Human modifications to estuaries correlate with the morphology and functional roles of coastal fish

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ABSTRACT

Animals can respond to human impacts by favouring different morphological traits or by exploiting different food resources. We quantified the morphology and diet of four functionally different fish species (n = 543 fish) from 13 estuaries with varying degrees of human modification in Queensland, Australia. We found differences in the responses of trophic groups to the environmental conditions of estuaries; principally the extent of seagrass in the estuary, and the amount of shoreline and catchment urbanisation. Here, seagrass and urbanisation extent correlated with the diet and morphology of zooplanktivores and detritivores; thereby indicating that human modifications may modify these species functional roles. Conversely, environmental variables did not correlate with the diet or morphology of zoobenthivores or piscivores thereby indicating that human modifications may have less an effect on these species functional roles. Our findings demonstrate that anthropogenic impacts to coastal ecosystems might extend from the traditionally measured metrics of abundance and diversity.

1. Introduction

Increasing and expanding human populations modify ecosystems globally (Vitousek et al., 1997). These landscape transformations modify the condition and connectedness of ecosystems (Kareiva et al., 2007), the structure of food webs (Lotze et al., 2011) and the distribution of biodiversity (Gámez-Virués et al., 2015). Landscape transformations also change the rate and modify the distribution of key ecological functions (Hector and Bagchi, 2007; Olds et al., 2018) resulting in further reductions in ecosystem condition and ecosystem services (Cardinale et al., 2012; Haddad et al., 2015). However, many species adapt and survive within modified ecosystems, and these species can help maintain key ecological functions that provide resistance to further ecosystem degradation (Aronson et al., 2014; Clavel et al., 2011). Whilst the effects of landscape transformation on biodiversity, food webs and ecological functions is increasingly well understood, the adaptive capacity of species that persist in modified ecosystems remains poorly understood (Cardinale et al., 2012; Haddad et al., 2015). An organism's functional role is defined by its dietary requirements, so structural

changes to ecosystems and food webs can modify the suite of available niches and the broader functioning of ecosystems (Toyama et al., 2018). Therefore, understanding the ways in which different species and functional groups can adapt to human stressors is an important research gap in many ecosystems.

Approximately 40% of the world's population lives within 100 km of coastlines (Chaudhary and Pisolkar, 2019). Coastal ecosystems are therefore hotspots for the combined influence of direct (e.g. habitat loss, overharvesting) and indirect (e.g. run-off from modified catchments, sedimentation) anthropogenic impacts that modify the condition and functioning of ecosystems (Halpern et al., 2007). Marine vegetation such as mangrove forests, salt marshes and seagrass meadows are particularly vulnerable to these threats (Firth et al., 2016; Tscharntke et al., 2012). These ecosystems have a disproportionately large effect on the abundance and distribution of marine fauna, so their loss significantly modifies the broader condition of coastal systems and the provision of ecosystems services like fisheries (Gilby et al., 2018; Kornis et al., 2017). For example, between 50 and 65 percent of tidal wetlands have been lost globally due to direct replacement by hardened shorelines (e.g. concrete

structures such as seawalls, jetties, and groins) (Kornis et al., 2017). This reduces the availability of quality habitat for fish, and can result in changes in fish species diversity and abundance at multiple spatial scales (Connolly, 2003; Gilby et al., 2018). Effluent discharge and run-off from agricultural lands into coastal systems can cause phytoplankton blooms, which can lead to eutrophication, food web de-stabilisation, habitat loss and subsequent change in faunal assemblages (Lee et al., 2006a). Therefore, increasing anthropogenic modifications to marine habitats alters the composition of fish and invertebrate assemblages within coastal ecosystems (Hooper et al., 2005; Whitfield and Elliott, 2002). Many coastal fish species are, however, adaptable to these landscape modifications and can change their diets and functional role within ecosystems to suit the resources available within ecosystems (Fox and Bellwood, 2011; Olds et al., 2018). The ways in which different species or functional groups respond to these anthropogenic impacts remains, however, poorly understood.

Estuaries support a suite of ecosystem services (e.g. nursery habitat for fish, coastal protection, nutrient sequestration), but are under increasing threat from human activities globally (Elliott et al., 2019). Many estuarine fish species can adapt to ecosystem modification because they are naturally plastic in their diets and morphology (Elliott et al., 2007; Whitfield and Elliott, 2002). Morphological changes in fish are often associated with diet, development, growth rate, nutrition and environmental conditions (e.g. habitat structure, water temperature, predation pressure, and currents) (Canty et al., 2018; Floeter et al., 2018). For example, urbanisation and other catchment modifications can change the quality, quantity and composition of food items in estuaries (e.g. Schlacher and Wooldridge, 1996). This can modify body condition and organism health (Schlacher et al., 2007; e.g. Whitfield and Elliott, 2002), internal (e.g. Mutchler et al., 2014) and external morphology (e.g. Burress et al., 2016), and the structure and function of feeding appendages (especially jaws, teeth, and mouth position) (e.g. Eggold and Motta, 1992). Changes in diet amount to changes in ecological niches and the functional role of species, and these changes can occur over a period of weeks to months (Bruno and O'Connor, 2005). Changes in diet and functional role of species therefore has broader implications across modified ecosystems over multiple time scales (Leitão et al., 2018). Changes in fish morphology are often used as a tool to predict the functional roles of fish within ecosystems (e.g. Goatley and Bellwood, 2009). Because diet and morphological changes can potentially be tied to changes in the condition of estuarine ecosystems and the species that inhabit them (some of which are of commercial and recreational significance), these valuable resources are a priority for conservation and management planning (Halpern et al., 2007; Unsworth and Cullen, 2010).

Modifications to ecosystems can lead to changes in the condition, diet and ecological niches of animals that perform important ecological roles and functions (Cardinale et al., 2012; Haddad et al., 2015) and this may prevent ecosystem collapse or provide ecosystem services (Devictor et al., 2008; Olds et al., 2018). The effects of landscape transformation have been well established for fish assemblage composition (Clynick et al., 2008) and for the body condition of animals in coastal ecosystems (Hartman, 2003; Taylor and Miller, 2001). However, the ways in which human modifications combine to modify both fish functional roles (i.e. diet) and morphology together remain poorly understood (Meillère et al., 2015). In this study, we test whether and how human modifications to estuaries and their catchments change the diet and morphology of fish. We quantify this for four fish species which each represent a key trophic group found in estuaries in eastern Australia; zoobenthivores (yellowfin bream *Acanthopagrus australis*), zooplanktivores (southern herring *Herklotsichthys castelnaui*), detritivores (sea mullet *Mugil cephalus*) and piscivores (dusky flathead *Platycephalus fuscus*). We hypothesised that changes in diet and morphology would correlate with changes in environmental conditions of estuaries, especially the level of urbanisation along the estuary and throughout the catchment, and the amount of marine vegetation (especially mangroves and seagrasses)

within the estuary, but that the direction and strength of these effects would differ among functional groups (Fig. 1). We also gauged whether changes to morphology are associated with changes to diet and vice versa (Fig. 1).

2. Methods

2.1. Study region

Fish were collected between July and September 2018 from 13 estuaries spanning approximately 230 km of coastline in southeast Queensland, Australia (Fig. 2). The region is an ideal location to test for the effects of urbanisation on estuarine systems due to growing population pressure (~4.7 million people increasing at >2% per year) (ABS, 2015) causing an expanding urban footprint at the cost of mangroves and seagrass in the coastal strip, and more intensive agriculture in the catchments (e.g. Elliott et al., 2019; Lee et al., 2006a). The estuaries sampled encompass a broad suite of environmental conditions, ranging from relatively undisturbed systems (e.g. Coochin Creek), to floodplains where the estuarine banks are entirely urban land (e.g. Nerang River) (for full details on the environmental attributes of each estuary, see Table S1).

2.2. Fish species and sample collections

We selected representative species from four functional groups to examine how human modifications to estuaries may affect estuarine fish species with different biological traits. The species chosen are the most abundant and widespread example of the main functional groups in the region (Gilby et al., 2018). Yellowfin bream *Acanthopagrus australis* is a zoobenthivore that feeds opportunistically on a variety of benthic invertebrates (e.g. molluscs, polychaetes, crustaceans) from a several substrates (e.g. rock, seagrass, mangroves, sand and mud) (Hadwen et al., 2007; Pollock, 1982a). Southern herring *Herklotsichthys castelnaui* is a small (~15 cm) zooplanktivore common in estuaries of the region during spring and summer (Abrantes and Sheaves, 2009; Waltham and Connolly, 2013). Sea mullet *Mugil cephalus* is a benthic detritivore abundant throughout the year in coastal waters of eastern Australia (Bell et al., 2005; Pastor et al., 1996). Dusky flathead *Platycephalus fuscus* is a piscivore, feeding as an ambush predator on the seafloor (Gray and Barnes, 2008). We quantified morphological measurements and diet composition for 543 fish; 118 yellowfin bream (zoobenthivore), 238 southern herring (zooplanktivore) 160 sea mullet (detritivore) and 27 dusky flathead (piscivore) (Table S2).

Fish were captured from the lower reaches of each estuary (to the seaward point in the estuary where winter salinity levels averaged 30 ppt over the previous 10 years), following the extent of previous surveys conducted in these estuaries (Gilby et al., 2018). Capture sites were distributed randomly throughout each estuary, with particular focus on spreading the capture sites of each species evenly across the sampling extent in each estuary, thereby ensuring maximum variation in our environmental variables of interest across the study region. Different capture techniques were used to suit each species. Herring were collected with cast nets, sea mullet were collected using gillnets at junction points in the estuary with the running tide, yellowfin bream and dusky flathead were collected using traditional angling methods around a mixture of urban and natural environments within the estuaries. All specimens were immediately euthanised (USC Animal Ethics approval ANA18126), preserved on ice in the field, transferred to the laboratory within 3 h and stored at −20 °C until processed.

2.3. Morphological measurements

Morphological measurements were quantified from photographs taken of the side of each fish and calculated in the *geomorph* package of the R statistical framework (Figure S1)(Adams et al., 2018). Fish images
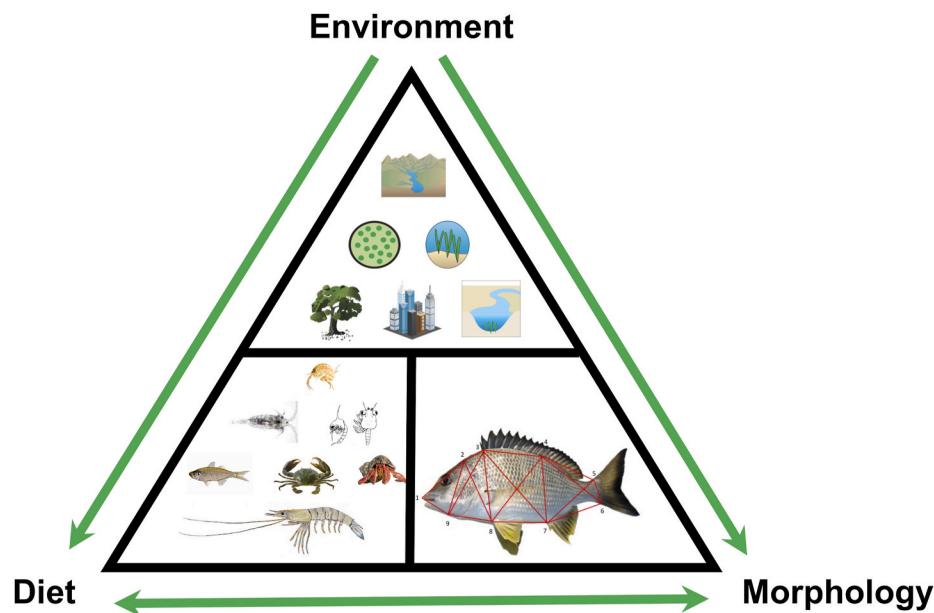
Fig. 1. Conceptual diagram illustrating the hypothetical relationship between fish and changes in the environmental conditions of estuaries and their catchments. We specifically tested whether fish morphology and diet composition change in response to anthropogenic landscape modifications (e.g. conversion of wetlands to urban lands), remaining marine vegetation (e.g. seagrass and mangrove areas), and water quality (e.g. turbidity, chl-a; Table 1).

were captured by horizontally mounting (checked using a tubular spirit level) a Nikon W300 digital camera (set on macro photograph mode) on a tripod positioned to fit the entire fish in the frame as closely as possible. Photographs were taken from the left side of each fish only and included a 30 cm ruler as a scalebar for subsequent image analyses. Morphological measurements were based on a standard truss network (Strauss and Bookstein, 1982), with additional measurements of the body width, head, jaw and fins of each fish (Table S3; Figure S2). Body width metrics (e.g. body width, interorbital width, jaw width, mouth gape) were measured with Vernier callipers in the laboratory. In total, 35 morphological measurements were made for each fish, yielding a total of 19,005 data points. All morphological measurements were standardised to a proportion of the individual's standard length (SL) for statistical analyses. There were few differences in the average standard lengths of individuals from the different estuaries (Table S2).

2.4. Diet measurements

We examined gut contents of all fish using a visual quantification of gut content, conducted following procedures in Linke et al. (2001) and Gilby et al. (2011). Here, the entire stomach content was extracted, weighed, sorted, and then identified to the lowest taxonomic level possible under a dissecting microscope. Each food item was recorded as the percentage of total gut weight. Where fish were captured using angling, any bait material identified in the stomach was excluded from the analysis.

2.5. Environmental variables

Twelve environmental variables were chosen based on their importance in predicting fish abundance and diversity in previous studies of estuaries in the region (Gilby et al., 2018; Olds et al., 2018) (Table 1). Measurements of habitat extent and connectivity are quantified at current-day extents in the estuaries sampled. As stated above, these estuaries represent a gradient of highly urbanised to relatively natural levels of condition; the regression analyses conducted therefore counteract any requirement to have a categorical variable of 'modified and unmodified' estuaries. Environmental variables can be broadly grouped into three categories. Firstly, site-specific variables are those which

quantified cover (in m²) of marine habitats and urbanisation within a 500 m buffer of each fish capture site. This buffer distance was selected based on the scales of movement of fish in estuaries over single tidal cycles within this region (Gilby et al., 2018; Olds et al., 2018). Secondly, estuary-scale variables are quantified as the current extent of urbanisation within catchments, or the current extent of marine ecosystems (intertidal flats, seagrass and mangroves) in each study estuary (Queensland Government, 2021). We normalised each of these metrics for the size of the catchment because larger catchments and estuaries will have bigger areas of each habitat type. We accounted for the potential effects of catchment size by also including catchment size as a variable in the analysis. Thirdly, water quality data are collected monthly by a regional water quality monitoring program across the study region (EHMP, 2018). Because water quality monitoring sites did not precisely match the sites where we captured fish, water quality values were interpolated to capture sites using inverse distance weighting (IDW) interpolations in QGIS. We chose to analyse the average of interpolated values from the 6 monthly monitoring events prior to fish capture because six months values correlated significantly with both three and one month values (EHMP, 2018), and because this longer time period enabled quantification of the longer-term effects of any declining water quality at each site.

2.6. Statistical analysis

Our analytical approach was to test each species separately for correlations between the suite of environmental metrics indexing anthropogenic landscape transformations of estuaries with two sets of multivariate data; one for morphology and one for diet (Fig. 1). We then identified the main variables driving these differences using multivariate BEST analyses and visualised these results using non-metric multidimensional scaling ordinations (nMDS).

We tested for correlations between environmental variables, and the diet and morphology (separately) of each species using the BEST (BIO-ENV) procedure in PRIMER E (Clarke and Gorley, 2015). The analysis identifies the combination of environmental variables that result in the best resemblances among samples within the dataset, and gives the best possible rank order match between inter-point dissimilarities and inter-point distances (Clarke and Gorley, 2015). BIOENV undertakes a
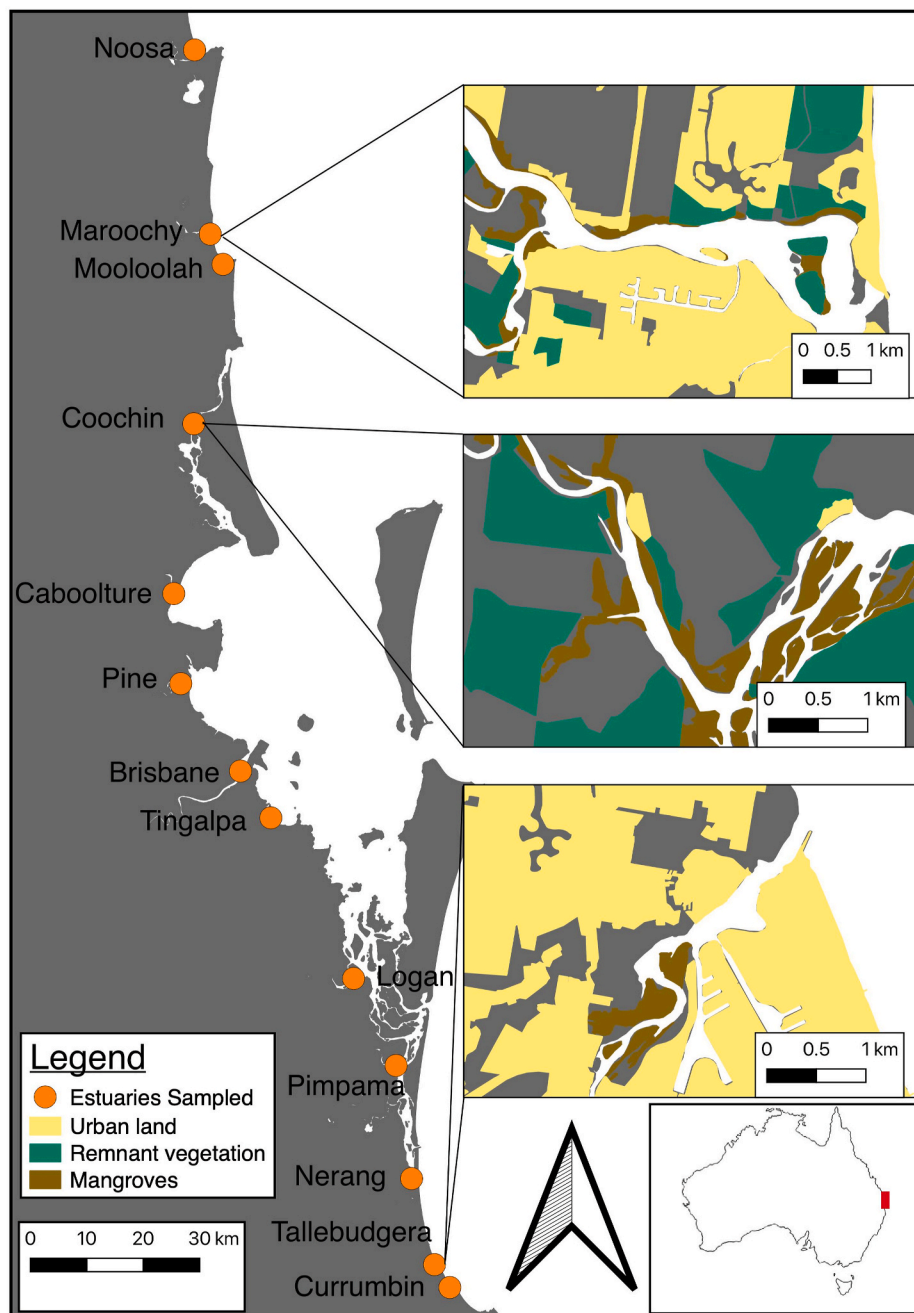
Fig. 2. Location of selected estuaries from which fish were sampled for analyses of their body shapes and diet composition in SE Queensland, Australia. Estuaries selected represent a range of habitat complexities within the estuaries. Inset maps give examples of intermediately (top panel), low (middle panel) and highly (bottom panel) urbanised estuaries within this region.

full search of all possible combinations of variables to explain patterns in morphometrics or diet data, and was restricted to finding the best combination of four or fewer variables. Tests were calculated on a normalised Euclidean distance dissimilarity matrix for environmental variables and morphometrics, and fourth root transformed Bray Curtis dissimilarity measures for diet data. The significance of these patterns was determined using the global BEST match test, which is generated by randomly permuting sample labels 999 times across the dataset. We visualised the directionality of these relationships by plotting vectors of variables from the best-fit model and dependent variables with correlation values greater that 0.4 on nMDS ordinations.

We tested for correlations between diet metrics and morphometrics of each species using the RELATE procedure in PRIMER (as opposed to

the BEST procedure) because we could not infer directionality or causality of one suite of variables on the other (i.e. we could not be certain that diet was modifying morphology, or vice versa). RELATE tests for trends in model structures in multivariate patterns (Clarke and Gorley, 2006). We visualised the directionality of these relationships by plotting vectors from both datasets with correlation values greater than 0.4 on nMDS ordinations.

3. Results

3.1. Correlations between environment, morphology and diet variables

We found no significant correlation between environmental

Table 1

Environmental variables included in statistical models, and their definitions. '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 fish capture sites measured at smaller spatial scales (within 500 m of the site where individual fish were captured).

Factor	Definition
Site-scale	
Intertidal flats area	Area (in m^2) of intertidal sandbanks, intertidal flats, and flood- and ebb-tide delta within a 500m buffer of each fish capture site (Queensland Government, 2021)
Mangrove area	Area (in m^2) of mangrove coverage within a 500m buffer of each fish capture site
Urban area	Area (in m^2) of urbanised land cover within a 500m buffer of each fish capture site (Queensland Government, 2021)
Seagrass area	Area (in m^2) of seagrass within a 500m buffer of each fish capture site (Queensland Government, 2021)
Estuary-scale	
Intertidal flats- catchment	Area (in percentage) of intertidal sandbanks, intertidal flats, and flood and ebb-tide delta for the whole estuary, corrected for the total area of the estuary (from the mouth to the upper limit of mangroves) (Queensland Government, 2021)
Mangroves- catchment	Area (in m^2/m) of mangrove coverage within the whole estuary corrected for total length of the estuary that supports mangroves (to account for the size of the estuary) (Queensland Government, 2021)
Urban-catchment	Percentage of the catchment classified as urbanised, including residential, utilities, and manufacturing and industrial areas (Queensland Government, 2021)
Seagrass-catchment	Area (in percentage) of seagrass coverage within the whole estuary, corrected for the total area of the estuary (from the mouth to the upper limit of mangroves) (Queensland Government, 2021)
Catchment Size	Total area (in m^2) of the catchment for each estuary (Queensland Government, 2021)
Water Quality	
Turbidity	Average water column turbidity levels (in nephelometric turbidity units) interpolated (inverse distance weighting) to each fish capture site over a 6 month sampling period from June–December 2018 prior to fish capture (EHMP, 2018)
Salinity	Average salinity (in PPT) interpolated (inverse distance weighting) to each fish capture site over a 6 month sampling period from June–December 2018 prior to fish capture (EHMP, 2018)
Chlorophyll A	Average water column chlorophyll *a* concentration (in mg/L) interpolated (inverse distance weighting) to each fish capture site over a 6 month sampling period from June–December 2018 prior to fish capture (EHMP, 2018)

variables and diet or morphology for yellowfin bream, and no correlation between yellowfin bream diet and morphology (Fig. 3). However, the environmental conditions of estuaries correlated significantly with both the morphology and diet of the southern herring and sea mullet (Fig. 3). A significant correlation between the morphology and diet of dusky flathead was found, but environmental variables were not correlated with either diet or morphology (Fig. 3).

3.2. Variables modifying diet and morphology

3.2.1. Southern herring- zooplanktivore

Environmental metrics that best explained variation in the morphology of southern herring were the extent of seagrass and urban structure at the site of fish collection, the percentage of mangroves within the catchment and catchment size (Fig. 4a, Table 2A). There were two prominent morphological changes evident. Firstly, fish that were captured at sites with greater seagrass area nearby, in estuaries with smaller areas of mangroves, had a longer pre-orbital length (morphometric PO), and larger pectoral fin height (morphometric PH) (Fig. 4A, Table S4). Secondly, fish in heavily urbanised estuaries draining a smaller catchment, had broader shoulders (morphometric HP) (Fig. 4A, Table S4).

Environmental metrics that best explained variation in the diet of

southern herring were the extent of seagrass near the collection site and catchment size (Fig. 4B, Table 2B). Diet composition correlated with the environment in two ways. Firstly, individuals from sites with greater extent of seagrass nearby and in estuaries with larger catchments ate higher volumes of harpacticoid copepods and gammarid amphipods in stomach contents (Fig. 4B, Table S4). Gammarid amphipods, on average made up 0.1% of the gut volume in individuals from estuaries with no or little seagrass, compared with 16% in individuals captured from areas with increased seagrass area. Harpacticoid copepods comprised 0.1% of the gut volume individuals from estuaries with no or little seagrass, compared with 1.5% in individuals captured from areas with higher seagrass areas. Secondly, individuals from sites with intermediate areas of seagrass nearby and intermediately sized catchments, ate higher volumes of crab larvae (Fig. 4B, Table S4).

3.2.2. Sea mullet- benthic detritivore

Environmental metrics that best explained variation in the morphology of sea mullet were the extent of seagrass and urbanisation nearby to the capture site, and average chlorophyll-a concentrations at the site of fish collection, and total catchment size (Fig. 4C, Table 2A). Individuals captured at sites with higher chlorophyll-a concentration, in larger catchments, at sites with lower extent of urban structure and seagrass nearby, tended to have larger thoraxes (morphometrics VBL, RDA, RDPF, DBL, FDA), wider peduncles (morphometric PW), a longer distance between the peduncle and anal fin (morphometric PA), and a shorter jaw (morphometric JL) (Fig. 4C, Table S5). Therefore, the thorax and tail region of fish tended to be larger, and the jaw length shorter in fish from larger, more productive estuaries, with less seagrass (Fig. 4C, Table S5).

Environmental metrics that best explained variation in the diet of sea mullet were the area of seagrass and the degree of urbanisation near the capture site, and the extent of mangroves and seagrass in the catchment (Fig. 4D, Table 2B). Fish captured at sites with increased seagrass areas and urban structure nearby, and in estuaries draining catchments with increased seagrass beds and fewer mangroves consumed higher volumes of gammarid amphipods (Fig. 4D, Table S5).

3.2.3. Dusky flathead- piscivore

We found a significant correlation between the diet and morphology of dusky flathead. These correlations extend in two ways. Firstly, fish with longer thoraxes (morphometric VBL) that were flatter (dorsal fin to anal fin length; RDA) ate increased volume of fish (percent of gut volume) and fewer mud crabs (percent of gut volume) (likely juvenile *Scylla serrata*) and penaeid prawns (Fig. 4E, Table S6). Conversely, fish with shorter thoraxes (morphometric VBL), and less flat (dorsal fin to anal fin length (RDA) with longer heads (HL) ate increased volume of mud crabs (percent of gut volume) and penaeid prawns (percent of gut volume) but fewer fish (percent of gut volume) (Fig. 4E, Table S6).

4. Discussion

The effects of human modifications to ecosystems on the abundance and diversity of animals are established in a number of settings (Foley et al., 2005). Many species can, however, adapt well to anthropogenic changes (Hoffmann and Sgro, 2011) by changing their functional roles and morphology, and this might have significant consequences for ecosystem functioning in impacted ecosystems (Gagic et al., 2015; Villéger et al., 2010). In this study, we found consistencies in the effects of the size of the catchment in which fish were captured and the extent of seagrass nearby to the capture site for both the morphology and diet of southern herring (zooplanktivore). We found consistencies in associations between the extent of seagrass and urban structure on both the morphology and diet of sea mullet (detritivore). Fish captured at sites with greater extents of seagrass and urban structure nearby tended to contain fish with smaller thoraxes and longer jaw lengths, that also tended to consume a greater proportion of gammarid amphipods in their
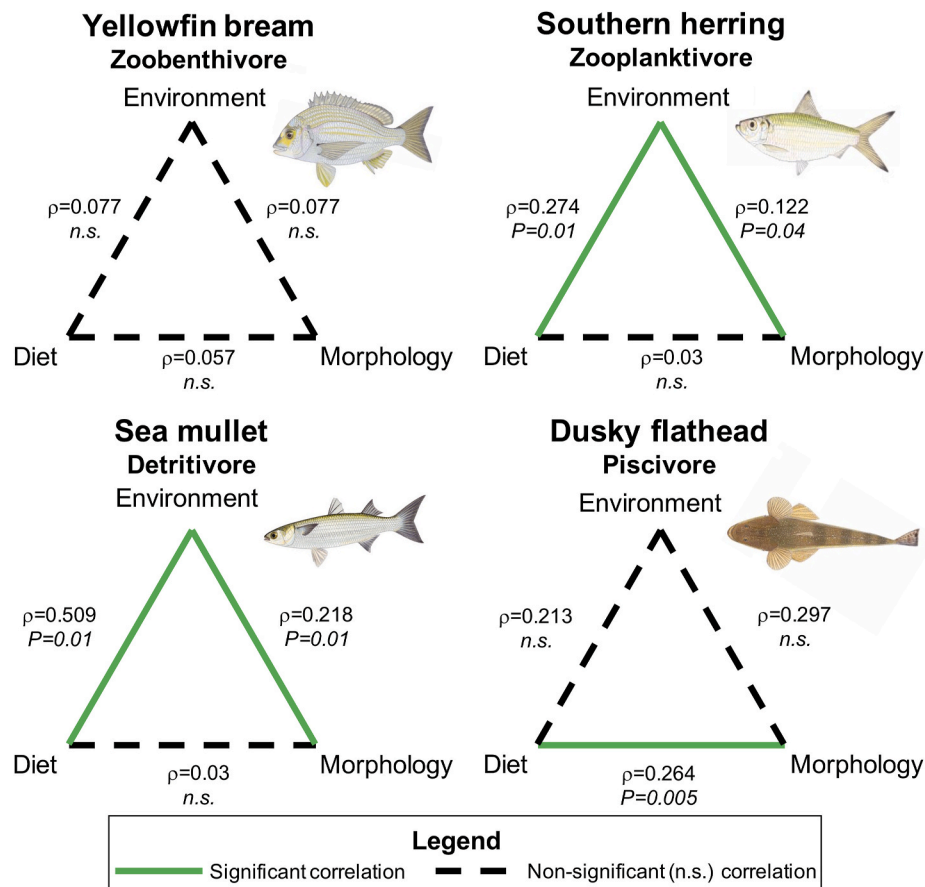
Fig. 3. Relationships between the three main multivariate matrices measured. The sides of the triangle represent the analysis (BEST procedure) testing for multivariate correlations between the set of environmental variables (Table 1) and the diet composition and morphology of the four fish species representing the main trophic groups. The base of the triangle represents a similar test (RELATE procedure) between diet and morphology (ρ = Spearman's Rho, n.s. = P > 0.05).

diets. We found consistent correlations between seagrass extent and urbanisation on the diet and morphology of southern herring and sea mullet in southeast Queensland estuaries. Consequently, it is possible that the effect of human impacts to estuaries could extend beyond simple changes in fish abundance and diversity. Conversely, yellowfin bream (zoobenthivore) and dusky flathead (piscivores) were not significantly affected by the condition of estuaries in this study. This may suggest that the morphology and functional role of yellowfin bream may be more resistant to broader landscape transformations yet, this will require further investigation. However, the small sample size of dusky flathead will require further investigation.

Diet is strongly tied to environmental conditions, as the availability and quality of some resources (e.g. plankton and detritus) depends on environmental conditions and the presence of key ecosystems (e.g. seagrasses) in estuaries (López-Vila et al., 2019; Telesh, 2004). Seagrass has been shown in many systems to be significant in structuring coastal food webs (Connolly and Waltham, 2015), especially when it is in close proximity to urbanised shorelines (Gilby et al., 2018), and our results support these findings. In this sense, the effects of seagrass and urbanisation could extend beyond modifications to the structure of fish assemblages (Gilby et al., 2018; Heck et al., 2008) as they correlate with the morphology, diet and functional role sea mullet and southern herring (Unsworth et al., 2007; Villéger et al., 2010). Despite this, we found no correlation between diet and morphology for three out of four of the functional groups. This may suggest that the effects of ecological demands on morphology and diet separately may have outweighed the relationship between the more common diet related morphological characteristics findings in the literature (Labropoulou, 1998).

In this study, changes to the morphology and diet of southern herring

(zooplanktivores) and sea mullet (detritivores) correlated most with the extent of seagrass and shoreline urbanisation nearby to the capture sites and the broader context of the estuary (i.e. catchment size). Both seagrass extent and urbanisation are key predictors of the structure of fish assemblages (Brook et al., 2018; Gilby et al., 2018) and the distribution of ecological functions across seascapes in this region (Henderson et al., 2019), and are key indicators of human impacts on coastal systems globally (Bishop et al., 2017). Seagrass meadows are a threatened (often due to urbanisation) but pivotal habitat for a range of animals in coastal ecosystems because they provide nurseries, sequester carbon and nutrients, and provide a food source (including through detrital pathways) (Connolly and Waltham, 2015; Heck et al., 2008; Waycott et al., 2009). Seagrass harbours grazing benthic amphipods that feed directly on the seagrass and free-living benthic harpacticoid copepods are abundant in productive seagrass meadows (Jankowska et al., 2019; Touchette and Burkholder, 2000). Increased abundance of gammarid amphipods and harpacticoid copepods were seen in the diets of sea mullet (detritivore) captured from locations with greater areas of seagrass. This may have simply been an incidental effect of greater seagrass availability, rather than a concerted switching of diet by these generalist detritivores. Nevertheless, variation in the gut content of individuals in association with seagrass availability constitutes a genuine change in the broader diets of these detritivores.

Greater seagrass extent correlated with longer pre-orbital lengths in southern herring (zooplanktivore); this modification may allow fish to better capture invertebrates associated with seagrass (Meyer et al., 2019; Walters and Bell, 1994). Increased pectoral fin heights may assist with manoeuvrability in complex habitats (i.e. seagrass beds), allowing increased effectiveness for slow movements of fish. This is an advantage
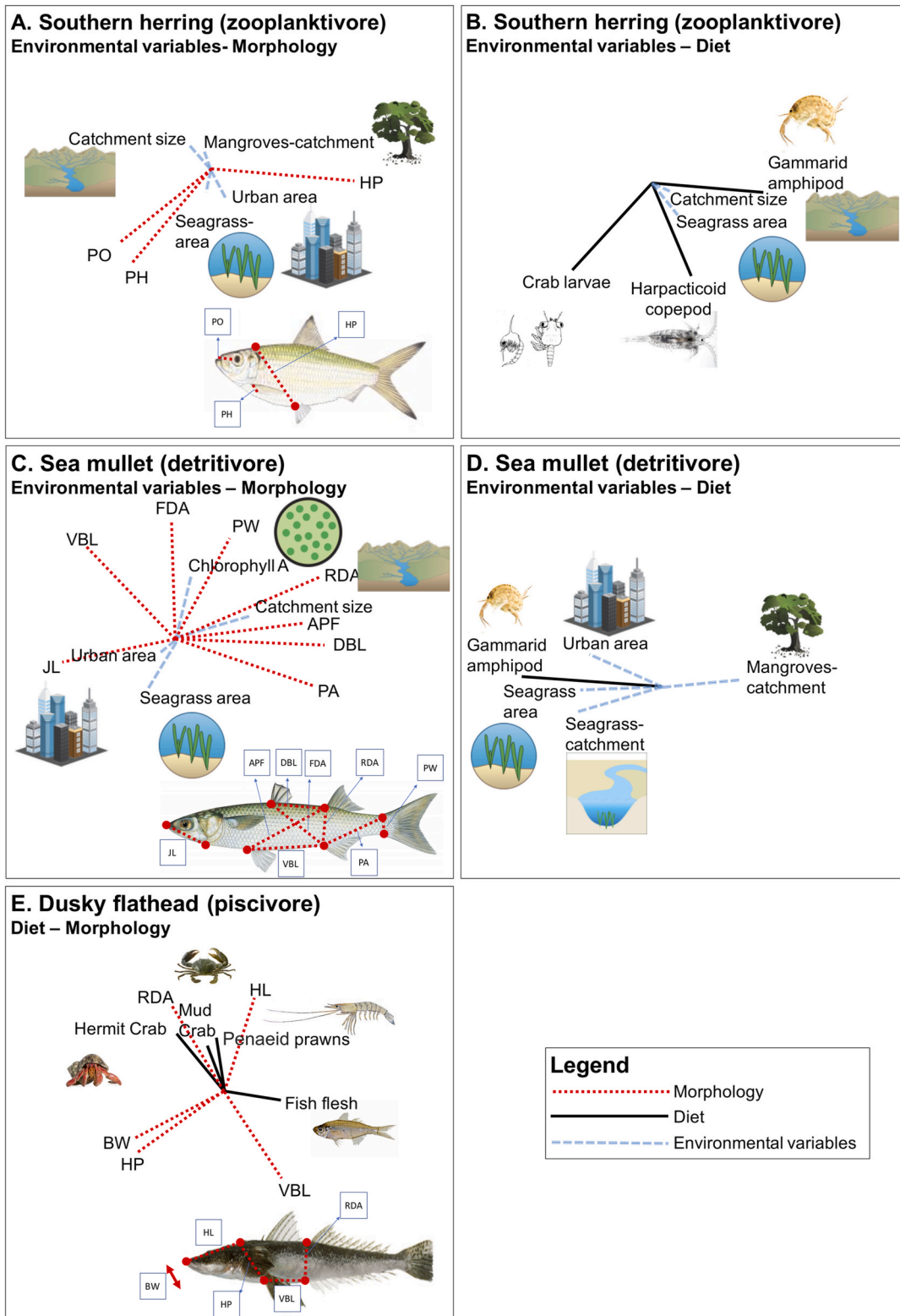
Fig. 4. Non-metric multidimensional scaling (nMDS) ordinations vectors illustrating significant relationships from Fig. 3 for; A) environmental variables and morphology for southern herring, B) environmental variables and diet for southern herring, C) environmental variables and morphology for sea mullet, D) environmental variables and diet for sea mullet, and E) diet and morphology for dusky flathead. Ordinations of centroid values for each estuary are provided in Figure S3. See Tables S4-6 for average diet and morphology values for each estuary.

to narrow-bodied, slow moving fishes as it may assist in more efficiently exploiting the available resources in their environment (e.g. complex seagrass habitats)(Drucker et al., 2005; Liao, 2007). Seagrass increases quality and availability of detritus in warm temperate estuaries, which

potentially attracts detritivore species (Franco et al., 2008). Therefore, this study shows the potential for changes in seagrass extent to be implicated in functional changes of southern herring and sea mullet and suggests that further investigations should be made into the mechanisms

Table 2

Best fit models from significant BEST analyses for correlations between environmental metrics and morphometrics, and environmental metrics and diet composition. ρ = Spearman's rho. P = Global model test from BEST analysis.

Species	BEST model	ρ	P
a. Environmental metrics and morphology			
Southern herring (zooplanktivore)	Seagrass area + Urban area + Mangroves-catchment + Catchment size	0.122	0.04
Sea mullet (benthic detritivore)	Seagrass area + Urban area + Chlorophyll-A + Catchment size	0.218	0.01
b. Environmental metrics and diet			
Southern herring (zooplanktivore)	Seagrass Area + Catchment Size	0.274	0.01
Sea mullet (benthic detritivore)	Seagrass Area + Urban Area + Mangroves-catchment + Seagrass-Catchment	0.509	0.01

underpinning these effects.

We identified significant effects of catchment size in several statistical models. Large catchments often have greater flow, sedimentation, and urbanisation extent, especially those with less extensive mangroves (e.g. Katopodis et al., 2019), and these factors have been shown in multiple settings to be deleterious for seagrass (Lambert et al., 2020; Lee et al., 2006b). This may explain some of the combined effects of seagrass area and catchment size for many relationships in this study. Catchment size was included in this study to offset the use of proportions in land use and marine habitat extents, such that a combined effects of proportion land use and catchment size would indicate some effect total aerial extent of a given attribute. Therefore, the effects of catchment size and mangrove-catchment indicate some effects of total mangrove area on the morphology of southern herring. Relationships between catchment size and diet for southern herring are less straight forward to explain, as the effect of catchment size was not also associated with any effects of whole catchment land use or marine habitat extent. This was, however, the relationship we found with the lowest correlation coefficient and highest P value, so this must be considered when interpreting trends. While catchment size was lower in explanatory power than seagrass area for herring diets, greater harpacticoid and crab larvae abundance was associated with greater and intermediate catchment sizes, respectively. The spatial distribution of crab larvae is modified by temperature (Baylon, 2010), salinity (Dos Santos et al., 2019), dissolved oxygen (Roman et al., 2019), depth and water currents (Eggleston et al., 1998). Crabs are also found in higher abundance in mangrove dominated systems (Walton et al., 2006). It is reasonable, therefore, to hypothesise that these variables are affected by catchment size to some degree, but these effects further testing.

We identified detrital material in the stomachs of all sea mullet but did not quantify its original source. Therefore, the effects on diet that we identified (i.e. differences in fauna consumption) were likely incidental. Higher primary production by phytoplankton improves food availability for detritivores, increases fish health and often results in higher body condition and larger thorax sizes (Gido, 2002; Vanni et al., 2005). Jaw length and morphology is tightly tied to fish feeding traits (Wimberger, 1991). In this sense, changes in jaw structure of sea mullet may have developed to take better advantage of different detrital sources (e.g. microphytobenthos vs seagrass detritus) (Wainwright and Richard, 1995). Modification to detrital pathways in many coastal ecosystems may lead to changes to the structure and functioning of coastal ecosystems (Pitt et al., 2018). Implications for detritivores, especially the sea mullet which is a commercially important fishery globally, should be explored in more detail on a continental scale as this species migrates to spawn, and so may be influenced by changes across diverse coastal ecosystems.

In this study, we found no significant correlation between environmental conditions and diet or morphology of either yellowfin bream (zoobenthivore) or dusky flathead (piscivore). Some species that remain

in urbanised ecosystems are resistant to ecosystem-wide changes because either their functional niches are not modified by impacts, or they consume a wide enough diet that they simply consume whatever is available (Devictor et al., 2008; Olds et al., 2018). The lack of pattern in yellowfin bream may be due to the extensive movements they make across estuaries and the diverse range of prey they consume (Hadwen et al., 2007; Pollock, 1982a). Yellowfin bream can occur in high abundance in marine ecosystems of the study region (Gannon et al., 2015; Taylor et al., 2013), especially around urban structure (Brook et al., 2018; Olds et al., 2018). Urbanisation impacts may be lessened for such generalist species as they are able to adapt with broad and variable diets across different ecosystem configurations (Clavel et al., 2011; Olds et al., 2018).

Dusky flathead are ambush predators in marine environments (Douglas and Lanzing, 1981), and feed predominantly on fish and small crustaceans; prey that remain in abundance even in urbanised estuaries (Clynick and Chapman, 2002). Dusky flathead, as with other species of flathead, have relatively small home ranges throughout their lives, meaning that their diet and possibly their morphology would theoretically be impacted significantly by urbanisation (Fetterplace et al., 2016). Morphological changes in piscivores often result from changes in predation method, which reflects the prey availability within an ecosystem and success of prey capture (Eklöv and Diehl, 1994). The smaller sample size of dusky flathead in this study might be considered insufficient in determining a clear result for this species, and so further studies need to be conducted. We did find, however, in the small sample size that dusky flathead that consumed a greater proportion of fish had larger thorax size and narrower heads. Therefore, our replication was sufficient to detect relationships between diet and morphology, but not with environmental variables. Indeed, it may be that dusky flathead simply are not affected by the variables we tested, or at the spatial scales that we quantified because the effects of urbanisation for dusky flathead are possibly more related to their distribution and abundance (Gilby et al., 2018). Findings of changes in head size and dimensions have been suggested in other studies as an adaptation to the maximum size of prey targeted (Scharf et al., 2000) and the potentially more nutritious fish-dominated diet (Barnes et al., 2011). Consequently, more intense urbanisation, and significant reductions in prey fish abundance, may lead to morphological changes in dusky flathead in the future. Despite these attractive hypotheses, the level replication for flathead was, however, lower than for the other species in this study, and so more robust conclusions can only be made for this species, and other piscivores, with further studies.

Quantifying the temporal scales of changes in diet and morphology occur may be instructive in optimising management outcomes. For example, diet may change over a period of hours or days due to environmental fluxes, whereas morphology may change over years or decades depending on whether changes are genotypic or phenotypic. For genetic change to occur within the species tested, conditions must be consistent over generational scales, and the populations must be semi or totally closed (Kelley and Evans, 2018; Vieira et al., 2016); both unlikely in the systems studied (EHMP, 2019; Pollock, 1982b). Consequently, the changes we found in morphology are likely to be localised anatomical responses within the anatomical plasticity spectrum of individuals. Further analysis (perhaps of genetic stocks and flows) of these patterns is, however, required to make substantive conclusions regarding these effects.

Changes to the diet and morphology of fish can alter their functional roles (Hjelm et al., 2003) and have consequences for ecosystem functioning and condition (Villéger et al., 2010). These considerations have important consequences for the management of human-modified coastal ecosystems. We found consistent correlations of seagrass and urbanisation with the diet and morphology of our representative zooplanktivore and detritivore species. Seagrass is a globally threatened habitat that provides shelter, nurseries and resources for many marine organisms, shaping assemblage structure, functional niches and ecological food

webs across seascapes (Heck et al., 2008; Waycott et al., 2009). Properly managing coastal seascapes for the persistence of structurally complex coastal ecosystems is vital because changes within these habitats can potentially expand to changes in diet, morphology and functional roles in some species of fish. Potential change in morphology and function of some coastal species along anthropogenic gradients, may suggest that anthropogenic alterations to ecosystems have the potential to trigger effects that extend beyond the traditionally measured metrics of species abundance and diversity. Measures like gross morphology or diet of target species may assist in detecting the effects of anthropogenic impacts on ecosystems that are not detected using traditional monitoring metrics like abundance or diversity. Incorporating these measures into traditional monitoring may serve to detect early changes more readily in the functioning of degraded ecosystems. Experimental studies must now be undertaken to establish causality of these trends, with priority placed on studies that investigate the underlying mechanisms for change within functional groups and confirming patterns for piscivores.

Author Statement

Felicity Osborne: Conceptualization, methodology, investigation, software, formal analysis, data curation, writing-original draft. Andrew Olds: Conceptualization, methodology, writing- review and editing, funding acquisition. Thomas Schlacher: Conceptualization, methodology, writing- review and editing, funding acquisition. Christopher Henderson: Methodology investigation, writing- review and editing. Tyson Martin: Methodology investigation, writing- review and editing. Rod Connolly: Conceptualization, writing- review and editing. Paul Maxwell: Conceptualization, writing- review and editing, funding acquisition. Ben Gilby: Conceptualization, methodology, resources, investigation, software, formal analysis, writing-original draft, supervision, funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2021.105443.

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