Fish Biomass in Tropical Estuaries: Substantial Variation in Food Web Structure, Sources of Nutrition and Ecosystem-Supporting Processes

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Abstract Quantification of key pathways sustaining ecosystem function is critical for underpinning informed decisions on development approvals, zoning and offsets, ecosystem restoration and for meaningful environmental assessments and monitoring. To develop a more quantitative understanding of the importance and variation in food webs and nutrient flows in tropical estuaries, we investigated the spatio-temporal distribution of biomass of fish across 28 mangrove-lined estuaries in tropical Australia. We evaluated the extent to which nekton biomass in tropical estuaries responded to spatial and temporal factors and to trophic identity. Biomass was dominated by two trophic groups, planktivores and macrobenthos feeders. Contributions by other trophic groups, such as detritivores and microbenthos feeders, were more variable. Total biomass and the biomass of all major trophic groups were concentrated in downstream reaches of estuaries. The consistent concentration of biomass downstream, and spatio-temporal differences in the contributions by the different trophic groups, indicates substantial differences in food web structure, differences in the contributions from different sources of nutrition and probably unequal flow of productivity into higher levels of the food web in different parts of the estuary. In turn, this suggests substantial qualitative and quantitative differences in ecosystem-supporting processes in different estuary reaches.

Keywords Mangrove · Nekton · Penaeid · Spatial prioritisation · Restoration · Offset

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Introduction

Although their high productivity and nursery-ground values make estuaries and their associated wetlands among the most valuable ecosystems on the planet (Choi and Wang 2004; Costanza et al. 1997; Eamus et al. 2005), threats from a diversity of anthropogenic factors mean they are also among the most threatened (Duke et al. 2007; Gehrke et al. 2011; Lotze et al. 2006). Their location at the interface between land and sea is attractive for human habitation; climates are usually mild and there is ready access to both terrestrial and marine resources. Consequently, estuaries are the focus for a substantial proportion of the world's population (Vitousek et al. 1997). Additionally, their setting, as coastal inlets linked to river systems, makes them key locations for transportation hubs and the focus of rapid, large-scale development (Corn and Copeland 2010; Edgar et al. 2000). The location of estuaries also means they are vulnerable to a range of natural forces; the joint influences of rivers and the sea exposes them to impacts from climate variability, extreme events and sea level rise. This conjunction of high value and intense threats makes ensuring their continued healthy functioning an issue of primary concern if they are to continue to provide their diverse ecosystem services for future generations (Erwin 2009).

Understanding the values of estuaries and how to assess and monitor changes in value is an important element in maximising environmental outcomes in the face of developmental pressures (Grech et al. 2013; Sheaves et al. 2015). It requires information about aspects such as habitat requirements and sources and flows of productivity that provide the vital support for ecosystem and fishery productivity (Nagelkerken et al. 2015). In particular, quantitative knowledge of the significance of particular trophic pathways in sustaining ecosystem function is needed to support informed decisions on development approvals, zoning and offsets and to underpin meaningful environmental assessments and monitoring (Creighton et al. 2015). Moreover, establishing the amounts of material flowing through food webs, and how that varies over space and time, provides the vital underpinning for valuing estuarine productivity (Cowley and Whitfield 2002; Weinstein and Litvin 2016), and so is crucial to efficient spatial prioritisation (Beger et al. 2010) and effective restoration (Sheaves et al. 2014; Weinstein and Litvin 2016). Unfortunately this information is extremely limited across most of the world's tropical waters (Sheaves et al. 2014).

Studies of fish in temperate estuaries focussed on the environmental factors underlying the distribution and biomass of species (e.g. Marshall and Elliott 1998) and the relative dominance of different feeding modes (e.g. Cowley and Whitfield 2002). This has been developed with the addition of further data from multiple estuaries and the incorporation of defined fish guilds, such as estuarine species and marine migrants (Elliott et al. 2007). Zoogeographical comparisons among estuaries have also proved informative. Based on fish distributions and abundances in 190 South African estuaries, Harrison and Whitfield (2008) demonstrated that fish guilds in cool-temperate estuaries were dominated by migratory species (estuarine migrants and marine opportunists), whereas those in warm-temperate and subtropical estuaries were dominated by estuarine-dependent species. Across the same systems, Harrison and Whitfield (2012) found some zoogeographic and estuarine typology (closed vs open) effects on the biomass composition among trophic guilds, yet all estuaries were dominated by detritivores. The approach in tropical estuaries has focussed more on the interplay between variation in assemblages among estuaries and the importance of different trophic groups (Sheaves et al. 2010). Few other studies have examined the distribution of biomass of the nekton assemblage within and among estuarine systems, and hence, our understanding of food web structure remains incomplete (Abrantes et al. 2015).

As an important step in gaining a more quantitative understanding of the importance and variation in food webs and nutrient flows in tropical estuaries, we investigated the spatio-temporal distribution of biomass of fish in extensive surveys in tropical Australia. We focussed on the primary and secondary consumers (fish and nektonic crustaceans) that link primary production with higher trophic levels. We specifically evaluated: (i) the extent to which spatial and temporal factors, and trophic identity, influence the distribution of nekton biomass in tropical estuaries; (ii) how overall nekton biomass is distributed among reaches along the upstream-downstream gradient within estuaries; (iii) how the relative contributions of different trophic groups to biomass vary in space and time; and (iv) how the biomass of each major trophic group is distributed among reaches of the estuary.
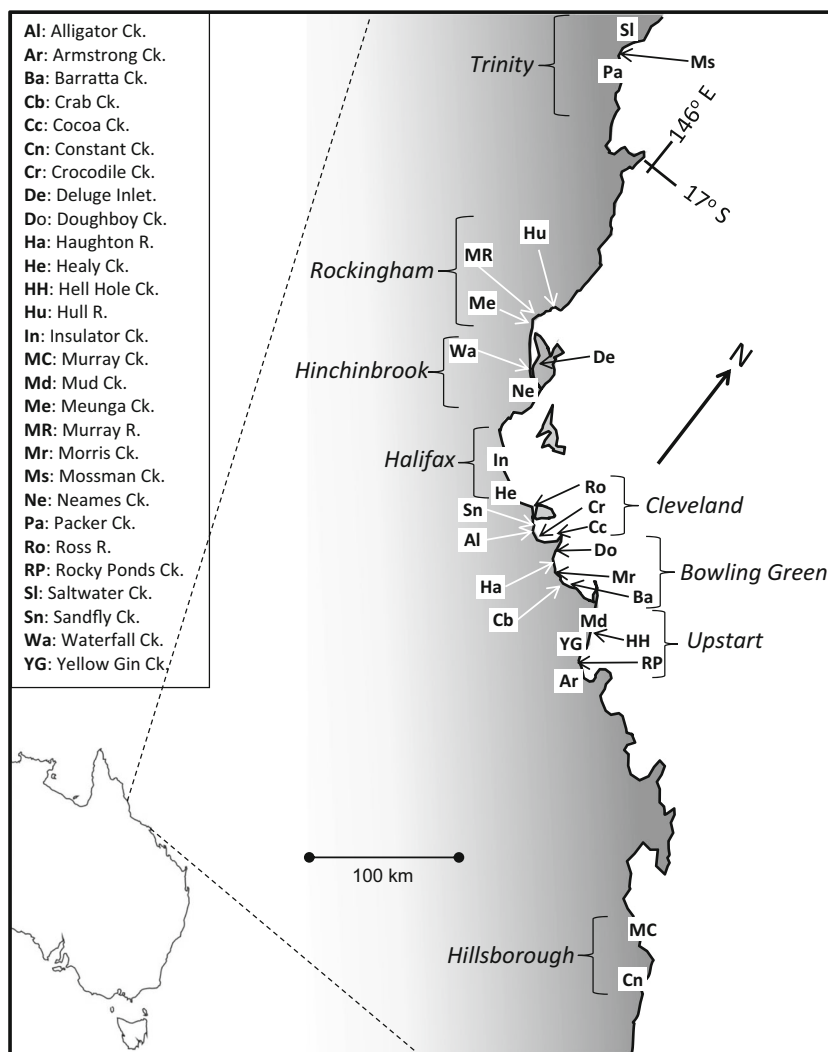
Methods

The data from two previous studies from north-eastern Australia (Sheaves and Johnston 2009; Sheaves et al. 2010) were combined to provide a data set from 28 mangrove-lined estuaries spanning over 650 km of coast (Fig. 1). Details of the estuaries and their environments, along with details of sampling designs, can be found in the studies of Sheaves and Johnston (2009) and Sheaves et al. (2010). While the previous studies reported data on numeric CPUE, the current work focusses on biomass, with cast net catch data expressed in terms of biomass per net (either for each trophic group or overall as appropriate) providing an estimate of biomass density.

The two studies used similar sampling methodologies: small mesh monofilament drawstring cast nets (2.4 m radius, 5 mm mesh) operated by a single individual from a 4.3-m dingy and deployed along the estuary banks over the lower part of the tide when fish are forced into the main channel and so accessible to the sampling gear. The use of cast nets allowed the greatest range of habitats to be sampled and provided a means of estimating the biomass in a defined volume of water (i.e. biomass density) but biased sampling towards smaller individuals. Consequently, the study focuses on small primary consumers and secondary consumers that link primary production with higher trophic levels. The bias towards smaller individuals is likely to have resulted in underrepresentation of two groups: large mobile nekton feeders (nektivores) and large detritivores (principally mugilids and *Chanos chanos*). The probable underrepresentation means that results for these trophic groups need to be treated with caution, and that, while the estimates allow spatial comparisons among estuaries and reaches, overall biomass estimates should be seen as minimum values.

In both studies, at least 15 (and as many as 30) replicate nets were collected per reach from each estuary (Sheaves and Johnston 2009; Sheaves et al. 2010). In most cases, three reaches (downstream, mid-estuary and upstream) were sampled, although this was reduced

Fig. 1 Location of the study sites along the northeast coast of tropical Australia. Estuaries are grouped into Bays indicated by *italicised text and braces*

Al: Alligator Ck.
Ar: Armstrong Ck.
Ba: Barratta Ck.
Cb: Crab Ck.
Cc: Cocoa Ck.
Cn: Constant Ck.
Cr: Crocodile Ck.
De: Deluge Inlet.
Do: Doughboy Ck.
Ha: Haughton R.
He: Healy Ck.
HH: Hell Hole Ck.
Hu: Hull R.
In: Insulator Ck.
MC: Murray Ck.
Md: Mud Ck.
Me: Meunga Ck.
MR: Murray R.
Mr: Morris Ck.
Ms: Mossman Ck.
Ne: Neames Ck.
Pa: Packer Ck.
Ro: Ross R.
RP: Rocky Ponds Ck.
Sl: Saltwater Ck.
Sn: Sandfly Ck.
Wa: Waterfall Ck.
YG: Yellow Gin Ck.

to only downstream and upstream reaches in the shorter estuaries (Online Resource Table 1). Reaches were approximately 1.5-km long, except in Healy Ck. where they were 700-m long. The downstream reach was defined as the area immediately inside the estuary mouth and the upstream reach as the area immediately downstream of the limit of navigation for the (4.3-m long) sampling dingy. Where mid-estuary samples could be collected, they were situated approximately mid-way between the downstream and upstream samples.

The two studies differed in their spatial and temporal extents. In one of the studies (Sheaves and Johnston 2009; hereafter referred to as the Spatial Study), the emphasis was on spatial patterns, with 21 estuaries sampled over 4 consecutive tidal cycles between August and October 2007. Five of the estuaries were sampled twice during the study, and the mean of those replicates are used in the present analysis. In addition, only one reach could be sampled in one of the estuaries (Victor Ck.), so this was omitted from the present analysis to leave 20 estuaries (Fig. 1). In the other study (Sheaves

et al. 2010; hereafter referred to as the Temporal study), 9 estuaries were sampled approximately monthly between November 2007 and January 2009, although inclement weather meant that not all estuaries could be sampled during all months. One estuary (Bluewater Ck.) was only long enough for a single reach so was omitted from this analysis. Two constructed estuarine lakes sampled by Sheaves et al. (2010) are not included in the present study. The final combined data set consisted of 28 estuaries (Estuaries) comprising either 2 or 3 reaches (Online Resource Table 1). To allow investigation of large-scale spatial patterns, the estuaries from both studies were grouped into "Bays" (Fig. 1), aligning with the definition of Bays in Sheaves and Johnston (2009).

Nekton were assigned to trophic groups (Online Resource Table 2) based on published literature (Baker and Sheaves 2005; Kent 2007; Salini et al. 1990; Salini et al. 1998; Wilson and Sheaves 2001). The trophic groups were Planktivore, Detritivore, Macrobenthivore, Penaeid, Microbenthivore, Herbivore, Insectivore and Nektivore (Online Resource Table 2) and were modified

from Elliott et al. (2007) to align with functional dietary categories rather than taxonomic categories. For instance, small juveniles of most macrobenthivores fed on much smaller prey (particularly microcrustaceans) than their adults so were assigned as microbenthivores. Although the group Penaeid refers to a taxonomic category, their diet comprises a mixture of organic particles and microzoobenthos, and they play different roles in

estuarine food webs to fish with similar diets (Baker and Sheaves 2005), hence our designation of this group by their taxonomic title. Nektivores were included in the general description of trophic group contribution (Figs. 2 and 3) but excluded from detailed analyses because the study focused on fish primary (herbivore and detritivore) and secondary (planktivores and others) consumers.

Fig. 2 Regression tree model of the contribution of spatial factors (Bay, Estuary and Reach), trophic groups and Trip (Temporal study only) to biomass density. *Bar graphs* indicate the relative frequency distribution of (4th root transformed) biomass density of samples forming each terminal node. *Numbers below bar graphs* are estimates of the (4th root transformed) mean biomass density for each terminal node, and *numbers in parentheses* indicate the sample size for each terminal node. **a** Spatial study. **b** Temporal study
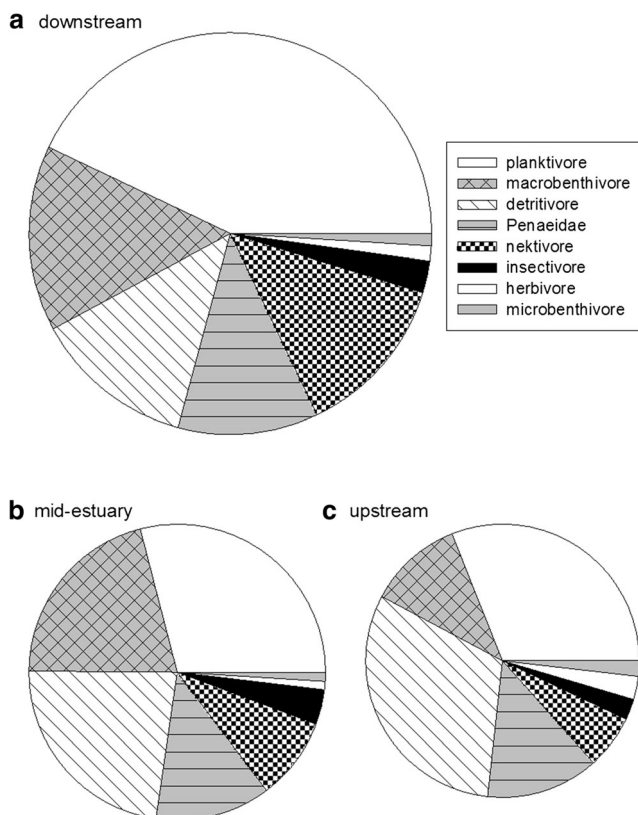
a downstream

b mid-estuary   c upstream
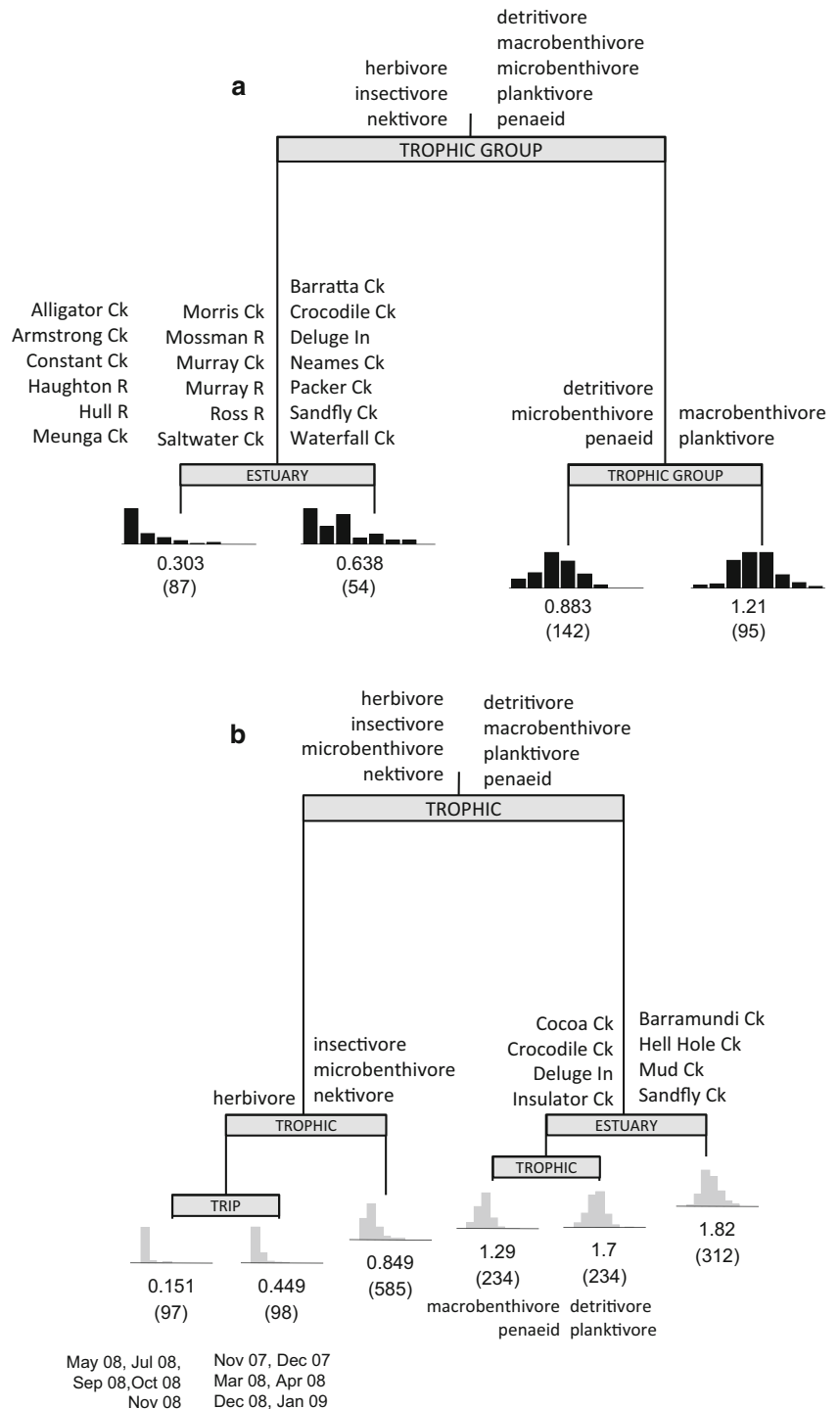
Fig. 3 Proportional contribution to biomass density for each reach, averaged across all estuaries. The relative size of each pie chart reflects overall biomass density in each reach

Data Analysis

Factors Influencing Biomass Variation

To determine the influence of spatial and temporal factors and trophic identity on overall biomass, we used Univariate Classification and Regression Trees (CARTs) to model the effects of Bay, Estuary, Reach (spatial factors) and trophic group for both studies. We also included Trip for the Temporal study. The response variable biomass density (i.e. biomass per net) was analysed separately for the two studies (Temporal and Spatial) using TreesPLUS software (De'ath and Fabricius 2000). Data were 4th root transformed prior to analysis to produce approximately symmetrical distributions of residuals and trees fitted by minimising absolute deviations, both measures aimed at limiting the biasing effect of extreme values. The tree models were fitted using 10-fold cross validation, and the final tree model selected as the 1-SE tree (the smallest tree within 1 Standard Error of the tree with the minimum cross validation error) (Breiman et al. 1984).

Distribution of Overall Biomass among Reaches

The distribution of overall biomass density among reaches was investigated graphically. Both data sets were combined,

with the mean over time for each estuary reach used to represent average biomass density.

Spatial and Temporal Variation in Contribution of Trophic Groups to Biomass

We used Multivariate Classification and Regression Trees (mCART) (De'ath 2002) to investigate the influence of spatial and temporal factors on the contributions by different trophic groups, analysing data from the two studies separately. Because substantial differences were detected in total biomass among estuaries, the data were row standardised to adjust for absolute differences in biomass among estuaries and reaches, allowing analyses to focus on differences in relative contribution of trophic groups. This produced dependent variable sets representing the relative contributions of the different trophic groups to biomass density for each reach. Predictor variables were Bay, Estuary and Reach for both studies, with the addition of Trip for the Temporal study. mCART analysis was conducted using TreesPLUS software paralleling the approach used above for univariate CARTs. Data were again 4th root transformed to produce approximately symmetrical distributions of residuals.

Reach-Specific Distribution of Individual Trophic Groups

The reach-specific concentration of trophic group biomass was assessed with a pairwise comparison of biomass density between downstream and upstream reaches using paired *t* tests separately for the two studies, with data 4th root transformed to improve homogeneity of variance. Because shorter estuaries were only divided into upstream and downstream reaches (Online Resource Table 1), data from the mid-estuary reach was omitted from this analysis to allow comparisons among all estuaries studied. While the pairwise approach affords overall comparison of upstream-downstream distributions of individual trophic groups, it does not allow spatial or temporal modifiers to be assessed. To do this, we again employed univariate CARTs as described above for each trophic group separately, for the two studies.

Results

The study included 121 identifiable fish taxa (resolved to species level except in the case of some Gobiidae and for juveniles too small for species identification) and 5 species of penaeids (Online Resource Table 3).

Factors Influencing Biomass Variation

CART modelling of the contributions of spatial factors and trophic groups to overall biomass density indicated that

trophic identity had the strongest influence on overall biomass in both the Spatial (Fig. 2a) and Temporal study (Fig. 2b). Planktivores, detritivores, penaeids and macrobenthivores made the largest contributions to biomass across both studies (occurring in the high density right branches of both trees Figs. 2a, b), while microbenthivores only provided substantial contributions in the Spatial study (Fig. 2a). Only a small proportion of the biomass was comprised of herbivores, insectivores and nektivores in either study. Of the high biomass groups, planktivores and macrobenthivores were particularly important in the Spatial study and planktivores and detritivores in the Temporal study.

Despite the strong influence of trophic group, the variables Location (Estuary) and Trip produced subsidiary tree splits, indicating variability in the biomass contributed by different trophic groups among estuaries and/or through time. The Estuary splits comprised a haphazard combination of estuaries from different Bays (Fig. 2a) reflecting the absence of Bay splits, indicating a lack of similarity among estuaries within Bays.

Distribution of Overall Biomass among Reaches

Across the whole data set, overall biomass density was greatest downstream and lowest upstream (Fig. 3). Four trophic groups,
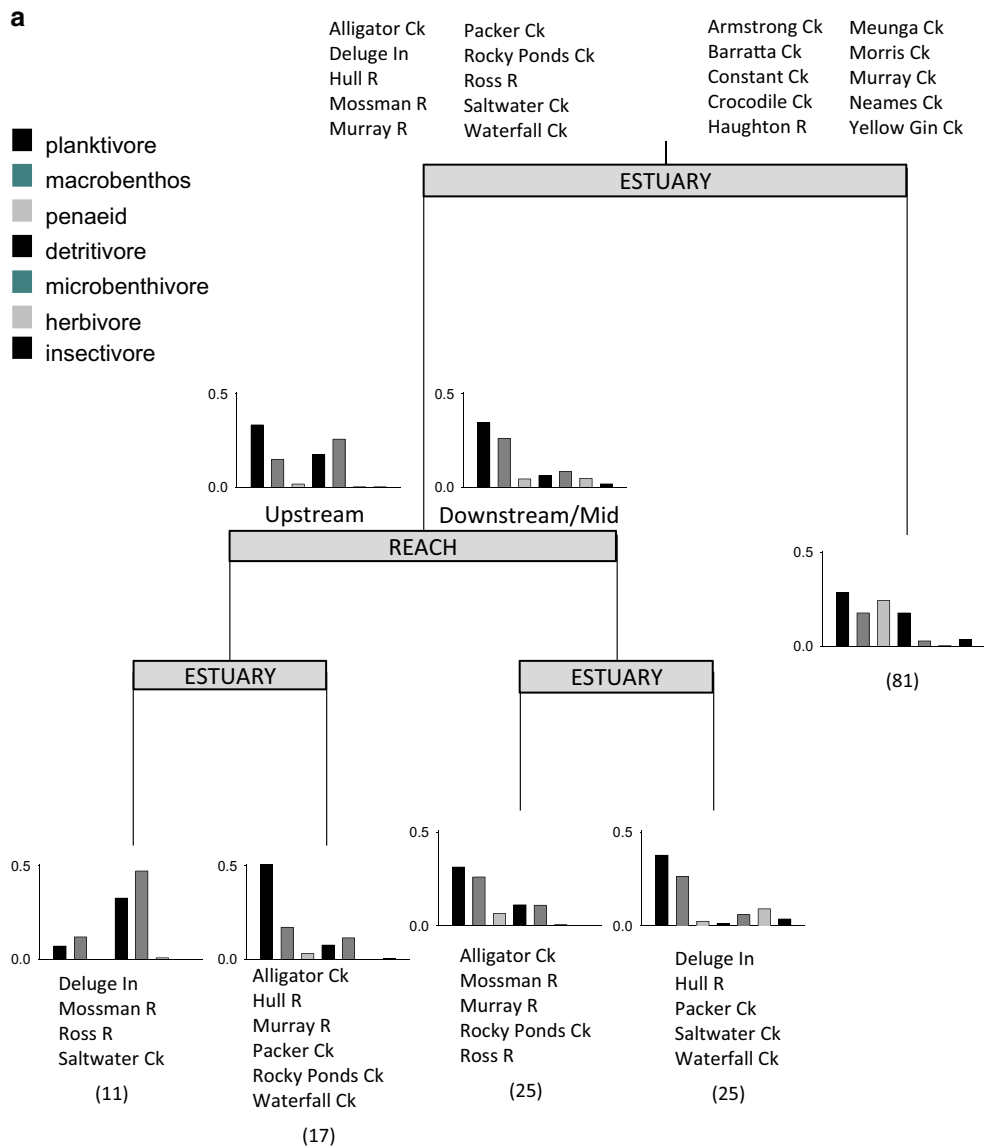
Fig. 4 Multivariate regression tree models of the influence of spatial (Bay, Location and Reach) and temporal (Trip) factors on the relative contribution to (4th root transformed; data row standardised to adjust for absolute differences in biomass among estuaries and reaches) biomass density of different trophic groups. **a** Data from the Spatial study (i.e. spatial factors only); **b** data from the Temporal study (i.e. spatial and temporal factors). *Numbers in parentheses below bar graphs* indicate the sample size for each terminal node. *Bar graphs* adjacent to nodes or below terminal nodes are the relative contribution of each trophic group to the overall biomass density. The trophic groups listed in the legend from *top to bottom* correspond to the bars from *left to right* in each bar graph
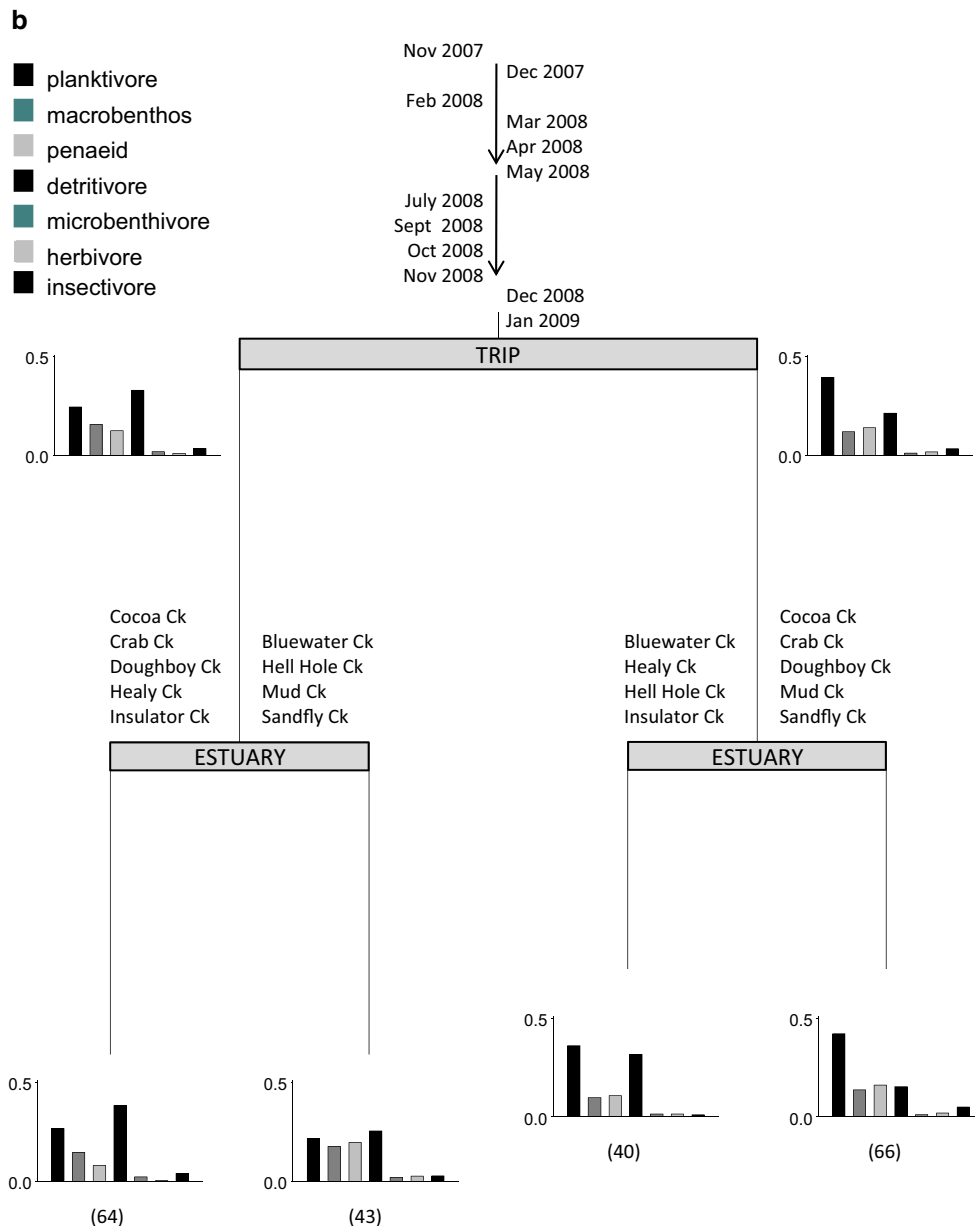
Fig. 4 (continued)

planktivores, macrobenthivores, penaeids and detritivores, made major contributions to overall biomass density, while contributions from nektivores were intermediate and other groups were consistently low (<3 %). Planktivores contributed the greatest proportion of biomass in all reaches, with the contribution declining from downstream to upstream, while detritivores showed the reverse pattern with the highest contributions in upstream reaches and lowest downstream (Fig. 3).

Spatial and Temporal Variation in Contribution of Trophic Groups to Biomass

Estuary identity, for some estuaries Reach, influenced the proportional contributions of the different trophic groups to

biomass in each of the studies (Fig. 4). The biomass composition was similar among reaches in half the estuaries in the Spatial study (right branch of primary split in Fig. 4a), with planktivores, detritivores, macrobenthivores and penaeids dominant throughout these estuaries. In the other ten estuaries, trophic composition varied substantially among reaches. In those estuaries, contributions by planktivores and macrobenthivores were high, and detritivores low in Downstream and Mid reaches, while contributions in Upstream reaches were dominated by planktivores and microbenthivores, with greatly increased detritivore but reduced macrobenthivore contributions. Microbenthivores made particularly large contributions in Upstream reaches of four estuaries (Deluge, Mossman, Ross and Saltwater). The

contributions of penaeids were small for the same four Upstream reaches but were substantial in other reaches across both studies. Overall, groupings of Estuaries in the Spatial study (Fig. 4a) appeared to be haphazard, with no indication of large-scale spatial groupings (e.g. Bays); rather, each Location group comprised estuaries from across the study area.

While planktivores and detritivores, and to a lesser extent macrobenthivores and penaeids, dominated biomass across the Temporal study (Fig. 4b), there were changes in the relative contributions of these groups over space and time. A primary temporal change was a function of a shift in dominance from detritivores in what was largely a 'late dry season' group (November 2007 and July to November 2008 plus February 2008) to planktivores in the 'wet season' group (December 2007, March to May 2008, December 2008, January 2009). Patterns of relative biomass density differed spatially for both seasonal groups, with Cocoa, Crab, Doughboy, Mud and Sandfly Creeks having particularly low detritivores biomass densities among the *wet season* samples, and Bluewater, Hell Hole, Mud and Sandfly Creeks having similar planktivore, macrobenthivore, penaeid and detritivore contributions among the *late dry season* samples.

Reach-Specific Distribution of Individual Trophic Groups

There was significantly greater biomass per net (i.e. higher biomass density) in samples from Downstream than from Upstream reaches of estuaries across both studies (Table 1). Planktivores and macrobenthivores mirrored this in both studies, while microbenthivores and penaeids showed significantly higher biomass density in downstream reaches only in the Temporal study. Detritivores and insectivores showed more even distributions of biomass between reaches in both studies. Despite total biomass density, and the biomass density of several trophic groups being significantly higher downstream than upstream, CART modelling (Table 2) shows this general distribution pattern was often

Table 1 Paired t tests comparing mean biomass density (4th root transformed) between downstream and upstream reaches. Positive t values indicate higher means downstream

	Spatial study			Temporal study		
	t	df	p	t	df	p
Total biomass	3.552	19	0.002	4.036	7	0.005
Planktivore	3.074	19	0.006	3.42	7	0.011
Detritivores	-0.745	19	0.465	-1.137	7	0.293
Macrobenthivore	3.4	19	0.003	2.547	7	0.038
Penaeids	2.016	19	0.058	4.052	7	0.005
Microbenthivore	0.342	19	0.736	5.43	7	0.001
Insectivore	0.186	19	0.854	1.078	7	0.317

Table 2 Results of CART analyses of downstream-upstream distribution of fish biomass in (a) the 20 estuaries from the Spatial study and (b) the 8 estuaries of the Temporal study. Where the overall reach effect is modified depending on estuary or trip, Reach Bias (the proportion of total biomass found within one reach: strong >0.8, moderate 0.7–0.8, weak <0.7) is displayed. For each instance of Reach Bias, the % of estuaries showing bias and the direction of bias are shown.

a) Spatial	Primary reach effect	Modifier of reach effect	Details of modified reach effect		
			Strong bias	Mod. Bias	Weak bias
Total biomass	DS > US	No modifiers			
Planktivore	DS > US	Estuary	60 % DS > US		40 % US > DS
Detritivore	no effects				
Macrobenthivore	DS > US	Estuary	30 % DS > US	30 % DS > US	40 % US > DS
Penaeids	No effects				
Microbenthivore	No effects				
Insectivore	No effects				

b) Temporal	Primary reach effect	Primary modifier of reach effect	Details of modified reach effect			Tertiary modifier of reach effect	Details of modified reach effect		
			Strong bias	Mod. Bias	Weak bias		Mod. Bias	Weak bias
Total biomass	(DS > US)	Estuary	50 % DS > US	64 % DS > US	36 % DS > US			
Planktivore	(DS > US)	Estuary		50 % DS > US				
Detritivore	No effects							
Macrobenthivore	(DS > US)	Trip		58 % DS > US	42 % US > DS	*Trip* split of moderate bias group	50 % DS > US	50 % US > DS
Penaeids	(DS > US)	No modifiers						
Microbenthivore	(DS > US)	Trip	67 % DS > US		33 % DS > US	*Estuary* split of weak bias group	36 % US > DS	64 % DS > US
Insectivore	No effects							

DS downstream, *US* upstream

modified by spatial and, in some cases, by temporal factors. In the Spatial data set (Table 2a), the models indicate the consistent downstream bias for Total biomass across estuaries, but this Reach bias varied among estuaries for planktivores and macrobenthivores. Reach bias was considered strong if >0.8 of total biomass was found in one reach, intermediate if 0.7–0.8 and weak if <0.7 of total biomass was concentrated in one reach. The overall reach bias, with planktivore biomass concentrated in downstream reaches, varied among estuaries; 60 % of estuaries showed a strong downstream bias with 90 % of the biomass in the downstream reach, while the remaining 40 % of estuaries showed a weak upstream bias with a little over 60 % of biomass upstream (Table 2a). Similarly, in 30 % of estuaries macrobenthivores showed a strong Downstream > Upstream bias, 30 % a moderate Downstream > Upstream bias and 40 % a weak Upstream > Downstream bias. For the Temporal study (Table 2b), all estuaries showed a moderate or weak Downstream > Upstream bias in biomass with no temporal effects. The situation was similar for microbenthivores, with all estuaries displaying a strong or weak Downstream > Upstream bias. Planktivores and macrobenthivores showed both spatial and temporal modification of their downstream Reach biases. Planktivores showed strong (50 % of Estuaries) to moderate (50 % of Estuaries) Downstream > Upstream biases across all estuaries, but the bias was weak during 50 % of Trips for the "moderate Estuary bias" group. Macrobenthivores showed moderate Downstream > Upstream bias for 58 % of Trips but weak Upstream > Downstream biases for the remaining Trips. However, the 'weak Trip bias' effect was averaged over a group of 36 % of Estuaries showing a moderate Upstream > Downstream bias and a group of 64 % of Estuaries showing a weak Downstream > Upstream bias. For penaeids, the Downstream > Upstream bias was not modified by Estuary or Trip. Herbivores showed a clear Downstream > Upstream bias but were not included in formal analyses because of the high number of samples from which they were absent (Spatial study: 55 % of downstream and 95 % of upstream samples; Temporal study: 52 % of downstream and 63 % of upstream samples).

Neither detritivores nor insectivores showed any consistent Downstream versus Upstream bias in either study. For insectivores, this may be due to a lack of power to detect differences because of their low overall biomass contribution (Fig. 3); however, this is not the case for detritivores, which contributed a major proportion of biomass, particularly in Upstream reaches.

Discussion

Biomass density was dominated across estuaries, among reaches and over time by planktivores and macrobenthivores, with more variable contributions by detritivores, penaeids and microbenthivores. Total biomass and the biomass of all major trophic groups were concentrated in downstream reaches, but the relative contributions from the different trophic groups varied over space and time. The consistent concentration of biomass downstream and spatio-temporal differences in the contributions by the different trophic groups indicates substantial differences in food web structure, differences in the contributions from different sources of nutrition and probably unequal flow of productivity into higher levels of the food web in different parts of the estuary. Taken together, these suggest significant functional differences among estuary reaches, with qualitative and quantitative differences in ecosystem-supporting processes. Beyond the implications for ecological functioning, there are substantial consequences for the prioritisation for development, conservation and restoration efforts, for strategic decisions on zoning and offsets and for the way that assessment and monitoring need to be conducted.

Among-Estuaries Variation in Biomass Density

Trophic identity had the strongest influence on overall biomass density, greater than spatial or temporal factors. Planktivores, detritivores, penaeids and macrobenthivores dominated biomass across both studies, while microbenthivores only provided substantial contributions in the estuaries of the Spatial study. Despite this consistent pattern of dominance, there were clear spatio-temporal differences in trophic composition, indicating food web structure varied from place to place and over time. Seasonal shifts related to a switch from high planktivore and penaeid biomass density during the wet season, to high macrobenthivore and detritivore biomass density by the end of the dry season, aligning with known seasonal shifts in sources of productivity (Abrantes and Sheaves 2010).

There was considerable estuary-to-estuary variation in the contributions of different trophic groups, but this tended to be haphazard rather than reflecting similarities between adjacent estuaries or latitudinal shifts in the contributions of different trophic groups. Similarly, while the magnitude of biomass density varied over time and among estuaries, the variability again appeared haphazard rather than relating to large scale spatial structure. This contrasts with what might be expected if estuary-to-estuary differences were influenced by estuary proximity (i.e. groupings of adjacent estuaries) or latitude. This among-estuary variation aligns with previous studies in the region (Sheaves and Johnston 2009) and internationally (e.g. Blaber and Milton 1990; Harrison 2005) that found similar low levels of estuary-to-estuary similarity in assemblage composition and abundance. Sheaves and Johnston (2009) found that at least some of the among-estuary variability could be explained by a range of what they termed 'estuary-scale ecological variables' such as intertidal area, tidal range and mangrove area. Sheaves (2016) further explored the drivers of among-estuary variability and suggested that much of it

could be explained by the interaction of these estuary-scale variables, spatially variable supply of larvae from offshore spawning sites and estuary-to-estuary differences in resident species population dynamics.

Reach-Specific Differences in Food Web Structure and Function

In contrast to the haphazard pattern of estuary-to-estuary differences, there were substantial systematic changes in the contributions of trophic groups among reaches in many of the estuaries, with upstream reaches usually having lower relative contributions from macrobenthivores, prawns and herbivores. These changes in contribution were matched by a consistent reach-specific pattern of substantially higher biomass densities Downstream than Upstream for all major trophic groups except detritivores and insectivores. Variability in channel width within reaches, among reaches and among estuaries, the large changes in water volume over the tidal cycle and the fact that the densities of many species are greater along banks than in mid-stream habitats (Sheaves and Johnston 2008), make it difficult to convert these biomass density data to estimates of total biomass or standing stock per reach. However, the estuaries across the study area are much larger downstream than upstream (the ratio of the main channel width of downstream: mid estuary: upstream reaches is approximately 6:3:1, with a similar ratio of low tide depths among reaches; Sheaves unpublished data). This means there is a much greater area of habitat and probably an order of magnitude greater biomass downstream than upstream.

The Downstream concentration of the biomass of groups like macrobenthivores and planktivores, that are important drivers of food web dynamics (Baker and Sheaves 2005; Prado et al. 2013), and the contrast in the pattern for detritivores compared to other trophic groups, strongly suggests that different food chains dominate in different parts of estuary. These three groups represent major food web pathways with energy and nutrients channelled upwards via: (i) phytoplankton productivity (planktivores), (ii) the integration of organic material into food chains by invertebrate benthos (macrobenthivores) and (iii) the direct conversion on detrital material into fish biomass (detritivores). Some caution are necessary in interpreting the pattern of detritivores biomass; the use of cast nets may have biased the data because of the potential to underrepresent larger mobile detritivores such large mugilids. However, this potential bias does not appear to have been important because the lack of downstream bias in detritivores biomass accords with data from gill netting and isolation fish-to-extinction experiments conducted by Blaber et al. (1989) in other northern Australian estuaries that should not have suffered from this potential bias.

The observed changes in the dominance of these pathways have far reaching implications for the relative importance of major ecological processes in different areas of tropical estuaries. The extent and nature of these differences indicate not only changes in food web structure, but also consistent differences in contributions by different sources of nutrition (primary producers) in different parts of the estuary. This adds up to the likelihood of functional differences among reaches, with changes in the importance of different trophic pathways and basal sources of nutrition. In turn, this suggests that the different reaches are the sites for qualitatively and quantitatively different ecosystem-supporting processes, an idea parallel to the Functional Process Zones of Thorp et al. (2006) for riverine ecosystems.

Spatio-temporal changes in food web structure are common (Baker et al. 2013; Bergamino et al. 2011), although the extent to which food webs are impacted by changes in trophic composition appears to be site- and situation-specific (Claudino et al. 2013). Where spatio-temporal change and variation in food web structure do occur, there are far reaching consequences for ecosystem processes, such as the alternation of biotic drivers (e.g. shifts between competition and predation depending on the location- or time-specific nature and size of predator assemblages (Orrock et al. 2008)), changes in the effects of trophic subsidies (Kostecki et al. 2010), changes in spatio-temporal coupling and interaction of resources (Marczak et al. 2007), or changes in the overall trophic transfer efficiencies (Jennings et al. 2002). These variations in ecosystem process often result in changes in community dynamics (Bergamino et al. 2011; Polis and Strong 1996) that can be important in maintaining biodiversity (Pasquaud et al. 2010) and promoting ecosystem resilience (Elliott and Quintino 2007). At the same time, variations in food web structure can require adaptation of feeding strategies to changing food availability (Olin et al. 2012) and optimisation of available food resources (Elliott and Quintino 2007).

The Role of Biomass in Food Web Understanding

The need to include biomass dynamics in food webs has long been understood (Polis 1999) but often seems to be overlooked in an era of stable isotope analysis-dominated food web studies. Concentrating on biomass leads to food web models (e.g. Fig. 5) with a very different emphasis to webs derived from stable isotope analysis (e.g. Abrantes and Sheaves 2009). At the most basic level, considering biomass focuses on feeding groups rather than species, which are generally the foci of stable isotope-based food webs. The focus on feeding groups and their biomasses means the emphasis is on biomass pools and magnitudes of flow rather than on sources of productivity (Walters et al. 2008); in contrast, stable isotope analysis provides information about sources of nutrition but provides limited information on the relative strengths of the different carbon pathways (e.g. which species mediate transfers and which particular pathways are conduits for the major

flows of carbon and nutrients) or which pathways are most important to ecosystem function. The biomass-based food web for this study (Fig. 5) emphasises the importance of planktivores and macrobenthivores, particularly in downstream parts of these tropical estuaries—information that greatly enhances the value of isotope based food webs. For example, including biomass flows to the isotope-based food web in Fig. 7 of Abrantes and Sheaves (2009) for Deluge Inlet, one of the study estuaries, would substantially expand the relevance of the isotope work in that study by quantifying the magnitude of production/energy flowing through each of the pathways in the foodweb.

The food web depicted in Fig. 5 also shows how large the gaps in our understanding of the trophic functioning of tropical estuaries are. For instance, although the present study provides some detail for fish consumer groups, and we have some idea of ultimate sources from stable isotope analysis (e.g. Abrantes and Sheaves 2009) and of the intermediate links from dietary studies (e.g. Baker and Sheaves 2005), there is no real understanding of the importance of individual invertebrate trophic groups or

species that mediate the flow of nutrients to higher tropic levels (Antonio et al. 2010). As a consequence, there is no understanding of the importance of many linking pathways—hence the depiction of sources and invertebrate trophic levels with equal size boxes and linkages with dashed lines in Fig. 5 to emphasise these knowledge gaps.

Integrating biomass, diet and stable isotope studies is critical for understanding food webs. Isotope studies provide information about the presence of flows, but not magnitudes, diets delineate specific linkages but not magnitudes (Baker et al. 2014); biomass adds this critical item of knowledge needed to quantify the importance of particular pathways and trophic interactions in supporting ecosystem function. An example of the importance of this complementary information can be seen in the dashed line dividing the planktivore boxes in Fig. 5; depicted this way to include the understanding from Abrantes and Sheaves (2009) that there are two isotopically distinct planktivore groups in Australia's tropical estuaries. One of the groups has a depleted δ^{13}C signature, apparently indicating feeding on 'estuarine'
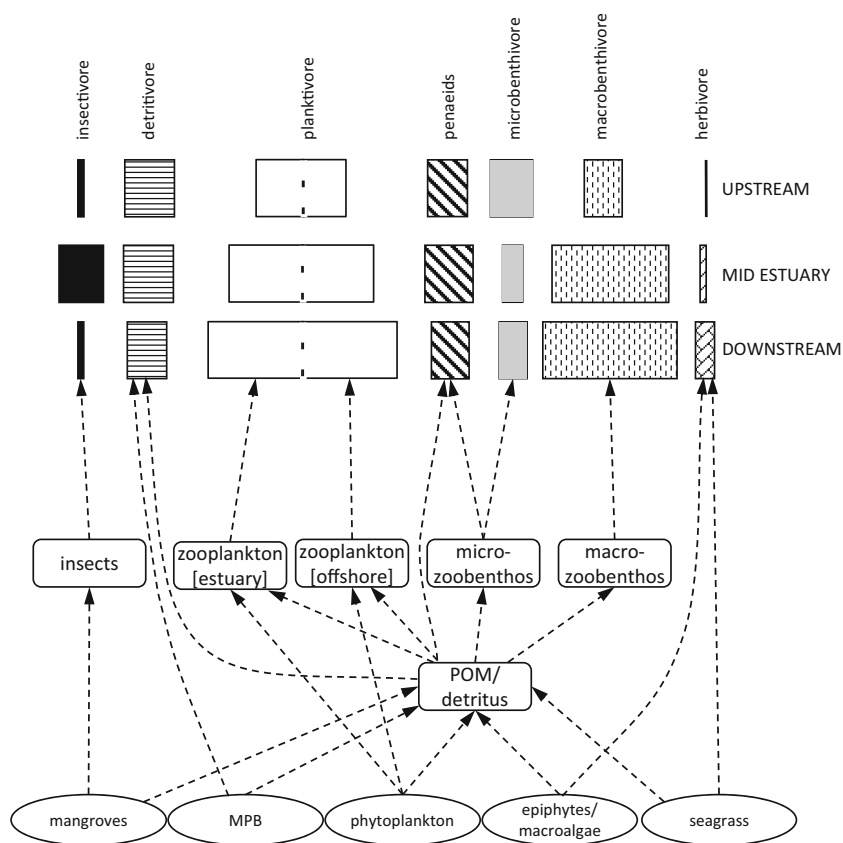

Fig. 5 A general food web based on biomass for tropical eastern Australian estuaries. *Box widths* for the trophic groups show the relative biomasses in each reach based on averages from across the study. NOTE: this is an 'average' food web for all the estuaries in the Spatial study with no attempt made to depict spatial differences. Assumed trophic linkages feeding in to the nekton trophic groups are depicted in the lower parts of the figures based on published literature; primarily Abrantes and Sheaves (2009) for the sources and invertebrate linkages, and Baker and Sheaves (2005) and Wilson & Sheaves (2001) for the invertebrate-fish linkages. These trophic components (rounded boxes and ellipses) are shown with equal sizes to emphasise that we have insufficient knowledge to differentiate their relative importances. *Arrows* feeding up into the nekton trophic components are *dashed* to indicate that there is insufficient knowledge of the details of the amounts flowing along each pathway or the specific organisms most responsible for transfers along the pathways

zooplankton compared with the second planktivore group that has a relatively enriched $\delta^{13}C$ signature, probably reflecting feeding on more 'marine' zooplankton. Combining approaches to gain deeper, more specific knowledge is critical given the increasing realisation of the intricacies and importance of spatio-temporal variation in food webs and nutrient flows across a variety of aquatic ecosystems (e.g. Bergamino et al. 2013; Burghart et al. 2013; Claudino et al. 2013).

Implications for Conservation and Management

The current study provides new ecological detail needed to support strategic decisions about the siting of development activities, the prioritisation of areas for conservation, the imposition of zoning, the location and nature of environmental offsets and the nature of ecosystem repair and remediation actions (e.g. Coles et al. 2015; Grech et al. 2013; Weinstein and Litvin 2016). The substantial within-estuary differences in the nature of food web support and the variation in productivity underlined by spatial change in biomass density make it clear that such management actions will have different outcomes depending on the location in which they occur. For instance, management of change in downstream estuarine areas needs to take particular care to minimise impacts on planktonic food webs, while a greater focus on detritivore food webs is required in upstream areas. Similarly, fundamental differences in tropic organisation mean that remediation actions in upper estuarine areas may be inappropriate as offsets for impacts occurring in the lower estuary.

The implications of this study go beyond the provision of ecological insights. The ability of the simple cast netting approach to produce estimates of biomass per unit area provides a new way to estimate the relative value of different estuary components. Outside of better studied areas of the world (Weinstein and Litvin 2016; Zimmerman et al. 1984), reliable quantitative estimates of biomass are uncommon. In other areas, such estimates are rare because of limited resources, the inability of many sampling approaches to provide data that relate to a defined spatial area (Baker and Minello 2011) and because few gears can be used across more than a few of the many habitats encountered in estuaries (Rozas and Minello 1997). The cast netting approach provides a simple, cost-effective alternative that provides estimates based on high replication and comparable across many estuary habitats, and so likely to be suitable to many situations (Baker and Minello 2011). Moreover, biomass relates to ecosystem productivity and directly to fisheries species. Such data is suitable for a variety of management applications that require biologically meaningful measures of value for assessment or spatial prioritisation (deciding among ecosystem repair options (e.g. Creighton et al. 2015) or evaluating different offset options (e.g. Coles et al. 2015)). They are particularly useful because they relate to values that are readily recognised by decision makers and understood by end-users (Dutra et al. 2015).

The current study does not provide all the detail necessary to completely remedy the deficiencies in current understanding; however, it does provide new knowledge of the extent of spatial variation in the flow of productivity that can provide

Table 3 Future research directions; needs and examples of studies

Need	Examples
Understand the details and generality of differences in trophic support in different estuary reaches	• Studies aimed at validating the results of the current study at more extensive spatial scales, and under different physical scenarios (e.g. climates, tides, system types, system sizes) • Collecting the detailed stable isotope, dietary and biomass data needed for reliable Ecopath modelling
Understanding the nature of sources of trophic support	• Spatio-temporally explicit, linked stable isotope, dietary and biomass studies to determine the extent to which nutrition of plankton-based food webs is derived from: ◦ Phytoplankton vs. particulate organic carbon; ◦ Allochthonous vs. autochthonous sources ◦ Inwelling vs. outwelling
Understand connectivity in the context of spatially- and temporally-specific sources of food web support	• Linking food web understanding to knowledge of life-history habitat utilisation and, within that, to knowledge of short term feeding migrations (tidal or day-to-day)
Understand the implications of spatial differences in food webs and trophic support for estuary repair and remediation	• Relate spatial patterns in food web structure and sources of carbon to areas already lost and to patterns of human development of estuaries
Understand temporal variation in food web support and the extent to which remediation needs to addresses alternation of supporting resources	• Long-term and multi-scale studies of the dynamics of food web support in different reaches
Developing assessments and monitoring programs that take account of spatio-temporal changes in food web structure and function	• Developing assessments programs, baseline studies and monitoring plans to incorporate and measure differences in the nature of ecosystem support in different reaches and over time

the impetus and direction for further work information (e.g. Table 3). Such studies should not be conducted in isolation because their values depend on the quality of complementary information. For instance, the value of understanding spatio-temporal variation in food web support is greatly diminished if the life-history utilisation of habitats or intra-mosaic dynamics are poorly resolved (Nagelkerken et al. 2015). It is also critical that they are supported by assessment and monitoring approaches able to provide sensitive detection of change (Teal and Weinstein 2002).

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