



Saltmarsh grass supports fishery food webs in subtropical Australian estuaries

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ABSTRACT

All fishery food webs are ultimately underpinned by organic matter produced by algae and plants, some of it supplied by primary producers at the fringes of fish habitats. This is no different in tropical and subtropical estuaries where secondary production by crustaceans and finfish may depend on coastal wetlands (e.g. mangroves, seagrass, saltmarshes) abutting channels. Coastal urbanisation is a major cause of wetland loss globally. Hypothetically, reduced wetland area may propagate to less fisheries production if wetland contributions to food webs are substantial – this is the prime question addressed here. We sampled key fisheries species in subtropical estuaries in reaches of moderate urbanisation (18–33% of shoreline hardened) and in reference locations dominated by wetlands, on the east coast of Australia. We used triple stable isotopes (C, N, S) to estimate (using mixing models) the trophic contributions of the key primary producers to regional fisheries species. Organic matter from wetland plants, particularly saltmarsh grass (*Sporobolus virginicus*), underpinned fishery food webs in most cases (with median contributions ranging from 18 to 88% for saltmarsh grass, followed by 6–70% for C3 wetland plants (e.g. mangroves, phragmites) and 3–36% by benthic algae). Moderate levels of urban transformation of estuarine margins did not change the dominance of wetland carbon for fish and crustaceans in settings without significant seagrass meadows. Given the demonstrated importance of saltmarshes, and other coastal wetlands, to regional fisheries production, conservation of these habitats is necessary in the face of multiple anthropogenic threats.

1. Introduction

All fisheries ultimately are underpinned by organic matter from plants. Thus, identifying the actual sources of plant-derived material supporting food webs is important to conserve and restore critical fish habitat (Whitfield, 2017). Most of the catch in coastal, inshore fisheries come from unvegetated soft-sediments (Melville and Connolly, 2005; Taylor et al., 2017). This means that organic matter supporting fisheries production comes either from in-situ algal production or from organic matter transferred from wetland sources, catchment fluxes, or other primary producer habitats (Connolly et al., 2009; Schlacher and

Wooldridge, 1996).

The specific nutritional contribution by different plants to fishery food webs can vary with location, topography, connectivity, season, and the types of wetland or marine plant habitats present (Abrantes and Sheaves, 2008; van de Merwe et al., 2016). For example, saltmarsh grass is an important source in fish food webs on the USA East Coast (Fry et al., 2003; Kneib, 2000), but rarely in Australia where seagrass is often the principal source of carbon (Connolly and Waltham, 2015; Loneragan et al., 1997; Melville and Connolly, 2005). Many tropical Australian estuaries, however, lack seagrass, and it is unclear what other carbon sources are important in these settings, including the role of saltmarshes

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in fish productivity (Abrantes and Sheaves, 2008; Raoult et al., 2018). Saltmarshes are facing multiple threats (e.g. agricultural land-use, trampling, mangrove encroachment, and storm damage (Kelleway et al., 2016; Rogers et al., 2019; Rogers et al., 2006; Turschwell et al., 2020)), making a solid understanding of their energetic role a critical component of inshore fisheries management.

Coastal urbanisation can impact water quality, promote harmful algal blooms, change productivity, modify organic matter provenance, and alter the diversity, composition and trophic role of fishes in urban estuaries (Brook et al., 2018; Docile et al., 2016; Henderson et al., 2019; Kneib, 2000; Lee et al., 2006; Olds et al., 2018; Schlacher et al., 2007). Significantly, urbanisation is also a major cause of wetland loss, potentially leading to a decline of primary producers underpinning fisheries production (Imhoff et al., 2000). Yet, it remains largely undetermined whether and how changes to wetland plants may propagate to fishery food webs (Nagelkerken et al., 2015; Wenger et al., 2009) – this question is pertinent given the global decline of coastal wetlands (Davidson, 2014) and is the prime rationale for this study. We specifically tested three key questions: 1) how important are different types of wetland primary producers to secondary production of crustaceans and fish species, via trophic transfers in estuarine fishery food webs; 2) do contributions of wetland primary producers change between wet and dry seasons and; 3) do modest levels of urban development of estuarine margins change the contribution of wetland sources to fishery food webs?

2. Material and methods

2.1. Site selection and conditions

We gauged the contribution of the main types of locally-available coastal wetland and marine plants to the tissue of several fish species commonly harvested in tropical and subtropical estuaries on the East Coast of Australia in Central Queensland. The area shows increasing land-use changes towards coastal urbanisation and port development and has a high occurrence of agriculture (cattle grazing or sugar cane). We sampled fish and carbon sources, using a paired design of natural and urban locations, in two regions of Central Queensland (Australia): Bundaberg and Rockhampton (Fig. 1). Mangroves and saltmarshes dominated the floodplains and no seagrass has ever been recorded at or near these sampling sites. We defined ‘urban’ locations as estuarine reaches abutted by artificial structures (using a 25 m buffer in QGIS), being 33% of the shoreline at Bundaberg (24°45′29.9″S, 152°24′24.1″E) and 18% at Rockhampton (23°23′31.4″S, 150°31′54.1″E). We compared these urban reaches with ‘natural’ reference areas selected to have intact natural wetlands and very few hardened shorelines (2–6%) (Bundaberg – Kolan River, 24°40′40.8″S, 152°12′01.8″E; Rockhampton – Fitzroy River, 23°22′23.9″S, 150°30′46.2″E; Fig. 1).

Because of pronounced seasonality in rainfall leading to variation in hydrological connectivity between wetlands and estuarine channels, we sampled at the end of the wet and dry season (hereon referred to as ‘wet’ and ‘dry’). Isotopic analysis of fish muscle tissue typically reflects diet over a period of approximately three months prior to capture (Hesslein et al., 1993). Hence, we sampled fish in May (2017) to represent diet during the wet season (typically from November to April), and in

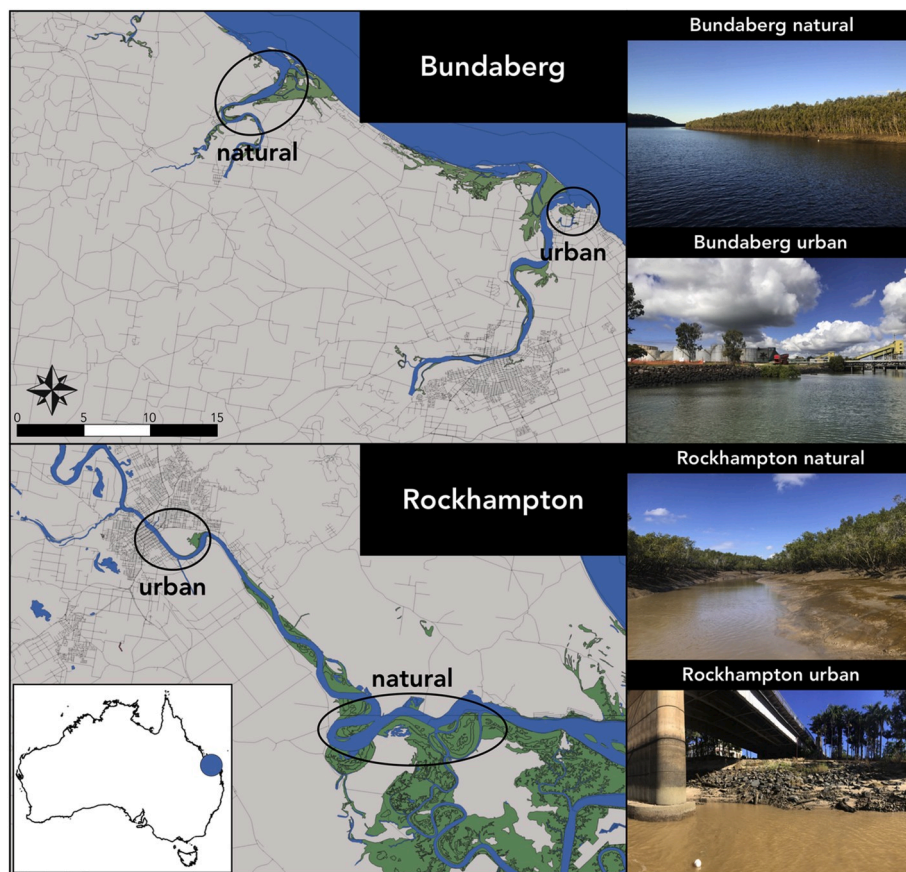


Fig. 1. Bundaberg and Rockhampton sampling regions in Central Queensland, Australia, and example habitats for natural and urban locations. Green shading indicates natural wetland area (map layer source: The State of Queensland, Department of Environment and Science, 2019). Inset map and blue dot show approximate location of Central Queensland within Australia. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

October (2017) for the dry season (typically from June to September). Rainfall in coastal catchments in the three months leading up to our wet season sampling was 421 mm, compared with 5 mm for dry season.

2.2. Sample collection and preparation

In each estuary, we collected key fisheries species representing inshore crustacean and finfish commonly harvested in central Queensland (Department of Agriculture and Fisheries, 2018; Webley et al., 2015), being two omnivorous crustaceans and five carnivorous finfish in our study (Table 1). Banana prawns (*Fenneropenaeus merguensis*) and mud crabs (*Scylla serrata*) are widely distributed throughout the Indo-west Pacific, the Middle East, southeast Asia to Japan, the western Pacific islands and northern Australia, with mud crabs also occurring along the coasts of south and east Africa (Food and Agriculture Organization, 2018). Grunter (*Pomadasys kaakan*) are found in the Indo-west Pacific, specifically the Red Sea, east coast of Africa, southeast Asia and northern Australia (Froese and Pauly, 2018). King threadfin (*Polydactylus macrochir*) have a limited distribution in the Indo-west Pacific from southern New Guinea to northern Australia (Froese and Pauly, 2018). Trumpeter whiting (*Sillago maculata*) are found along the east coast of Australia (McKay, 1992) and Yellowfin bream (*Acanthopagrus australis*) are found along the east and west coasts of Australia (Carpenter, 2001). Fish and crustaceans were caught using a range of techniques and equipment including seine nets, cast nets, gill nets, line fishing and crab pots. Catches (species and size ranges) differed for finfish between estuaries (Table 1).

We concurrently collected common primary producers potentially supporting fishery food webs: mangroves (*Avicennia marina* and *Rhizophora stylosa*), C3 saltmarsh succulent (*Suaeda australis*), C4 saltmarsh grass (*Sporobolus virginicus*), and benthic algae (consisting predominantly of cyanobacteria and diatoms). At one region, Rockhampton Urban, *A. marina*, *R. Stylosa* and *S. australis* were not the most common sources; instead we collected *Aegiceras corniculatum*, *Melaleuca* sp. and *Phragmites australis* (Table S2). We attempted to collect phytoplankton samples from the water column during both the wet and dry season, however only a single clean sample could be obtained from a single region at one location and time period, potentially due to the high turbidity of these estuaries that is known to limit phytoplankton

production (Cloern, 1987). We therefore had to exclude phytoplankton from analyses and used only benthic algae to represent in-situ sources. No substantial seagrass areas were identified in the vicinity of any of the sites, and macroalgae growing on rocks or urban structures was extremely limited, and thus assumed not to be a major contributing source.

All animal and plant samples were dried to constant weight (60 °C) and ground in preparation for isotopic analysis. All animal samples were white muscle tissue with low lipid concentrations, and isotope values were therefore not corrected for lipid content. Green leaves were analysed from all plant samples. Benthic algae samples were collected in scrapes of the top 0.5 cm of sediment, then sieved and centrifuged in silica following Hamilton et al. (2005). Resulting samples were visually checked for purity and quantity of algal cells, and the centrifuging process occasionally repeated where necessary.

2.3. Analyses

We used stable isotopes of carbon (C), nitrogen (N) and sulfur (S), and mathematical mixing models to estimate source contributions to each species at each region and location. Isotope samples were analysed on an elemental analyser isotope ratio mass spectrometer (EA-IRMS) at the Griffith University Stable Isotope Facility, Queensland. Precision of the mass spectrometer, calculated as the 95% confidence interval of differences between paired values from duplicate samples, was 0.04, 0.05 and 0.10 for C, N and S respectively, well within acceptable levels (Jardine and Cunjak, 2005).

The relative contribution of potential plant sources to animals was assessed using the stable isotope mixing model MixSIAR (Stock and Semmens, 2013), where we included the residual error term (Parnell et al., 2010). To assess the extent that the isotope data informed on diet contributions, we calculated the Hellinger distance for each model and source (Brown et al., 2018). Values of the Hellinger distance range from 0 to 1 and values closer to one indicate greater differentiation of the estimated source contributions when compared to the priors of the model. We adjusted isotope values individually for each of the fishery species based on their trophic levels, where each trophic level was assumed to enrich each isotope by 1.0‰, 2.5‰ and 0‰, for C, N and S respectively (Table 1, based on McCutchan et al. (2003)). The MixSIAR

Table 1

Fishery species collected in the Bundaberg region in Queensland, Australia, and contributions from primary producers to the food web (median; 95% CI). Highest contributing source in bold for each species/season combination. Trophic enrichment factors (TEF) for each species are based on published values (Connolly and Guest, 2005; Froese and Pauly, 2018). Crustaceans were measured using carapace length and finfish using total length. C3 wetland plant sources include *Avicennia marina*, *Rhizophora stylosa* and *Suaeda australis* with sources combined a-priori for mixing models and; saltmarsh grass is *Sporobolus virginicus*. *Significant difference in contributions between seasons where 95% CIs do not overlap with medians.

Fishery species	TEF	Location	Season	Size (mm)	n	Contributions			
						Benthic algae	C3 wetland plants	Saltmarsh grass	
Crustaceans	Banana prawn (<i>Fenneropenaeus merguensis</i>)	natural	wet	60–80	6	19; 0-57	28; 2-53	41; 19-82	
			dry	60–80	6	36; 19-51	35; 18-52	29; 17-42	
		urban	wet	60–100	7	10; 0-73	18; 1-46	67; 14-93	
			dry	60–80	6	30; 5-68	16; 4-30	54; 21-77	
		Mud crab (<i>Scylla serrata</i>)	natural	wet	60–140	10	11; 0-35	40; 22-54*	48; 33-62
			dry	110–140	6	33; 10-52	18; 2-38*	49; 32-67	
Finfish	Javelin grunter (<i>Pomadasys kaakan</i>)	natural	wet	170–240	5	32; 2-78	22; 2-56	41; 11-74	
			dry	210–260	6	23; 3-44	40; 19-61	37; 17-55	
		urban	wet	160–320	6	27; 1-92	16; 1-68	45; 4-89	
			dry	200–240	6	15; 1-61	26; 7-47	56; 21-79	
		Trumpeter whiting (<i>Sillago maculata</i>)	natural	Wet	40	3	8; 0-40	23; 1-50	66; 40-90
			Dry	50–90	3	16; 1-47	12; 1-41	68; 36-92	
	Yellowfin bream (<i>Acanthopagrus australis</i>)	natural	Wet	80–110	5	12; 0-59	42; 12-60	45; 17-66	
			Dry	30–60	4	6; 0-36	35; 7-62	58; 18-82	
		urban	Wet	90–110	6	14; 0-84	33; 6-50	49; 7-71	
			Dry	40–70	4	5; 0-50	34; 5-67	59; 15-85	

models included two treatment factors: location (two levels, natural and urban) and animal size (as a covariate), with separate models run for each species at each region and season. The explanatory power of employing isotopes of three elements is normally very high, but because N isotopes have a large trophic enrichment factor (TEF) relative to the total range of values for plants and animals, N isotopes can potentially detract rather than add to modelling based only on C and S (Connolly et al., 2004). To assess the utility of retaining N, we tested the sensitivity of MixSIAR outputs by running models using only C and S. Although median estimates of source contributions varied slightly when N was excluded, the rank order of importance did not change, so we retained all three elements for analyses.

When all possible primary producers were included in the model, the breadth of solutions in MixSIAR outputs prevented clear conclusions about relative contributions. Primary producers with similar isotopic signatures can be combined before model fitting to reduce the number of sources and enable a unique conclusion to be drawn from the mixing model (Phillips et al., 2005). The mangrove species (*Avicennia marina* and *Rhizophora stylosa* and *Aegiceras corniculatum*), the C3 saltmarsh succulent (*Suaeda australis*) and the two alternative wetland sources at Rockhampton urban (*Melaleuca* sp. and *Phragmites australis*) had similar,

depleted C isotope values (Tables S1–S2). Because of the similar C isotopes and because we were interested in main wetland types, we combined our sources into three distinct isotopic categories: 1) C3 plants (comprised of *A. marina*, *R. stylosa* and *S. australis* for Bundaberg natural and urban and Rockhampton natural locations, and; *A. corniculatum*, *Melaleuca* sp. and *P. australis* at Rockhampton urban location); 2) Saltmarsh grass (the C4 plant *S. virginicus* only); and 3) Benthic algae.

We presented results as marginal contributions of each source to fisheries species diets because inspection of posterior estimates of contributions indicated no strong correlations. We therefore defined statistically significant differences between seasons as cases where the 95% credible intervals did not overlap with the seasonal medians of other sources.

3. Results

Fisheries species relied substantially on organic matter produced by wetland plants, especially exported primary production by the saltmarsh grass, *Sporobolus virginicus*. Plants in abutting wetlands contributed, on average, at least 75% to fish secondary production whilst the likely contribution of benthic algae was less than 25%. The median

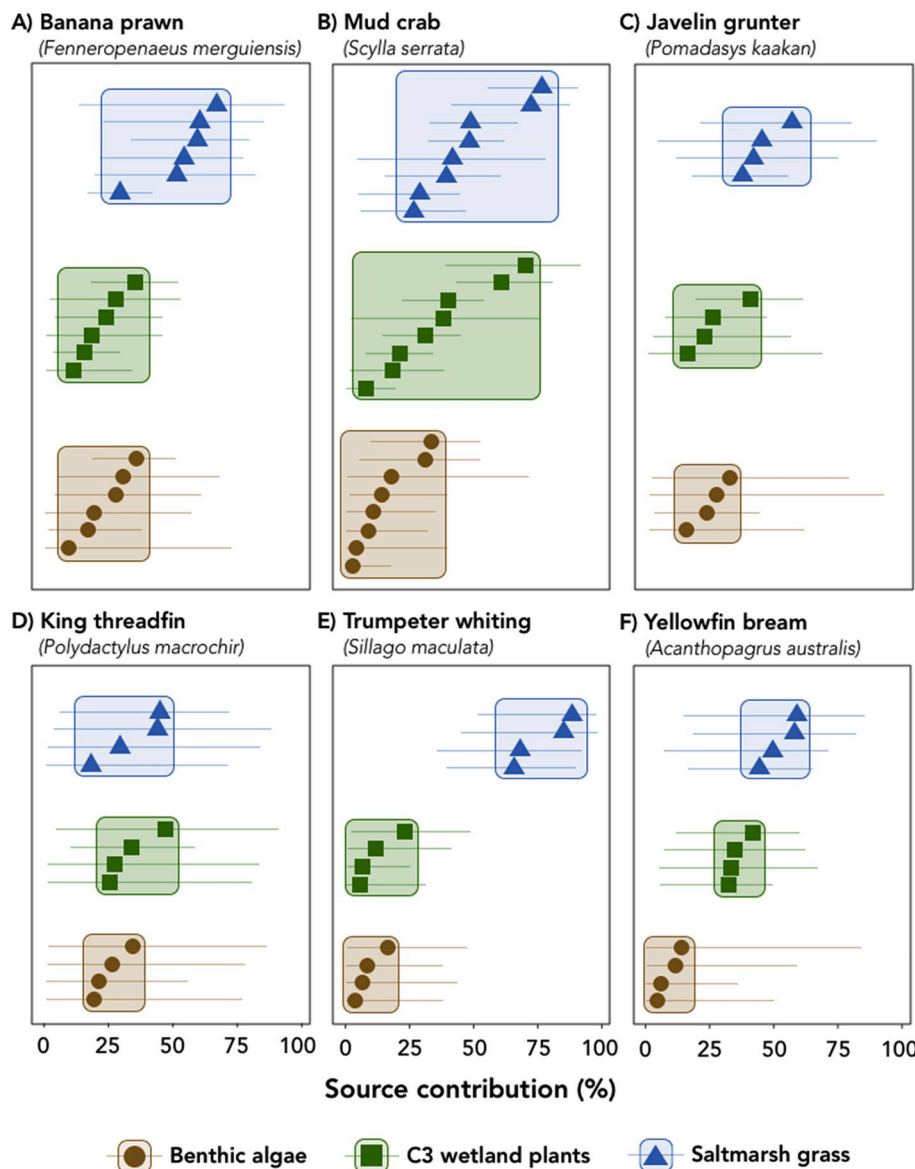


Fig. 2. Contribution (median, 95% CIs) of benthic algae, C3 wetland plants and saltmarsh grass to six fishery food webs in two regions in Central Queensland, Australia. Values for each species in the Bundaberg region are shown in Table 1 and in the Rockhampton region in Table 2. Colour boxes are positioned to highlight differences among sources and are not determined statistically. Replicates within boxes (four combinations of location/season, except for banana prawns and mud crabs which have six and eight combinations of region/location/season, respectively) are ordered from highest to lowest mean contribution for that source – precise details for each combination are given in Tables 1 and 2 (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

contribution of saltmarsh grass to fish tissue ranged from 18 to 88%, followed by 6–70% for C3 wetland plants (e.g. mangroves, phragmites) and 3–36% by benthic algae (Fig. 2; Tables 1–2). The Hellinger distance was, on average, further from zero for saltmarsh grass when compared with other sources (Table S3), which indicates that the isotope data had a strong influence on the estimated contribution of saltmarsh grass to animal diets. Consumer tissue signatures for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ varied from -21.1 to -13.2‰ , 7.5 – 11.2‰ and 12.3 – 18.5‰ respectively for Bundaberg, and -22.6 to -16.3‰ , 8.6 – 15.8‰ and 12.1 – 15.5‰ respectively for Rockhampton (Tables S1–S2).

The relative importance of primary producers to food webs varied little between the wet and dry seasons. Mud crabs were the only species that showed any significant changes in source contributions between seasons. Even for this species, however, changes varied across regions or locations (Tables 1–2). We found no evidence that the contribution of wetland plants was consistently lower in urban areas. Instead, we found that the combined contributions of wetland plants to fishery food webs was consistently high at both urban and natural locations, in two regions and across two seasons (Fig. 3; Tables 1–2).

4. Discussion

Wetlands contributed a high proportion of primary productivity to several commonly targeted finfish and crustaceans across the two regions studied in central Queensland, regardless of the presence of urban structures. We have shown that saltmarsh grass is an important contributor to fisheries productivity in locations where seagrass is not found. This result is important, because while seagrass is well recognised for its contribution to fishery food webs, saltmarsh is often seen to be less important (Connolly and Waltham, 2015; Gilby et al., 2018; Melville and Connolly, 2005). These are key findings because of the threats facing saltmarsh habitats from anthropogenic activities and the current lack of protection that saltmarshes receive (Wegscheidl et al., 2016).

Our findings on the importance of saltmarsh grass, *Sporobolus virginicus*, support findings elsewhere in Australia. In temperate south-eastern Australia, for instance, fishery food webs within two major estuaries, the Clarence and Hunter Rivers, showed strong reliance on saltmarsh grass (Raoult et al., 2018). In tropical northern Australia, food webs supporting fisheries species in small, land-locked lagoons were dominated by the most prevalent habitat on the lagoon edges, with one lagoon dominated by saltmarsh grass (Abrantes and Sheaves, 2008). Saltmarsh grass has been demonstrated as an important primary producer supporting food webs of penaeid prawns, crabs (*Scylla serrata*) and bream (*Acanthopagrus* spp.) on the east coast of Australia in tropical (Abrantes and Sheaves, 2008), temperate (Raoult et al., 2018) and now

subtropical regions (this study). Strong saltmarsh grass isotope signals have also been reported in food webs supporting whiting (*Sillago* spp.) in tropical (Abrantes and Sheaves, 2008) and subtropical (this study) regions, and flathead (*Platycephalus* spp.) in tropical (Abrantes and Sheaves, 2008) and temperate (Raoult et al., 2018) regions of Australia. Our results, from natural and urban locations at two regions during two seasons for multiple species, combined with other studies, highlight the value of saltmarsh grass to Australian fishery food webs in open estuarine systems when seagrass is absent.

The important role of saltmarsh in supporting fishery food webs demands these habitats receive greater recognition than they currently do, particularly in places where seagrass is absent. Saltmarsh in Australia is generally undervalued and management and protection is inconsistent across states (Wegscheidl et al., 2016). Saltmarsh habitats face a range of threats from both natural and anthropogenic activities, including from agricultural activities, changes in hydrology, and fragmentation (Saintilan et al., 2014). Further, sea level rise could lead to a greater loss of these habitats due to hardening of shorelines preventing landward migration of saltmarsh, and by facilitating mangrove encroachment (Enwright et al., 2016; Saintilan et al., 2014; Schuerch et al., 2018). Although mangrove encroachment into saltmarsh habitat could have some benefits, such as increasing the carbon storage capacity of coastal wetlands (Kelleway et al., 2016), fishery food webs will likely be adversely affected, given the evidence for saltmarsh habitat as a primary source of productivity to fishery food webs in Australia (Raoult et al., 2018; Taylor et al., 2018). Furthermore, many of the fisheries species analysed here also occur in Asia, where saltmarsh systems are at risk of additional threats from invasive species and are lesser-known than those in Australia (Lee and Khim, 2017; Patro et al., 2017).

Internationally, the saltmarsh grass *Spartina* is renowned for its productivity, which is transported to deeper estuarine waters where it supports numerous fisheries species (Kneib, 2000). Findings for *Spartina* marshes are mostly from North America (Bouillon et al., 2011), where marshes grow much lower in the intertidal zone than in South Asia and Australia (Patro et al., 2017; Saintilan and Rogers, 2013). However, Australian marsh plants are typically less productive and saltmarsh is inundated less frequently, which makes the substantial role of saltmarsh in Australian food webs more surprising (Abrantes et al., 2015). The incorporation of saltmarsh carbon into Australian fishery food webs may therefore be better explained by trophic connections due to pore and surface water exchange. For example, burrows created by invertebrates living in saltmarsh can increase pore water exchange without complete tidal inundation, thereby enhancing the exchange between saltmarsh soil and estuarine waters (Xin et al., 2009). Microbial conversion of dissolved organic carbon could then form trophic transfers into the

Table 2

Fishery species collected in the **Rockhampton** region in Queensland, Australia, and contributions from primary producers to the food web (median; 95% CI). Highest contributing source in **bold** for each species/season combination. Trophic enrichment factors (TEF) for each species are based on published values (Connolly and Guest, 2005; Froese and Pauly, 2018). Crustaceans were measured using carapace length and finfish using total length. C3 wetland plant sources were combined a-priori for mixing models and include; *Avicennia marina*, *Rhizophora stylosa* and *Suaeda australis* at the natural location, and *Aegiceras corniculatum*, *Melaleuca* sp. and *Phragmites australis* at the urban location and; saltmarsh grass is *Sporobolus virginicus*. *Significant difference in contributions between seasons where 95% CIs do not overlap with medians.

Fishery species	TEF	Location	Season	Size (mm)	n	Contributions		
						Benthic algae	C3 wetland plants	Saltmarsh grass
Crustaceans	Banana prawn (<i>Fenneropenaeus merguensis</i>)	natural	wet	60	3	20; 2-43	13; 2-35	66; 41-89
			Dry	60–80	6	18; 3-34	22; 5-41	60; 40-78
		urban	wet	–	–	–	–	–
			Dry	–	–	–	–	–
	Mud crab (<i>Scylla serrata</i>)	natural	wet	90–160	8	28; 2-48	35; 19–53*	38; 20-55
			Dry	90–150	11	14; 2-31	56; 43-70*	29; 14-44
Finfish	King threadfin (<i>Polydactylus macrochir</i>)	natural	wet	500–660	3	34; 2-86	25; 1-80	30; 1-84
			Dry	570–640	6	21; 1-56	34; 10-58	45; 6-71
		urban	wet	540–650	3	19; 1-77	27; 1-83	44; 3-88
			Dry	460–630	3	26; 1-78	47; 4-91	18; 1-71

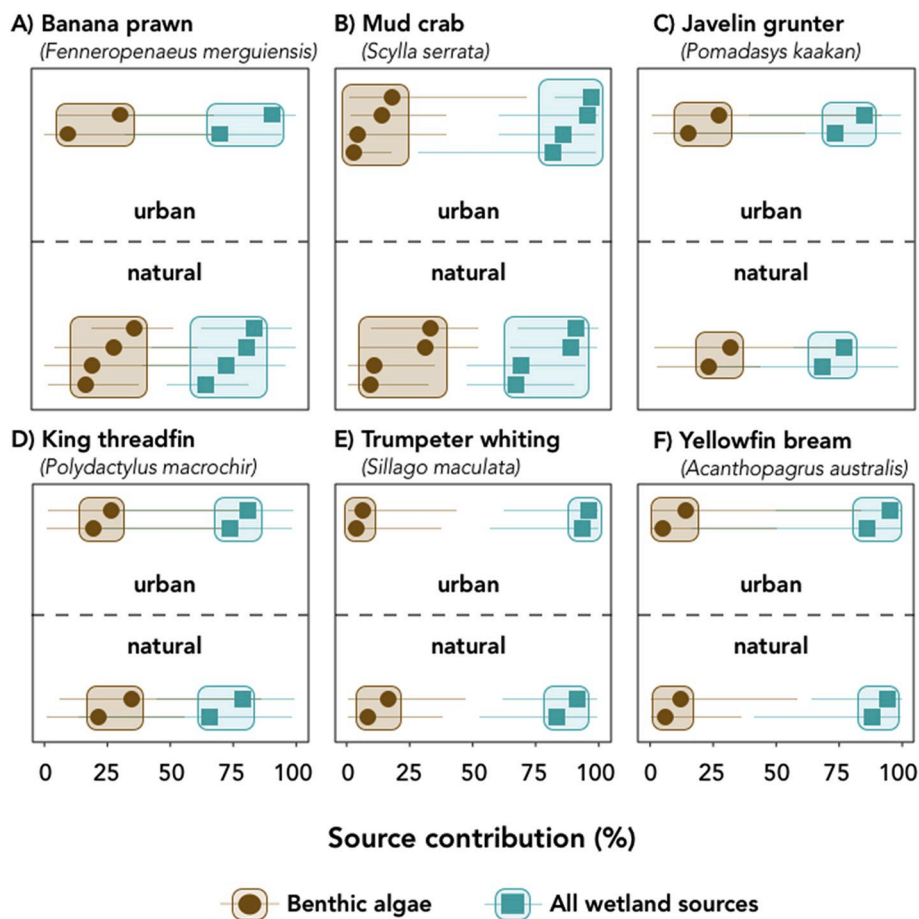


Fig. 3. Contribution (median, 95% CIs) of benthic algae and wetland sources to six fishery food webs in urban and natural locations in two regions in Central Queensland, Australia. Values for the wet and dry seasons for each species in the Bundaberg region are shown in Table 1 and in the Rockhampton region in Table 2. Colour boxes are positioned to highlight differences among sources and are not determined statistically. Replicates within boxes (the two regions, and four combinations of location/season for mud crabs) are ordered from highest to lowest mean contribution for that source – precise details for each combination are given in Tables 1 and 2 (all wetland sources are the combined contributions of C3 wetland plants and saltmarsh grass). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

microbial loop through phytoplankton consumed by burrowing invertebrates. This exchange between pore and surface water as a result of burrowing invertebrates has been demonstrated for both saltmarsh and mangrove-dominated estuaries (Santos et al., 2019; Xin et al., 2009).

We found no prominent pattern of change in source contributions between the wet and dry seasons. A single species at one region (mud crabs in the Fitzroy region) showed a change in contribution, from saltmarsh dominating in the wet season to mangrove dominating in the dry season. However, this finding was not consistent for mud crabs in the Bundaberg region, suggesting this is a region or location-specific finding (e.g. perhaps due to the varied diet of mud crabs). Previously, wet-dry seasonal differences have been shown for banana prawns and finfish in tropical north Queensland (Abrantes and Sheaves, 2008), and for finfish in subtropical Queensland (van de Merwe et al., 2016). Saltmarsh grows on the upper inter-tidal zone in Australia and is therefore less connected to estuaries through water movement from rainfall in the dry season (Saintilan and Rogers, 2013). Consequently, there should be greater opportunity for saltmarsh carbon to be transported to estuarine waters during the wet season to support fishery food webs. However, saltmarsh prey species that are likely to support fishery food webs, such as crab and gastropod larvae, spawn in great numbers during particularly high spring tidal cycles; these tidal cycles occur during both winter and summer in subtropical Australia, and thus increase the opportunity for saltmarsh carbon to be incorporated into food webs regardless of the season (Hollingsworth and Connolly, 2006; Saintilan and Mazumder, 2017). Our findings provide very little support for the influence of seasonal river flow on these lower estuarine, inshore food webs, and instead could be partly explained by tidal inundation patterns. Alternatively, wet season rainfall or flooding of saltmarsh habitat might play a significant role in providing organic material to support food webs

throughout the year. We recommend further investigation at the local scale, as seasonal differences in food webs might be location-specific, rather than species-specific.

Although we found no effect of urbanisation on fishery food webs at our study locations, the role of urbanisation in fishery food webs warrants further investigation. It is possible that urbanisation at higher levels than is found in the central Queensland region might have effects on the contribution of wetland sources to food webs. While there were measurable differences in the proportion of armoured shorelines at the study sites, the overall impact of urbanisation on wetlands could be considered at the lower end of the scale, with enough wetland habitats still thriving in proximity to the sites to support fisheries productivity. Urbanisation, defined by the proportion of artificial structures, may not be the most important measure when it comes to examining how urbanisation affects fishery food webs. Using alternatives such as proportion imperviousness of the catchment (Wang et al., 2001) and the number of point sources present in the system, may reveal stronger impacts, and this is an avenue for future fishery food web research.

Furthermore, other carbon sources could have contributed to the lack of differences found in natural and urban locations. Unidentified sources from run-off (e.g. from sugarcane farming or agricultural activities) that have similar signatures to wetland sources (e.g. C4 plant signatures such as *Sporobolus virginicus*), may be introduced into these estuarine systems, mimicking the effects of saltmarsh contribution found in natural locations. The patterns observed at our regions, could therefore be symbolic of broader-scale input at the catchment level including alternative C4 plant sources. Alternatively, if the substantial fluxes of saltmarsh carbon in the system and the fisheries species we sampled are representative of 'average whole-of-system levels', this could indicate that wetlands are contributing an even greater amount than otherwise

thought.

It is also prudent to compare our findings for each species with their expected dietary intake and movement into wetlands. For example, mud crabs showed the most variation in contribution from wetland sources, which can be attributed to their varied, omnivorous diet (Webley, 2008). Juvenile banana prawns and yellowfin bream are known to migrate with the tide into mangrove and saltmarsh habitat for feeding opportunities or protection (Mazumder et al., 2006; Vance et al., 2002) and thus a high contribution from saltmarsh would be expected for these species. The two carnivorous finfish, javelin grunter and king threadfin, feed on crustaceans and small fish along muddy or sandy estuarine environments (Abrantes and Sheaves, 2009; Motomura, 2004), and whiting are benthic carnivores feeding on crustaceans, polychaetes and molluscs, predominantly in sandy and muddy habitats (Burchmore et al., 1988). For these species, the saltmarsh contribution presumably comes from organic matter transported to the unvegetated areas via currents or detrital transport, rather than direct consumption (Table 1).

It has been shown previously that the presence of urban structures on estuary edges can alter fish abundance and diversity (Henderson et al., 2019; Kneib, 2000) and fish diets (Connolly, 2003; Waltham and Connolly, 2006), and that habitat fragmentation resulting from artificial structures can affect the resilience of key predatory fisheries (Layman et al., 2007). While we found no difference in wetland contribution between natural and urban locations, there are still significant considerations for the productivity of fisheries species whose abundance, diversity, isotopic composition or trophic position might be affected in response to the presence of urban structures, and where primary sources of productivity are threatened by habitat loss.

5. Conclusions

Coastal vegetated habitats such as mangroves, saltmarsh and seagrass all play important roles in coastal protection, carbon storage, and habitats for juvenile fish (Barbier et al., 2011; Macreadie et al., 2017). These ecosystem services are under threat from urbanisation and the loss of coastal habitats. Ultimately if primary sources of productivity are lost to urbanisation, the availability of plant matter to support food webs will be diminished and may lead to effects on fisheries productivity we are yet to fully understand. Consistently strong, species-specific results demonstrating the supporting role that saltmarsh plays, can be used to value saltmarsh habitat economically (Abrantes et al., 2019; Taylor et al., 2018). Such valuations can support initiatives for greater protection and restoration of this vulnerable and under-appreciated habitat. Management decisions need to be made to limit the ongoing development of artificial structures that replace or prevent the migration of critical coastal habitats (Schuerch et al., 2018) such as the saltmarsh grass, *Sporobolus virginicus*, particularly where this habitat is a primary source of productivity in the absence of seagrass habitat.

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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.

CRediT authorship contribution statement

Kristin I. Jinks: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Michael A. Rasheed:** Resources, Writing - review & editing, Funding acquisition. **Christopher J. Brown:** Formal analysis, Writing - review & editing, Supervision. **Andrew D. Olds:** Conceptualization, Writing - review & editing, Funding acquisition. **Thomas A. Schlacher:** Writing - review & editing, Visualization, Funding acquisition. **Marcus Sheaves:** Funding acquisition. **Paul H. York:** Resources, Writing - review & editing, Funding acquisition. **Rod M. Connolly:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2020.106719>.

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Glossary

- C3 plant*: A plant that utilises a C₃ carbon fixation pathway for photosynthesis
- C4 plant*: A plant that utilises a C₄ carbon fixation pathway for photosynthesis
- TEF (Trophic enrichment factor)*: The difference between the stable isotope signature of a consumer and the food source, based on the feeding behaviour and physiology of the consumer
- $\delta^{13}\text{C}$ or *C isotope*: Ratio of two stable isotopes of carbon, $^{13}\text{C}:^{12}\text{C}$
- $\delta^{15}\text{N}$ or *N isotope*: Ratio of two stable isotopes of nitrogen, $^{15}\text{N}:^{14}\text{N}$
- $\delta^{34}\text{S}$ or *S isotope*: Ratio of two stable isotopes of sulfur, $^{34}\text{S}:^{32}\text{S}$