

Seascape-scale trophic links for fish on inshore coral reefs

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Received: 1 January 2014 / Accepted: 25 July 2014 / Published online: 12 August 2014
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Abstract It is increasingly accepted that coastal habitats such as inshore coral reefs do not function in isolation but rather as part of a larger habitat network. In the Caribbean, trophic subsidies from habitats adjacent to coral reefs support the diet of reef fishes, but it is not known whether similar trophic links occur on reefs in the Indo-Pacific. Here, we test whether reef fishes in inshore coral, mangrove, and seagrass habitats are supported by trophic links. We used carbon stable isotopes and mathematical mixing models to determine the minimum proportion of resources from mangrove or seagrass habitats in the diet of five fish species from coral reefs at varying distances (0–2,200 m) from these habitats in Moreton Bay, Queensland, eastern Australia. Of the fish species that are more abundant on reefs near to mangroves, *Lutjanus russelli* and *Acanthopagrus australis* showed no minimum use of diet sources from mangrove habitat. *Siganus fuscescens* utilized a

minimum of 25–44 % mangrove sources and this contribution increased with the proximity of reefs to mangroves ($R^2 = 0.91$). Seagrass or reef flat sources contributed a minimum of 14–78 % to the diet of *Diagramma labiosum*, a species found in higher abundance on reefs near seagrass beds, but variation in diet among reefs was unrelated to seascape structure. Seagrass or reef flat sources also contributed a minimum of 8–55 % to a fish species found only on reefs (*Pseudolabrus guentheri*), indicating that detrital subsidies from these habitats may subsidize fish diet on reefs. These results suggest that carbon sources from multiple habitats contribute to the functioning of inshore coral reef ecosystems and that trophic connectivity between reefs and mangroves may enhance production of a functionally important herbivore.

Keywords Stable isotope · Connectivity · Ecosystem function · Mangrove · Seagrass · Herbivore

Communicated by Ecology Editor Dr. Alastair Harborne

Electronic supplementary material The online version of this article (doi:10.1007/s00338-014-1196-4) contains supplementary material, which is available to authorized users.

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Introduction

Connectivity among habitats is a focal concept in ecology and an important consideration in contemporary conservation planning (Beger et al. 2010; Nagelkerken et al. 2013). Habitat connectivity refers to the way landscape structure may facilitate or obstruct a range of ecological processes and ecosystem functions, such as carbon fluxes, organism movement and dispersal, breeding, and resource use (Crooks and Sanjayan 2006). High connectivity can also enhance ecosystem resilience (Cumming 2011) or the adaptive capacity and ability of ecosystems to recover from disturbance (Gunderson 2000). This is due to the functional effects of mobile organisms on key ecological processes, such as grazing (McNaughton 1985; Olds et al. 2012a),

predation (Fortin et al. 2005; Andrews and Harvey 2013), and propagule dispersal (Hougnier et al. 2006; Viana et al. 2012).

Cross-habitat subsidies (i.e., trophic links) support production in many ecosystems (Polis et al. 2004), and their functional importance often depends on the structure of the landscape or seascape (Massol et al. 2011; Hyndes et al. 2014). Inshore coral reefs are a useful model system for exploring the influence of seascape connectivity on such trophic links due to their frequent proximity to mangrove forests and seagrass beds. While reef, seagrass, and mangrove habitats are highly productive in their own right, their functioning is enhanced where seascape connectivity facilitates the exchange of carbon and organisms among habitats (Sheaves 2009; Nagelkerken et al. 2013). For example, tropical seagrass beds provide significant carbon subsidies to adjacent habitats through ontogenetic movement and daily migration of fishes, and detrital-based transport processes (Heck et al. 2008).

Mangroves support fish biomass on coral reefs in both the Caribbean and the Indo-Pacific by providing shelter and food to these species as juveniles (e.g., Mumby and Hastings 2008; Kimirei et al. 2013). The role of mangroves and seagrass beds as juvenile nurseries for reef fishes is one mechanism for carbon movement between coastal habitats and coral reefs (Dorenbosch et al. 2005; McMahon et al. 2012).

Most studies of the transfer of carbon subsidies from seagrass beds and mangroves to the diet of fish on coral reefs have been done in the Caribbean (Berkström et al. 2012). Caribbean seagrass beds are linked to inshore coral reefs via the nocturnal feeding migrations of coral reef fishes (Eggleston et al. 1998; Nagelkerken et al. 2000, 2008; Peterson et al. 2013). Reefs closer to seagrass beds facilitate access to additional diet resources for reef fishes, while both habitats potentially benefit from nutrients available in fish excretions (Meyer and Schultz 1985; Burkepile et al. 2013; Layman et al. 2013). Although some of the most abundant and functionally important fishes in coral reef ecosystems, including herbivores (Igulu et al. 2013) and juvenile lutjanids (Sheaves and Molony 2000; McMahon et al. 2011), rely more heavily on dietary items from mangroves than species in other feeding guilds, this relationship has only been identified for fish collected from habitats other than coral reefs. Finally, the transfer of detritus from seagrass and mangrove habitats may support invertebrates on inshore coral reefs (Granek et al. 2009; Lai et al. 2013), but whether this subsidizes the diet of reef fishes remains unexplored.

The juveniles and subadults of numerous species of reef fishes (including harvested species, reef-herbivores, and apex predators) are found in mangroves and seagrass beds in the Indo-Pacific region (Sheaves 2009; Unsworth and

Cullen 2010). As in the Caribbean Sea (reviewed by Grober-Dunsmore et al. 2009; Boström et al. 2011), the density of adult fish on inshore coral reefs is positively influenced by connectivity with adjacent seagrass (e.g., Dorenbosch et al. 2005; Unsworth et al. 2008; Campbell et al. 2011; Olds et al. 2014) and mangrove habitats (e.g., Nagelkerken 2007; Berkström et al. 2012; Olds et al. 2013).

While mechanisms for carbon transfer through ontogenetic movement have been supported (McMahon et al. 2011; Kimirei et al. 2013), no studies have investigated the importance of carbon sources from non-reef habitats in the diet of fishes on inshore coral reefs in the Indo-Pacific. In addition, the contribution of carbon transfer to the production of reef fishes in the Indo-Pacific may differ from the Caribbean due to differences in the magnitude of tidal exchange between the two regions (Krumme 2009; Sheaves 2009). Inshore habitats in the Indo-Pacific are macrotidal, meaning that they are only accessible during high tide, which could limit the degree of trophic transfer by fish movement in comparison with those which are constantly inundated in the Caribbean. On the other hand, tidal currents are known to transport carbon from habitats such as mangroves to adjacent waters (Guest et al. 2006). It is important, therefore, to clarify whether processes observed in the Caribbean can be generalized across latitudes and tidal regimes to maximize the effectiveness of seascape management in the Indo-Pacific region.

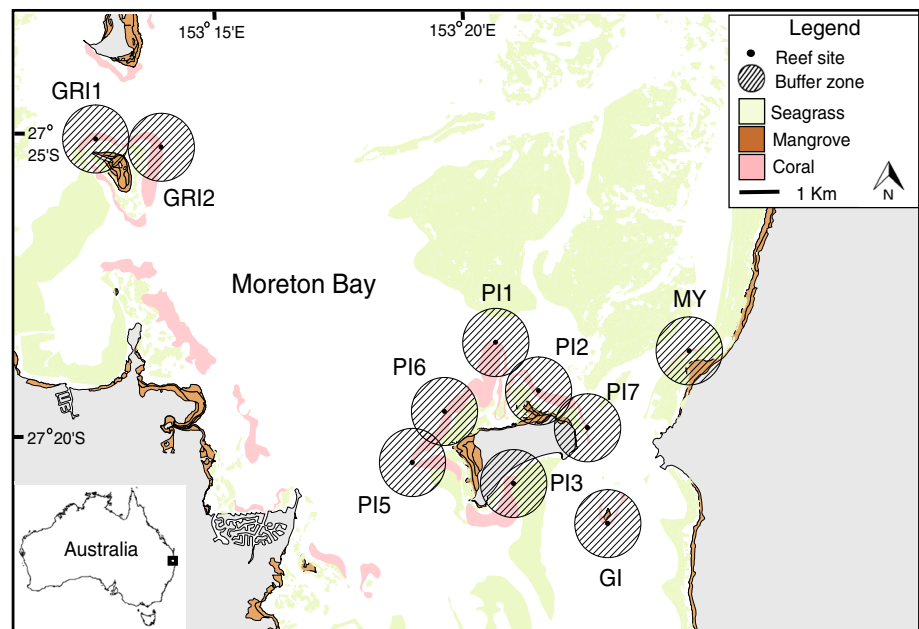
The goal of this study was to investigate whether fish on inshore coral reefs in the Indo-Pacific utilize food sources from adjacent seagrass and mangrove habitats. We tested the hypothesis that the contribution of sources from seagrass and mangroves to the diet of fish on inshore reefs would be greater on reefs nearer to each habitat. We expected that increased connectivity between coral reefs and seagrass or mangrove habitats would facilitate trophic transfer from these habitats to the diet of fish on the reef, either through fish moving off the reef to feed or via the water borne transport of organic material to reefs. We tested the hypothesis by using stable carbon isotope analysis to characterize the proportion of non-reef sources in the diet of five reef fishes collected from reefs at varying distances to mangrove and seagrass habitats.

Materials and methods

Study location

The study was done in Moreton Bay, a semi-enclosed, subtropical embayment in southeast Queensland, Australia (27°S, 153°E; 1,582 km²). Moreton Bay has a semi-diurnal tidal range of ~1.7 m, so intertidal areas including

Fig. 1 Geographic location of reefs sampled for fish in Moreton Bay, Queensland, Australia. Hashed circles indicate the 1,000-m buffer zones surrounding each reef that were used to calculate seascape metrics



fringing mangroves, seagrass beds, and reef flats are inundated only intermittently during high tide. Fishes were collected from ten coral reefs along a gradient of isolation (0–2,200 m) from adjacent fringing mangrove and seagrass habitats (Fig. 1). Habitat connectivity and area (Electronic Supplementary Materials, ESM Table 1) were characterized within a mean daily home range that is typical of these fishes (<1,000 m; Sheaves 1993; Verweij and Nagelkerken 2007; Butcher et al. 2010; Fox and Bellwood 2011) for seagrass, reef, and mangrove habitats at each study site using benthic habitat maps for Moreton Bay and ArcGIS (ESRI ArcGlobe 2010).

Study species

Five species of common reef fishes were collected from reefs to examine whether their diet was supported by carbon sources from alternate habitats. Three species (*Siganus fuscescens*, *Lutjanus russelli*, and *Acanthopagrus australis*) were selected because they are more abundant on reefs near to mangroves than on those further away (67–80, 118–146 and 86–98 % for the three species, respectively; Olds et al. 2012c). *Diagramma labiosum* was selected because variation in its abundance is best explained by the proximity of reefs to seagrass (Olds et al. 2012b). *Pseudolabrus guentheri*, which shows strong site attachment (Talbot et al. 1978) was also collected to test for the detrital transfer of carbon from mangroves or seagrass to reefs.

Fish diets were characterized from the literature to help interpret isotope results. *Siganus fuscescens* is a roving herbivore that consumes fleshy macroalgae, and although it prefers rhodophytes (Pillans et al. 2004), it will exploit the most abundant macroalgal sources available at a particular

location (Debenay et al. 2011). The remaining fish species are zoobenthivores. In particular, *A. australis* is an opportunistic omnivore, preferring to consume decapod crustaceans, bivalves, polychaetes, and some algae (Hadwen et al. 2007). *Diagramma labiosum* feeds mainly on benthic invertebrates such as crustaceans, annelids, and some small fishes (Salini et al. 1994; Sommer et al. 1996). *Pseudolabrus guentheri* feeds primarily on small benthic crustaceans (Westneat 2001), while *L. russelli* feeds on penaeid and brachyuran crustaceans, molluscs, and small fish (Salini et al. 1990). We did not collect planktivorous or solely piscivorous fishes that might utilize transient diet sources that would not reflect the carbon value of the feeding habitat of interest.

Data collection

Fishes collected from reefs (Table 1) were euthanized, measured (SL \pm 1 mm), and dissected to remove a sample of liver tissue. Liver tissue was used for stable isotope analysis rather than muscle tissue as it best reflects recent diet (\sim 20 d; Buchheister and Latour 2010). This allowed us to reduce the likelihood of variability in isotope values associated with seasonal changes in diet sources or spawning migrations. Further, although fish size varied among individuals, reduced tissue turnover times in smaller fish was not considered a problem given our interest was only in short term diet source use. A subset of five liver samples from each species was lipid extracted to account for variation in the lipid content among individuals (Fry 2002). Evaluation of these samples showed that the lipid corrections developed by Fry (2002) could be applied to the reef fish sampled and lipid-corrected carbon isotope values are reported here (Table 1).

Table 1 Minimum proportion of diet from mangrove (% Mg) or seagrass/reef flat (% Sg) sources, $\delta^{13}\text{C}$ mean, standard deviation (SD), total number (N), and range of standard lengths (SL) of each fish species collected from each of ten reefs in Moreton Bay (see Fig. 1 for locality information)

Species	Location	GI	GRI1	GRI2	MY	PI1	PI2	PI3	PI5	PI6	PI7
<i>Siganus fuscescens</i>	% Mg/Sg (min)	44/0	–	31/0	34/0	28/0	–	25/0	30/0	–	39/0
	Mean $\delta^{13}\text{C}$	–18.1	–	–18.2	–17.0	–16.5	–	–16.1	–17.4	–	–16.8
	SD	1.4	–	1.2	0.5	0.2	–	2.7	1.0	–	0.7
	N	5	–	5	3	3	–	5	5	–	5
	SL (cm)	11–17	–	12–20	10–11	10–12	–	11–17	11–16	–	7–14
<i>Acanthopagrus australis</i>	% Mg/Sg (min)	0/0	0/0	0/0	0/0	0/0	0/0	0/11	0/0	0/18	0/3
	Mean $\delta^{13}\text{C}$	–15.5	–16.3	–16.5	–16.0	–14.9	–15.6	–13.4	–16.0	–14.1	–15.0
	SD	1.3	1.3	1.0	2.9	1.7	1.2	1.9	1.6	0.8	0.9
	N	5	5	5	5	5	5	5	5	5	5
	SL (cm)	23–27	23–29	24–27	21–26	24–27	21–26	24–30	22–29	22–28	22–28
<i>Lutjanus russelli</i>	% Mg/Sg (min)	0/29	–	–	–	0/49	0/35	0/35	–	0/42	0/36
	Mean $\delta^{13}\text{C}$	–14.4	–	–	–	–11.9	–12.4	–11.7	–	–12.9	–12.5
	SD	0.1	–	–	–	1.1	1.5	1.8	–	3.0	1.7
	N	3	–	–	–	5	5	5	–	5	5
	SL (cm)	17–18	–	–	–	17–21	17	18–19	–	18–20	17–20
<i>Diagramma labiosum</i>	% Mg/Sg (min)	0/72	–	0/14	0/24	0/35	0/41	0/17	0/30	0/78	0/16
	Mean $\delta^{13}\text{C}$	–12.8	–	–15.0	–14.2	–12.6	–12.1	–13.0	–13.0	–11.2	–14.0
	SD	0.8	–	0.6	1.4	0.5	0.4	0.4	0.7	0.3	0.9
	N	5	–	5	5	5	5	5	5	5	5
	SL (cm)	24–46	–	30–41	29–40	33–39	31–38	23–37	28–37	31–38	33–51
<i>Pseudolabrus guentheri</i>	% Mg/Sg (min)	0/14	0/33	0/8	–	0/25	0/32	0/15	0/30	0/55	–
	Mean $\delta^{13}\text{C}$	–15.0	–13.5	–15.4	–	–13.1	–12.5	–13.1	–12.9	–12.3	–
	SD	1.1	1.0	1.0	–	0.8	2.1	0.6	0.5	1.4	–
	N	4	5	4	–	5	3	4	5	4	–
	SL (cm)	10–13	16–18	16–18	–	15–17	12–14	12–16	15–17	15–18	–

Dash indicates fish were unavailable from a particular reef

Three replicates of potential macroinvertebrate and plant diet sources of fish were collected from each reef and the nearest reef flat, mangrove, and seagrass habitat. Plant samples were cleaned in filtered seawater, and any epifauna were removed. Muscle tissue was dissected from invertebrates. All samples were dried to constant weight at 60 °C, ground, and placed in tin capsules. Samples were analyzed for stable carbon isotopes ($\delta^{13}\text{C}$) on a Sercon Hydra 20–22, Sercon Europa EA-GSL mass spectrometer. Isotopic ratios are expressed in delta notation according to the formula: ^{13}C (in ‰) = $1,000 * (\delta^{13}\text{C}:^{12}\text{C}_{\text{sample}} / ^{13}\text{C}:^{12}\text{C}_{\text{standard}}) - 1,000$. The standard is Vienna PeeDee Belemnite (Coplen 1995).

Data analysis

With several possible diet sources for each fish and only one tracer ($\delta^{13}\text{C}$), it was not possible to calculate a unique contribution from each source. Values of $\delta^{15}\text{N}$ were not included in this analysis because we were most interested in the carbon contribution of seagrass and mangrove habitats to reef fishes.

We considered mixing models that calculated the mean as well as maximum and minimum carbon contributions for each habitat type and present here the minimum source contributions from mangrove and seagrass habitats. In mixing models, maximum diet contributions give a potential value, while minimum contributions represent a more conservative but reliable value (Fry 2013). The diversity of potential dietary items available to consumers was taken into account (ESM Table 2) before narrowing choices to two sources for the percentage-minimum source contribution calculations based on prior knowledge of fish diets.

The particular carbon sources used in a mixing model determine the proportion each habitat contributes to consumer diet, and using alternative carbon sources can modify the perceived contributions. Therefore, mixing model results should be interpreted as best estimates, rather than exact contributions to consumer diet. Calculations were estimated using two-source mixing models in IsoError (Phillips and Gregg 2001), which incorporates the variability in carbon values for both sources and mixtures into the source

proportion estimate (ESM Table 5). Each model included a carbon source from the habitat of interest (i.e., mangrove or seagrass), the mixed sample (i.e., fish tissue), and the reef source with the closest $\delta^{13}\text{C}$ value to the mixture. If mixtures fell between two sources that did not include the habitat of interest, the minimum contribution to fish diet from this habitat was considered to be zero. Thus, for example, if a fish had a -15‰ value that could be explained by consumption of -10‰ seagrass invertebrates and -20‰ consumption of plankton-feeding invertebrates, then there is no necessary contribution of -27‰ mangrove sources, and the minimum mangrove contribution would be 0‰ .

Plant sources were used to estimate habitat contributions for the herbivorous fish (*S. fuscescens*), while benthic invertebrate sources were used for zoobenthivorous fish (ESM Table 3 and 4). Mean $\delta^{13}\text{C}$ values (\pm SE) of potential food items from habitats at each site were used as source contributors to the mean $\delta^{13}\text{C}$ value of fish species at each reef. Dietary fractionations ($\Delta\delta^{13}\text{C} = \text{consumer } \delta^{13}\text{C} - \text{diet source } \delta^{13}\text{C}$) were accounted for in the herbivore mixing model by adding 1.9‰ to plant diet source $\delta^{13}\text{C}$ values, a figure based on fractionation estimated for another species of siganid (Igulu et al. 2013). In zoobenthivore models, a factor of 0.4‰ was added to source values of invertebrate prey to reflect fractionation typical of aquatic organisms with mixed protein diets (McCutchan et al. 2003). Fractionation factors can vary among fish due to diet choice and metabolic rates, so we tested the sensitivity of our results to the assumed $\Delta\delta^{13}\text{C}$ for each mixing model within ranges typical of coral reef fishes ($0\text{--}3\text{‰}$; Wyatt et al. 2010; ESM Figs. 1–3).

In the herbivore model, the minimum mangrove contribution was estimated for *S. fuscescens* using mangrove leaf (*Avicennia marina*) and reef macroalgae (*Lobophora variegata*) values. Although *L. variegata* (-12.1 to -15.4‰) is less palatable than some other algae, it was the only species available at all reefs sampled and had similar carbon values to other common algae found in Moreton Bay, including *Sargassum* spp. (-14.1 to -16.3‰) and *Dictyota* spp. (-12.7 to -15.8‰ ; Black and Bender 1976; Fry et al. 1982). All three algae have been observed to be consumed by *S. fuscescens* on coral reefs (Debenay et al. 2011). A sensitivity analysis of the results to the assumed algal isotope values at each reef was run to account for the true range of algae available to rabbitfish. The minimum contributions from mangrove habitats were of interest, and both macroalgae and mangrove leaves could contribute to the habitat signal. Isotope values of a red alga on mangrove pneumatophores (*Catenella nipae*) were similar to those of mangrove leaves but were unavailable from some locations (mean *C. nipae*; $-28.9 \pm 0.6\text{‰}$, *A. marina*; $-27.9 \pm 0.4\text{‰}$). Mangrove leaves were available from all locations, and so in the mixing models, mangrove leaves were used to represent ^{13}C -depleted carbon sources (red algae + mangroves) available in mangrove habitats.

In the zoobenthivore mixing model, invertebrates from each habitat were used as sources because they represent an integrated value for available basal carbon sources. Gastropods of the same species (*Calthotia indistincta*) were collected from seagrass and intertidal reef flat habitats, and their carbon isotope values were not significantly different (ESM Table 2), and thus, they were pooled to represent ^{13}C -enriched non-reef carbon sources. Mangrove gastropods (*Austrocochlea constricta*) and *C. indistincta* are both algal grazers. The reef gastropod (*Cronia aurantiaca*) is a carnivore; however, it represents integrated reef-based diet sources available to reef fishes as it is similar in $\delta^{13}\text{C}$ to reef macroalgae (ESM Table 3 and 4). Fish in this study feed on invertebrates from planktonic and microalgal food chains (i.e., molluscs, small shrimp, and fish) with relatively depleted carbon values ($\delta^{13}\text{C} \sim -14$ to -19‰ ; Fry et al. 1983; Rodelli et al. 1984) as well as macroalgal food chains, so we also included an invertebrate representative of planktonic reef-based sources (a bivalve, *Trichomya hirsuta*). Using the zoobenthivore model, minimum mangrove contributions were estimated for all zoobenthivorous fish using mangrove-gastropod and reef-bivalve values. Also, in the zoobenthivore model, minimum seagrass/reef flat contributions were estimated for all species using seagrass/reef flat-gastropod and reef-gastropod values (ESM Table 4).

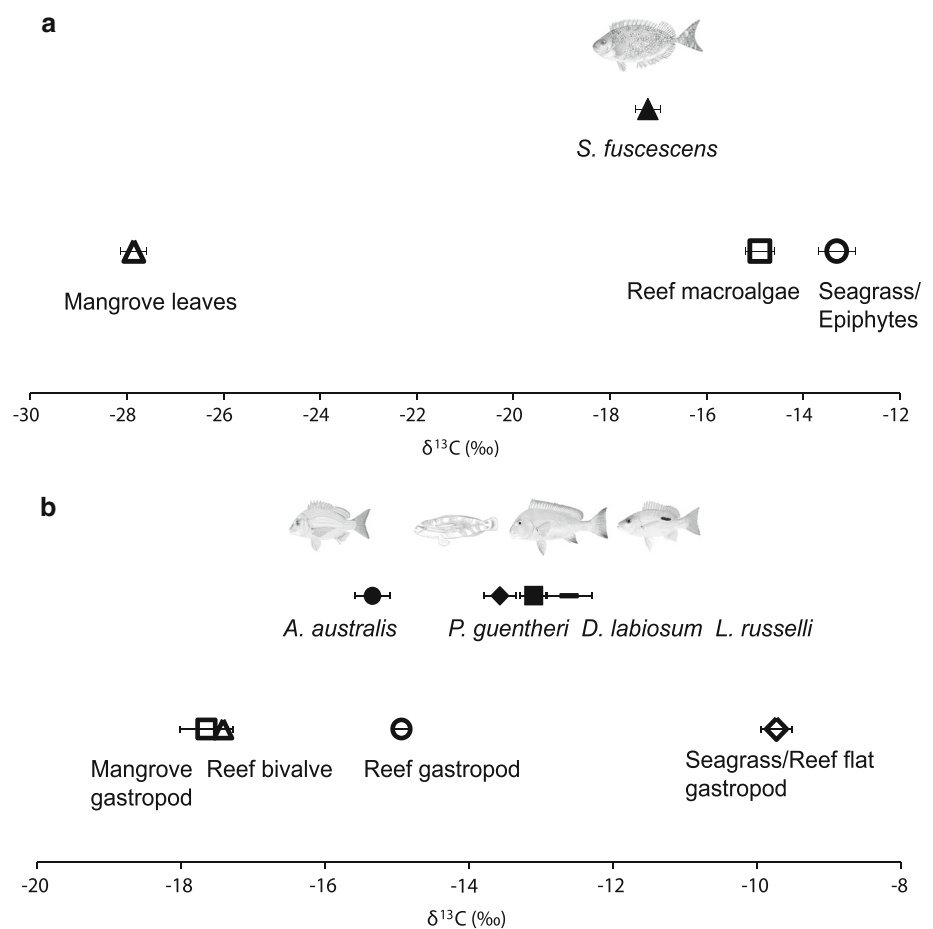
Seascape variables were first tested for normality and collinearity, and were transformed or eliminated where necessary. Variables were then ranked using a distance-based linear model (DistLM; Legendre and Anderson 1999) to test the predictive power of the seascape metric ‘isolation of reef to mangroves’ on the proportion of mangrove habitat sources and ‘proximity to seagrass’ on the proportion of seagrass habitat sources in the diet of reef fishes. Isolation refers to the edge-to-edge distance between two habitats, while proximity incorporates both isolation and the area of the neighboring habitat (ESM Table 1). These metrics were chosen based on the best predictors of patterns in local fish abundance (Olds et al. 2012b). In addition to mangrove isolation and seagrass proximity, the analysis also included variables of habitat area for mangrove, seagrass, and reef habitats as predictors of variation in fish diet. The model was fitted using stepwise selection, and the strongest model was chosen using a corrected Akaike’s information criterion (AIC_c).

Results

Liver tissue $\delta^{13}\text{C}$ for fish predicted to utilize mangrove habitat sources

Mean $\delta^{13}\text{C}$ values of *S. fuscescens* varied across reefs from -16.1 to -18.2‰ (Table 1; Fig. 2a), and the minimum contribution of mangrove habitat resources to fish diet

Fig. 2 Mean $\delta^{13}\text{C}$ liver tissue value of **a** *Siganus fuscescens* and potential plant diet sources from each habitat and **b** $\delta^{13}\text{C}$ liver tissue values for zoobenthivorous fish (*Acanthopagrus australis*, *Pseudolabrus guentheri*, *Diagramma labiosum* and *Lutjanus russelli*) and potential invertebrate prey sources including a mangrove gastropod (*Austrocochlea constricta*), reef bivalve (*Trichomya hirsuta*), reef gastropod (*Cronia aurantiaca*), and an aggregated value for a gastropod collected from intertidal seagrass and reef flat habitats (*Calthalotia indistincta*). Error bars represent ± 1 SE. Fish illustrations sourced from www.efishalbum.com



ranged from 25 ± 9 to 44 ± 5 % among reefs (Fig. 3). Of the seascape variables evaluated for their influence on fish diet, only ‘isolation of reef to mangroves’ was significant and it explained 78 % of the variability in the proportion of mangrove habitat sources in the diet of *S. fuscescens* (Table 2). Plotting residuals showed that the relationship between mangrove source use and isolation was not linear, so we fit a quadratic curve to the relationship which generated an r^2 value of 0.91 and present this curve in Fig. 3. A t test confirmed that fish received significantly higher minimum contributions from mangroves at locations within predicted fish home range in Moreton Bay (500 m; Olds et al. 2012a) than those outside this range ($p < 0.05$). The minimum contribution of seagrass and reef flat sources to rabbitfish diet was 0 % at all locations.

The minimum contribution of mangrove-based carbon was determined to be zero for all zoobenthivorous fish because reef-bivalve sources were more enriched in ^{13}C than mangrove-gastropod sources (Table 1; Fig. 2b). Mean $\delta^{13}\text{C}$ values of *A. australis* varied across reefs from -13.4 to -16.5 ‰. Minimum contributions of seagrass/reef flat resources to *A. australis* ranged from 0 to 18 ± 9 %

(Table 1). Mean $\delta^{13}\text{C}$ values of *L. russelli* varied across reefs from -11.7 to -14.4 ‰ (Table 1; Fig. 2b), and the minimum contribution of seagrass/reef flat resources to *L. russelli* ranged from 29 ± 6 to 49 ± 11 % (Table 1).

Liver tissue $\delta^{13}\text{C}$ for fish predicted to utilize seagrass habitat sources

Mean $\delta^{13}\text{C}$ values of *D. labiosum* varied across reefs from -11.2 to -15.0 ‰, and the minimum contribution of seagrass/reef flat habitat resources to fish diet ranged from 14 ± 4 to 78 ± 4 % (Table 1; Fig. 2b). The proportion of seagrass/reef flat resources in the diet of *D. labiosum* was not significantly correlated with any seascape variable (Table 2).

Liver tissue $\delta^{13}\text{C}$ for fish predicted to utilize reef habitat sources

Mean $\delta^{13}\text{C}$ values of *P. guentheri* varied across reefs from -12.3 to -15.0 ‰, and seagrass/reef flat sources contributed 8 ± 9 to 55 ± 15 % of fish diet (Table 1; Fig. 2b).

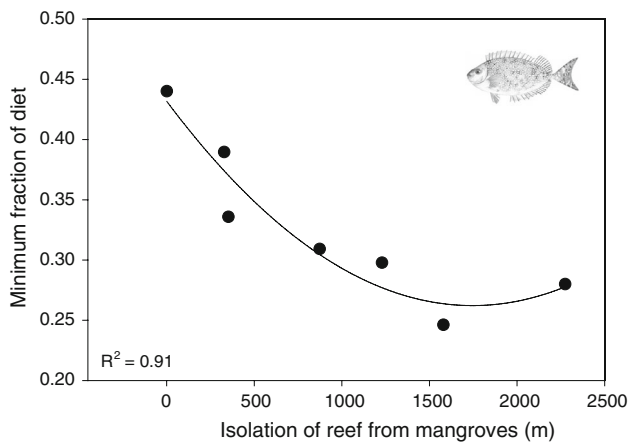


Fig. 3 Relationship between the estimated minimum proportion of sources from mangrove habitat in the diet of *Siganus fuscescens* and the distance of each reef from adjacent mangroves with line of best fit (quadratic). Fish illustration sourced from www.efishalbum.com

Table 2 Results of distance-based linear models (DISTLM) relating the proportion of mangrove habitat sources in the diet for (a) *Siganus fuscescens* and the proportion of seagrass/reef flat habitat sources for (b) *Diagramma labiosum* and (c) *Pseudolabrus guentheri* diet with seascape variables in a stepwise selection procedure based on Euclidean distance similarity

Species	Variable	F	P	Prop. ^a
(a) <i>S. fuscescens</i>	Mangrove isolation	17.59	0.00	0.78
	Reef area	5.26	0.08	–
	Mangrove area	0.25	0.67	–
	Seagrass area	1.59	0.24	–
	Seagrass proximity	0.78	0.41	–
(b) <i>D. labiosum</i>	Mangrove isolation	1.16	0.31	0.14
	Seagrass area	0.39	0.59	–
	Seagrass proximity	0.22	0.65	–
	Reef area	0.03	0.87	–
	Mangrove area	0.03	0.94	–
(c) <i>P. guentheri</i>	Mangrove area	0.68	0.41	0.10
	Reef area	0.43	0.53	–
	Mangrove isolation	0.31	0.60	–
	Seagrass area	0.20	0.65	–
	Seagrass proximity	0.25	0.59	–

Values in bold indicate $p < 0.01$

^a Proportion of explained variance

The proportion of seagrass/reef flat-derived resources in the diet of *P. guentheri* was not significantly correlated with any seascape variable (Table 2).

Model sensitivity to trophic fractionation and source pool estimates

The minimum mangrove contribution to the diet of *S. fuscescens* varied only 4 % with each 0.5 ‰ change in fractionation and became stronger with larger $\Delta^{13}\text{C}$ (ESM Fig. 1a; ESM Table 5a). Results for the minimum seagrass contribution to zoobenthivores, particularly for *L. russelli* and *P. guentheri*, however, were sensitive to our estimate for $\delta^{13}\text{C}$ fractionation, varying ~10 % with each 0.5 ‰ change in fractionation (ESM Fig. 1b-d; Table 5b-d). Sensitivity of *S. fuscescens* to the assumed algal carbon value on reefs revealed the minimum mangrove contribution to fish diet only decreased by 5 % with each 1 ‰ decrease in algal $\delta^{13}\text{C}$. When algal values were depleted by 3 ‰, mangrove contributions were near zero at sites further away from mangroves, while the largest minimum contribution at sites within the 500 m home range was 27 % (ESM Fig. 2).

Discussion

Stable isotope analysis illustrated cross-habitat trophic links from mangroves, reef flats, or seagrass beds to inshore coral reefs for four common species of reef fishes in Moreton Bay. The variability in mangrove-based diet sources with habitat connectivity for *S. fuscescens* is consistent with the idea that increased connectivity facilitates the transfer of trophic subsidies from mangrove habitats (Fig. 3). As an abundant herbivore comprising 33–72 % of the biomass of roving herbivores in Moreton Bay (Olds et al. 2012b), *S. fuscescens* likely plays a key role in controlling algal growth on coral reefs (Olds et al. 2012a), which in turn may enhance reef resilience to major disturbances such as flood events (Olds et al. 2014). The trophic link for *S. fuscescens* emphasizes the importance of recognizing functionally important relationships at the ecosystem level (Mouquet et al. 2013), while the contribution of ^{13}C -enriched seagrass or reef flat sources to the remaining fish species highlights the need to take into account how trophic links are unconstrained by habitat borders.

Resources from mangrove habitats contributed a minimum of >40 % to the *S. fuscescens* diet at some reefs despite only being available to fish at high tide (about a third of the time). Variation in the amount of resources from mangrove habitats in the diet of *S. fuscescens* was most strongly related to mangrove-reef connectivity, while reef and seagrass habitat variables did not explain variation in diet. The diet of *S. fuscescens* on reefs near to fringing mangroves in Moreton Bay might, therefore, be sustained by a trophic subsidy from mangrove habitats as

hypothesized. While mangroves are an important nursery habitat for some juvenile fish, it is unlikely that the biomass of *S. fuscescens* on reefs near to mangroves is supported by this mechanism. Mangroves in Moreton Bay do not appear to act as nurseries for juvenile *S. fuscescens* (Laegdsgaard and Johnson 1995), and mangroves near reefs provide poor nursery habitat given that they are utilized by high numbers of predators (Olds et al. 2012c). Also, siganids generally recruit to seagrass beds as juveniles, only moving to reefs or other structured habitats as subadults (Mellin et al. 2007).

S. fuscescens utilized the highest proportion of mangrove-based resources on reefs <500 m from mangroves. This might reflect the importance of a home range threshold since abundances of *S. fuscescens* in Moreton Bay are also highest when mangroves are within 500 m of coral reefs (Olds et al. 2012c). The fact that fish from reefs distant to mangroves still received around 20 % contribution from mangrove habitat is surprising as we did not expect fish to be accessing mangrove resources at these reefs, although reef fishes are known to make large scale daily movements at times (Chateau and Wantiez 2009). Error analysis on the estimated carbon value of algal sources used in the herbivore mixing model revealed that while fish on reefs further away received negligible contribution from mangroves, fish on the reef nearest to mangroves still received a contribution of 27 %. Given that the mangroves are only available to fish for a limited portion of each day, this contribution is still important to consider.

Mangrove-reef proximity may be a measure of the accessibility of mangroves for *S. fuscescens*, but it may also be a proxy for numerous interacting mechanisms. Proximity between habitats reduces the energy required for a fish to access external resources (Dill 1978; Sheaves 2005) and could reduce the time spent moving across unstructured habitats between reefs and mangroves where risk of predation may be higher (Beukers and Jones 1998; Grober-Dunsmore et al. 2009). Proximity may also facilitate the tidal transfer of detrital and algal sources from mangroves to reefs (Granek et al. 2009), although this is not consistent with the negligible contribution from mangroves to the diet of the obligate reef fish (*P. guentheri*). Regardless of the mechanism, this result suggests that habitat connectivity may facilitate trophic processes.

Our conservative estimate of mangrove habitat contribution provided no evidence that mangrove sources contributed to the diets of *L. russelli* or *A. australis* despite occurring in higher abundances on reefs near to mangroves. However, as these diet proportions were minimum estimates, mangroves may still contribute to fish diet to some degree. When occurring in the mangroves, these species may utilize some carbon sources from mangrove

food webs or sources from planktonic or other food webs that are present in the mangroves but do not reflect mangrove carbon sources. For example, *L. russelli* feeds predominantly on penaeid prawns and small fish (Salini et al. 1990; Baker and Sheaves 2005), and *A. australis* consumes small fishes in mangrove-lined estuaries (Mazumder et al. 2011); both prey items occur in mangroves and might or might not be linked to mangrove-based food webs (Abrantes and Sheaves 2009; Heithaus et al. 2011).

Fringing mangroves often provide negligible contributions of carbon to primary consumers, but provide important refuges for invertebrates and juvenile reef fishes, and thus play an indirect role in supporting coral reef food webs (Kieckbusch et al. 2004). Carbon values for crabs and gastropods collected from fringing mangroves in this study were enriched in ^{13}C relative to mangrove carbon values and were closest to those of plankton and macroalga on the reef (ESM Table 2). Therefore, even if zoobenthivores were feeding in the mangroves, this would be difficult to trace using carbon isotopes. Alternatively, these species may utilize mangrove habitat for shelter rather than feeding, as some predatory fish do in the Caribbean (Verweij et al. 2006). The lack of any minimum contribution of mangrove resources in the diet of *P. guentheri*, a reef obligate fish, suggests that there is limited detrital transfer of mangrove carbon sources across habitat boundaries to fringing coral reefs and supports the idea that *S. fuscescens* exploits mangrove resources through tidal migration.

Resources from seagrass and reef flat habitats provided nearly half of the diet of *D. labiosum*, *P. guentheri*, and *L. russelli* at some reefs, revealing that these sources may contribute to ecosystem functioning on inshore coral reefs. The contribution of ^{13}C -enriched diet sources to the reef-specific species, *P. guentheri*, suggests that there may be some transfer of seagrass or reef flat-based carbon sources to inshore coral reefs. This is not surprising as seagrass carbon has been observed to fuel productivity over large scales between adjacent coastal ecosystems (Nelson et al. 2012). Invertebrates on reefs may be enriched in ^{13}C due to the assimilation of seagrass organic matter (Lai et al. 2013) or the waste products of mobile fauna that move between the two habitats (Peterson et al. 2013). However, these results should be considered less robust than those for *S. fuscescens* and *D. labiosum* given their sensitivity to the assumed degree of carbon fractionation. While *D. labiosum* and *L. russelli* may access ^{13}C -enriched sources by exploiting benthic sources in seagrass beds or intertidal reef flats during feeding migrations as other haemulids and lutjanids do in the Caribbean (Nagelkerken et al. 2000), the contribution of these sources to the diet of *P. guentheri* suggests that they may exploit benthic sources from the

coral habitat that are enriched in ^{13}C via the detrital transfer of seagrass or reef flat sources.

The contribution of ^{13}C -enriched sources to the diet of *D. labiosum* was not related to the proximity of reefs to seagrass beds as predicted, suggesting that the biomass of these species on reefs nearer to seagrass is not supported by increased accessibility to prey sources in these areas. Alternatively, the increased abundances of *D. labiosum* on reefs near to seagrass may result from greater juvenile settlement as they migrate from adjacent seagrass habitat. Seagrass beds are a preferred habitat for juvenile haemulids (Nagelkerken and Van der Velde 2004; Kwik et al. 2010). Although the utilization of ^{13}C -enriched diet sources was not related to the degree of reef-seagrass connectivity for *D. labiosum*, these sources clearly contribute an important subsidy to their diet on some reefs.

Although we expected mangroves would provide a strong contribution to fish diet based on patterns in fish abundance observed previously, carbon isotope analysis suggested that there was a moderate contribution for only one of the three species investigated. Fringing mangroves may function as a prey refuge for zoobenthivore diet sources rather than contributing to fish diet. Alternatively, fringing mangroves may serve primarily as high-tide predation refuges for adult fish. In areas where inshore reefs and fringing mangroves are well connected, the increased size of the habitat network itself may allow for higher holding capacities of reef fishes. Carbon sources from seagrass and reef flats supported three of the five species, suggesting that these habitats may make important contributions to the diet of fishes on some reefs.

The results of this study emphasize the need to manage coastal habitats at a seascape scale, taking into consideration trophic interactions among multiple habitats while also considering how these relationships vary among species and functional groups. While seagrass, reef flat, and mangrove habitats can contribute to fish diet on inshore reefs, the degree and type of contribution may vary widely among feeding guilds as well as with the degree of seascape connectivity. These productive inshore habitats face increasing fragmentation from coastal development, which could reduce the degree of trophic connectivity among them. Future ecosystem-based management will be more effective where critical trophic links are identified and prioritized for conservation.

Acknowledgments We thank D. Bezerra, C. Clarke, S. Davies, K. Davis, A. Fontes, C. Henderson, C. Huijbers, S. Lauchlan, T. Martin, P. Maxwell, R. Win, and staff at Moreton Bay Research Station for their assistance with field work and A. Budarf for comments on the manuscript. This work was funded by an Australian Research Council grant (to R.M.C. and K.A.P.) in collaboration with the Queensland Government.

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