators of smaller zooplanktivores, are positively correlated with armoured shorelines, potentially reflecting predator-avoidance strategies (Whitfield & Blaber 1978). We suggest that piscivores might, therefore, shelter among the complex structures of armoured shorelines and make feeding migrations to other natural habitats that support a higher abundance of zooplanktivores and other prey items; this hypothesis requires further testing.

This study demonstrates that estuaries with low levels of urbanisation can support a high diversity and abundance of estuarine fishes, which aggregate near high relief habitats, encompassing both natural and man-made structures. Paradoxically, the habitat values of armoured shorelines for fishes appear to be greatest in estuaries that also support mangroves, which are more structurally complex. These findings stress the importance of conserving a diverse seascape where a mosaic of habitat types provides complementary and alternative areas for a diversity of fishes. Consequently, maximising the diversity and abundance of fish in estuaries and optimising the habitat values of armoured shorelines for many species necessitates preservation of natural ecosystems, especially mangroves, across estuarine seascapes. Because fish move regularly between natural and artificial habitats in urban estuaries, it will also be necessary to conserve, and restore, critical spatial linkages (e.g. movement corridors, hydraulic connections) between natural ecosystems and urban fish habitats (Soulé et al. 2004, Olds et al. 2016).

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