



## Landscape context and nutrients modify the effects of coastal urbanisation

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### ABSTRACT

Estuaries are focal points for coastal cities worldwide, their habitats frequently transformed into engineered shorelines abutting waters with elevated nutrients in an urbanised landscape. Here we test for relationships between shoreline armouring and nutrients on the diversity and trophic composition of fish assemblages across 22 estuaries in eastern Australia. Urbanisation was associated with fish diversity and abundance, but there were differences in the effects of shoreline armouring and nutrient level on the trophic composition of fish assemblages. Fish diversity and the abundance of most trophic groups, particularly omnivores, zoobenthivores and detritivores, was greatest in highly urban estuaries. We show that estuarine fish assemblages are associated with urbanisation in more nuanced ways than simple habitat transformation would suggest, but this depends on the broader environmental context. Our findings have wider implications for estuarine conservation and restoration, emphasizing that ecological benefits of habitat measures may depend on both landscape attributes and water quality in urban settings.

### 1. Introduction

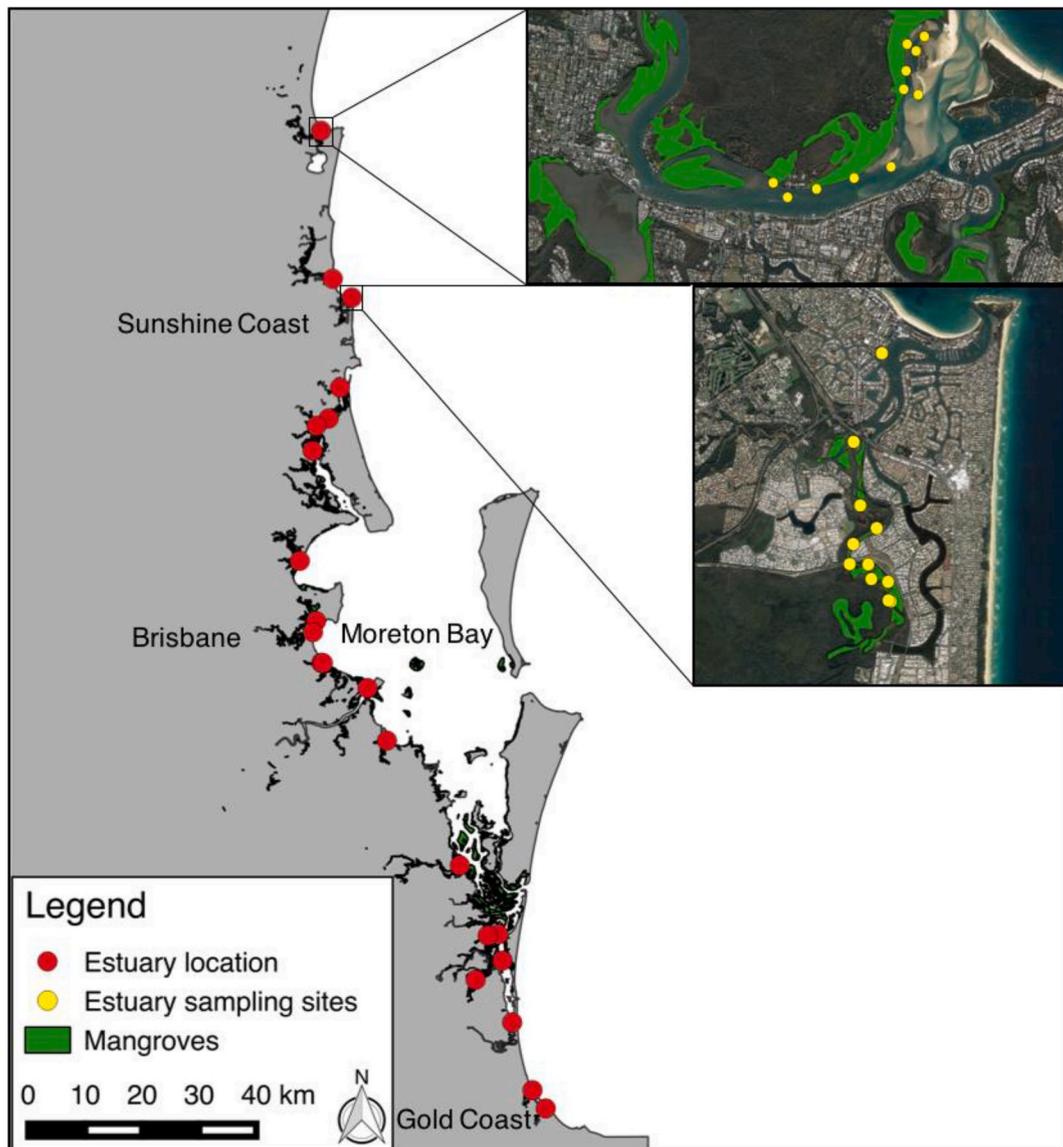
Natural ecosystems have been profoundly modified by human actions, with widespread and frequently negative effects on the diversity of organisms, structure of food-webs, and distribution of ecological functions (Chapin et al., 2000; Grimm et al., 2008a; Tschardt et al., 2012). Urbanisation is the most ubiquitous agent of landscape transformation (Grimm et al., 2008a; Seto et al., 2012). Typically, urbanisation alters populations and assemblages across numerous terrestrial, marine and freshwater ecosystems through the replacement of natural habitats with engineered structures and impervious surfaces (Cheptou et al., 2008; Loreau and Mazancourt, 2013; McPhearson et al., 2016), or increases in nutrient loadings via increased runoff and human waste or treated sewage (Seto and Shepherd, 2009). Well-known examples that illustrate the pervasive effects of urbanisation include changes to plant and animal assemblages in forests and grasslands near large cities (Aronson et al., 2014; McKinney, 2008), losses of key feeding and resting habitats for migratory birds and mammals (Johnson et al., 2006; Ordeñana et al., 2010; Runge et al., 2015), and reductions in the diversity and abundance of fish and invertebrates in modified lakes and estuaries (Carpenter et al., 1998; Collen et al., 2014; Radinger et al., 2016). The impacts of

different urban stressors are, however, typically assessed in isolation, and the potential combined effects from habitat transformation and nutrient enrichment are rarely tested with empirical data (Beninde et al., 2015; Grimm et al., 2008b; McPhearson et al., 2016).

The size, type and configuration of natural ecosystems (e.g. forests, grasslands, mangroves) across landscapes (hereafter called 'landscape context') shapes the distribution and availability of resources (e.g. food, shelter), biodiversity, and the provision of key ecological functions (e.g. herbivory, scavenging, predation) (Hodgson et al., 2011; Huijbers et al., 2016; Olds et al., 2016). The direct replacement of natural habitats with hard structures and impervious surfaces (e.g. buildings, bridges, rock walls) alters the context within which natural habitats sit, and can negatively affect biodiversity, ecological functions and ecosystem services by fragmenting landscapes, reducing landscape heterogeneity, and facilitating the spread of some exotic species (Bulleri and Chapman, 2010; Layman et al., 2014; Lindenmayer and Fischer, 2013; Olds et al., 2018). The indirect effects of intense urbanisation include changes to topography, hydrology and atmospheric conditions, and the accumulation of human waste in the vicinity of cities (Dafforn et al., 2015; McPhearson et al., 2016; Seto and Shepherd, 2009). These impacts can lead to nutrient enrichment and pollution of the air, soil and water, and

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**Fig. 1.** Location of study estuaries in southern Queensland, Australia. Insets illustrate the location of sampling sites along: (A) a relatively natural estuary with abundant mangroves (Noosa); and (B) a highly urbanised estuary where shorelines are dominated by artificial structures (Mooloolah).

can shape the distribution, abundance and diversity of plants and animals across modified landscapes (Howarth, 2008; Nyenje et al., 2010; Smith, 2003). Therefore, it is likely that variation in landscape context due to urbanisation might influence how animal assemblages respond to the relative or combined effects of urbanisation, but this is yet to be tested with empirical data.

The ecological effects of urbanisation are not universally negative as numerous species can flourish in urban environments (Sushinsky et al., 2013). Opportunistic taxa that can cope with the combined effects of nutrients and pollution can take advantage of empty niches in urban habitats. For example, birds and mammals shelter in city forest fragments and forage on human refuse (Mainwaring, 2015; Ordeñana et al., 2010; Shochat et al., 2010), amphibians breed in artificial wetlands used for stormwater control (Brand and Snodgrass, 2010; Chester and Robson, 2013), and fish and invertebrates can live in estuarine lakes built to limit sedimentation and nutrient inputs (Clynick et al., 2008; Layman et al., 2014; Waltham and Connolly, 2011). Despite notable benefits for some species, the composition of 'urban assemblages' often differs to those inhabiting natural areas (Firth et al., 2013; Henderson et al., 2019), and there is likely a threshold in certain abiotic factors (e.g. pollution, excessive nutrients) beyond which these taxa can no longer

survive (Carpenter et al., 1998; Vitousek et al., 1997). The direct effects from habitat loss have been reported widely, and for most taxonomic groups, but it is not clear whether, and how, these impacts interact with other indirect human stressors (e.g. nutrients) that also modify animal assemblages and ecological functions in urban landscapes.

Most of the global human population inhabits coastal areas (Schlacher et al., 2016; Seto et al., 2012). Rapid, and concentrated, urbanisation has fragmented coastal ecosystems and altered the distribution of coastal biodiversity globally (Heery et al., 2017; Huijbers et al., 2015; Martínez et al., 2007). This coastal urbanisation is concentrated in estuarine environments, which have been extensively modified (e.g. canals, artificial lakes, armoured shorelines) to cater for the needs of a growing human population (Bishop et al., 2017; Waltham and Connolly, 2011). The widespread, and intense, modification of estuaries has significantly impacted the condition of nearshore habitats (Chapman and Underwood, 2011; Waycott et al., 2009), altered the composition of animal assemblages (Dugan et al., 2008; Henderson et al., 2019; Sheaves et al., 2012), and modified the distribution of ecological functions (Barbier et al., 2011; Huijbers et al., 2015) across coastal seascapes. Estuaries provide many important ecosystem services for people (e.g. fisheries, good water quality, shoreline protection), and these are

intrinsically linked to abundance and diversity of estuarine biota, and the ecological functions they perform (e.g. estuaries provide important nursery habitats for many harvested fish species) (Barbier et al., 2011; Beger et al., 2010; Nagelkerken et al., 2015; Saunders et al., 2014).

Throughout history, estuaries have been key sites for the development and growth of coastal urban nodes, with many of the global great cities situated on or near estuaries. This concentration of human activity abutting estuarine shores means that estuarine ecosystems experience multiple stressors that are typically associated with cities, most prominently habitat loss and changes to the chemical and physical environmental conditions (Grimm et al., 2008b; Kennish, 2002; Neilson and Cronin, 2012). In many urban estuaries, a prominent form of habitat change is hardening of natural shorelines with engineered defences (e.g. rock walls, revetments) and the placement of jetties, pontoons and similar structures, whilst chemical conditions are frequently altered by inputs of sediments and nutrients, resulting in extreme cases of eutrophication (Gilby et al., 2017b; Gorman et al., 2017). Responses of estuarine fish to shoreline armouring and nutrient inputs are evident in many systems (Breitburg et al., 2009; Bulleri and Chapman, 2010; Kennish, 2002; Smith and Schindler, 2009; Strain et al., 2018) but it remains largely unknown whether and how these types of stressors interact, and whether these responses are influenced by landscape context – this is the test of this paper.

## 2. Materials and methods

### 2.1. Study seascape

We sampled fish assemblages from 22 estuaries in southern Queensland, Australia (Fig. 1). Estuaries were distributed over 200 km of coastline from the Noosa River in the north, to Currumbin Creek in the south (26°22' S, 153° 04' E – 28° 07' S, 153°29' E). Estuaries were sampled in random order between June and August 2015. Estuaries in the region differ considerably in their level of urban modification, and nutrient status (Gilby et al., 2017b; Maxwell et al., 2015), and are therefore ideal for testing how landscape context might influence the effects of shoreline armoring and nutrients on estuarine fish assemblages (Blaber, 2013; Sheaves et al., 2010).

### 2.2. Fish surveys

Fish assemblages were surveyed at ten sites in each estuary using baited remote underwater video stations (BRUVS). We selected BRUVS as they are suitable for sampling fish communities that are representative of an entire estuary and not just a specific habitat within that estuary (Gilby et al., 2017b). BRUVS can be effective for surveying fish from all functional groups in estuaries, with stations that are baited with pilchards performing as well as, or better than those that remain unbaited (Henderson et al., 2019c; Wraith et al., 2013), however this may not be the case in non-estuarine ecosystems where other methods may be more suitable (Goetze et al., 2015). Sites were sampled on two separate occasions over a three-day period (i.e.  $n = 20$  per estuary). We sampled the marine reach of each estuary, which was classified as the section of the waterway from the estuary mouth to where long-term (i.e. based on 10-year average) salinity levels were  $\geq 30$  psu (EHMP, 2016). Sites were distributed evenly along this marine reach in each estuary, with distances between sites ranging between 240 m and 1.3 km. BRUVS were deployed in water depths of  $\sim 2$  m for 1-h over unvegetated substrate within 30 m of adjacent banks, to control for potential connectivity effects with shoreline vegetation. BRUVS consisted of a high definition GoPro camera mounted on a 5-kg weight, and a bait bag fixed to a PVC pipe 0.5 m from the camera. The standard bait used across all deployments was  $\sim 500$  g of pilchards (*Sardinops sagax*) in a  $20 \times 30$  cm mesh bag with 0.5 cm openings. Bottom water clarity was quantified using a  $20 \times 20$  cm visibility calibration disk with three equal width vertical stripes (i.e. white, grey, and black) attached to the end of each

PVC arm. Water clarity was considered high when all three colours were visible, and poor if only grey and white stripes were visible. To account for possible effects of variation in water clarity among survey sites, we only counted fish that were recorded between the camera and the visibility disk. Fish abundance, species richness and assemblage composition were quantified from video footage using the Max N statistic; which describes the maximum number of individuals of each species recorded at one time (Gladstone et al., 2012; Murphy and Jenkins, 2010). Fish were then categorised into five trophic groups: piscivores, zoobenthivores, detritivores, zooplanktivores, and omnivores (Elliott et al., 2007).

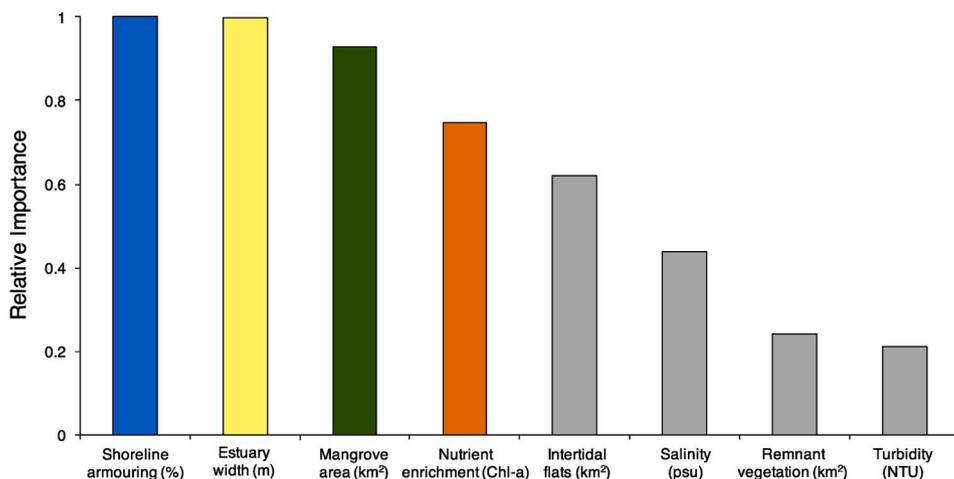
### 2.3. Quantifying spatial metrics

To test how the extent of shoreline armouring and level of nutrients modify fish assemblages in estuaries, we quantified the proportion of urban shoreline in the sampled reach of each estuary and measured the concentration of chlorophyll-a (chl-a) at each site (following Gilby et al., 2017b). Water quality data (e.g. turbidity and salinity) was measured at each site, and long-term datasets (e.g. chlorophyll-a) were obtained for each estuary from a local ecosystem health monitoring program (EHMP) (EHMP, 2016). The area of natural marine ecosystems (i.e. mangroves, intertidal flats) and remnant terrestrial vegetation within 500 m of each site was calculated from digitized habitat maps using Quantum GIS (Queensland Government, 2014, 2015). A buffer distance of 500 m was chosen to encompass the daily home-range movements of fishes in the study region (Olds et al., 2012; Sheaves, 1993). In the studied estuaries, the extent of shoreline armouring was significantly and positively correlated to the total area of urban land in the catchment ( $df = 438$ ,  $P < 0.001$ ,  $F = 79.2$ ), which makes it a suitable index for urbanisation in estuaries (Breitburg et al., 2009; Hart et al., 2015). Chl-a is a more suitable indicator of nutrient levels in estuaries than simple nutrient concentrations (Hart et al., 2015) and, in this study Chl-a was significantly, and positively, correlated with total nitrogen concentration ( $df = 438$ ,  $F = 61.5$ ,  $P < 0.001$ ). We also measured water quality (salinity, turbidity), the size of each estuary (i.e. width at the mouth), the area of natural marine ecosystems (mangroves, intertidal flats), and the area of remnant terrestrial vegetation in each river catchment to allow us to test for possible confounding effects of variation in these attributes among estuaries.

### 2.4. Data analyses

We used multivariate random forests (MRFs) to determine the relative importance of shoreline armouring, nutrients and other environmental attributes in explaining spatial variation in fish assemblage composition (Miller et al., 2014). MRFs advance on traditional multivariate regression trees by running many permutations of the data, thereby reducing relative error and improving the accuracy of factor importance estimates (Sega and Xiao, 2011). All MRFs were calculated on Hellinger transformed data. We constructed MRFs with 100, 200, 300, 500, and 1000 trees; model performance did not improve after 300 trees, so this was chosen as the maximum number to be included (Miller et al., 2014). Factor importance is determined by randomly fitting factors to the model, with the most important factors having the greatest relative effect on mean squared error (Breiman, 2001; Miller et al., 2014). MRFs produce a similarity matrix based on the positions of cases in the terminal nodes of trees; consequently, this matrix includes information regarding both the structure of fish communities and the environmental variables of interest. This similarity matrix was used to create a multi-dimensional scaling (MDS) ordination to visualise the influence of 'important' environmental variables (i.e. those with importance values  $> 0.7$ ) on fish assemblages.

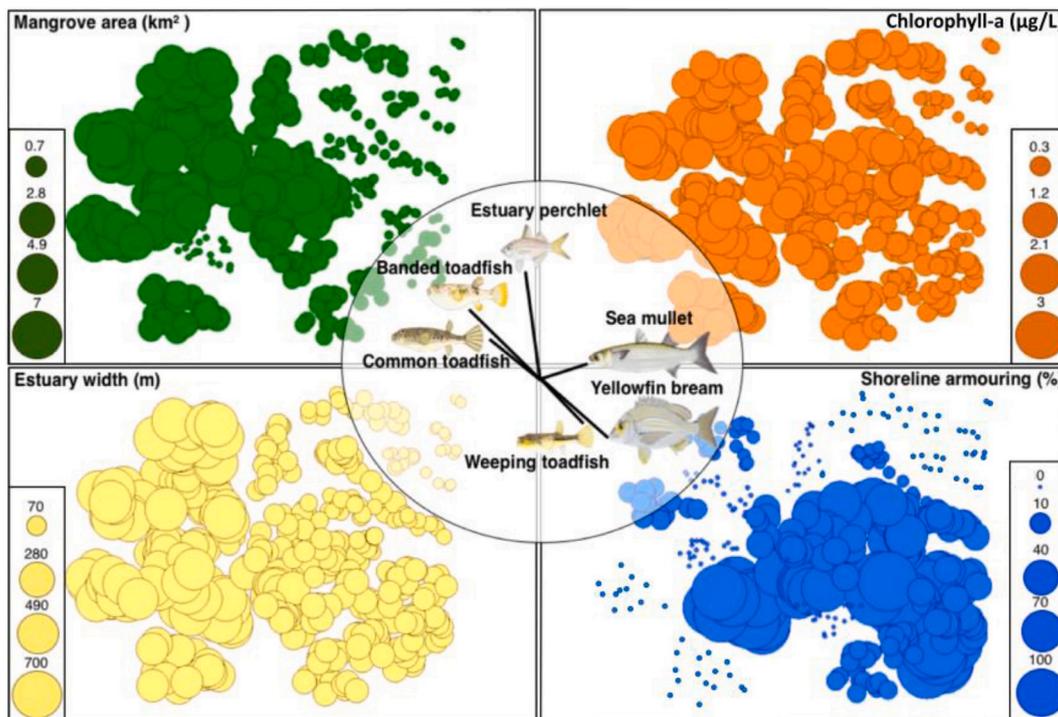
The MRF model identified that the extent of shoreline armouring and level of nutrients both explained significant variation in the composition of estuarine fish assemblages (Fig. 2). Estuary width and the area of mangrove habitat were also important features for estuarine fishes. To



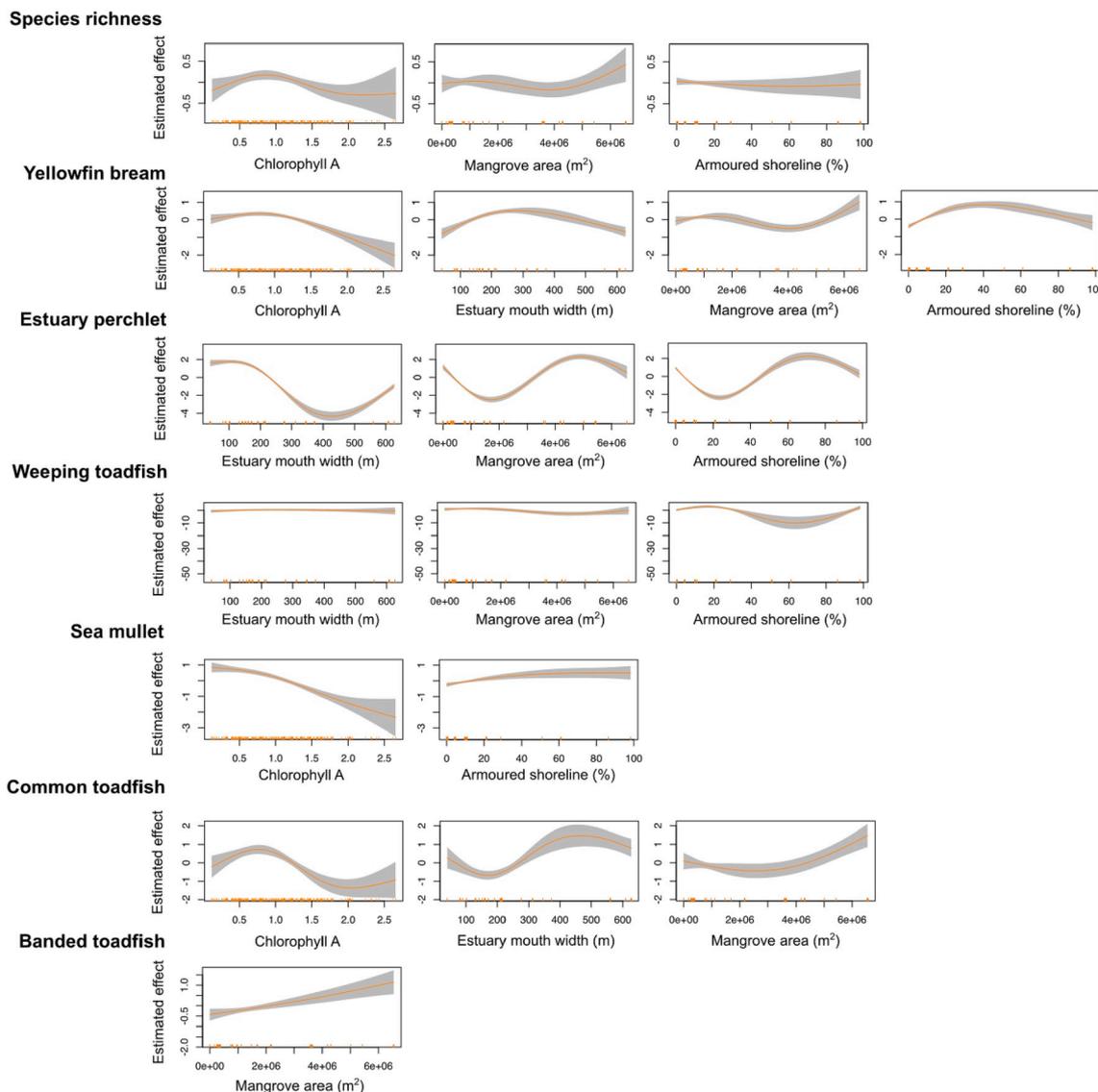
**Fig. 2.** Relative importance of shoreline armouring, nutrients level, landscape context and other environmental variables to the composition of estuarine fish assemblages. Importance values are the results of Multivariate Random Forests (MRFs) models; larger values (shaded in colour) are of higher ecological significance, whereas smaller values (<0.7 and shaded in grey) have little or no effect on fish assemblages. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

further examine differences in the effects of shoreline armouring and nutrients on fish assemblages, we grouped sites into upper and lower quartiles for both of these features (i.e. to examine the effects at the upper and lower ‘extremes’ of environmental features) and used permutational multivariate analysis of variance (PERMANOVA) to test for differences in the species and trophic composition of fish assemblages (Anderson, 2001). We chose to separate our sites into quartiles for the PERMANOVA analysis as we were interested in understanding how fish communities differ relative to the extremes of these environmental variables. MDS was used to visualise significant factors following PERMANOVA. To assess how variation in environmental variables influences variation in species richness and the abundance of dominant fish species (based on vectors from the MDS) between estuaries, we used generalised additive models (GAMs) in R using the *mgcv* and *MuMIn* packages (Bartoń, 2013; Wood and Wood, 2015). GAMs were chosen instead of other regression models because we could not assume linear

relationships. We fit models with all possible combinations of four or fewer environmental variables and restricted individual models to four polynomial functions or fewer to minimise model overfitting. Models were compared using Akaike information criterion (AICc) corrected for small sample sizes and assessed models for auto-correlation using the *acf* function in R. Best fit models were considered to be those with the lowest AICc value. The relative importance of variables in each model was calculated by summing weighted AICc values across all models containing the variable of interest. We identified the most ‘important’ factor across all models, based on summed importance values across best-fit GAM models for each different metric. Dufrene-Legendre indicator species analysis was then used to identify trophic groups that best characterised sites with high and low shoreline armouring, and high and low nutrient levels (Dufrene and Legendre, 1997; Roberts, 2013). We then used a multi-dimensional scaling (MDS) segmented bubble plot to display the effects of shoreline armouring, nutrients and landscape



**Fig. 3.** Multi-dimensional scaling (MDS) ordination displaying the effects of shoreline armouring, chlorophyll-a and landscape context on estuarine fishes. Vectors show species correlations with the ordination space (e.g. yellowfin bream were positively correlated with shoreline armouring and banded toadfish were positively correlated with chlorophyll-a and mangrove area). Fish illustrations sourced from [www.efishalbum.com/](http://www.efishalbum.com/).



**Fig. 4.** Generalised additive model (GAM) partial plots illustrating the significant associations between species richness and the abundance of important species (cf. Fig. 3). Grey shaded areas represent the 95% confidence interval.

context on fish trophic groups. This was based on significant Dufrene-Legendre indicator species analysis on trophic groups which compared sites at high and low levels of shoreline armouring and nutrients.

**3. Results**

The composition of estuarine fish assemblages was associated with the combined effects of shoreline armouring, nutrients, and the landscape context (i.e. estuary width and mangrove area) of individual estuaries (Fig. 2). Highly modified estuaries with extensive urban shorelines (i.e. with 60–100% of shorelines hardened with artificial structures), and few mangroves ( $\leq 6 \text{ km}^2$ ), were dominated by yellowfin bream (*Acanthopagrus australis*), sea mullet (*Mugil cephalus*), and weeping toadfish (*Torquigener pleurogramma*) (Figs. 3 and 4). By contrast, estuaries that were characterized by abundant mangroves ( $\geq 6 \text{ km}^2$ ) were dominated by banded toadfish (*Marylina pleurostricta*) (Figs. 3 and 4). Narrow estuaries ( $< 100 \text{ m}$  wide) with few mangroves ( $\leq 6 \text{ km}^2$ ), and oligotrophic conditions (chlorophyll-a concentrations  $\leq 0.6 \text{ mg/L}$ ), were dominated sea mullet (Figs. 3 and 4). Estuaries that were characterized by low or high mangroves and estuary mouth widths contained

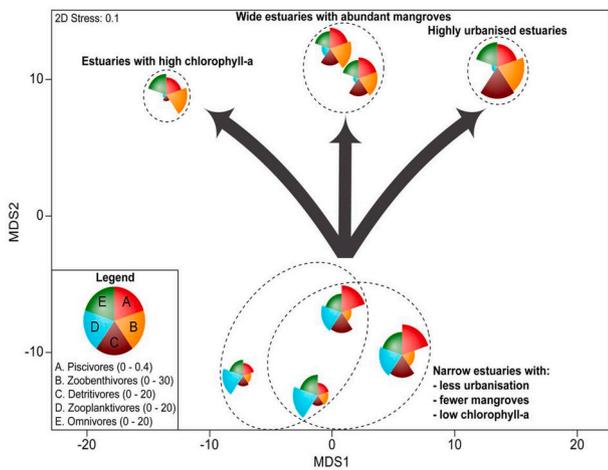
**Table 1**

Summary of permutational multivariate analysis of variance (PERMANOVA), and pairwise comparisons, testing for effects at the extremes (i.e. low vs high quartile values) of shoreline armouring, chlorophyll-a, and landscape context on the trophic composition of estuarine fish assemblages. Values in **bold** are significant at  $\alpha = 0.05$ .

Source of variation	F/t value	p-value
Main test		
High vs low modification (d.f. = 7)	15.884	<b>0.001</b>
<b>Pairwise comparisons</b>		
<b>High vs low modification</b>		
Shoreline armouring	4.6117	<b>0.001</b>
Chlorophyll-a	4.7276	<b>0.001</b>
Mangrove area	5.0049	<b>0.001</b>
Estuary width	5.4513	<b>0.001</b>

abundant estuary perchlet (*Ambassis marianus*) (Figs. 3 and 4). Common toadfish (*Tetractenos hamiltoni*) dominated estuaries that contained more mangroves ( $\geq 6 \text{ km}^2$ ) and were wide ( $> 300 \text{ m}$  wide) (Figs. 3 and 4).

The joint effects of shoreline armouring, nutrients, and landscape context were also associated with the trophic composition of fish



**Fig. 5.** Multi-dimensional scaling (MDS) segmented bubble plot displaying the effects of shoreline armouring, chlorophyll-a and landscape context on fish trophic groups. Bold arrows indicate significant differences in assemblage structure between the upper and lower quartiles of shoreline armouring, nutrients and landscape context. For example, zoobenthivores are more abundant in estuaries with high chlorophyll *a*, compared to those with lower levels. Dashed lines delineate coherent groups ( $p < 0.05$ ) defined by pairwise tests following permutational multivariate analysis of variance. Numbers in parentheses indicate the range of the average abundance of each functional group.

assemblages (Table 1, Figs. 3 and 5). Fish assemblages differed between estuaries with extensive urban shorelines and those that were characterized by high nutrient levels (Tables 2 and 3, Figs. 3 and 5). Highly modified estuaries with extensive urban shorelines were dominated by abundant omnivores (yellowfin bream; crescent perch, *Terapon jarbua*; tarwhine, *Rhabdosargus sarba*), zoobenthivores (common silverbiddy, *Gerres subfasciatus*; whipfin silverbiddy, *G. filamentosus*; weeping toadfish) and detritivores (sea mullet; striped scat, *Selenotoca multifasciata*) (Tables 3 and 4, Fig. 5). By contrast, less urbanised estuaries were characterised by low fish diversity and an abundance of zooplanktivores (estuary perchlet; southern herring, *Herklotsichthys castlenau*; common hardyhead, *Atherinomorus vaigiensis*) (Tables 3 and 4, Fig. 5). Estuaries that were characterized by high chl-*a* loads were dominated by abundant zoobenthivores (banded toadfish; common silverbiddy; common toadfish) (Tables 3 and 4, Fig. 5). By contrast, estuaries with low nutrient levels were dominated by zooplanktivores (estuary perchlet; southern herring; common hardyhead) (Tables 3 and 4, Fig. 5).

**4. Discussion**

Urbanisation can alter the structure of estuarine assemblages and the functioning of ecosystems by replacing natural habitats with hardened

shorelines, and via the effects of nutrients and pollution (Alberti, 2010; Grimm et al., 2008a). However, the potential combined effects of these different urban stressors are rarely tested with empirical data (Concepción et al., 2016; McPhearson et al., 2016). We show that shoreline armouring, nutrient levels, and landscape context combine to shape the diversity, abundance and trophic composition of fish assemblages in moderately degraded estuaries. There were, however, distinct trophic effects from these different components of urbanisation. Armoured shorelines were associated with greater fish diversity and an abundance of omnivores, zoobenthivores and detritivores, whereas zoobenthivores were associated with high nutrient levels, and natural estuaries (i.e. those with low levels of nutrient input and reduced shoreline armouring) were characterised by abundant zooplanktivores. These results indicate that the effects of urbanisation on the trophic composition of animal assemblages can depend on both the level of nutrients and landscape context in which urban structures are embedded (sensu Alberti, 2010; Bishop et al., 2006; Diaz and Rosenberg, 2008; Lee et al., 2006).

The positive association between armoured shorelines and fish diversity and abundance, and the trophic composition of assemblages indicate that the ecological impacts of urbanisation are not universally negative (sensu Becker et al., 2013; Dafforn et al., 2015; McPhearson et al., 2016). The abundance of most fish trophic groups (i.e. omnivores, zoobenthivores and detritivores) in estuaries was, however, only greater in urban environments that were also characterised by low nutrients. These findings have important implications for the spatial management of highly modified estuaries, and other similar degraded coastal ecosystems, and indicate that the ecological performance of coastal conservation and ecosystem engineering projects might depend on both the level of nutrients experienced, and the spatial position of ecosystems in urban landscapes. For example, the hardened shorelines and artificial structures that characterise urban estuaries can provide abundant food (e.g. sessile epibiota, infaunal invertebrates) and shelter (e.g. rock walls, pylons) for fish (Chapman and Underwood, 2011; Toft et al., 2013; Waltham and Connolly, 2013). Despite growing evidence suggesting

**Table 3**

Summary of Dufrene-Legendre indicator species analysis results testing how shoreline armouring and chlorophyll-a modify the trophic composition of estuarine fish assemblages.

Impact/Trophic group	Primary habitat	Indicator value	p-value
<b>Shoreline armouring</b>			
Omnivores	High urbanisation	0.61	0.001
Zoobenthivores	High urbanisation	0.87	0.001
Detritivores	High urbanisation	0.80	0.001
Zooplanktivores	Low urbanisation	0.34	0.001
<b>Chlorophyll-a</b>			
Zoobenthivores	High nutrients	0.72	0.001
Zooplanktivores	Low nutrients	0.22	0.001

**Table 2**

Best-fit general additive models (GAMs) relating the species richness and abundance of most dominant species to the upper and lower extremes of environmental variables. For linear relations, arrows indicate whether the variable is associated with an increase or decrease in fish abundance. Important values are included in parentheses (larger values indicate stronger correlation with fish abundance).

Richness or species	Variables included in best-fit models		d.f.	Models
Species richness	Mangrove area (1.0) <sup>b</sup>	Armoured shoreline (0.74) <sup>b</sup>	Chlorophyll <i>a</i> (1.0) <sup>a</sup>	10 2
Yellowfin bream	Armoured shoreline (1.0) <sup>a</sup>	Chlorophyll <i>a</i> (1.0) <sup>c</sup>	Estuary width (1.0) <sup>a</sup>	Mangrove area (0.88) <sup>b</sup> 11 1
Estuary perchlet	Armoured shoreline (1.0) <sup>b</sup>	Estuary width (0.99) <sup>c</sup>	Mangrove area (0.88) <sup>b</sup>	9 2
Weeping toadfish	Armoured shoreline (0.88) <sup>a</sup>	Mangrove area (0.92) <sup>c</sup>	Estuary width (0.69) <sup>a</sup>	8 3
Sea mullet	Armoured shoreline (0.51) <sup>d</sup>	Chlorophyll <i>a</i> (0.51) <sup>d</sup>		4 9
Common toadfish	Mangrove area (1.0) <sup>b</sup>	Chlorophyll <i>a</i> (1.0) <sup>c</sup>	Estuary width (1.0) <sup>b</sup>	10 2
Banded toadfish	Mangrove area (1.0) <sup>b</sup>			4 8

<sup>a</sup> Non-linear responses (see Fig. 4).  
<sup>b</sup> Positive correlations.  
<sup>c</sup> Negative correlations.  
<sup>d</sup> Neutral response.

**Table 4**

Effects of shoreline armouring and chlorophyll-a on the abundance (mean  $\pm$  SE) of fish trophic groups and dominant fish species. Abundances highlighted in bold represent those functional groups that were significant in the Dufrene-Legendre indicator species analysis.

Trophic group	Mean abundance (SE) at high levels	Mean abundance (SE) at low levels	Common name	Scientific name	Mean abundance (SE) at high levels	Mean abundance (SE) at low levels
<b>Shoreline armouring</b>						
Omnivores	<b>10.71 (1.65)</b>	3.95 (0.48)	Yellowfin bream	<i>Acanthopagrus australis</i>	<b>9.31 (0.92)</b>	3.56 (0.45)
			Crescent perch	<i>Terapon jarbua</i>	<b>0.45 (0.27)</b>	0.09 (0.05)
			Tarwhine	<i>Rhabdosargus sarba</i>	<b>0.33 (0.11)</b>	0.1 (0.03)
Zoobenthivores	<b>3.66 (2.08)</b>	2.5 (0.24)	Common silverbiddy	<i>Gerres subfasciatus</i>	<b>1.30 (0.88)</b>	0.54 (0.10)
			Whipfin silverbiddy	<i>Gerres filamentosus</i>	<b>0.36 (0.34)</b>	0.04 (0.02)
			Weeping toadfish	<i>Torquigener pleurogramma</i>	<b>0.14 (0.06)</b>	0.07 (0.02)
Detritivores	<b>7.94 (4.73)</b>	1.95 (0.35)	Sea mullet	<i>Mugil cephalus</i>	<b>7.86 (4.73)</b>	1.49 (0.28)
			Striped scat	<i>Selenotoca multifaciata</i>	0.08 (0.04)	<b>0.36 (0.14)</b>
Zooplanktivores	8.66 (4.19)	<b>9.05 (2.50)</b>	Estuary perchlet	<i>Ambassiss marianus</i>	8.58 (4.19)	<b>8.64 (2.04)</b>
			Southern herring	<i>Herklotsichthys castlenai</i>	0.06 (0.05)	<b>0.34 (0.33)</b>
			Common hardyhead	<i>Atherinomorus vaigiensis</i>	0.01 (0.01)	<b>0.18 (0.11)</b>
<b>Chlorophyll-a</b>						
Zoobenthivores	<b>4.99 (0.71)</b>	2.96 (0.45)	Banded toadfish	<i>Marilyna pleurostricta</i>	<b>0.96 (0.18)</b>	0.37 (0.12)
			Common silverbiddy	<i>Gerres subfasciatus</i>	<b>0.70 (0.21)</b>	0.51 (0.19)
			Common toadfish	<i>Tetractenos hamiltoni</i>	0.64 (0.12)	<b>0.74 (0.15)</b>
Zooplanktivores	5.95 (2.37)	<b>8.74 (3.10)</b>	Estuary perchlet	<i>Ambassiss marianus</i>	4.76 (2.36)	<b>5.81 (1.53)</b>
			Southern herring	<i>Herklotsichthys castlenai</i>	0.05 (0.04)	<b>2.83 (2.47)</b>
			Common hardyhead	<i>Atherinomorus vaigiensis</i>	0.08 (0.09)	<b>1.12 (1.03)</b>

that anthropogenic nutrient-enrichment can enhance productivity in many oligotrophic estuaries prior to reaching a threshold where the effects become negative (Bishop et al., 2006; York et al., 2012), the abundance of prey and the quality of sheltering opportunities for fish may be reduced in estuaries with high nutrient and sediment loads because these conditions limit the recruitment of both fish, and the invertebrates they eat (Anderson et al., 2002; Breitbart et al., 2009; Kemp et al., 2005; Whitfield and Elliott, 2002). We might, therefore, expect better ecological outcomes from coastal management, when urban conservation and restoration projects target estuaries that experience lower nutrient loads (Cloern, 2001; Rabalais et al., 2009; Smith and Schindler, 2009; Snickars et al., 2015). It follows that ecological engineering projects, which seek to maximise the habitat values of armoured shorelines and artificial structures for fish, might also experience greater success in estuaries with good water quality, and low nutrient and sediment loads (Brook et al., 2017; Dafforn et al., 2015).

The effects of urbanisation on fish diversity and abundance were associated with the distribution of yellowfin bream, weeping toadfish and sea mullet, which were most abundant in highly modified estuaries. These taxa are dominant omnivores, zoobenthivores and detritivores, respectively, in estuaries and use artificial shorelines and urban waterways as feeding habitats and sheltering sites (Dafforn et al., 2015; Sheaves et al., 2014; Waltham and Connolly, 2013; Whitfield et al., 2012b). Yellowfin bream are of great significance to anglers and commercial fisheries on the east coast of Australia (Meynecke et al., 2008; Olds et al., 2012; Taylor et al., 2012). In conjunction with this, yellowfin bream are a large omnivore that feeds predominantly on fish and benthic invertebrates, and aggregate over a range of structurally complex habitats (e.g. reefs, seagrass meadows, woody snags, artificial structures) (Curley et al., 2013; Gilby et al., 2018; Sheaves et al., 2014; Strain et al., 2018). By contrast, weeping toadfish are small zoobenthivores that feed on benthic crustaceans and molluscs, which utilise both soft-sediment and structurally complex ecosystems as habitat (Hyndes et al., 2003; Miller and Skilleter, 2006; Valesini et al., 2004). Similar to

yellowfin bream, sea mullet are harvested widely in commercial fisheries in Australia (Gilby et al., 2017a; Whitfield and Patrick, 2015). Sea mullet feed on organic detritus and benthic microalgae, and occur over a diverse range of habitats across freshwater, estuarine and oceanic systems (Blaber, 1976; Lawson and Jimoh, 2010; Whitfield et al., 2012a). Armoured shorelines and artificial structures (i.e. jetties, pontoons, rock walls) are ubiquitous features of estuaries in the study area, which have also been extensively modified by human activities (i.e. dredging, channelization, trawling), and are therefore characterised by their lack of naturally complex habitats (e.g. rock bars, woody snags) (Waltham and Connolly, 2011). These artificial habitats typically support a diverse community of epibiota and shelter an abundance of infaunal invertebrates in the underlying soft-sediments (Clynick et al., 2007; Connell and Glasby, 1999; Davis et al., 2014). Hence, the aggregation of yellowfin bream and weeping toadfish in highly urban estuaries (i.e. 60-100% of shorelines armoured with artificial structures) is likely a response to the abundant opportunities for both feeding and sheltering that these locations provide. By contrast, the high abundance of sea mullet in estuaries with heavily armoured shorelines likely reflects the abundance of soft-sediment benthos, which provides favourable conditions for locating detritus and benthic microalgae year round (Elliott and Whitfield, 2011; Whitfield et al., 2012a). Given that these omnivorous, zoobenthivorous and detritivorous fishes were most abundant in urban estuaries, and that many of these species perform important functions (e.g. carrion consumption, predation, nutrient processing) in coastal seascapes (Gilby et al., 2017a; Porter and Scanes, 2015; Whitfield et al., 2012a), we suggest that coastal urbanisation might not always result in the functional loss of these critical ecological processes from modified estuaries (sensu McPhearson et al., 2016; Olds et al., 2018).

Estuaries that experienced high nutrient levels, but still retained a large area of mangroves ( $\geq 6$  km<sup>2</sup>), were associated with abundant toadfishes (i.e. banded and common toadfish). Both toadfish species are zoobenthivores, and are abundant in the estuaries of the study area, they utilise mangroves, saltmarsh, seagrass and soft-sediment ecosystems as

habitat and feed on benthic invertebrates (e.g. crustaceans, molluscs) (Jelbart et al., 2007; Piah and Bucher, 2014; Platell and Freewater, 2009). Increased nutrient loads stimulates benthic productivity in estuaries, and can enhance the diversity, abundance and size of benthic invertebrates that are available as food for benthic feeding fishes like toadfish (Breitburg, 2002; Burford et al., 2009). Estuaries in the study area are subjected to high nutrient and sediment loads from the combined effects of coastal urbanisation (e.g. storm water run-off), catchment modification (e.g. land clearing for agriculture) and nutrient enrichment (e.g. wastewater discharge) (Leigh et al., 2013; Maxwell et al., 2014). The abundance of banded and common toadfish in estuaries that were characterized by high nutrient levels might, therefore, be an indirect response to an increased abundance of benthic prey in these locations (Breitburg, 2002; Laursen et al., 2002; Nozais et al., 2005). To better understand these potential functional effects of nutrients, we need empirical data to test how nutrient loads, benthic productivity and food availability shape the abundance of toadfishes, and other zoobenthivores, in urban estuaries.

We show that the ecological effects of urbanisation interact with both the level of nutrients, and spatial context of ecosystems, in coastal landscapes. We report positive trophic effects of armoured shorelines and artificial structures on certain components of fish assemblages, and suggest that urbanisation might not lead to the loss of important ecological functions from modified estuaries with good water quality. Our findings have wider implications for the management of degraded ecosystems, because they suggest that the outcomes of conservation, restoration and ecosystem engineering projects are likely shaped by both the spatial context of ecosystems in urban landscapes, and the level of nutrient loading they experience.

#### Declaration of competing interest

There are no conflicts of interest for any author associated with this manuscript.

#### CRedit authorship contribution statement

**Nicholas A. Yabsley:** Writing - original draft. **Ben L. Gilby:** Writing - original draft. **Thomas A. Schlacher:** Writing - original draft. **Christopher J. Henderson:** Writing - original draft. **Rod M. Connolly:** Writing - original draft. **Paul S. Maxwell:** Writing - original draft. **Andrew D. Olds:** Writing - original draft.

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#### Appendix A. Supplementary data

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