Community structure and dietary pathways for invertebrates on intertidal coral reef flats

Jean P. Davis [a,*], Kylie A. Pitt [a], Rod M. Connolly [a], Brian Fry [b]

[a] *Australian Rivers Institute — Coast and Estuaries, and Griffith School of Environment, Griffith University, Gold Coast, Queensland 4222, Australia*
[b] *Australian Rivers Institute — Coast and Estuaries, and Griffith School of Environment, Griffith University, Nathan, Queensland 4111, Australia*

ABSTRACT

Intertidal reef flats cover extensive inshore areas of coral reef ecosystems but their contribution to coral reef food webs remains largely unknown. We measured benthic invertebrate abundance using quadrat surveys and traced sources supporting the production of three abundant invertebrates from different feeding guilds using stable isotope measurements of carbon (C) and nitrogen (N) along reef flats bordered by mangroves in Queensland, Australia. Filter feeding bivalves, detritivorous hermit crabs, and grazing gastropods were the most abundant trophic groups on the reef flat and occurred most commonly distant from the shoreward mangroves. Isotope values of bivalves did not vary among sampling positions and these animals depended on a consistent pelagic food source. Gastropods collected at the center of the reef flat had unusually enriched C isotope values compared to those at the reef edge, indicating increased contributions from autochthonous benthic food sources, probably benthic microalgae. The C isotope values of hermit crabs also varied among sampling positions, but were less consistently enriched. The N isotope values of both hermit crabs and gastropods were lower at the reef flat center and mangrove edge, suggesting a decreased reliance on pelagic sources away from reef edge positions. Grazers and detritivores on reef flats in this study depend on benthic sources with greatly enriched C isotope values; these sources are common on reef flats globally. Trophic sources on reef flats should receive greater consideration in coral reef food webs, especially given their widespread occurrence and use by mobile consumers.

© 2015 Elsevier Inc. All rights reserved.

1. Introduction

Understanding how marine habitats function as trophic networks is a growing priority in coastal ecology (Berkström et al., 2013). Movement of energy in the form of particulate or dissolved organic carbon can subsidize the growth and reproduction of organisms in adjacent habitats (Sheaves, 2009) and significantly modify food web dynamics (Polis et al., 1997; Hyndes et al., 2014). Tropical coastal environments, in particular, offer a complex array of both terrestrial and marine dietary sources to consumers. While trophic functioning in subtidal coral reef, seagrass, and mangrove habitats has been investigated in many studies (Nagelkerken, 2009; Hyndes et al., 2014), little is known about the trophic ecology of intertidal coral reef flats.

Coral reef flats are back reef habitats that usually consist of carbonate and sand substrates in shallow water and occur on many reefs globally (Yamano, 2000; Harborne, 2013). They are especially important areas for exploring food web dynamics, since they link productive habitats such as subtidal coral reefs and seagrass beds to intertidal fringing mangrove forests in some locations (Neil, 2000; Shibuno et al., 2008; Granek et al., 2009). Exclusion experiments and visual surveys show that intertidal reef flats are important foraging areas for grazing reef fish (Stephenson and Searles, 1960; Miller, 1983; Thacker et al., 2001). In addition to providing benthic algal food sources, intertidal coral rubble habitats also support highly diverse benthic invertebrate assemblages (Meesters et al., 1991; Gischler and Ginsburg, 1996; Walker et al., 2008). Carnivorous fish cross reef flats in eastern Australia during tidal migrations (Olds et al., 2012) and gut contents (Heupel and Bennett, 1998), stable isotope analyses (Davis et al., 2014) and video surveys (Fig. 1) suggest that benthic invertebrates from reef flats support the diet of these consumers. Thus, reef flat invertebrates may serve as important trophic links between primary producers and predatory fish in coral reef ecosystems.

The exchange of organic matter (OM) among coastal habitats occurs via animal movement and the waterborne transfer of dissolved (DOM) or particulate organic matter (POM) (Hyndes et al., 2014). In coastal areas stable isotope analysis is useful for quantifying energy transfer among habitats (Bouillon and Connolly, 2009; Sheaves et al., 2014). Primary producers in tropical mangrove and seagrass habitats typically have unique $\delta^{13}C$ values relative to other food sources, making it possible to trace the movement of mangrove and seagrass OM to adjacent habitats and its assimilation by consumers (Marguillier et al., 1997; Heithaus et al., 2011).

* Corresponding author.
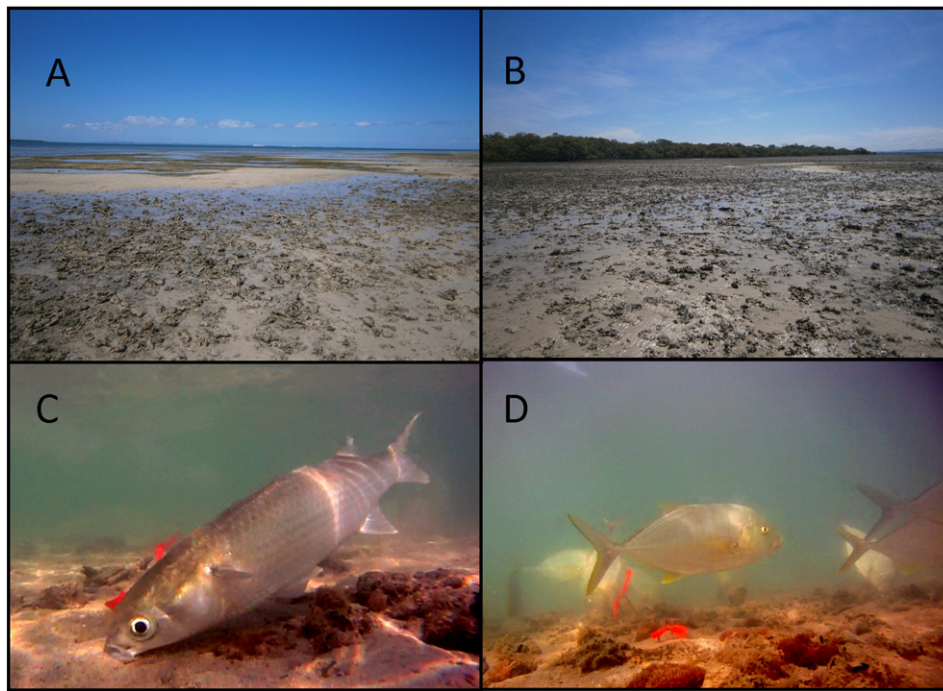*E-mail address:* jean.davis@griffithuni.edu.au (J.P. Davis).

Fig. 1. Photograph of typical coral rubble substrate on an intertidal reef flat in Moreton Bay, Queensland, facing (A) seaward towards seagrass beds and the reef crest, and (B) landward towards fringing mangroves. Images of fish foraging over reef flat habitat in Moreton Bay include; (C) sea mullet (*Mugil cephalus*) and (D) golden trevally (*Gnathanodon speciosus*).

In contrast to the broad literature on the trophic ecology of mangroves and seagrasses, studies of the primary sources of production on coral reef flats are limited to observations of feeding movements of ophiuroids (Oak and Scheibling, 2006) and an isotope study of intertidal invertebrates in the Caribbean Sea (Mallela and Harrod, 2008). Both studies suggest that primary consumers on reef flats typically depend on offshore or allochthonous sources of production that are depleted in ^{13}C. However, some grazing invertebrates in the study by Mallela and Harrod (2008) depended on food sources enriched in ^{13}C and stable isotope studies that included secondary consumers (fish) collected from reef flats suggest that primary producers are enriched in ^{13}C relative to the reef crest (Kolasinski et al., 2009; Wyatt et al., 2012a). This result is consistent with consumption of autochthonous benthic sources such as cyanobacterial mats and benthic or endolithic microalgae that are enriched in ^{13}C (Kolasinski et al., 2011; Hilting et al., 2013).

The objective of this study was to characterize the invertebrate community on intertidal reef flats and to use stable isotopes to determine the sources of production that support abundant primary consumers there. We tested 3 hypotheses: (1) organism abundances vary across positions on the reef flat (2) diets differ among species due to variation in feeding mode, and (3) diets of individual species vary across positions on the reef flat due to the availability of external detrital and pelagic foods.

2. Methods

2.1. Sampling location

Four reef flat locations were sampled in central Moreton Bay, Queensland, Australia, during the winter of 2012 (Fig. 2). Intertidal reef flats in Moreton Bay are composed of low relief coral rubble, sand and mud substrates, and extend 100 to 250 m from mangroves seaward to subtidal fringing reefs and seagrass beds. Habitat boundaries in this ecosystem are clearly defined by the mean low tide limit at the subtidal edge and the presence of mangrove pneumatophores at the landward margin. The bay is macrotidal (2 m tidal range) and reef flats and mangroves are inundated twice each day. The dominant seagrass species in Moreton Bay is *Zostera muelleri* (Alismatales: Zosteraceae),

mangroves are mainly *Avicennia marina* (Lamiales: Acanthaceae), the most common coral is *Favia speciosa* (Scleractinia: Mussidae) and the most abundant macroalgae on coral reefs is *Lobophora variegata* (Dictyotales: Dictyotaceae). No conspicuous autotrophic source including algal mats or seagrass meadows was observed on the reef flats, although small patches (<1 m^2) of seagrass were present in some locations.

2.2. Sample collection and processing

Invertebrate abundance was surveyed across three positions at each reef flat location; within ten meters of the reef edge, at the center of the reef flat, and within ten meters of the mangrove edge. Positions were separated by 50–100 m depending on the width of the reef flat. Starting at the reef edge at mean low tide, ten 1 m^2 quadrats were randomly placed along a 60 m transect laid horizontal to the shoreline. These transects were repeated at the center of the reef flat and the mangrove edge. In each quadrat, substrate type and sessile invertebrates (barnacles, oysters, mussels, sponges and live coral) were quantified as percent cover since individuals were often indistinguishable, while motile invertebrates (crabs, gastropods, sea stars, polychaetes and sea cucumbers) were counted individually. Abundances of animals were sampled on four reef flats, while isotope analyses were performed for animals from three or four of these reef flat communities depending on availability.

For isotope analysis, three feeding guilds, each represented by a single species, were chosen to reflect different producers; the grazing gastropod (*Calthalotia indistincta* (Archaeogastropoda: Trochidae)) was an indicator of algal production (Gacia et al., 2009), the suspension feeding mussel (*Trichomya hirsuta* (Mytiloida: Mytilidae)) of particulate organic matter (POM) (Price et al., 2012) and the detritivorous hermit crab (*Clibanarius taeniatus* (Decapoda: Diogenidae)) of detrital plant sources that might support productivity on the reef flat (Kunze and Anderson, 1979). While the types of producers that might contribute to the diets of each invertebrate species were known, the planktonic vs. benthic vs. mangrove origins of these sources were unknown. Each species was common, usually dominating its respective guild.

Invertebrates were collected for isotope analysis at the same locations and positions as described for surveys of abundance. At each position,
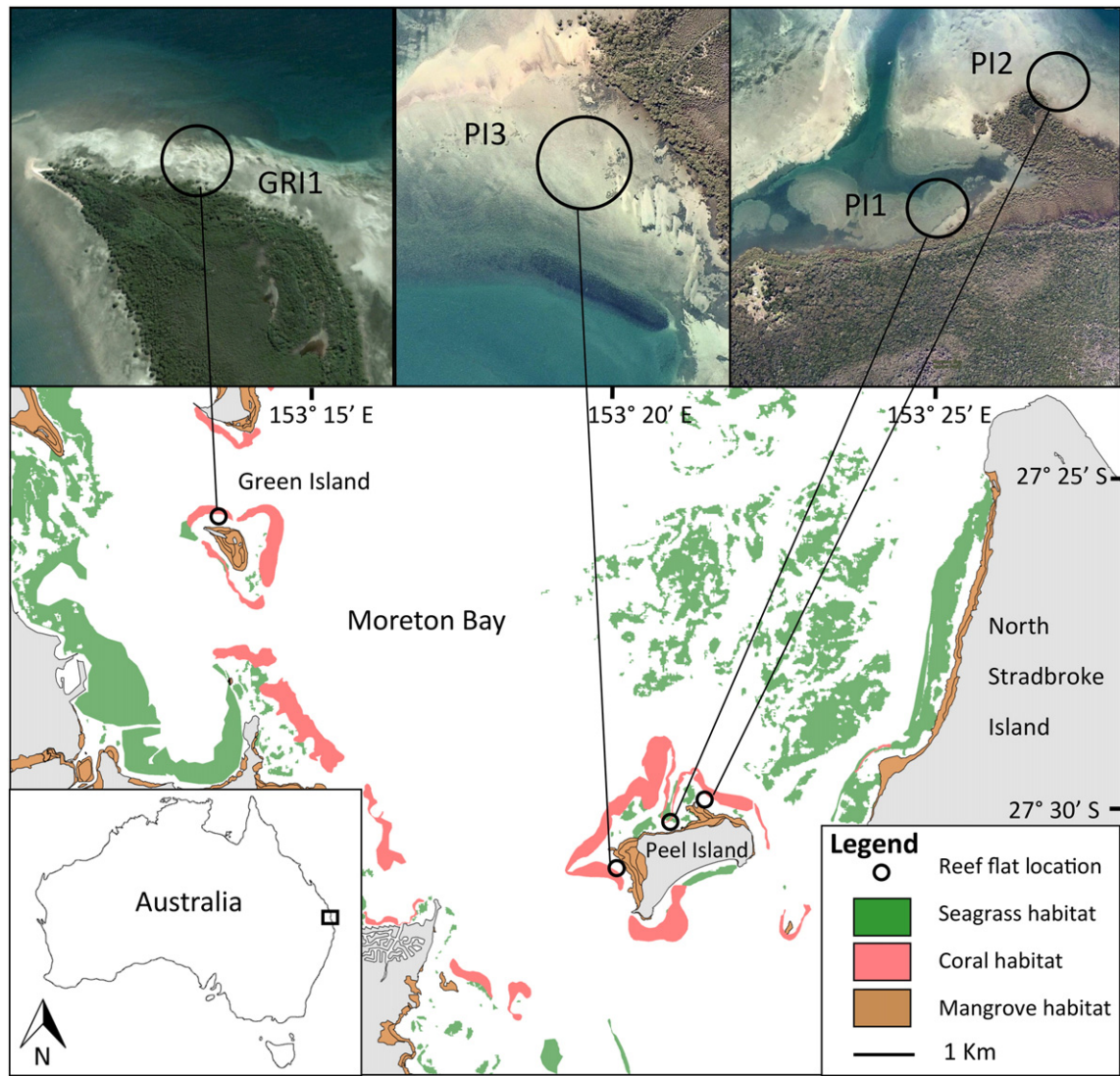
Fig. 2. Reef flat locations sampled in Moreton Bay, Queensland, Australia, and surrounding coral reef, seagrass and mangrove habitats.

samples of each species (n = 3) were collected directly adjacent to a randomly chosen point along a transect placed parallel to the shoreline. Gastropods and hermit crabs were unavailable at one location each (Table 1). Three fresh samples of dominant autotrophic sources including *L. variegata*, *Z. muelleri*, *F. speciosa* and *A. marina* were collected at the nearest point to the reef flat at each location. Because microphytobenthos

(MPB; cyanobacteria plus benthic microalgae) were in low density, the samples isolated from sediment collected from the center of the reef flat were pooled, resulting in a single sample for each location.

In-situ measurements of POM were not collected for this study due to the typically high temporal variability in this source (~4‰) (Wainright and Fry, 1994; Vizzini and Mazzola, 2003) relative to the long turnover

Table 1
δ^{13}C and δ^{15}N values (mean, SE) for a gastropod (*Calthalotia indistincta*), hermit crab (*Clibanarius taeniatus*) and mussel (*Trichomya hirsuta*) (n = 3) collected from three positions along the reef flat at each location. Dash indicates that species were unavailable from that location. GRI refers to Green Island and PI refers to Peel Island locations.

Location	GRI1		PI1		PI2		PI3	
	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N
Mussel								
Mangrove edge	−18.1 (0.2)	7.1 (0.2)	−16.4 (0.8)	5.4 (0.4)	−15.7 (0.0)	5.7 (0.4)	−17.0 (0.1)	6.5 (0.2)
Reef flat center	−18.6 (0.4)	6.8 (0.1)	−16.2 (0.3)	5.3 (0.2)	−16.8 (0.3)	6.1 (0.2)	−17.1 (0.2)	6.5 (0.0)
Reef edge	−18.0 (0.4)	6.8 (0.1)	−16.4 (0.4)	5.3 (0.4)	−17.0 (0.1)	6.2 (0.1)	−17.4 (0.1)	6.5 (0.0)
Gastropod								
Mangrove edge	−9.3 (0.2)	3.9 (0.1)	–	–	−10.1 (0.2)	3.9 (0.0)	−8.2 (0.3)	3.0 (0.1)
Reef flat center	−9.3 (0.4)	4.2 (0.2)	–		−8.8 (1.0)	4.0 (0.5)	−8.6 (0.7)	3.8 (0.2)
Reef edge	−11.5 (0.8)	4.9 (0.6)	–		−11.0 (0.3)	4.6 (0.1)	−9.6 (0.3)	4.7 (0.1)
Hermit crab								
Mangrove edge	−9.9 (0.4)	5.8 (0.2)	−10.4 (0.2)	7.6 (0.2)	−8.4 (0.2)	6.9 (0.2)	–	–
Reef flat center	−9.2 (0.1)	6.7 (0.1)	−9.6 (0.1)	7.7 (0.4)	−8.1 (0.2)	6.7 (0.3)	–	–
Reef edge	−10.9 (0.6)	8.0 (0.4)	−9.9 (0.1)	8.5 (0.3)	−11.2 (0.5)	7.9 (0.5)	–	–

time of tissues in filter feeding invertebrates (Raikow and Hamilton, 2001). Isotope values of filter feeders (mussels) collected in this study and the average POM value from the literature were considered more robust proxies. We reference a POM value typical of inshore coral reefs; -20.1 ± 1‰ $\delta^{13}C$, 5 ± 0.5‰ $\delta^{15}N$, based on Mallela and Harrod (2008) and Wyatt et al. (2013). Phytoplankton samples were not collected due to the difficulty of isolating phytoplankton from non-living POM and the spatial and temporal variability of plankton found in inshore systems (Bergamino and Richoux, 2014). Instead, we reference an average lipid-normalized value from the literature based on near-surface (<5 m depth) zooplankton collected from offshore areas in eastern Australia; -18.7 ± 0.1‰ $\delta^{13}C$, 6.5 ± 0.2‰ $\delta^{15}N$ (Couturier et al., 2013).

Macroalgae and turf algae were not visually evident on the reef flat so MPB were isolated to account for benthic microscopic sources. However, isotope results for consumers suggested that autotrophs with unusually elevated values of $\delta^{13}C$ were important diet sources. Literature on inshore coral reef autotrophs shows that cyanobacteria on reef flats have enriched carbon values (Table 2). Cyanobacteria mats are the most probable source with enriched ^{13}C on reef flat food webs because they occur frequently on reef flats worldwide (Moriarty et al., 1985; Thacker et al., 2001; Kuffner et al., 2006) and are consumed by benthic invertebrates (Cruz-Rivera and Paul, 2006). Other plant and algal foods found on reef flats such as the seagrasses *Syringodium* and *Thalassia* and the alga *Caulerpa* are similarly enriched in $\delta^{13}C$ (Fry et al., 1987; Kolasinski et al., 2011) but there is no evidence that they are abundant on reef flats in this study, or that they are important foods for consumers. In our figures, therefore, in addition to MPB we include a value for cyanobacteria (-6.5 ± 1.8‰ $\delta^{13}C$, 0.9 ± 1.9‰ $\delta^{15}N$) as averaged from all available values for cyanobacteria collected on reef flats and similar settings (Table 2). Hilting et al. (2013) have also isolated coral reef benthic microalgae with values in this range.

Muscle tissue of invertebrates was removed from shells and cleaned in deionized water. All plant material was cleaned of sediment in filtered seawater and any epiphytes removed. MPB were collected by scraping sediment samples from the top 1 cm of the reef flat. A single MPB sample was isolated from the sediment as in Hamilton et al. (2005). All plant and animal tissue was dried at 60 °C for 72 h and homogenized. Subsamples of animal tissue (1–3 mg) and plant material (7 mg) were weighed and placed in tin capsules for stable isotope analysis. Samples were analyzed by a Sercon Hydra 20–22, Sercon Europa EA-GSL mass spectrometer. Isotopic ratios are expressed in delta notation according to the formula: $\delta X = [(R_{smpl} / R_{std}) - 1] * 1000$, where X represents ^{13}C or ^{15}N and R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio respectively. Nitrogen is expressed relative to atmospheric nitrogen and carbon relative to Vienna Pee-Dee Belemnite.

2.3. Data analysis

Abundances of the most common classes of invertebrates were summed by feeding guild (filter feeding bivalves, grazing gastropods and detritivorous hermit crabs). Variation in the untransformed abundance of each species among sampling positions (a fixed factor with 3 levels) and locations (a random factor with 4 levels) was tested using a two-way PERMANOVA based on a Euclidean distance similarity matrix with 9999 permutations. Variation in measured isotope values of each invertebrate species was tested using a two-way PERMANOVA of the same design. Values of $\delta^{13}C$, $\delta^{15}N$ and a combined C and N isotope value ($\delta CN = \delta^{15}N - \delta^{13}C$) as in Fry et al. (2008) were analyzed separately. Significant terms and interactions were further explored using posteriori-pairwise comparisons with the PERMANOVA t-statistic.

The relative contribution of benthic and pelagic food sources to invertebrate diet was calculated using single isotope, two source mixing models of $\delta^{13}C$, $\delta^{15}N$ and δCN in IsoError (Phillips and Gregg, 2001), which incorporates source variability into source proportion estimates. Given the number of food sources available on coral reefs, mangroves and seagrass beds, calculating diet contributions for all possible food sources was not viable. The isotope values of pelagic sources on inshore reefs, such as POM, are typically depleted in ^{13}C and enriched in ^{15}N relative to benthic foods like microalgae or cyanobacteria (Fig. 4). We used the five most ^{13}C depleted mussel values as a proxy for pelagic sources and the five most ^{13}C enriched gastropod values as a proxy for benthic source use. Endmember values were (mean $\pm$ SD) -18.6 ± 0.4‰ $\delta^{13}C$, 6.9 ± 0.3‰ $\delta^{15}N$ and 25.5 ± 0.5 δCN for pelagic foods and -7.7 ± 0.5‰ $\delta^{13}C$, 3.3 ± 0.3‰ $\delta^{15}N$ and 11 ± 0.6 δCN for benthic foods. These values were not perfect estimates of 100% pelagic or benthic source pools but they were consistent with isotope values of POM and cyanobacteria on fringing reefs (Fig. 4), and using them eliminated the uncertainty in estimating the fractionation between foods and consumers. We used the mussel values most depleted in ^{13}C to reflect pelagic foods rather than the average of all mussels to take into account the possibility of benthic algal sources being assimilated into some mussel diets (Larsen et al., 2013). Additionally, the isotope value for benthic diet may have been more enriched in ^{13}C than the endmember used, but variation within 2–4‰ would not greatly affect model results as the benthic and pelagic endmembers were already separated by about 10‰.

No adjustment for fractionation was made for mussels or gastropod consumer isotope values since mixing model sources were already primary consumers. The detritivorous hermit crab typically feeds on decaying plant matter but also some animal foods (Benvenuto, 2003), so $\delta^{15}N$ values were adjusted (3.2‰) to the baseline of the primary consumers, using the method described by Post (2002). Trophic adjustments for $\delta^{13}C$ were considered negligible (0‰) for these consumer-

Table 2
Enriched values of $\delta^{13}C$ for invertebrates and benthic autotrophs collected from intertidal flats in marine settings.

Location of study	Habitat	Source	N	Mean $\delta^{13}C$ (‰)	SD	Source
Plants						
Northwestern Hawaiian Islands	Coral reef	Benthic microalgae	8	−8.6	3.2	Hilting et al. (2013)
Reunion Island, SW Indian Ocean	Inner reef flat and back reef	Cyanobacteria	5	−6.9	2.3	Kolasinski et al. (2011)
		Benthic detritus	5	−7.6	1.3	
New Caledonia	Lagoon	Turf algae	3	−4.0		Carassou et al. (2008)
Bahamas Islands	Intertidal reef flat	Algal mat	1	−6.5		Fry et al. (1987)
Al-Khor Bay, Qatar	Intertidal flat	Cyanobacteria	3	−7.6	1.0	Al-Maslamani et al. (2012)
Sinai Peninsula, Egypt	Rock pools	Cyanobacteria	1	−4.0		Schidlowski (1985)
Primary consumers						
Moreton Bay,	Intertidal reef flat	*Calthalotia indistincta*	3	−8.6	0.7	Davis et al. (this study)
QLD, Australia		*Clibanarius taeniatus*	6	−8.0	0.2	
Bahamas Islands	Intertidal reef flat	*Chiton spp.*	4	−4.8	0.4	Fry et al. (1987)
		Cerithium lutosum	1	−7.0		
		Merita versicolor	1	−7.3		
Trinidad, Caribbean	Intertidal reef flat	Multiple grazers	6	−8.1	1.3	Mallela and Harrod (2008)

based mixing models (Post, 2002). These adjustments in C and N brought all animals to the same trophic level baseline, so that they could be considered as members of the same generalized consumer population in the $\delta^{13}C$, $\delta^{15}N$ and δCN mixing models.

3. Results

3.1. Invertebrate abundance

A total of 47 benthic invertebrate species were observed across all locations (Table 3). The most common invertebrates on the reef flat were bivalves, gastropods and hermit crabs, which reached 66% cover, 46 individuals, and 6 individuals m^{-2}, respectively, at some locations. Abundances of filter feeding bivalves differed across the reef flat and variation among positions differed slightly among locations (Table 4). There was a general trend, however, for bivalves to be more abundant on the reef edge and the center of the reef flat than at the mangrove edge (Fig. 3A). Abundances of hermit crabs also varied among sampling positions but no consistent patterns were evident among locations (Table 4, Fig. 3B). Abundances of gastropods varied among locations but not among positions (Table 4). They were sparse at all locations except GRI1 where they were abundant at all positions (Fig. 3C). The substrate at Green Island was mainly hard calcareous material (39–66% cover), while Peel Island locations were predominantly soft sediment with only 5–20% cover of hard calcareous material.

3.2. Autotroph $\delta^{13}C$ and $\delta^{15}N$

The $\delta^{13}C$ values for autotrophs varied from −28 to −10‰ and mangroves and seagrasses were easily distinguishable from other sources (Fig. 4). Mangroves were the most depleted source, while POM and plankton (based on the literature), MPB, and reef macroalgae had intermediate values, and seagrass was the most enriched source collected. Values of $\delta^{13}C$ of cyanobacteria found on reef flats in other studies are more enriched than the seagrass we measured (−7‰; Kolasinski et al., 2011). The $\delta^{15}N$ values of autotrophic sources ranged from −0.4 to 6.5‰, with mangroves, cyanobacteria and seagrass being the lowest and reef macroalgae and plankton the highest (Fig. 4).

Table 4
Results of 2-level PERMANOVA tests of variation in abundance of (a) filter feeding bivalves, (b) detritivorous hermit crabs, and (c) grazing gastropods across sampling positions at all locations. Terms in bold indicate significant effects.

	df	P (perm)
(a) Bivalve		
Location	3	<0.001
Position	2	0.027
Loc. × position	**6**	**<0.001**
(b) Hermit crab		
Location	3	<0.001
Position	2	0.875
Loc. × position	**6**	**0.001**
(c) Gastropod		
Location	**3**	**<0.001**
Position	2	0.104
Loc. × position	6	0.424

3.3. Spatial variation in invertebrate $\delta^{13}C$ and $\delta^{15}N$

Carbon stable isotope values for gastropods varied among locations and positions (Table 5) and were more enriched at the center of the reef flat versus the reef edge (Fig. 5). Values of $\delta^{13}C$ for gastropods at the center of the reef flat were more enriched than any food sources that were collected but were consistent with values of cyanobacteria from the literature (Fig. 4). Nitrogen stable isotope and δCN values of the gastropod varied among positions on the reef flat (Table 5), becoming more enriched at the reef edge compared to the reef flat center and mangrove edge (Fig. 5). Values of $\delta^{15}N$ of the hermit crab varied among locations and positions (Table 5). As with the gastropod, the hermit crab had higher values of $\delta^{15}N$ at the reef edge compared to the center of the reef flat and the mangrove edge (Fig. 5). Values of $\delta^{13}C$ and δCN of hermit crabs also varied among positions (Table 5) but patterns were not consistent among locations. At GRI1 and PI2 hermit crabs were more enriched in ^{13}C at the center of the reef flat than at the reef edge (t = 2.85, p < 0.05 and t = 4.89, p < 0.01 respectively), while at PI1 this trend was absent (Fig. 5). At GRI1 and PI2 hermit crabs had higher δCN at the reef edge compared to the center of the reef flat (t = 3.05, p < 0.05 and t = 3.44, p < 0.05 respectively) and mangrove edge (t = 3.03, p < 0.05 and t = 3.86, p < 0.05 respectively) but there was no

Table 3
Abundance or cover m^{-2} (mean, SE) of abundant taxa observed at four locations in Moreton Bay at three positions across the intertidal coral reef flat. No. spp. = the number of species in each group. GRI refers to Green Island and PI refers to Peel Island locations.

Abundance (#/m^{-2})					Cover (%)				
Locations	Polychaeta	Polyplacophora	Gastropoda	Crustacea	Echinodermata	Holuthuria	Bivalvia	Porifera	Cnidaria
GRI1									
MG edge			15.1 (4.9)	46.3 (11.8)					
Middle	0.1 (0.1)		16 (5.4)	37.4 (12.5)	0.1 (0.1)		3.3 (4)		
RF edge			13.5 (2.4)	18.1 (3.9)	0.1 (0.1)		1.6 (2)		
PI1									
MG edge			1.8 (1.1)	0.2 (0.1)			16.3 (12)		
Middle			0.5 (0.2)	1.9 (0.5)			35.5 (10)	0 (2)	2.8 (1)
RF edge			0.3 (0.2)	1.2 (0.5)			41.6 (13)	0 (5)	8.7 (0)
PI2									
MG edge			3.1 (0.5)	0.9 (0.5)			0 (2)		
Middle			1.6 (0.7)	13.7 (3.1)			5.4 (5)	0.5 (6)	4.3 (1)
RF edge		0.1 (0.3)	3.4 (1.1)	25.7 (5.1)		0.8 (0.5)	15.5 (9)	1.2 (2)	25.1 (2)
PI3									
MG edge		0.2 (0.0)	1.0 (0.6)	1.1 (0.7)			2.6 (6)		
Middle			4.5 (1.0)	6.4 (1.0)	0.1 (0.1)		61.6 (19)	1.5 (11)	15 (3)
RF edge			0.4 (0.2)	1.6 (0.8)			66.3 (23)	1.2 (3)	5.1 (2)
No. spp.	1	1	17	11	3	1	3	3	7

(A) Bivalves (filter feeders)

(B) Hermit crabs (detritivores)
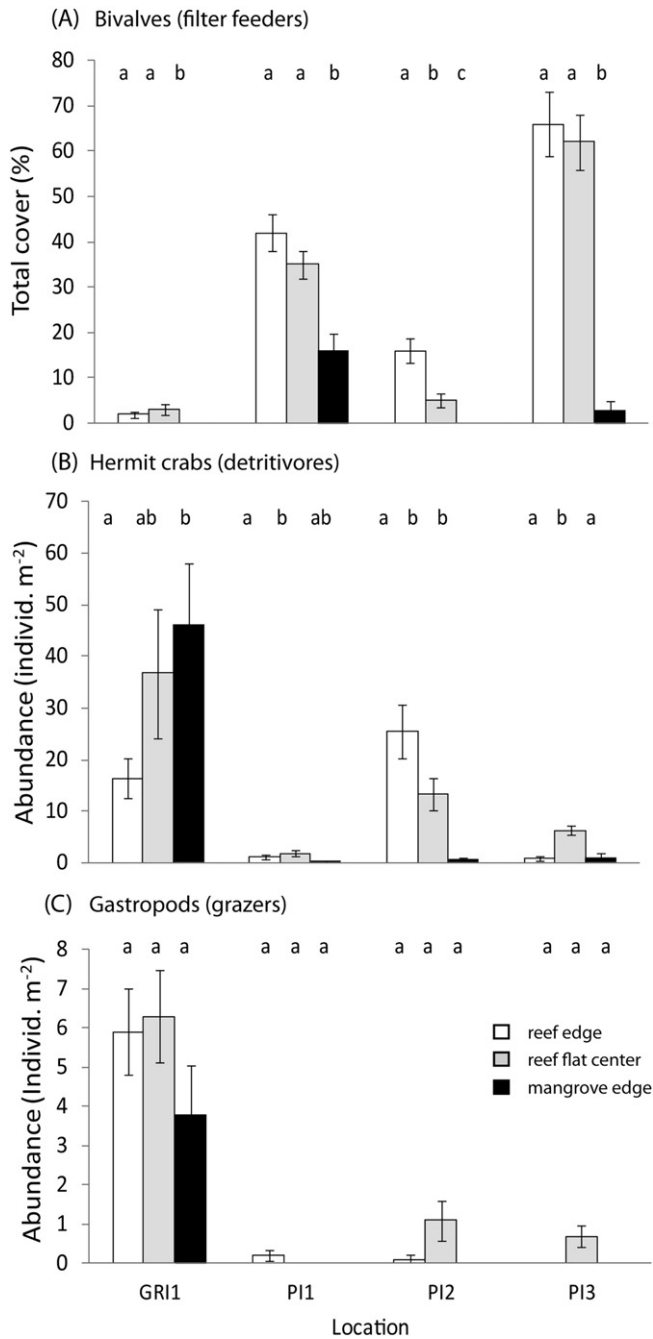

(C) Gastropods (grazers)

Fig. 3. Percentage cover of all species of sessile filter feeding bivalves, and abundance of detritivorous hermit crabs and grazing gastropods, at three positions across the reef flat at each location. Letters indicate significant differences among sampling positions at each location. Data are means ± SE. GRI refers to Green Island and PI refers to Peel Island locations.

trend in δCN at PI1 (Fig. 5). All hermit crabs had relatively enriched carbon isotope values similar to that of cyanobacteria or seagrass (Fig. 4). The $\delta^{13}C$, $\delta^{15}N$ and δCN of mussels did not vary among positions but did vary among locations (Table 5). Their isotope values were consistently low in $\delta^{13}C$ and similar to pelagic food sources (Fig. 4).

3.4. Contribution of food sources to invertebrate diet

The results of 2-source mixing models using $\delta^{13}C$, $\delta^{15}N$ and δCN indicate that both pelagic and benthic food sources were important to invertebrate diet on reef flats, but that dependence on these sources varied among species and also across positions for two species. Models

using $\delta^{13}C$ showed that mussel diet was predominantly (83–87%) from pelagic food sources at all positions on the flat. Hermit crabs and gastropods used mostly benthic food sources (64–78% and 73–91% respectively) but the proportion of pelagic food sources in their diets increased >10% at the reef edge (Fig. 6A). Mixing models using $\delta^{15}N$ also showed the diet of mussels did not vary across positions and was predominantly pelagic (83–87%), while gastropods and hermit crabs used more benthic sources at positions shoreward of the reef edge (Fig. 6B). The combined δCN models again indicated that the use of pelagic resources decreased at positions towards the mangrove edge for gastropods and hermit crabs but remained consistently high for mussels (Fig. 6C).

4. Discussion

4.1. Dietary pathways for reef flat invertebrates

Intertidal reef flats are undervalued habitats relative to their area and distribution on coral reefs, especially given the food sources they provide for both humans (Hauzer et al., 2013; Nordlund et al., 2013) and fishes (Thacker et al., 2001; Miller, 1983). These habitats are different from other reef zones because reef flat animals are more exposed to physiological stresses from the extremes of tidal exposure, temperature changes and high turbidity than on subtidal reef flats or reef crests. This study provides a first look at the primary sources supporting productivity on intertidal reef flats. Filter feeding bivalves depended predominantly on pelagic sources as expected, however the $\delta^{13}C$ values for gastropods and hermit crabs on the center of the reef flat were more enriched than any autotrophic sources identified and mixing models indicated they depend on predominantly benthic foods. Indeed, they had similar carbon isotope values to autotrophic benthic sources found on reef flats such as cyanobacteria or turf algae (Table 2). Our results highlight a trend for increased consumer dependence on benthic autotrophic sources with enriched carbon isotopes in inshore coral reef food webs (Wyatt et al., 2012a; Hilting et al., 2013) that could have important implications for our understanding of trophic functioning in these areas.

4.2. Spatial patterns in abundances of benthic invertebrates

Three trophic guilds (filter feeders, detritivores and grazers) occurred across most of the reef flat at all locations. Filter feeding bivalves commonly colonized positions distant from the mangrove edge, where access to pelagic dietary sources is presumably greater (Peterson and Black, 1987; Bayne et al., 1988), and the risk of desiccation and thermal stress at low tide is less (Lent, 1969). The variability in abundances of detritivorous hermit crabs among locations and positions was not unusual given these species are relatively mobile (Benvenuto et al., 2003) and may preferentially target resources on different parts of the reef flat. Gastropods did not favor any position on the reef flat but were often absent from the mangrove edge, perhaps reflecting reduced food availability (Underwood, 1984) or reduced resistance to desiccation (Broekhuysen, 1940).

Although we did not focus on differences in abundance among sampling locations, there were clear differences in community structure among reef flats, with mussels more abundant at Peel Island locations and gastropods and hermit crabs most abundant at Green Island. Differences in community structure are probably due to substrate characteristics of the reef flats. There are major differences in geomorphology between the islands. Green Island was created from Tertiary volcanic lava, while Peel Island is composed of softer Mesozoic sandstone (Maxwell, 1970). Mussels may be less exposed to predation when partially buried in the softer sand and mud substrates at Peel Island (Downing et al., 2000), whereas gastropods and hermit crabs may have better mobility and access to preferred foods on the harder substrate of the reef flat at Green Island.
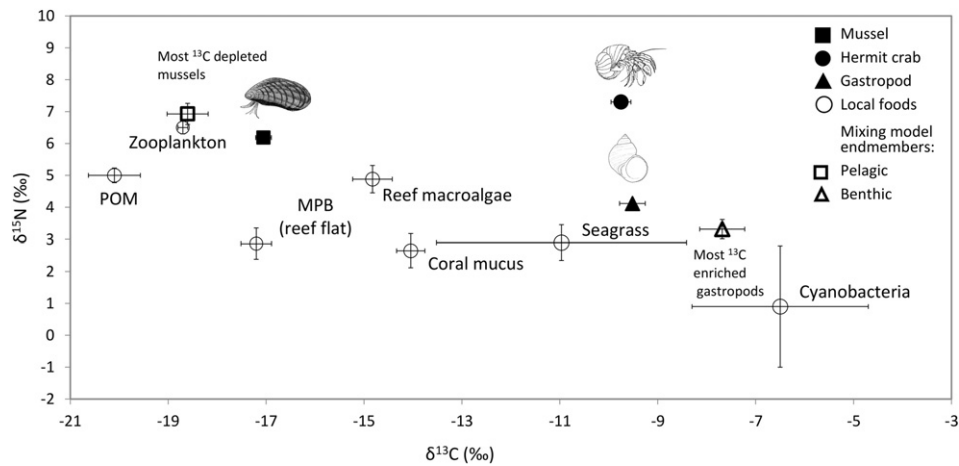
Fig. 4. Mean (± SE) carbon and nitrogen isotope values of mussels (*Trichomya hirsuta*), hermit crabs (*Clibanarius taeniatus*) gastropods (*Calthalotia indistincta*) and six autotrophs. *POM* particulate organic matter; *MPB* microphytobenthos; reef macroalgae (*Lobophora variegata*); seagrass (*Zostera muelleri*), coral mucus (*Favia speciosa*) and cyanobacteria. Zooplankton, POM and cyanobacteria values taken from Couturier et al. (2013), Mallela and Harrod (2008) and Table 2, respectively. Mixing model endmembers are the 5 most ^{13}C enriched and depleted organisms collected. Mangrove sources were −28‰ δ^{13}C and 3‰ δ^{15}N, and are not shown.

4.3. Spatial variation in stable isotopes and diet of invertebrates

Isotope values of mussels were consistent among positions and mixing model results suggested they fed on pelagic-based foods at all positions on the reef flat. Isotope analyses of intertidal mussels in the USA and New Zealand indicates that they selectively feed on high quality phytoplankton sources (Bracken et al., 2012), which supports the idea that mussels in this study were exploiting pelagic subsidies rather than MPB. Increased abundances of mussels at the reef edge and at the center of the reef flat is consistent with a dependence on pelagic sources, since individuals at these positions are submerged for longer periods (i.e., have better access to pelagic sources) (Peterson and Black, 1987) than those at the mangrove edge. Reef flats in Moreton Bay and elsewhere (Walker et al., 2008) support large populations of filter feeders, and these consumers increase the complexity of the benthic habitat, allowing other organisms to settle and grow (Gutiérrez et al., 2003) so pelagic sources are probably important for ecosystem functioning on reef flats.

Variation in values of δ^{13}C and δ^{15}N for gastropods suggests either that they incorporate more pelagic sources at the reef edge or that isotopes of a single source change across positions. Allochthonous detrital or pelagic sources were considered minor contributors to gastropod diet at the reef edge, because no obvious sources of drift algae or seagrass

were observed there and carbon isotope values of grazers remained enriched relative to pelagic sources. Gastropod δ^{13}C values at the mangrove edge were not depleted relative to other positions, therefore it is also unlikely gastropods assimilate substantial diet sources from fringing mangroves. This observation is consistent with other studies that have found little evidence for the assimilation of mangrove carbon by consumers in adjacent habitats (Bouillon et al., 2008).

Gastropods assimilated sources with unusually enriched δ^{13}C values at the center of the reef flat and showed a high dependence on benthic autotrophic foods there. Although we did not identify the source in this study, similarly highly enriched sources have been observed for cyanobacteria (Table 2), which are common to reef flats worldwide (Thacker et al., 2001; Fonseca et al., 2012). Values of δ^{13}C for benthic autotrophs in intertidal areas typically become enriched due to high light levels (Bootsma et al., 1996; Pages et al., 2014) and thick boundary layers (France, 1995). Therefore, the change in isotope values for gastropods at the reef edge may simply reflect a change in the isotopes of the same benthic food source; primary producers at the reef edge might have more depleted δ^{13}C values and enriched δ^{15}N values relative to the center of the reef flat due to reduced light levels and exposure time at the subtidal boundary. Gastropods were present at both the reef edge and at the center of the reef flat, which suggests the variation in source contribution did not affect productivity, while their absence from the mangrove edge may be caused by the increased risk of desiccation.

Patterns in hermit crab δ^{15}N were similar to those observed for gastropods, suggesting that they either assimilated more pelagic sources or that the isotopic values of sources changed at the reef edge. Despite the enrichment in ^{13}C of hermit crabs at some positions away from the reef edge and a strong dependence on benthic foods, trends in δ^{13}C among sampling positions were not consistent at all locations, and showed little variation among positions at PI1. Hermit crabs at PI1 may not have shown the same diet trends due to differences in physical characteristics. Site PI1 was the most sheltered reef flat sampled, being located in a back-reef channel with high sediment loads. These physical factors may have reduced the growth of autotrophic sources with enriched δ^{13}C values which appeared important at the other locations. Finer grain sizes on intertidal flats can reduce the growth of in-situ autotrophs (Cahoon et al., 1999; Schiel et al., 2006) and thus their availability to consumers (Herman et al., 2001). Hermit crabs were in very low abundance and gastropods were not present at the PII location but both species were more abundant at locations where they had diets enriched in δ^{13}C, suggesting enriched benthic sources are an important component of their diet.

Table 5

Results of 2-level PERMANOVA tests of variation in δ^{13}C, δ^{15}N and δCN across 3 positions (reef edge, reef flat center and mangrove edge) for a gastropod (*Calthalotia indistincta*), mussel (*Trichomya hirsuta*) and hermit crab (*Clibanarius taeniatus*) at all locations. Terms in bold indicate significant effects. The df = 2, 2, 4 for Location, Position and Loc. × Pos. for gastropods and hermit crabs, and df = 3, 2, 4 for mussels.

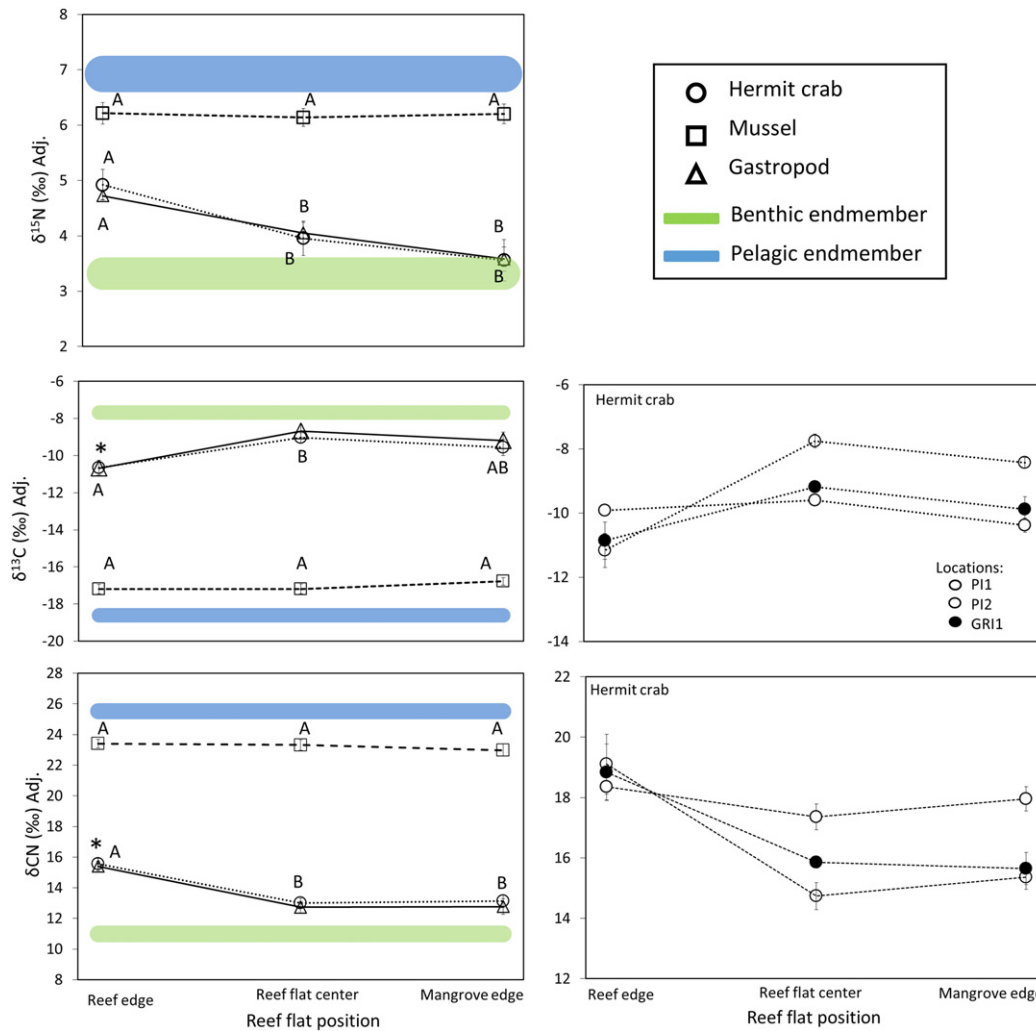|	Gastropod	Mussel	Hermit Crab
	P	P	P
δ^{13}C			
Location	**0.013**	**<0.001**	**0.029**
Position	**0.025**	0.162	**<0.001**
Loc. × position	0.202	0.291	**0.002**
δ^{15}N			
Location	0.120	**<0.001**	**0.002**
Position	**0.019**	0.711	**0.032**
Loc. × position	0.444	0.587	0.266
δCN			
Location	**0.016**	**<0.001**	**<0.001**
Position	**0.019**	0.353	0.068
Loc. × position	0.588	0.381	**0.003**

Fig. 5. Spatial patterns in values of invertebrate tissue nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$) and combined C and N isotopes (δCN) averaged across locations and then by location for hermit crabs. Hermit crab $\delta^{15}N$ is adjusted -3.2‰ to account for trophic level. Data are mean ($\pm$SE) for each position. The width of the lines for mixing model endmembers represents the error.

Differences in feeding strategy and mobility for hermit crabs may also have resulted in more variable trends in carbon source use. While the gastropod probably feeds in a small radius due to limited mobility, large hermit crabs like *Clibanarius taeniatus* can travel up to several meters to find a preferred food source (Benvenuto et al., 2003). Increased mobility may allow for more opportunistic feeding forays to access detrital or benthic sources, which may explain the variability in abundances of hermit crabs across positions on the reef flat. Although largely dependent on decaying plant material, these hermit crabs may also assimilate some animal material (Kunze and Anderson, 1979) and the patchy availability of animal food sources could have resulted in altered patterns in carbon source use compared to gastropods.

4.4. Trends in consumer diets on coral reef flats

Although few studies have investigated trophic dynamics at the landscape scale for coral reef flats, there does appear to be a regular enrichment in $\delta^{13}C$ and depletion in $\delta^{15}N$ values in consumers on inshore areas of coral reefs globally (Fry et al., 1987; Kolasinski et al., 2009; Wyatt et al., 2012a, 2013). Both Wyatt et al. (2012a) and Hilting et al. (2013) noted that fishes depend on high levels of benthic reef production (sources enriched in $\delta^{13}C$) on inshore portions of coral reefs. Hilting et al. (2013) hypothesized that the unusually enriched values of $\delta^{13}C$ for benthic microalgae may be due to cyanobacteria or increased use of HCO_3^- during photosynthesis. There is also a concurrent decrease in

$\delta^{15}N$ moving shoreward on reef flats for fish in most feeding guilds (Wyatt et al., 2012a), consistent with some nitrogen fixation by cyanobacteria within symbioses (Lesser et al., 2007) or detrital reworking and release (Wyatt et al., 2012b; De Goeij et al., 2013). These isotope findings are very similar to patterns observed for grazers and detritivores in the current study, suggesting that this may be a typical trophic pattern on inshore coral reefs. This pattern implies that reef flats are strong source regions for local food webs on inshore fringing coral reefs, providing in situ benthic sources of organic matter to local consumers, and likely exporting organic matter to adjacent habitats.

Nitrogen isotopes of gastropods and hermit crabs became depleted at positions away from the reef edge, and this change suggests pelagic sources of nitrogen may be an external subsidy that supports the growth of autotrophic foods across the reef flat. Thus, the decay of plankton inside Moreton Bay may fertilize the growth of microalgae in intertidal habitats as is observed on coastal shelfs (Darrow et al., 2003). Such nutrient subsidies and enhanced primary productivity may help explain increased fish abundances associated with reef flats and nearby fringing mangroves locally (Olds et al., 2012).

One caveat of our study is that invertebrates and their foods were not collected across seasons. While seasonal sampling is useful for describing variability in source values, invertebrates such as filter feeders can have stable isotope turnover times of nearly a year (Raikow and Hamilton, 2001; Cabanellas-Reboredo et al., 2009), making seasonal sampling of sources inconsequential. Additionally, winter marine food
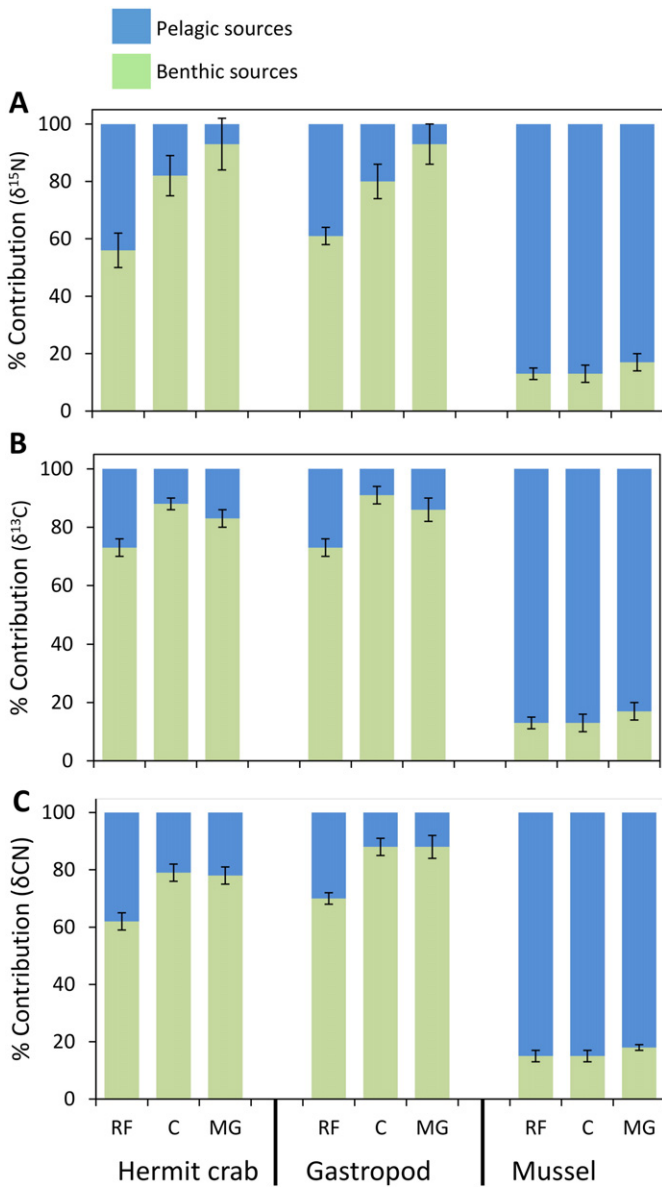
Fig. 6. Mean percentage contribution of the pelagic and benthic source groups (±SE) to consumer diets at each position on the reef flat and averaged across locations, calculated from $\delta^{13}C$ (A), $\delta^{15}N$ (B) and combined C and N isotopes (δCN) (C) using IsoError (Phillips and Gregg, 2001). RF = Reef edge, C = Reef flat center and MG = Mangrove edge.

webs are typically more depleted in $\delta^{13}C$ due to decreased irradiance levels, and thus, carbon demand (Vizzini and Mazzola, 2003), so the conclusion about the importance of enriched benthic carbon sources in reef flat food webs appears robust. Future studies of trophic functioning on reef flats might aim to capture temporal trends, as well as including a greater range of species and trophic levels to delineate food web structure.

4.5. Conclusion

The results of this study indicate that invertebrate communities depend on both autochthonous benthic and external pelagic sources. Although abundant filter feeders appeared to feed on planktonic food sources, detritivore and grazer diets apparently relied on sources with unusually enriched values of $\delta^{13}C$, indicative of benthic production. Community structure on intertidal reef flats is especially susceptible to the impending effects of climate change and sea level rise due to their intertidal nature and location at the land–sea interface (Walker et al.,

2008; Harborne, 2013). In addition, fish from subtidal habitats move over reef flats during daily tidal fluxes and feed (Harborne, 2013), so invertebrates may be an important trophic link between benthic producers and mobile consumers on coral reefs. We recommend that benthic producers with enriched carbon stable isotope values should be given increased attention in future food web studies of coral reefs, and that intertidal reef flats receive greater consideration when predicting the future of vulnerable coral reef ecosystems.

References

Al-Maslamani, I., Walton, M., Kennedy, H., Le Vay, L., 2012. Sources of primary production supporting food webs in an arid coastal embayment. Mar. Biol. 159, 1753–1762.

Bayne, B., Hawkins, A., Navarro, E., 1988. Feeding and digestion in suspension-feeding bivalve molluscs: the relevance of physiological compensations. Am. Zool. 28, 147–159.

Benvenuto, C., Sartoni, G., Gherardi, F., 2003. Foraging behaviour of the hermit crab *Clibanarius erythropus* in a Mediterranean shore. J. Mar. Biol. Assoc. UK 83, 457–461.

Bergamino, L., Richoux, N.B., 2014. Spatial and temporal changes in estuarine food web structure: differential contributions of marsh grass detritus. Estuar. Coasts http://dx.doi.org/10.1007/s12237-014-9814-5.

Berkström, C., Lindborg, R., Thyresson, M., Gullström, M., 2013. Assessing connectivity in a tropical embayment: fish migrations and seascape ecology. Biol. Conserv. 166, 43–53.

Bootsma, H., Hecky, R., Hesslein, R., Turner, G., 1996. Food partitioning among Lake Malawi nearshore fishes as revealed by stable isotope analyses. Ecology 77, 1286–1290.

Bouillon, S., Connolly, R.M., 2009. Carbon exchange among tropical coastal ecosystems. In: Nagelkerken, I. (Ed.), Ecological Connectivity Among Tropical Coastal Ecosystems. Springer, London, pp. 45–70.

Bouillon, S., Connolly, R.M., Lee, S.Y., 2008. Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J. Sea Res. 59, 44–58.

Bracken, M.E., Menge, B.A., Foley, M.M., Sorte, C.J., Lubchenco, J., Schiel, D.R., 2012. Mussel selectivity for high-quality food drives carbon inputs into open-coast intertidal ecosystems. Mar. Ecol. Prog. Ser. 459, 53–62.

Broekhuysen, G., 1940. A preliminary investigation of the importance of desiccation, temperature, and salinity as factors controlling the vertical distribution of certain intertidal marine gastropods in False Bay, South Africa. Trans. R. Soc. S. Afr. 28, 255–292.

Cabanellas-Reboredo, M., Deudero, S., Blanco, A., 2009. Stable-isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of different tissues of *Pinna nobilis* Linnaeus, 1758 (Bivalvia): isotopic variations among tissues and between seasons. J. Molluscan Stud. 75, 343–349.

Cahoon, L., Nearhoof, J., Tilton, C., 1999. Sediment grain size effect on benthic microalgal biomass in shallow aquatic ecosystems. Estuaries 22, 735–741.

Carassou, L., Kulbicki, M., Nicola, T.J., Polunin, N.V., 2008. Assessment of fish trophic status and relationships by stable isotope data in the coral reef lagoon of New Caledonia, southwest Pacific. Aquat. Living Resour. 21, 1–12.

Couturier, L.I., Rohner, C.A., Richardson, A.J., Marshall, A.D., Jaine, F.R., Bennett, M.B., Townsend, K.A., Weeks, S.J., Nichols, P.D., 2013. Stable isotope and signature fatty acid analyses suggest reef manta rays feed on demersal zooplankton. PLoS One 8, e77152.

Cruz-Rivera, E., Paul, V.J., 2006. Feeding by coral reef mesograzers: algae or cyanobacteria? Coral Reefs 25, 617–627.

Darrow, B.P., Walsh, J.J., Vargo, G.A., Masserini, R.T., Fanning, K.A., Zhang, J.-Z., 2003. A simulation study of the growth of benthic microalgae following the decline of a surface phytoplankton bloom. Cont. Shelf Res. 23, 1265–1283.

Davis, J., Pitt, K., Fry, B., Olds, A., Connolly, R., 2014. Seascape-scale trophic links for fish on inshore coral reefs. Coral Reefs 33, 891–896.

De Goeij, J.M., van Oevelen, D., Vermeij, M.J., Osinga, R., Middelburg, J.J., de Goeij, A.F., Admiraal, W., 2013. Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science 342, 108–110.

Downing, J.A., Van Leeuwen, H., Di Paolo, L.A., 2000. Substratum patch selection in the lacustrine mussels *Elliptio complanata* and *Pyganodon grandis grandis*. Freshw. Biol. 44, 641–648.

Fonseca, C., Villaça, R., Knoppers, B., 2012. Reef flat community structure of Atol das Rocas, Northeast Brazil and Southwest Atlantic. J. Mar. Biol. http://dx.doi.org/10.1155/2012/179128.

France, R., 1995. Carbon-13 enrichment in benthic compared to planktonic algae: food web implications. Mar. Ecol. Prog. Ser. 124, 307–312.

Fry, B., Macko, S., Zieman, J., 1987. Review of stable isotopic investigations of food webs in seagrass meadows. Fla. Mar. Res. Publ. 42, 189–209.

Fry, B., Cieri, M., Hughes, J., Tobias, C.R., Deegan, L.A., Peterson, B.J., 2008. Stable isotope monitoring of benthic–planktonic coupling using salt marsh fish. Mar. Ecol. Prog. Ser. 369, 193–204.

Gacia, E., Costalago, D., Prado, P., Piorno, D., Tomas, F., 2009. Mesograzers in *Posidonia oceanica* meadows: an update of data on gastropod–epiphyte–seagrass interactions. Bot. Mar. 52, 439–447.

Gischler, E., Ginsburg, R.N., 1996. Cavity dwellers (coelobites) under coral rubble in southern Belize barrier and atoll reefs. Bull. Mar. Sci. 58, 570–589.

Granek, E.F., Compton, J.E., Phillips, D.L., 2009. Mangrove-exported nutrient incorporation by sessile coral reef invertebrates. Ecosystems 12, 462–472.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101, 79–90.

Hamilton, S.K., Sippel, S.J., Bunn, S.E., 2005. Separation of algae from detritus for stable isotope or ecological stoichiometry studies using density fractionation in colloidal silica. Limnol. Oceanogr. 3, 149–157.

Harborne, A., 2013. The ecology, behaviour and physiology of fishes on coral reef flats, and the potential impacts of climate change. J. Fish Biol. 83, 417–447.

Hauzer, M., Dearden, P., Murray, G., 2013. The fisherwomen of Ngazidja Island, Comoros: fisheries livelihoods, impacts, and implications for management. Fish. Res. 140, 28–35.

Heithaus, E.R., Heithaus, P.A., Heithaus, M.R., Burkholder, D., Layman, C.A., 2011. Trophic dynamics in a relatively pristine subtropical fringing mangrove community. Mar. Ecol. Prog. Ser. 428, 49–61.

Herman, P.M., Middelburg, J.J., Heip, C.H., 2001. Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. Cont. Shelf Res. 21, 2055–2071.

Heupel, M., Bennett, M., 1998. Observations on the diet and feeding habits of the epaulette shark, *Hemiscyllium ocellatum* (Bonnaterre), on Heron Island Reef, Great Barrier Reef, Australia. Mar. Freshw. Res. 49, 753–756.

Hilting, A.K., Currin, C.A., Kosaki, R.K., 2013. Evidence for benthic primary production support of an apex predator–dominated coral reef food web. Mar. Biol. 160, 1681–1695.

Hyndes, G., Nagelkerken, I., McLeod, R., Connolly, R., Lavery, P., Vanderklift, M., 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. Biol. Rev. 89, 232–254.

Kolasinski, J., Frouin, P., Sallon, A., Rogers, K., Bruggemann, H.J., Potier, M., 2009. Feeding ecology and ontogenetic dietary shift of yellowstripe goatfish *Mulloidichthys flavolineatus* (Mullidae) at Reunion Island, SW Indian Ocean. Mar. Ecol. Prog. Ser. 386, 181–195.

Kolasinski, J., Rogers, K., Cuet, P., Barry, B., Frouin, P., 2011. Sources of particulate organic matter at the ecosystem scale: a stable isotope and trace element study in a tropical coral reef. Mar. Ecol. Prog. Ser. 443, 77–93.

Kuffner, I.B., Walters, L.J., Becerro, M.A., Paul, V.J., Ritson-Williams, R., Beach, K.S., 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar. Ecol. Prog. Ser. 323, 107–117.

Kunze, J., Anderson, D., 1979. Functional morphology of the mouthparts and gastric mill in the hermit crabs *Clibanarius taeniatus* (Milne Edwards), *Clibanarius virescens* (Krauss), *Paguristes squamosus* McCulloch and *Dardanus setifer* (Milne-Edwards)(Anomura: Paguridae). Mar. Freshw. Res. 30, 683–722.

Larsen, T., Ventura, M., Andersen, N., O'Brien, D.M., Piatkowski, U., McCarthy, M.D., 2013. Tracing carbon sources through aquatic and terrestrial food webs using amino acid stable isotope fingerprinting. PLoS One 8, e73441.

Lent, C.M., 1969. Adaptations of the ribbed mussel, *Modiolus demissus* (Dillvvyn), to the intertidal habitat. Am. Zool. 9, 283–292.

Lesser, M.P., Falcón, L.I., Rodríguez-Román, A., Enríquez, S., Hoegh-Guldberg, O., Iglesias-Prieto, R., 2007. Nitrogen fixation by symbiotic cyanobacteria provides a source of nitrogen for the scleractinian coral Montastraea cavernosa. Mar. Ecol. Prog. Ser. 346, 143–152.

Mallela, J., Harrod, C., 2008. δ ^{13}C and δ ^{15}N reveal significant differences in the coastal food webs of the seas surrounding Trinidad and Tobago. Mar. Ecol. Prog. Ser. 368, 41–51.

Marguillier, S., Van der Velde, G., Dehairs, F., Hemminga, M., Rajagopal, S., 1997. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by delta ^{13}C and delta ^{15}N. Mar. Ecol. Prog. Ser. 151, 115–121.

Maxwell, W., 1970. The sedimentary framework of Moreton Bay, Queensland. Mar. Freshw. Res. 21, 71–88.

Meesters, E., Knijn, R., Willemsen, P., Pennartz, R., Roebers, G., Soest, R.W.M., 1991. Sub-rubble communities of Curaçao and Bonaire coral reefs. Coral Reefs 10, 189–197.

Miller, A., 1983. Effects of differential fish grazing on the community structure of an intertidal reef flat at Enewetak Atoll, Marshall Islands. Pac. Sci. 36, 467–482.

Moriarty, D., Pollard, P., Hunt, W., Moriarty, C., Wassenberg, T., 1985. Productivity of bacteria and microalgae and the effect of grazing by holothurians in sediments on a coral reef flat. Mar. Biol. 85, 293–300.

Nagelkerken, I., 2009. Ecological Connectivity Among Tropical Coastal Ecosystems. Springer Verlag, Heidelberg.

Neil, D., 2000. Characteristics and significance of a sub-tropical 'Low Wooded Island': Green Island, Moreton Bay, Australia. J. Coast. Res. 16, 287–294.

Nordlund, L., de la Torre-Castro, M., Erlandsson, J., Conand, C., Muthiga, N., Jiddawi, N., Gullström, M., 2013. Intertidal zone management in the western Indian Ocean: assessing current status and future possibilities using expert opinions. Ambio http://dx.doi.org/10.1007/s13280-013-0465-8.

Oak, T., Scheibling, R., 2006. Tidal activity pattern and feeding behaviour of the ophiuroid *Ophiocoma scolopendrina* on a Kenyan reef flat. Coral Reefs 25, 213–222.

Olds, A., Connolly, R., Pitt, K., Maxwell, P., 2012. Habitat connectivity improves reserve performance. Conserv. Lett. 5, 56–63.

Pages, A., Grice, K., Ertefai, T., Skrzypek, G., Jahnert, R., Greenwood, P., 2014. Organic geochemical studies of modern microbial mats from Shark Bay: part I: influence of depth and salinity on lipid biomarkers and their isotopic signatures. Geobiology 12, 469–487.

Peterson, C.H., Black, R., 1987. Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. Limnol. Oceanogr. 32, 143–166.

Phillips, D.L., Gregg, J.W., 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127, 171–179.

Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu. Rev. Ecol. Syst. 28, 289–316.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Price, A., Maher, W., Kirby, J., Krikowa, F., Duncan, E., Taylor, A., Potts, J., 2012. Distribution of arsenic species in an open seagrass ecosystem: relationship to trophic groups, habitats and feeding zones. Environ. Chem. 9, 77–88.

Raikow, D.F., Hamilton, S.K., 2001. Bivalve diets in a midwestern US stream: a stable isotope enrichment study. Limnol. Oceanogr. 46, 514–522.

Schidlowski, M., 1985. Carbon isotope discrepancy between Precambrian stromatolites and their modern analogs: inferences from hypersaline microbial mats of the Sinai coast. Orig. Life Evol. Biosph. 15, 263–277.

Schiel, D.R., Wood, S.A., Dunmore, R.A., Taylor, D.I., 2006. Sediment on rocky intertidal reefs: effects on early post-settlement stages of habitat-forming seaweeds. J. Exp. Mar. Biol. Ecol. 331, 158–172.

Sheaves, M., 2009. Consequences of ecological connectivity: the coastal ecosystem mosaic. Mar. Ecol. Prog. Ser. 391, 107–115.

Sheaves, M., Baker, R., Nagelkerken, I., Connolly, R.M., 2014. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. Estuar. Coasts 38, 401–414.

Shibuno, T., Nakamura, Y., Horinouchi, M., Sano, M., 2008. Habitat use patterns of fishes across the mangrove-seagrass-coral reef seascape at Ishigaki Island, southern Japan. Ichthyol. Res. 55, 218–237.

Stephenson, W., Searles, R., 1960. Experimental studies on the ecology of intertidal environments at Heron Island. I. Exclusion of fish from beach rock. Mar. Freshw. Res. 11, 241–268.

Thacker, R., Ginsburg, D., Paul, V., 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. Coral Reefs 19, 318–329.

Underwood, A., 1984. The vertical distribution and seasonal abundance of intertidal microalgae on a rocky shore in New South Wales. J. Exp. Mar. Biol. Ecol. 78, 199–220.

Vizzini, S., Mazzola, A., 2003. Seasonal variations in the stable carbon and nitrogen isotope ratios (^{13}C/^{12}C and ^{15}N/^{14}N) of primary producers and consumers in a western Mediterranean coastal lagoon. Mar. Biol. 142, 1009–1018.

Wainright, S.C., Fry, B., 1994. Seasonal variation of the stable isotopic compositions of coastal marine plankton from Woods Hole, Massachusetts and Georges Bank. Estuaries 17, 552–560.

Walker, S., Degnan, B., Hooper, J., Skilleter, G., 2008. Will increased storm disturbance affect the biodiversity of intertidal, nonscleractinian sessile fauna on coral reefs? Glob. Chang. Biol. 14, 2755–2770.

Wyatt, A.S., Waite, A., Humphries, S., 2012a. Stable isotope analysis reveals community-level variation in fish trophodynamics across a fringing coral reef. Coral Reefs 31, 1029–1044.

Wyatt, A.S., Falter, J.L., Lowe, R.J., Humphries, S., Waite, A.M., 2012b. Oceanographic forcing of nutrient uptake and release over a fringing coral reef. Limnol. Oceanogr. 57, 401–419.

Wyatt, A.S., Lowe, R.J., Humphries, S., Waite, A.M., 2013. Particulate nutrient fluxes over a fringing coral reef: source–sink dynamics inferred from carbon to nitrogen ratios and stable isotopes. Limnol. Oceanogr. 58, 409–427.

Yamano, H., 2000. Sensitivity of reef flats and reef islands to sea-level change. Proceedings of the Ninth International Coral Reef Symposium, Bali, pp. 1193–1198.