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Stable isotopes as tracers of residency for fish on inshore coral reefs

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ABSTRACT

Understanding the migratory movements of fish between habitats is an important priority for fisheries management. Carbon (C) and nitrogen (N) stable isotopes were used to evaluate the degree of movement and residency for five fish species collected from coral reefs in Queensland, Australia. Isotope values of fish were measured and compared between slow-turnover muscle tissue and fast-turnover liver tissue, with isotopic agreement between liver and muscle generally indicating resident animals, and relatively low C isotope values in muscle indicating migrants. Three fish species, rabbitfish (*Siganus fuscescens*), painted sweetlips (*Diagramma labiosum*) and Guenther's wrasse (*Pseudolabrus guentheri*) showed relatively consistent carbon isotope values between muscle and liver tissue as expected for resident populations. One quarter of bream (*Acanthopagrus australis*) individuals showed much lower $\delta^{13}C$ values in muscle than liver. These low values diverged from the −10 to −15‰ values of residents and were more similar to the −20‰ values of fish collected from coastal riverine habitats, the presumed migration source. Moses perch (*Lutjanus russelli*) also showed substantial differences between muscle and liver C isotopes for about a quarter of individuals, but the overall higher C values of these individuals indicated they may have switched diets within island habitats rather than migrating. Our results were consistent with previous studies of fish residency and indicate that measuring stable isotopes in multiple tissues provides a useful methodology for characterizing fish residency in inshore areas.

1. Introduction

Characterizing the movements of fish between coral reefs and other habitats has become a focus for improving our understanding of habitat connectivity and population dynamics in tropical seascapes (Green et al., 2014). Reef fish make movements at scales of a few hundred meters to kilometers for feeding and spawning, and when they transition between juvenile and adult habitats (Berkström et al., 2012). These movements are challenging to measure. Historically, fish movement was investigated using labor intensive tagging and recapture studies employing dyes, plastic tags, and data from acoustic transmitters which offer detailed and explicit evidence of movement patterns (Gillanders, 2009). Using artificial tags can be costly however, and can involve handling effects on behavior and mortality, and overall have low recapture efficiency (Gillanders, 2009). More recently, natural biochemical markers such as stable isotopes have proven useful for characterizing fish movement (Elsdon et al., 2008; McMahon et al., 2013) and because they are naturally present in all animals many of the difficulties associated with artificial tags are avoided.

Stable isotope values of carbon in animal tissues typically indicate diet, while isotopes of nitrogen reflect trophic level (Fry, 2006). The accuracy of stable isotopes as tracers of animal diet, however, depends on the assumed equilibrium between the tissue measured and the food sources consumed. Fish tissues have different turnover times depending on their rate of growth and metabolism (Hesslein et al., 1993; Perga and Gerdeaux, 2005; Carleton and Del Rio, 2010). Muscle tissue in fish has a slow turnover time and isotopic ratios of this tissue reflect long term diet for foods consumed during growth (approximately 100 days), while liver tissue has continuous protein turnover, and isotope ratios in liver reflect diet within the last 10–20 days (Perga and Gerdeaux, 2005; Logan et al., 2006; Buchheister and Latour, 2010). Consequently, fishes with dissimilar liver and muscle isotope values may be new arrivals to a habitat. In contrast, fishes with similar isotope values in these two tissues are more likely to be residents (Haas et al., 2009).

For stable isotopes to be effective indicators of fish residency, the habitats that fish move between must have foods diet sources

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with unique isotopic values. This makes estuarine habitats valuable study areas as they typically have well-characterized differences in isotope values between freshwater and marine food sources (Bouillon et al., 2011). Stable isotope ratios of C and N in multiple tissues, though rarely used, have successfully shown changes in residency of brown shrimp (Fry et al., 2003), riverine fish (Haas et al., 2009) and blue crabs (Gelpi et al., 2013) in estuarine habitats. Isotopes are therefore likely to provide useful natural tags for investigating fish movement in inshore reefal systems, and may help identify key nursery areas (Fry, 1981; Herzka, 2005).

The aim of this study was to investigate whether concurrent measurements of $\delta^{13}C$ and $\delta^{15}N$ in fish liver and muscle tissue could be used to characterize variability in residency among fishes common to inshore coral reefs in southeast Queensland. It was hypothesized that isotopic values of muscle and liver tissues would be consistent for fish that occupy small home ranges on reefs. For non-resident fish muscle tissue isotopes would diverge from those typical of reef values and instead reflect isotope values of fish frequenting coastal riverine habitats. These ideas were tested relative to the known isoscape distributions in the Moreton Bay area (Fig. 1).

1.1. Study area and fish movement across the Moreton Bay isoscape

Moreton Bay is a large (3400 km^2) subtropical embayment which supports extensive recreational and commercial fisheries. Habitats in the bay range from mangrove creek, salt marsh and seagrass habitats in the coastal riverine areas (referred to here as "coastal riverine habitats"), to seagrass, fringing coral reefs and fringing mangroves towards the ocean entrance (referred to here as "island habitats") (Fig. 1). The reefs consist of boulder corals (*Favia* spp.) and some branching corals (*Acropora* spp.) and are located within 1000 m of intertidal reef flats, fringing mangroves (*Avicennia marina*) and seagrass beds (*Zostera muelleri*).

To explore fish movement on inshore coral reefs in Moreton Bay a geographic isotope seascape or "isoscape" was developed. There is a gradient for $\delta^{13}C$ and $\delta^{15}N$ values of fishes and invertebrates in estuarine coastal areas of eastern Australia relating to local rivers (Connolly et al., 2009). Due to the increased availability of terrestrial sources and organic matter from mangroves and associated flora in coastal riverine areas, lower $\delta^{13}C$ values of −17 to −21‰ and higher $\delta^{15}N$ values (16‰ ^{15}N) should be found in muscle tissue of fish which have spent time feeding in coastal riverine habitats in Moreton Bay (Connolly, 2003). Fish that are long-term residents of island habitats nearer to the open ocean should have $\delta^{13}C$ isotope values in the −9 to −16‰ range usually seen for coral reef residents (Wyatt et al., 2012; Davis et al., 2014) and lower $\delta^{15}N$ values (approximately 14‰) (Fig. 1). Although mangroves are found in both coastal riverine and island habitats, those on the mainland are riverine mangroves with high levels of sediment input where fish are known to feed (Laegdsgaard and Johnson, 2001). Island habitats have dry sandy fringing mangroves that do not offer many ^{13}C-depleted foods to reef fish (Davis et al., 2014).

The criteria for resident fish in the coral reef islands of Moreton Bay were that (1) they have relatively similar liver and muscle isotope values reflecting a consistent long-term diet, and that muscle values of $\delta^{13}C$ were in the range usually seen for coral reef residents. Two other feeding strategies could also reflect residency; (2) inconsistent $\delta^{13}C$ values in liver and muscle tissue, but with values in the range consistent with island habitat foods, suggesting diet switching within the island habitat and (3) equilibrium for foods depleted in ^{13}C. This last strategy is highly unlikely given the typical range of isotope values in island habitats.

Lower $\delta^{13}C$ values and a strong difference in muscle vs. liver values are expected for animals migrating from coastal riverine areas. Foods very depleted in ^{13}C are not typically observed in the diet of fish collected from island habitats (Davis et al., 2014), ruling

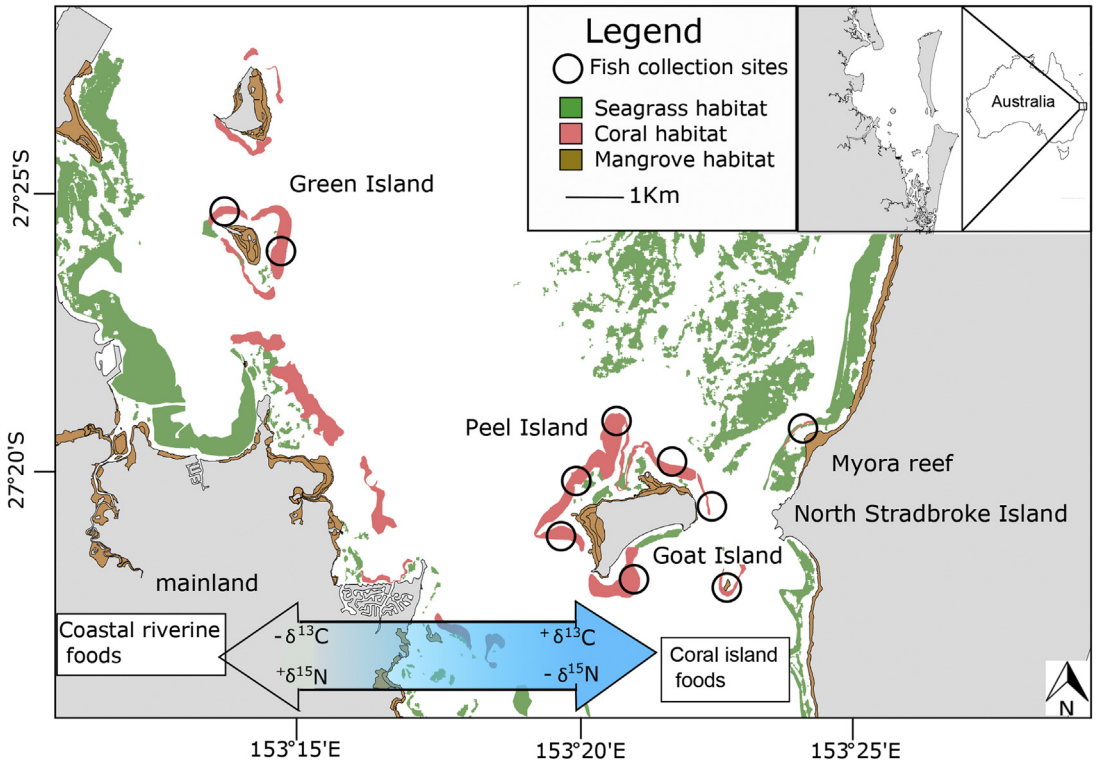

Fig. 1. Location of sampling sites in Moreton Bay, Queensland, Australia, and predicted trends in carbon stable isotope values (blue arrow). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

out the possibility of these isotopic changes reflecting small scale movement or changes in diet over time within the same habitat.

To test these patterns of movement and residency, individuals from five fish species were collected around mid-bay coral reef islands, with three species expected to be mostly composed of residents, and greater degrees of movement expected for the remaining two species. The resident species were Guenther's wrasse (*Pseudolabrus Guentheri*), dusky rabbitfish (*Siganus fuscescens*) and painted sweetlips (*Diagramma labiosum*), while those expected to be more mobile were (*Acanthopagrus australis*) and Moses perch (*Lutjanus russelli*). Differences in size-frequency distributions among habitats suggest Moses perch make ontogenetic movements from inshore mangroves to coastal fringing reefs (Newman and Williams, 1996), while tagging studies indicate juvenile bream make small scale movements (<6 km) for feeding and adult bream make large scale movements (10–90 km) for spawning (Pollock, 1982). Haemulids like painted sweetlips make small daily movements, but may make ontogenetic migrations from estuaries to coral reefs (Verweij and Nagelkerken, 2007). Conversely, tropical congeners of the rabbitfish (e.g. *Siganus lineatus*) and wrasse have home ranges restricted to coral reefs (Eckert, 1987; Fox and Bellwood, 2011). These five species were compared to establish isotope patterns of residency and movement across the Moreton Bay isoscape.

2. Methods

2.1. Sample collection

A total of 195 fish of the five species (wrasse, painted sweetlips, rabbitfish, bream and Moses perch) were collected by line and spearfishing from inshore fringing coral reefs in Moreton Bay during the winter of 2012. Three to five fish of each species were collected from six reef sites at Peel Island, a large continuous area of coral reef in central Moreton Bay, and from four smaller coral reefs in both eastern and western parts of the bay (Fig. 1). While a range of size classes was targeted for each species, bream and Moses perch were mainly juveniles based on length at maturity (Pollock, 1982) and gonad development, respectively. The time of collection coincided with the spawning season for bream, so the majority of adult fish were probably at sand bar spawning sites (Pollock, 1982) rather than at reef sampling sites. Only juvenile Moses perch are observed in inshore habitats (Sheaves, 1995) while adults are typically found on offshore reefs (Newman and Williams, 1996) so adult individuals may be absent within Moreton Bay.

2.2. Sample analysis

Fish were euthanized by pithing. The standard length was measured (SL ± 1 mm) (Table 1) and fish were dissected to remove liver tissue and a sample of muscle tissue from the left dorsolateral side. All tissue was rinsed with deionized water, dried at 60° C for 72 h and homogenized. Isotopes of subsamples of animal tissue (1–3 mg) were analyzed on a Sercon Hydra 20–22, Sercon Europa EA-GSL mass spectrometer. Isotopic ratios are expressed in delta notation according to the formula: $\delta X = [(R_{sample}/R_{standard}) - 1]$ *1000, where $X = {}^{13}C$ or ${}^{15}N$ and R is the respective ${}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ ratio. Nitrogen results are expressed relative to atmospheric nitrogen and carbon results are expressed relative to Vienna Pee-Dee Belemnite with analytical SD within 0.4‰.

Fish liver tissues typically exhibit higher lipid content than muscle (Sweeting et al., 2006), therefore a subset of five liver samples from each species was lipid-extracted using hexane (Fry, 2002) to account for variation in the lipid content among individuals. Evaluation of these samples showed that the lipid-corrections developed by (Fry, 2002; Gelpi et al., 2013) could be applied to these reef fish, and only lipid-corrected carbon isotope values of liver tissue are reported. Muscle contained very little lipid in these species and was not lipid-corrected. Removing lipids controlled for the effect of differences in lipid content on stable isotopes among individuals relative to reproductive status or maturity.

Table 1
Summary of the number (N) and standard length (SL) (cm) of fishes collected from coral reefs in Moreton Bay.

Species	Location	Small reefs (Green and Goat Islands, Myora reef)	Peel Island reefs
Guenther's wrasse			
	N	16	23
	SL (cm)	10–18	12–18
Painted sweetlips			
	N	15	30
	SL (cm)	24–41	23–51
Rabbitfish			
	N	20	20
	SL (cm)	11–20	7–17
Bream			
	N	20	30
	SL (cm)	21–29	21–30
Moses perch			
	N	6	25
	SL (cm)	17–18	17–21

2.3. Statistical analysis

Isotope data for fish collected at all reefs on Peel Island were pooled and then across all remaining locations, since the remaining reefs were much smaller in area. Residency was then evaluated for fish collected from only the Peel Island reefs to assess variability on large continuous reefs. A linear regression and the coefficients of determination (r^2) were used to describe the consistency in $\delta^{13}C$ or $\delta^{15}N$ values between liver and muscle tissue for each species at Peel Island. Higher r^2 values indicate a stable diet and, therefore, higher residency or diet specialization among individuals, while lower r^2 values indicate lower residency or more generalist feeding habits among individuals, depending on the range of $\delta^{13}C$ values.

Some species had a natural offset in $\delta^{13}C$ between liver and muscle tissues. This offset may be due to differences in fractionation, or how tissues turn over (Pinnegar and Polunin, 1999). The tissue-based offset ($\Delta^{13}C_{muscle\ -\ liver}$) was accounted for by taking the average difference between muscle and liver stable isotope values for all individuals considered resident for each species and adjusting any perceived differences between tissues of all individuals by that value. Relationships for each species from which offsets were derived were $r^2 = 0.67$, 0.63, 0.68, 0.59 and 0.71 for wrasse, painted sweetlips, rabbitfish, bream, and Moses perch, respectively (all relationships were statistically significant $p < 0.01$). The offset corrections were −0.3‰ for bream, 0.7‰ for rabbitfish and −0.7‰ for Moses perch, painted sweetlips and wrasse. Rabbitfish were the only species with muscle tissue that was more enriched than liver tissue on average, perhaps due to the higher fractionation in muscle tissue of herbivores compared to carnivores and omnivores (Igulu et al., 2013).

Fish with <2‰ difference in $\delta^{13}C$ between muscle and liver tissue generally had $\delta^{13}C$ values typical of foods available on inshore reefs (−10 to −17‰) (Davis et al., 2014), while fish with >2‰ variability in carbon isotopes between tissues, above the aforementioned offsets, were well separated from the rest of the samples for each species and were mostly depleted in ^{13}C (see

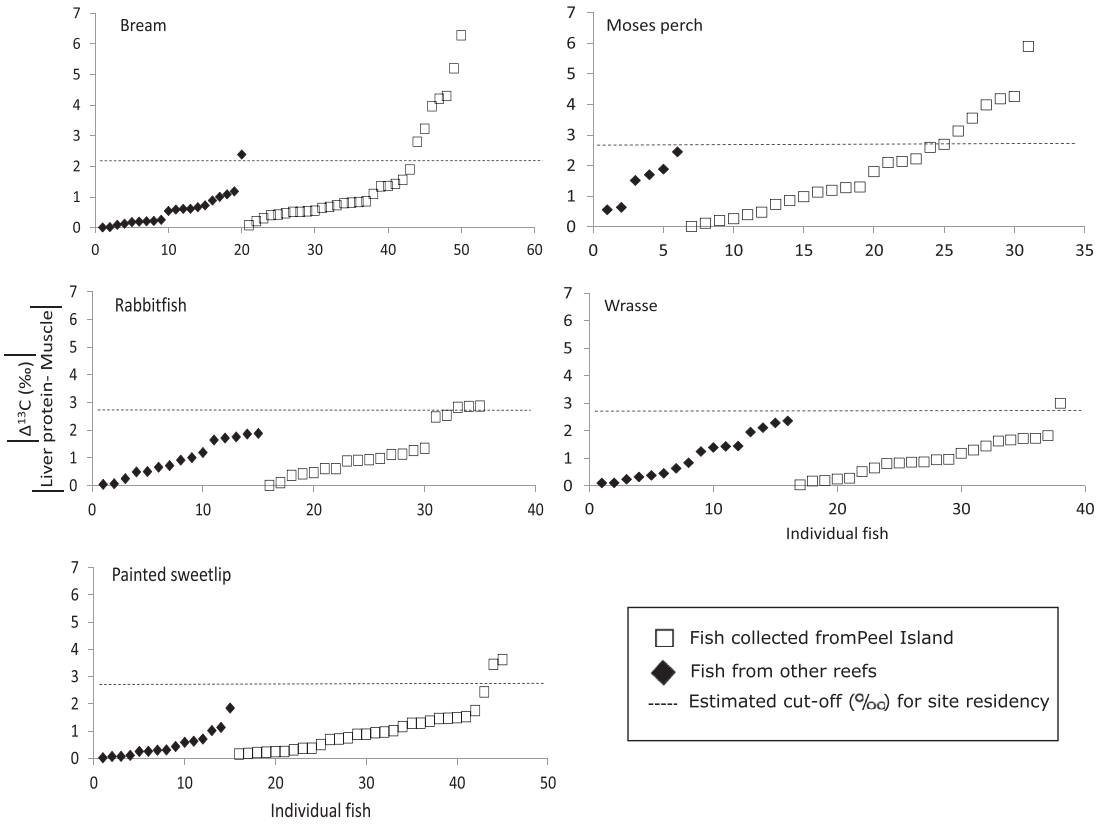

Fig. 2. Absolute values of differences in $\delta^{13}C$ (‰) between muscle and liver tissue for individual bream (*Acanthopagrus australis*), Moses perch (*Lutjanus russelli*), painted sweetlips (*Diagramma labiosum*), rabbitfish (*Siganus fuscescens*) and wrasse (*Diagramma labiosum*).

Figs. 2 and 3 below). Thus individuals with > |2‰| differential between tissues were considered to be non-resident, or to have recently switched diet sources. Although this threshold was not statistically derived, it represents a conservative estimate of residency that easily incorporates the small natural variability observed between fish liver and muscle tissue during controlled feeding experiments (Pinnegar and Polunin, 1999; Trueman et al., 2005; Malpica-Cruz et al., 2012; Varela et al., 2012). These small differences may be attributed to differences in amino acid and protein composition between liver and muscle (Estrada et al., 2005) or lipid content (Pinnegar and Polunin, 1999; Madigan et al., 2012).

3. Results

3.1. General stable isotope patterns

Fish from reefs in Moreton Bay had a wide range of stable isotopic values in both muscle $\delta^{13}C$ (−21.6 to −10.8‰) and $\delta^{15}N$ (8.0–15.8‰) and in liver tissue $\delta^{13}C$ (−20.7 to −9.1‰) and $\delta^{15}N$ (7.5–13.3). Bream and Moses perch had the widest range of carbon isotope values in muscle tissue (10‰), while wrasse and painted sweetlips had only a 5‰ range in $\delta^{13}C$ for muscle tissue. Bream had the highest $\delta^{15}N$ value (16‰) in muscle tissue and the greatest range in $\delta^{15}N$ (7‰), while rabbitfish had the lowest $\delta^{15}N$ value (7‰) in muscle tissue and the smallest range (2‰). Painted sweetlips, wrasse and Moses perch were intermediate.

Isotope values of liver tissue for two species (bream and Moses perch) collected from coral reefs in this study were depleted in ^{15}N and enriched in ^{13}C relative to individuals collected in coastal riverine habitats in previous studies (Table 2), and these data were used to illustrate resident values for fish in coral reef and coastal riverine habitats in Moreton Bay.

3.2. Consistency in isotope values between tissues

All species except bream and Moses perch had few individuals with large differences in $\delta^{13}C$ between tissues. Bream and Moses perch had the highest range in $\delta^{13}C$ (7 and 8‰ respectively), while painted sweetlips, rabbitfish and wrasse had lower ranges (5–6‰).

Differences in $\delta^{15}N$ of liver and muscle tissue were small and did not vary much among or within species, or correspond with changes in $\delta^{13}C$. Liver tissue was approximately 1.5‰ more depleted in ^{15}N for most species, except for rabbitfish that were slightly enriched (approximately 0.3‰).

3.3. Residency

Wrasse had consistent $\delta^{13}C$ values between tissue types ($r^2 = 0.58$ ($p < 0.0001$) and enriched $\delta^{13}C$ values overall (Fig. 3). Rabbitfish and painted sweetlips also had similar $\delta^{13}C$ values between tissues ($r^2 = 0.44$, $p < 0.01$ and 0.50, $p < 0.01$ respectively), but rabbitfish diet in general was depleted in ^{13}C relative to reef based foods (Fig. 3). Bream had very inconsistent $\delta^{13}C$ values between tissues ($r^2 = 0.21$, $p < 0.01$), and the individuals with the largest differences had muscle tissue depleted in ^{13}C (−15 to −21‰) and liver tissue with more enriched values (−11 to −18‰; Figs. 3 and 4). These individuals also had muscle tissue that was enriched in ^{15}N compared to liver tissue (Fig. 4), though a similar

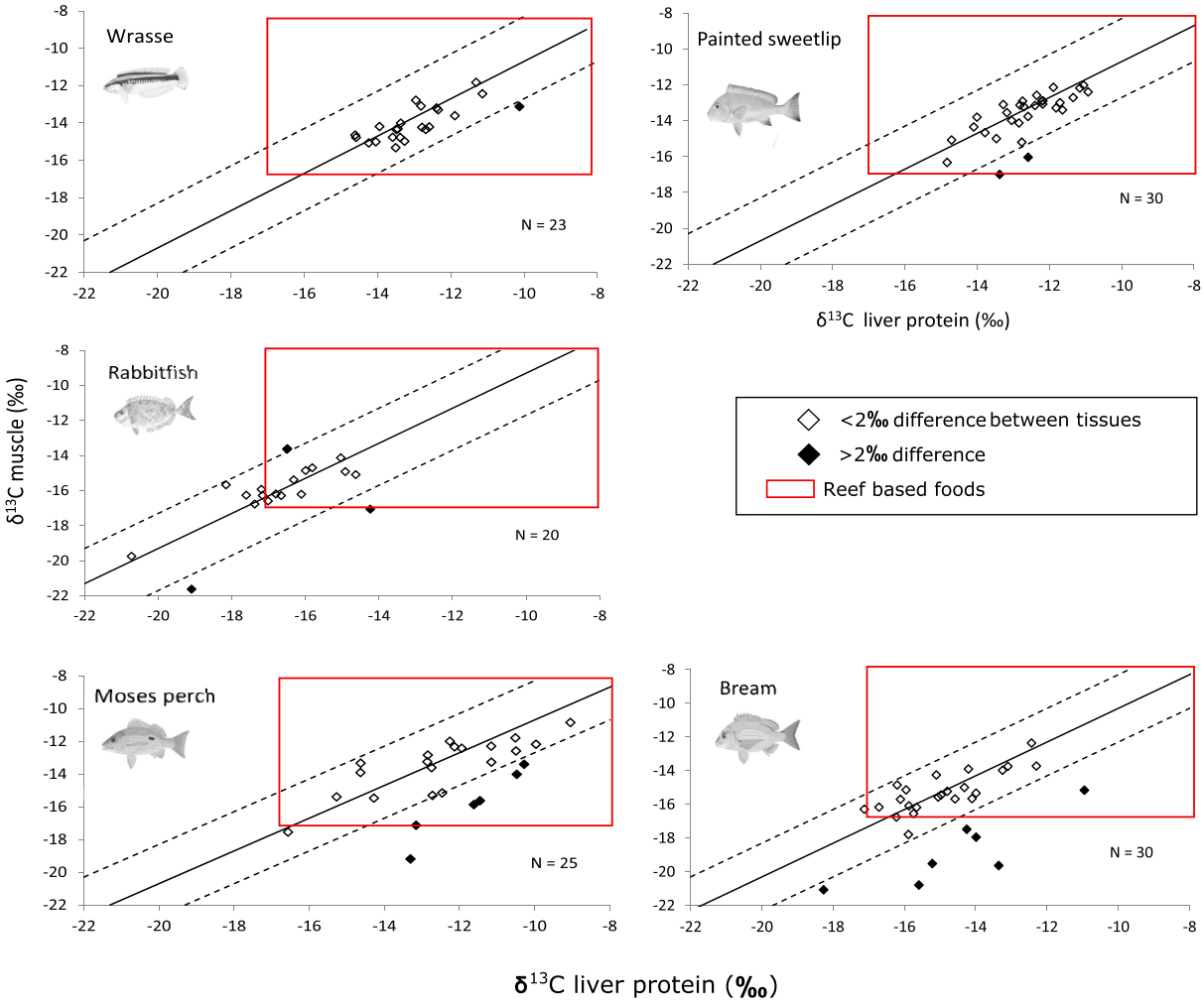

Fig. 3. The relationship between $\delta^{13}C$ values of liver and muscle tissue for all fishes collected from coral reefs at Peel Island, and individuals with >2‰ difference between tissues are highlighted. Hashed lines enclose the area within which fish were considered residents. Solid lines represent a one-to-one relationship between tissues, adjusted for natural offsets (detailed in Methods) within each species. N = total number of individuals.

Table 2
Carbon and nitrogen isotope ranges of muscle tissue of fishes (±SD) from coastal riverine habitats compared to liver tissue from fishes on inshore coral reefs (salinity 35‰).

Sampling region	Species sampled	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Source
Coastal riverine habitats				
Moreton Bay, QLD	*L. russelli*	−18.0 ± 0.8	12.9 ± 0.4	Lauchlan (pers. comm.) 2012
	A. australis	−20.0 ± 3.0	11.0 ± 1.0	Connolly, 2003
	A. australis	−17.0		Van De Merwe (pers comm.) 2012
Belongil Creek, NSW	*A. australis*	−19.4 ± 0.3	11.3 ± 0.7	Hadwen et al. 2007
Island habitats				
Moreton Bay QLD	*L. russelli*	−14.9 ± 1.8	10.3 ± 1.2	This study
	A. australis	−15.5 ± 1.6	10.9 ± 1.2	This study

pattern was observed in most species. Several Moses perch had low $\delta^{13}C$ values in muscle tissue compared to liver tissue ($r^2 = 0.34$, $p < 0.01$). The isotope values for Moses perch muscle tissue were higher than for bream, however, and largely fit within the range expected for reef diet sources (Fig. 3). There was no correlation between change in $\delta^{13}C$ values and size class for bream or Moses perch (Fig. 5).

4. Discussion

Estuarine habitats are important nursery areas and feeding habitats for fishes which make movements to coral reefs (Nagelkerken et al., 2014; Sheaves et al., 2014). Tracking fish in shallow estuarine areas is difficult, however, so little is known about the movement patterns of most species. In this study stable C and N isotopes in multiple tissues were successfully used to

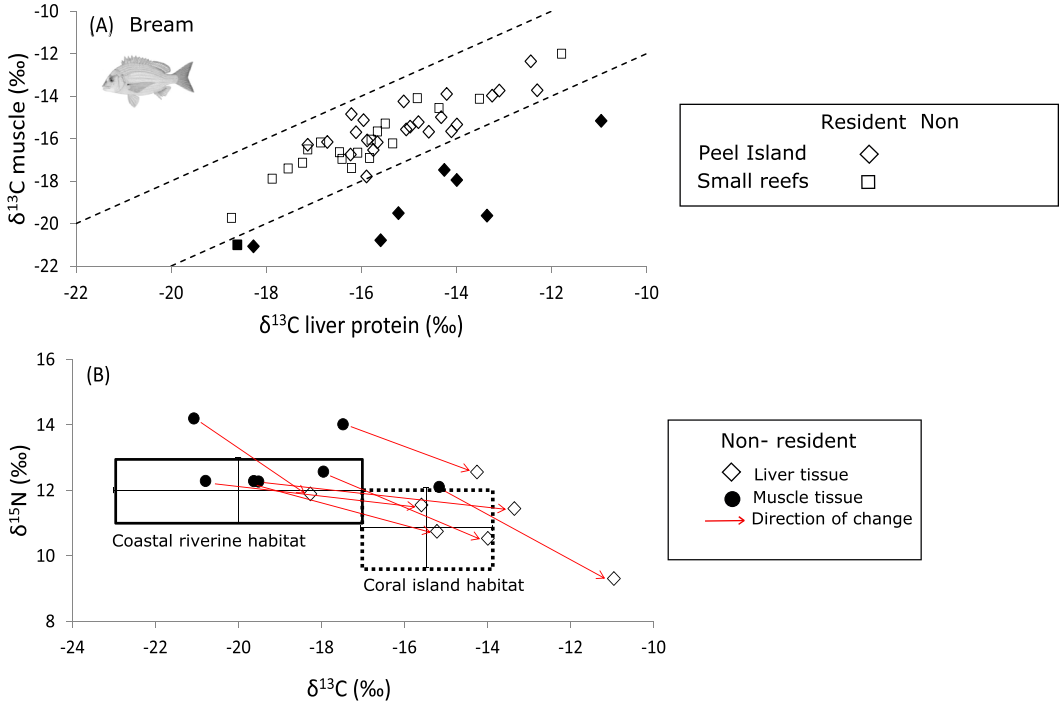

Fig. 4. (A) The relationship between muscle and liver $\delta^{13}C$ for bream (*Acanthopagrus australis*) collected from all locations, with non-resident individuals highlighted and (B) $\delta^{13}C$ and $\delta^{15}N$ of liver and muscle tissue for 'non-resident' bream collected from Peel Island, with the isotope range (±SE) of values for bream collected from coral island habitats (this study), compared to fish collected from coastal riverine habitats in Moreton Bay overlaid. Riverine mangrove fish values taken from (Connolly, 2003).

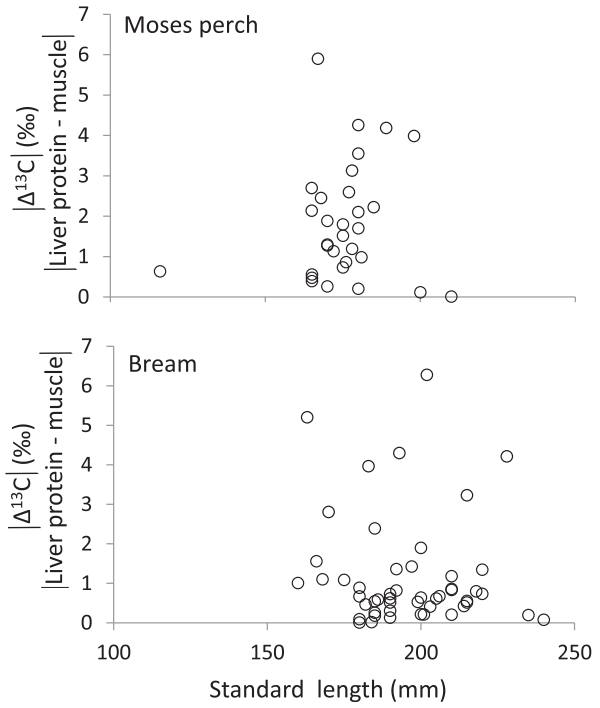

Fig. 5. Relationship between residency ($|\delta^{13}C_{liver} - \delta^{13}C_{muscle}|$) and the standard length of individual fish (open circles) at all locations for Moses perch (*Lutjanus russelli*) and bream (*Acanthopagrus australis*).

characterize the level of residency for fishes on inshore coral reefs in Moreton Bay. The hypothesis that fishes known to make large-scale migrations would have lower residency than those thought to have small home ranges was largely supported because (1) Moses perch and bream had much lower consistency in muscle and liver tissue $\delta^{13}C$ compared to the remaining three species, (2) individuals of bream and Moses perch with the largest differences between tissue types had long term diet values which were not consistent with food sources typically found on or near the reef, and (3) the lower values of $\delta^{13}C$ in muscle tissue matched those of resident bream collected in coastal riverine habitats of southeast Queensland in other studies (Connolly, 2003; Hadwen et al., 2007).

Values of $\delta^{15}N$ were less useful for characterizing the degree of residency among species. Using $\delta^{15}N$ to trace animal diet is more difficult because prey signals are confounded by several factors. Values of $\delta^{15}N$ may have been influenced by variable trophic fractionation (typically 3.2‰ compared to 1‰ for $\delta^{13}C$), and localized differences in nutrient loading (McCutchan et al., 2003; Pitt et al. 2009). Additionally, fish size affects the relationship between liver and muscle tissue isotopes (Trueman et al., 2005) and variability in the composition of essential and non-essential amino acids among tissues can contribute to inconsistency in $\delta^{15}N$ (Pinnegar and Polunin, 1999).

4.1. Overall range of diet sources

The range of carbon isotope values of resident individuals within a species was surprisingly broad. This was especially true for bream and Moses perch. The range in $\delta^{13}C$ among individuals was high compared to reef fish in other studies (Greenwood et al., 2010; Plass-Johnson et al., 2013) and fish sampled from areas with uniform foods (Fry and Parker, 1979). Fish in shallow benthic habitats typically exhibit a wide range in $\delta^{13}C$ however (Fry et al., 1999; Escalas et al., 2015) and diet plasticity in predatory reef fish may occur due to high site fidelity and specialization on multiple local food sources (Layman and Allgeier, 2011). Alternatively, the wide isotope ranges for these species could be due to the presence of

very recent migrants from mangrove creek or seagrass habitats that have not attained equilibrium with local reef diets. Fish in tropical inshore habitats often exploit a wide range of foods (Hammerschlag-Peyer and Layman, 2010) making it difficult to evaluate residency. In this study however, the presence of riverine mangroves and associated depleted diet sources still allowed us to successfully test for off-reef movements. This approach is not limited to areas with terrestrial habitats however, and could work for any food webs that have well-separated isotope values.

The large range in carbon stable isotopes among individuals could indicate local variation in food source isotopes (Fry et al., 1999) or variation in individual diets over time. Fish may have access to the same array of foods but individuals may have specific diet preferences. Alternatively, the mix of resources may vary across the island habitats, and this altered mix along with the relatively narrow home ranges of fish may explain the diversity in isotope values for resident fish. Future studies comparing fin clips to stomach content analysis could help test these hypotheses (Wyatt et al., 2010).

4.2. Residency among species

Carbon stable isotopes from liver and muscle tissue were useful for describing the degree of residency of fish on fringing reefs in Moreton Bay. Wrasse showed the highest level of residency to reefs on Peel Island, and a specialist diet strategy based on high consistency in $\delta^{13}C$ values between tissues. This species is small (max. length 18 cm) (Randall et al., 1997), lives on shallow reefs at all life stages (Talbot et al., 1978; Westneat, 2001), and exhibits territoriality around coral heads (pers. obs), suggesting it is very localized. For wrasse, the agreement between observations of home range and those from isotopic predictors of residency, suggests that $\delta^{13}C$ values in muscle and liver tissues may be a valuable tool for predicting residency in reef fish.

Bream in this study had longer term diets (i.e. muscle isotopes) that were similar to fish collected from coastal riverine habitats in previous studies (Connolly, 2003; Hadwen et al., 2007), suggesting that some fish had recently arrived at reefs from these habitats. Bream make large-scale (10–90 km) movements for spawning, but spawning events only last a few weeks and fish are far from their feeding areas during the migration (Pollock, 1982). It is unlikely that spawning movements explain the long-term ^{13}C-depleted diet of non-resident bream in this study because these movements only last for a short portion of the year and fish do not focus much effort on feeding during spawning events (Blaber, 2008). Additionally, most bream collected in this study were late juvenile (<21 cm FL) or newly matured fish, rather than large adults. A more probable explanation is that coastal riverine habitats are important nursery areas for bream, and some cohorts of fish move out towards central bay reefs to access additional food sources when nearing maturity. This type of habitat transition is observed for a congener of the bream in this study, the western yellowfin bream (*Acanthopagrus latus*) in Shark Bay, Western Australia (Platell et al., 2007). Western yellowfin bream shelter and feed as juveniles on sources such as crabs and gastropods in mangrove creeks, then move to rocky reefs and feed on bivalves as they near adulthood.

Similar to bream, Moses perch collected in this study were juveniles, and several showed large isotopic shifts from ^{13}C-depleted long-term diets, to enriched recent diets. This isotopic trend suggests Moses perch may also make movements from mangrove creeks towards coral reefs when reaching maturity. Ontogenetic transitions are typical of lutjanids and lethrinids in the Caribbean and Indo-Pacific (Wyatt et al., 2012; Kimirei et al., 2013a) and are predicted for Moses perch in eastern Australia based on size frequency distributions (Newman and Williams, 1996). Lutjanids move from nursery habitats to reefs to access better food sources when they reach a size where predation risk is reduced (Kimirei et al., 2013b). However, only two of six Moses perch with large isotopic shifts had muscle tissue $\delta^{13}C$ values consistent with fish collected from coastal riverine habitat. Thus, most of the >2‰ shifts could also reflect changing feeding strategies within reefs at Peel Island. For example, one cohort of Moses perch may have a diet composed mainly of ^{13}C-depleted pelagic foods such as small fish, and plankton but may have switched recently to specialize on more ^{13}C-enriched benthic foods. Foraging movements and diets of lutjanids in the Atlantic suggest there are high levels of individual specialization within species, with some fish moving to other habitats to feed while others consistently forage in a limited area (Hammerschlag-Peyer and Layman, 2010). The isotope values for Moses perch in this study could be consistent with both long-distance movements between coastal riverine habitats and islands as well as localized diet switching.

Both bream and Moses perch may make large-scale movements between coastal riverine habitats and coral reefs in Moreton Bay. While mangroves do occur on coral islands in the central bay, they are clear-water fringing mangroves which offer few carbon-depleted mangrove-based food sources for most fishes (Kieckbusch et al., 2004). Riverine mangroves occur in deeper sediments with low tidal exchange, and contribute more mangrove-associated food sources to benthic invertebrates than mangroves in open systems (Bouillon et al., 2004). These infauna can offer important food sources for carnivorous fishes (Sheaves, 2009), and fishes that feed in these habitats have low $\delta^{13}C$ values associated with mangle food webs (Lugendo et al., 2007; Abrantes et al., 2015). Additionally, although there was no relationship between fish size and variation in isotopic composition between tissues, Moses perch and bream were collected within narrow size ranges that were composed of late-juvenile or early adult life-stages. A relationship between ontogeny and residency may have been observed if a broader size range of fishes was collected (i.e. post-larval to mature adult).

Our predictions of home range for dusky rabbitfish and painted sweetlips were based on data from congeners of these species. Home range estimates for siganids at Lizard Island on the Great Barrier Reef suggest they remain localized to reefs (Fox and Bellwood, 2011), and isotopic data in this study shows this to be largely true for rabbitfish in Moreton Bay. A few individuals showed isotopic shifts between tissues, but with no specific trend, which suggests rabbitfish exhibit multiple diet strategies. The generally low $\delta^{13}C$ values in rabbitfish diets suggest they may depend on ^{13}C-depleted algal foods, such as the red alga *Catenella nipae* (Davis et al., 2014).

Painted sweetlips are part of the family Haemulidae (grunts), several species of which make large scale ontogenetic migrations between inshore nursery habitats and reefs and remain localized once settled (Appeldoorn et al., 2009). Fish collected in this study were all mature adults based on coloration and morphology (Davie, 2011), and as expected appeared largely resident to reefs at Peel Island. Fish in juvenile and adult size classes would need to be targeted to test whether isotopes could reflect ontogenetic movement for this species.

This study presents an initial investigation into a methodology that will be useful for more widespread characterizing of fish movement. Future studies might be able to increase robustness of results by collecting both juvenile and adult samples of each species in all habitats. This would provide clearer isotopic endmembers (isotope values of residents) for each habitat type. The next step would be to validate isotope measures of residency using complementary methods. Movement data based on acoustic telemetry or tag and recapture, for example, could be coupled with isotope data

from fin or scale tissue biopsies to validate results from dual tissue analysis. Additionally, compound specific analysis can better resolve habitat source values for N as well as C isotopes (McMahon et al., 2013) and may help in future studies of fish movement and residency.

The size of a fish can affect the rate of turnover in its tissues (Campana et al., 2010), however there was no relationship between fish size and muscle-liver isotopes among individuals in this study. Differences in turnover among different tissues may also occur among species depending on metabolic rates (Buchheister and Latour, 2010) but size-based differences in liver–muscle relationships among species were not observed here. The fishes in the median size range (bream and Moses perch) exhibited the largest differences in isotopes between tissues, while the largest (painted sweetlips) and smallest (rabbitfish and wrasse) species showed little difference. Future studies would benefit from species-specific estimates of tissue turnover, however, to confirm the particular time-scales reflected by the isotope values of diet sources in each tissue.

4.3. Conclusion

The movement of fish across inshore seascapes is pervasive but poorly understood, and research on this topic has been hampered by labor-intensive tagging methods. Isotopes of carbon in two tissues with different turnover rates provided a useful natural tracer of fish residency on coral reefs in an inshore embayment. Of the five fish species analyzed, two were identified as potentially making migrations between coastal riverine habitats and coral island habitats. These movements have important implications for the scale and location of protection measures such as marine reserves in inshore tropical ecosystems. Isotope analysis of multiple tissues is an underutilized tool for tracing fish movement, and can provide useful data for fisheries management in inshore areas where clear gradients in isotopic values occur.

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