

Urbanisation supplements ecosystem functioning in disturbed estuaries

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Abstract

Humans have urbanised and fragmented landscapes across the globe, with detrimental impacts to biodiversity, habitats and food webs in most biomes. Urbanisation might also modify the provision of ecological functions, but these putative effects of landscape transformation are rarely measured. Coastal cities are typically located near estuaries, and we tested for potential impacts of these on ecological functions. Our study used 22 estuaries in eastern Australia as model systems to examine how urbanisation shapes the consumption of carrion by fish, a pivotal ecological function in estuaries. Fish assemblages varied among estuaries according to the extent of shoreline hardening, and this was correlated with changes in the rate of carrion consumption. In estuaries with low levels of shoreline hardening and abundant remnant mangroves, most carrion was consumed by toadfishes (Tetraodontidae). By contrast, in moderately urban estuaries (i.e. where 20-60% of shorelines had been hardened with artificial structures) yellowfin bream (Sparidae) replaced toadfish and performed the bulk of the scavenging function. Bream are particularly effective scavengers that utilize artificial structures as habitat for both foraging and sheltering. We show that by augmenting habitat for an important species of scavenger, the moderate addition of urban structures to estuarine shorelines also helped to supplement a key ecological function in estuaries. Urbanisation impacts diversity in all ecosystems, but many opportunistic species flourish in urban habitats. Identifying and conserving taxa that perform important roles in urban environments is now a critical conservation challenge for maintaining ecological functions across disturbed landscapes.

Keywords: carrion consumption, coastal management, estuaries, fish, landscape ecology, scavenging, urbanisation

Introduction

Keep a mid course between two extremes

Ovid

Humans have fundamentally altered landscapes and modified ecosystem function on land and in the sea (Chapin et al. 2000, Tscharntke et al. 2012). Transformation of natural landscapes into cities is ubiquitous and the footprint of urbanisation is expanding globally with widespread and detrimental environmental effects on biodiversity, habitats and ecosystem services (Grimm et al. 2008, Firth et al. 2016). The ecological effects of urbanisation are pervasive and occur mainly through the loss, transformation and fragmentation of natural habitats, the impacts of pollution and the effects of feral animals (Lindenmayer and Fischer 2007, Schlaepfer et al. 2011, Aronson et al. 2014). Widely-reported impacts of urbanisation include reductions in both the diversity and abundance of plants and animals, changes to migration patterns, modification to the structure of food-webs, and declines in some ecosystem services (Beninde et al. 2015, McPhearson et al. 2016, Heery et al. 2017, Olds et al. 2018). Urbanisation can also modify ecological processes (e.g. pollination, seed dispersal, predation) (Cheptou et al. 2008, Lowenstein et al. 2015), but the possible effects of urban habitats on ecosystem functioning are rarely tested or reported (McPhearson et al. 2016, Bishop et al. 2017, Mayer-Pinto et al. 2018).

A large part of the global human population lives in coastal cities (Seto et al. 2012, Dafforn et al. 2015). The impacts of urbanisation on coastal ecosystems are widely reported, encompassing changes to the distribution, diversity and abundance of most animal and plant groups (Chapman et al. 2009, Schlacher et al. 2014, Firth et al. 2016, Heery et al. 2017). Urbanisation alters habitat condition and ecosystem functioning in the sea, as it does on land, by changing a number of ecological processes (e.g. herbivory, predation, filtration rates, carrion consumption), productivity and food-web dynamics (Layman et al. 2007, Gilby et al. 2015, Huijbers et al. 2015, Mayer-Pinto et al. 2018). Mitigating negative effects of urbanisation on ecosystem functioning is increasingly recognised as a priority in conservation (Sheaves et al. 2014a, Maxwell et al. 2015), but empirical data on the relationship between urbanisation and ecological function are typically lacking for estuarine and marine systems (Olds et al. 2014, Bishop et al. 2017, Heery et al. 2017, Mayer-Pinto et al. 2018).

In situations where assemblages have high internal functional redundancy (i.e. multiple species perform an ecological function and differ in their sensitivity to disturbance), key ecological processes might be maintained across natural and urban landscapes by different taxa that perform the same ecological functions (Fig. 1) (Elmqvist et al. 2003, Schlaepfer et al. 2011, Huijbers et al. 2016). By contrast, when assemblages contain limited redundancy (i.e. few species fulfil a particular function), an ecological process might be lost from urban settings that no longer support key species (Fig. 1) (Bellwood et al. 2003, Mori et al. 2013, Brown et al. 2015). An alternative model is where urban settings provide habitat for species that are adept at performing particular ecological functions (Becker et al. 2013, Layman et al. 2014, Huijbers et al. 2015). This could result in a 'supplementation effect' at moderate levels of urbanisation until other detrimental effects of cities (e.g. food availability, water quality, disturbance) become more prominent, leading to declines in overall function (Fig. 1). In estuaries, this might occur where artificial structures (e.g. jetties, pontoons, rock walls) add habitat

complexity, and provide food, for species that perform important ecological functions (e.g. oysters, mussels, barnacles that filter estuarine waters, and fish that scavenge carrion) (Hindell 2007, Chapman et al. 2009, Heery et al. 2017, Mayer-Pinto et al. 2018).

Here we test the above models of how ecological function responds to urbanisation in coastal seascapes, focusing on carrion consumption as a key function in estuaries. The consumption of animal carcasses by scavengers is a pivotal process in all ecosystems; many organisms scavenge and their actions recycle nutrients in food-webs and help maintain ecosystem functioning in disturbed landscapes (Wilson and Wolkovich 2011, Barton et al. 2013). Fish are prominent scavengers in estuaries (Webley 2008, Porter and Scanes 2015) and urbanisation is a key driver of estuarine fish assemblages (Whitfield and Elliott 2002, Chapman et al. 2009, Sheaves et al. 2012, Gilby et al. 2017a). We surveyed scavenging fish and measured carrion consumption in estuaries of southeast Queensland, Australia (Fig. 2). These estuaries have been the focus of a long-term (>15 years) habitat and water quality monitoring program (EHMP 2016), and are subject to strong regional gradients in urbanisation, water quality and habitat diversity (Leigh et al. 2013, Gibbes et al. 2014, Gilby et al. 2017b); hence, they provide a suitable natural laboratory for examining how urbanisation shapes ecosystem functioning in coastal seascapes.

Methods

Study seascape

We surveyed fish assemblages and quantified the rate at which carrion was consumed by fishes across 22 estuaries in southeast Queensland, Australia (Fig. 2). The estuaries stretch 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), and range from relatively natural systems with abundant mangroves to highly urbanised waterways (Supplementary material Table S1).

Urbanisation was quantified as the proportion of hardened shoreline in the sampled reach of each estuary, and the area of urban land in each catchment, measured from digitised habitat maps and satellite imagery using Quantum GIS (source: Healthy Waterways) (Waltham and Connolly 2011). We sampled the lower reach of each estuary, from the mouth to the point where salinity decreased to 30 psu, as this was where urban development was concentrated (following Gilby et al. 2017b). To verify that effects of urbanisation on carrion consumption were not modified by co-variation of other estuarine characteristics we tested for possible correlation with the availability of fish habitat (mangrove area), estuary width, water quality, and latitude. The area of mangroves in each sampled reach and the width of each estuary at the mouth were quantified from digitised habitat maps using Quantum GIS. Water quality data were sourced from Healthy Waterways (EHMP 2016), which conducts monthly monitoring of water quality in estuaries across the study region. We acquired data on salinity, turbidity and chlorophyll-a (variables of known significance for estuarine fishes; Sheaves et al. 2010, Blaber 2013) for each estuary in winter 2015, and interpolated (using inverse distance weighting) these metrics to each site from data collected across each estuary (EHMP 2016) (Supplementary material Table S1).

Fish surveys

We sampled the 22 estuaries in random sequence over 2 months during the austral winter of 2015. Scavenging fishes were indexed with baited remote underwater video stations (BRUVS), sampling ten sites in each estuary (separated by ≥ 250 m). Each estuary was sampled twice within three days (i.e. $n = 20$ BRUVS deployments per estuary). Our main objective was to examine the influence of urbanisation and other habitat attributes on ecological function. Because salinity is a key determinant of fish in estuaries (and hence likely to influence function) we standardised for salinity by spacing BRUVS evenly (at salinity increments of 0.5 psu) from the mouth of each estuary to the point where salinity had decreased to 30 psu (based on 10 yrs of salinity data; EHMP 2016) (Fig. 2). BRUVS were deployed within two hours of high tide and positioned in water depths of 1.5 – 2 m, over non-vegetated muddy or sandy substrate within 30 m of estuarine banks.

BRUVS consisted of a high definition GoPro camera, which was attached to a 5 kg weight and a bait bag that was held 0.5 m in front of the camera by a PVC pipe. Pilchards (*Sardinops sagax*) were used as the standard bait in all deployments; 500 g of pilchards was deployed inside each BRUVS bait bag (Harvey et al. 2007, Gilby et al. 2017a). Each unit was also fitted with a disk (15 X 15 cm) for visibility calibration that was placed 1 m from the camera. Visibility disks had three vertical stripes of white, grey and black paint, that were used to quantify and standardise visibility among estuaries. When analysing footage, observers noted which stripes were seen and this was used to index visibility (i.e. white only=low visibility, white and grey=moderate, white, grey and black = high): we found that the composition of fish assemblages did not differ significantly between classes of visibility (permutational multivariate analysis of variance; $p > 0.15$) and hence visibility was not included in further analyses (Gilby et al. 2017b). Each BRUVS deployment lasted for one hour, giving a total video sampling time of 440 hours for the study. The first five minutes of footage from each deployment was discarded to limit disturbance effects. Fish were defined as scavengers when they were observed to feed on deployed pilchards. Scavenger abundance, species richness, and assemblage composition was quantified from video footage using the standard Max N statistic (Murphy and Jenkins 2010, Gladstone et al. 2012).

Quantifying carrion consumption

Experimental assays have been widely adopted as tools for quantifying ecological functions, well-known examples include the use of: algae to measure herbivory on coral reefs (Olds et al. 2012b, Yabsley et al. 2016), tethered fish to measure predation in estuaries (Baker and Sheaves 2007), and fish carcasses to measure scavenging on beaches and in estuaries (Porter and Scanes 2015, Huijbers et al. 2016). We followed the approach of previous work on carrion consumption in estuaries (Webley 2008, Porter and Scanes 2015), and deployed fish carcasses to quantify carrion consumption at all sites where BRUVS surveys were conducted ($n = 220$). This was done by attaching two pilchards of known weight to the upper surface of each BRUVS bait bag. Pilchards were then re-weighed immediately after deployment and carrion consumption was recorded as the change in pilchard weight during each one-hour deployment. Pilchards were deployed on the upper surface of each bait bag so that carrion consumption could be measured, and were also deployed inside each bait bag to ensure consistency with the standard approach adopted in other BRUVS surveys (Gladstone et al. 2012, Wraith et al. 2013, Borland et al. 2017, Henderson et al. 2017). The contribution of each scavenger species to carrion consumption was determined later through analysis of

BRUVS footage. For each species that fed upon exposed pilchards we recorded both the total number of bites taken (i.e. pieces of carrion taken and consumed) and the proportion of bait consumed.

Data analysis

Spatial variation in total carrion consumption among sites was examined for correlation with urbanisation (i.e. shoreline hardening and area of urban land in the surrounding catchment), mangrove area, estuary width, water quality and latitude variables using Generalized Additive Models (GAMs) (Hastie and Tibshirani 1986) with the *mgcv* package in R. Separate analyses were conducted to examine potential effects of: (1) shoreline hardening, and (2) the area of urban land in the surrounding catchment, and to test for correlation between these two measures of urbanisation. Identical GAMs analyses were conducted to test for urbanisation effects, and the possible influence of other environmental variables, on: (1) carrion consumption by dominant scavengers; and (2) the distribution of dominant scavengers in estuaries. Sampling sites were nested within estuaries in all analyses, but nesting did not alter model performance as ‘site’ was never included in best-fit models (Tables S3-S5). Model overfitting was reduced by running all possible combinations of four or fewer factors, and by restricting individual models to 4 or fewer knots (i.e. individual polynomial functions that combine to smooth GAMs) (Zuur et al. 2009). Models were compared using Akaike Information Criterion corrected for finite sample sizes (AICc) with the MuMIn package in R. Best-fit models were considered to be those with the lowest AICc value and those within 2 Δ AICc units (Burnham and Anderson 2002). The relative importance of variables in each model was calculated by summing weighted AICc values across all models containing the variable of interest; values closer to one indicate a greater and more consistent association of a predictor and the response variable. To verify that there was no confounding effect of handling or abiotic factors (i.e. water movement) on rates of carrion consumption we confirmed that the weight of pilchards did not change on BRUVS deployments where no scavenging was recorded (paired t-test, $n = 41$, $p = 0.06$).

Results

Urbanisation was the strongest predictor of carrion consumption by scavenging fishes (Fig. 3). Variation in the rate of carrion consumption was linked to both the extent of shoreline hardening in estuaries, and the area of urban land in surrounding catchments (Supplementary material Fig. S1). Shoreline hardening was, however, the better predictor of carrion consumption (Fig. S1), and fish consumed the most carrion in moderately urbanised estuaries (i.e. where between 20 and 60% of shorelines had been hardened with artificial structures) (Fig. 3). The area of natural mangrove habitat, width of estuaries, salinity and latitude were also correlated with spatial variation in carrion consumption (Fig. S2). Overall, carrion consumption was greatest in estuaries that were characterised by moderately hardened shorelines with relatively urbanised catchments, comparatively large areas of mangroves ($\geq 6 \text{ km}^2$), wider openings to the sea ($\geq 200 \text{ m}$), and salinity levels close to seawater ($\geq 35 \text{ psu}$). Carrion consumption also varied with latitude, and was highest in the moderately urban estuaries to the north and south of the study area (Fig. S2).

Twenty-three fish species consumed carrion (Table S2), most are either omnivores or zoobenthivores that are known to feed on necromass (Elliott et al. 2007, Webley 2008, Porter and Scanes 2015). Carrion was also consumed by numerous species that are

targeted in local fisheries (e.g. yellowfin bream; *Acanthopagrus australis*) and by several nominally herbivorous taxa, which are not commonly thought of as scavengers (e.g. dusky rabbitfish; *Siganus fuscus*). Spatial variation in carrion consumption was positively correlated with changes in fish abundance, but not species richness (Fig. S3). This relationship was, however, rather weak because carrion consumption was dominated by only three species, which consumed >85% of all deployed necromass: yellowfin bream consumed 61% of carrion; banded toadfish (*Marilyna pleurosticta*) 17%; and common toadfish (*Tetractenos hamiltoni*) 8% (Fig. 4, Table S2). These 'top' scavengers differed, however, in their response to urbanisation.

Banded and common toadfish consumed more carrion in estuaries with a large area of mangroves ($\geq 5 \text{ km}^2$) (Fig. 4). Carrion consumption by toadfish (Tetraodontidae) was also correlated with estuary width, salinity, turbidity and chlorophyll-a, but not with the extent of urbanisation (Fig. S4). By contrast, yellowfin bream (Sparidae) consumed the most carrion in estuaries with moderately hardened shorelines (20-60% of shorelines hardened) (Fig. 4). Carrion consumption by yellowfin bream was also correlated with estuary width and the level of chlorophyll-a in the water column, but not with the area of mangroves (Fig. S4).

The spatial distribution of dominant scavengers reflected their effects on carrion consumption. Banded and common toadfish were most abundant in estuaries with large areas of mangroves (Fig. 5). Their distribution was also correlated with estuary width, salinity, turbidity and chlorophyll-a, but not with the extent of urbanisation (Fig. S5). By contrast, yellowfin bream were most abundant in estuaries with moderately hardened shorelines (Fig. 5). Their distribution was also correlated with estuary width and salinity, but not with the area of mangroves (Fig. S5).

Discussion

The ecological effects of urbanisation are widespread, but it is often untested to which extent changes to species composition and abundance propagate to changes in ecosystem function (Loreau and Mazancourt 2013, McPhearson et al. 2016, Bishop et al. 2017, Mayer-Pinto et al. 2018). Depending on the ecology of key species, and the internal redundancy of assemblages, urbanisation might result in either the loss, replacement, or supplementation of ecological functions (Fig. 1). Our results show, for the first time, that urbanisation might supplement ecological functions in moderately disturbed ecosystems. Shoreline hardening, and the area of urban land in surrounding catchments, were strongly correlated with fish assemblage composition and carrion consumption in estuaries. In natural mangrove-lined estuaries, the majority of necromass was consumed by toadfish (Tetraodontidae). In estuaries that had been moderately urbanised (i.e. where 20-60% of shorelines had been hardened with artificial structures), this function was dominated by yellowfin bream (Sparidae), which removed the bulk of carrion. In highly urbanised estuaries (i.e. where 60-100% of shorelines had been hardened), no species avidly fed upon exposed carrion and the rate of consumption declined as the extent of shoreline modification increased. These findings illustrate functional complementarity in resource use by estuarine scavengers (i.e. species co-exist by utilising similar resources in different contexts; Loreau 2004), and suggest that yellowfin bream might replace toadfish in moderately urban estuaries. Yellowfin bream were the dominant scavengers (removing $\approx 61\%$ of carrion) in this study, and consumed most carrion in moderately urban seascapes, but both bream abundance and carrion

consumption declined in highly urbanised estuaries. Limited urbanisation might, therefore, supplement the rate of carrion consumption in subtropical estuaries where key species benefit from urban structures. Effects of urbanisation are not universally negative, with many species capitalising on the regular supply of food and abundance of shelter in human modified landscapes (Aronson et al. 2014, Dafforn et al. 2015, Firth et al. 2016, Bishop et al. 2017). Species that perform important ecological processes, and which are also capable of exploiting resources in urban settings might, therefore, be important in sustaining ecological functions in disturbed ecosystems (Hobbs et al. 2006, Huijbers et al. 2016, Mayer-Pinto et al. 2018).

Diversity and functional redundancy are pivotal components of ecosystems that underpin their capacity to withstand disturbance, but both ecological features are particularly sensitive to landscape modification (Tschardt et al. 2012, Olds et al. 2016, Mayer-Pinto et al. 2018). We report moderate diversity in the scavenging guild of estuarine fishes, with carrion being consumed by 23 different species. Despite this diversity, we demonstrate that three species consumed >85% of all necromass, and show that each other taxa consumed <5% of deployed carrion. This result suggests that subtropical estuaries, which are under increasing pressure from multiple human impacts (Hindell 2007, Elliott et al. 2014, Firth et al. 2016), might have limited redundancy with regards to the ecological function of carrion consumption. A similar pattern of moderate diversity and limited redundancy characterises the guild of scavengers on exposed sandy beaches in the same region as this study was conducted. Carrion consumption is high and dominated by raptors on beaches that retain a buffer of natural vegetation, but scavenging rates decline on urban beaches where carcasses are typically removed by introduced canines (Brown et al. 2015, Huijbers et al. 2015). Because many animals can consume carrion, high diversity and redundancy are often thought to be characteristics of scavenging guilds (Wilson and Wolkovich 2011, Barton et al. 2013). There is, however, a striking similarity in the impacts of urbanisation across both estuaries and beaches in southern Queensland, which suggests that limited redundancy might be a prevalent feature of certain scavenger assemblages. Nevertheless, we have shown that toadfish dominate carrion consumption in mangrove-lined estuaries and are replaced by yellowfin bream in urban seascapes, but it is not clear whether similar functional replacement or complementarity, occurs in estuaries that have been modified by other human impacts (e.g. fishing, eutrophication, pollution, invasive species). The consumption of carrion by estuarine fishes appears to be sensitive to changes in water quality and fishing pressure (Webley 2008, Porter and Scanes 2015), but we do not yet know whether these effects result from human impacts to fish abundance, diversity or feeding ecology.

The spatial distributions of toadfish and yellowfin bream were correlated with their effects on carrion; toadfish were common in mangrove-lined estuaries, whereas yellowfin bream were concentrated around urban structures and hardened shorelines. Both species are abundant in the study area, and are avid scavengers that regularly consume carrion in estuaries and coastal waters (Webley 2008, Porter and Scanes 2015, Vargas-Fonseca et al. 2016). Toadfishes (both banded and common) are small zoobenthivores that feed mostly on benthic crustaceans and molluscs, they are estuarine residents, which migrate tidally into inundated mangrove forests and saltmarshes to feed (Tibbetts et al. 1998, Saintilan et al. 2008, Piah and Bucher 2014). By contrast, yellowfin bream are large zoobenthivores that feed opportunistically on fish and benthic

invertebrates across a range of coastal ecosystems; juveniles recruit into shallow seagrass meadows and migrate to structurally complex habitats (e.g. reefs, woody debris, artificial structures) as either sub-adults or adults (Meynecke et al. 2008, Sheaves et al. 2014b, Gilby et al. 2018). Humans have, however, removed much of the natural subtidal structure from Australia's estuaries to improve their navigability for shipping, and through the combined effects trawling, dredging and channelization (Hindell 2007, Sheaves et al. 2014a). Thus, artificial structures within estuaries (e.g. jetties, pontoons, rock walls) may partially compensate for this loss of natural in-stream habitat structure (Chapman et al. 2009, Waltham and Connolly 2011), whilst also providing settlement sites for a diversity of epifauna (e.g. oysters, mussels) that are eaten by zoobenthivorous fishes (Moreau et al. 2008, Bishop et al. 2017, Mayer-Pinto et al. 2018). The large numbers of yellowfin bream that we observed in urban estuaries likely relates to the presence of both abundant food and shelter under artificial structures (Clynick 2008, Folpp et al. 2013). Empirical data on the spatial distribution of potential prey items (i.e. fish and invertebrates) and the habitat values of hardened shorelines are, however, needed to test this hypothesis. Yellowfin bream are also a primary target for both recreational and commercial fishers, whereas toadfishes are not harvested in the study area (Tibbetts et al. 1998, Olds et al. 2012a, Curley et al. 2013). Thus, differences in the ecology and economic importance of toadfish and yellowfin bream suggest that the effects of species replacement might also shape the spatial distribution of other ecological functions (e.g. predation on fish and invertebrates), modify food-web structure and alter fisheries catches in urban estuaries.

The rate at which carrion is consumed in estuaries might be further modified by seasonal variation in the abundance and foraging activity of pivotal scavengers. We sampled during the austral winter, when yellowfin bream are particularly abundant in the lower reaches of estuaries (Meynecke et al. 2008, Curley et al. 2013), and it is possible that other species might be important scavengers at other times of the year. For example, mud crabs (*Scylla serrata*) are abundant, and avid scavengers of carrion, in estuaries over the austral summer (Webley 2008). The availability of carrion to estuarine scavengers might also vary as a function of seasonality, or with changes in the extent of shoreline modification (Huijbers et al. 2016). Large accumulations of animal carcasses were not observed in any of the estuaries we studied, which suggests that substantial differences in carrion availability were not a major factor in contributing to observed patterns in scavenging function. Nevertheless, to better characterise how human actions shape carrion consumption in disturbed estuaries we require empirical data to test for effects of urbanisation on the spatial and temporal availability of carrion and the abundance and foraging activity of estuarine scavengers.

We demonstrate that urbanisation can alter ecological function, albeit in somewhat unexpected ways: this is a common contention in urban ecology, but it is rarely tested with empirical data. Hardened shorelines were associated with fish assemblages of distinct composition. This structural shift did, however, not result in a decline in carrion consumption – the key ecological function tested by us. Instead, taxa that consumed carrion in natural settings were replaced in urban seascares by a particularly effective scavenger (yellowfin bream), which aggregated around artificial structures. Thus, moderate shoreline hardening was correlated with a greater abundance of this key scavenger in estuaries and, subsequently, with the overall function of carrion consumption in urban seascares. Human actions have eroded the spatial heterogeneity

and structural complexity of many ecosystems, but as we have shown here, some species can thrive in some urban settings. Identifying and conserving urban species that perform important ecological processes will be critical for maintaining ecosystem functioning across disturbed landscapes.

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Supplementary material

Supplementary material (Appendix ECOG-03551 at www.ecography.org/readers/appendix). Tables S1–S5, Figures S1–S5.

Figure Legends

Fig. 1. Conceptual diagram outlining three potential responses of ecological function to urbanisation: (1) complete replacement (green line) when functional redundancy is high; (2) loss (yellow line) when redundancy is low; or (3) limited supplementation (grey line) when urban structures provide habitat for species that perform important ecological functions.

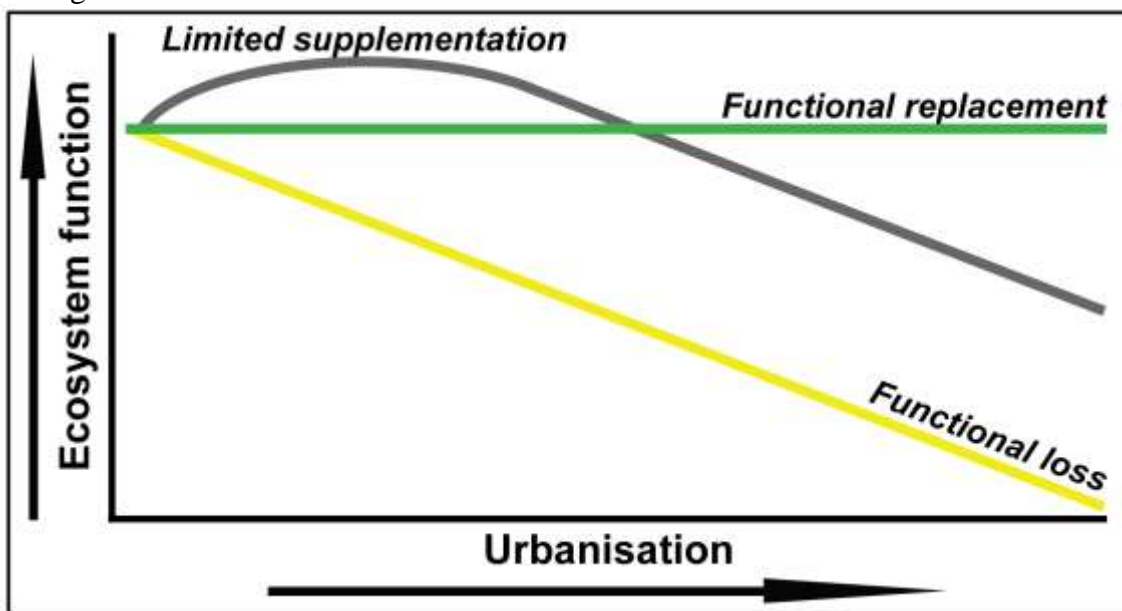


Fig. 2. Location of study estuaries in eastern Australia. Insets illustrate the location of sampling sites along: (A) a relatively natural estuary with abundant mangroves (Noosa); and (B) a highly urbanised estuary where hardened shorelines are dominated by artificial structures (Nerang).



Fig. 3. Moderate urbanisation supplemented the rate at which carrion was consumed by scavengers in estuaries. Correlations were tested with General additive models (GAMs): y-axis values in estimated effects plots denote the estimated degrees of freedom of the term in GAMs; shaded regions indicate 95% confidence intervals; importance values indicate the relative contribution of urbanisation to GAMs. Larger importance values indicate stronger correlation with carrion consumption; smaller values (i.e. < 0.60) have little or no effect.

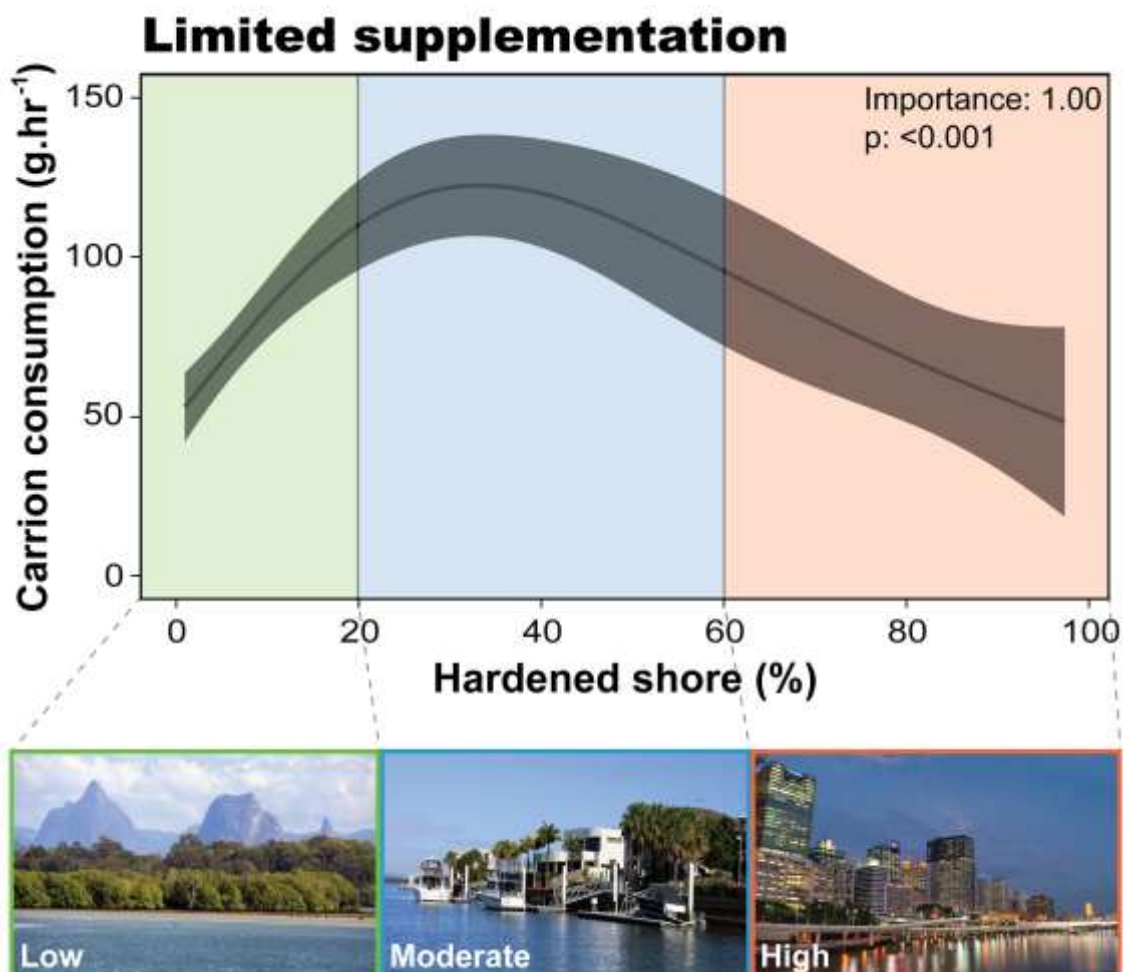


Fig. 4. Carrion consumption was dominated by yellowfin bream (*Acanthopagrus australis*), banded toadfish (*Marilyna pleurosticta*) and common toadfish (*Tetractenos hamiltoni*), which consumed >85% of all deployed carrion. Yellowfin bream dominated carrion consumption in moderately urban estuaries. By contrast, both banded and common toadfish consumed more carrion in estuaries with large areas of mangroves. Correlations were tested with General additive models (GAMs): y-axis values in estimated effects plots denote the estimated degrees of freedom of the term in GAMs; shaded regions indicate 95% confidence intervals; importance values indicate the contribution of each variable to GAMs models.

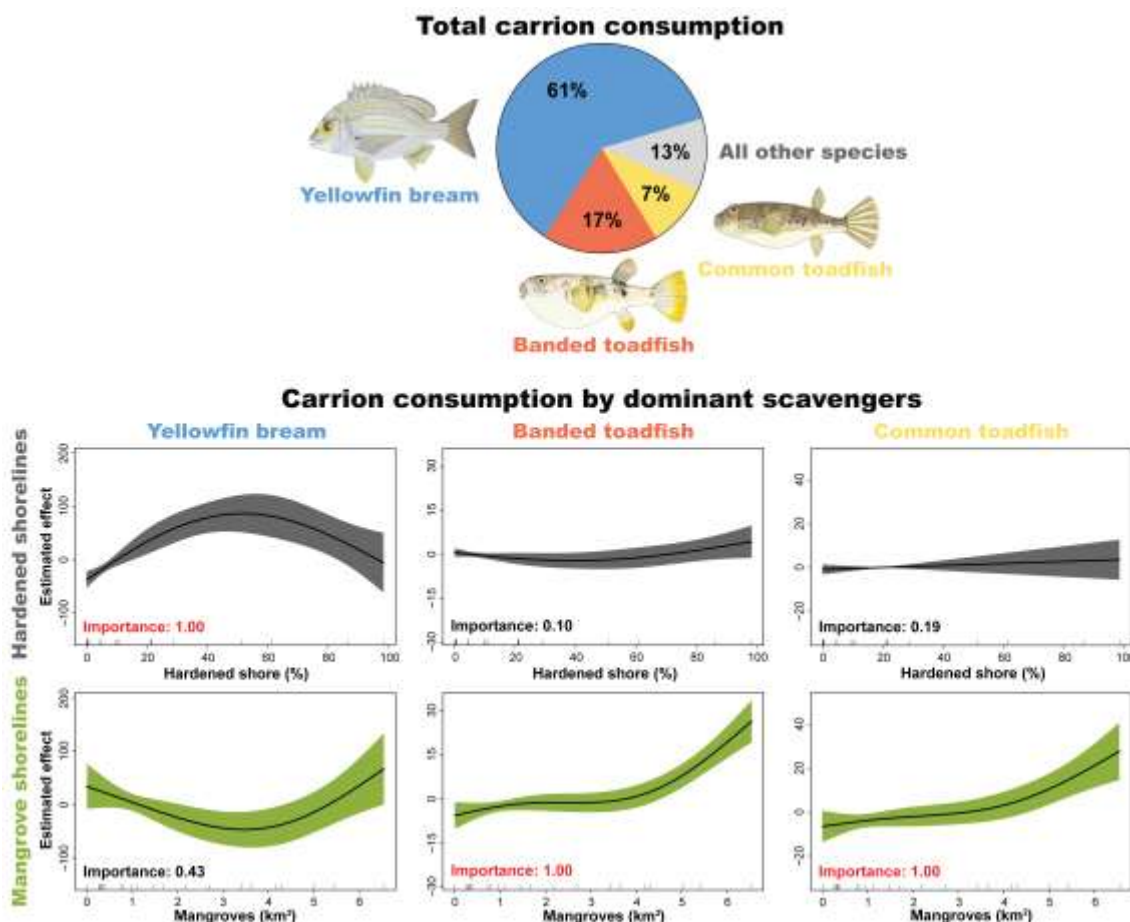


Fig. 5. Yellowfin bream were most abundant in moderately urban estuaries, whereas banded and common toadfish were most abundant in estuaries with large areas of mangroves. Correlations were tested with General additive models (GAMs): y-axis values in estimated effects plots denote the estimated degrees of freedom of the term in GAMs; shaded regions indicate 95% confidence intervals; importance values indicate the contribution of each variable to GAMs models.

