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REPORT

Elucidating the trophodynamics of four coral reef fishes of the Solomon Islands using δ^{15}N and δ^{13}C

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Abstract Size-related diet shifts are important characteristics of fish trophodynamics. Here, body size–related changes in muscle δ^{15}N and δ^{13}C of four coral reef fishes, *Acanthurus nigrofuscus* (herbivore), *Chaetodon lunulatus* (corallivore), *Chromis xanthura* (planktivore) and *Plectropomus leopardus* (piscivore) were investigated at two locations in the Solomon Islands. All four species occupied distinct isotopic niches and the concurrent δ^{13}C′ values of *C. xanthura* and *P. leopardus* suggested a common planktonic production source. Size-related shifts in δ^{15}N, and thus trophic level, were observed in *C. xanthura, C. lunulatus* and *P. leopardus*, and these trends varied between location, indicating spatial differences in trophic ecology. A literature review of tropical fishes revealed that positive δ^{15}N-size trends are common while negative δ^{15}N-size trends are rare. Size-δ^{15}N trends fall into approximately equal groups representing size-based feeding within a food chain, and that associated with a basal resource shift and occurs in conjunction with changes in production source, indicated by δ^{13}C. The review also revealed large scale differences in isotope-size trends and this, combined with small scale location differences noted earlier, highlights a high degree of plasticity in the reef fishes studied. This suggests that trophic size analysis of reef fishes would provide a productive avenue to identify species potentially vulnerable to reef impacts as a result of constrained trophic behaviour.

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Introduction

Size-correlated shifts in diet are a common feature of many marine fish species (Jennings et al. 2001). Such shifts may be due to ontogenetic environmental factors such as habitat utilisation (Bellwood 2006), or result from correlations with body size including prey restrictions from gape dimensions (Mumby et al. 2006) and swimming speed (Schmidt-Nielsen 1984). Diet shifts can manifest as changes in trophic level (TrL), and/or production source sustaining individuals and populations. Such patterns have been observed in a range of coral reef fish species (Kingsford 1992; Eggleston et al. 1998); however, size-related shifts are not ubiquitous among all species (e.g., Cassermiro et al. 2007), particularly in complex ecosystems where multiple primary production sources support highly variable trophic assemblages (Layman et al. 2005) as occurs in coral reefs.

Traditionally trophodynamics studies are undertaken using gut content analysis; however, this technique assesses diet over very small temporal scales (Hyslop 1980), requires high sampling effort, a major disadvantage in diverse tropical systems, and may underestimate the extent of generalist and detritus feeding (Carassou et al. 2008). Stable isotope analysis (SIA) provides alternative measures of TrL and production source, and circumvents many of the weakness inherent in gut content data. SIA utilises naturally occurring differences in ^{15}N/^{14}N (δ^{15}N) and ^{13}C/^{12}C (δ^{13}C) ratios in tissues between consumers and their diet. These differences arise due to preferential retention of heavier isotopes and excretion of lighter isotopes, leading to relative enrichment in ^{15}N and ^{13}C between consumer and consumed, termed trophic fractionation. δ^{15}N fractionation at each trophic step ($\Delta\delta^{15}$N) in fish is large, ~3.2‰ (Sweeting et al. 2007b), allowing estimation of TrL relative to a suitable reference point (Post 2002). $\Delta\delta^{13}$C in fish is ~1.5‰ (Sweeting et al. 2007a) and is used to estimate the contributions of different production sources utilised in an individual's diet which typically differ in δ^{13}C.

SIA has proved particularly valuable in elucidating fish trophodynamics, suggesting that size-related feeding is common, although the strength of these relationships varies between species (Jennings et al. 2001) and within species in both space (Deudero et al. 2004) and time (Polis and Strong 1996). However, it is far from clear to what extent and over what scale differences may occur.

Despite the potential insights that SIA can provide, it remains a largely unused tool in coral systems and variability in size/trophic parameters among locations remains poorly understood. This study assesses whether four species of coral reef fish exhibited trends in isotopic signatures indicative of size-related feeding, and whether such trends varied spatially. Four species were chosen to represent a range of typical trophic guilds: herbivore, planktivore, corallivore and piscivore. A literature review of size-related trends in tropical fishes is also used to assess the ubiquity of size-related trends and extent of spatial variation at a range of scales.

Materials and methods

Study locations and sample collection

Target species were selected based on local abundance, determined by the Solomon Islands Marine Assessment (Green et al. 2006) and visual census, and to represent a wide range of trophic strategies. The species selected were *Acanthurus nigrofuscus* (herbivore), *Chaetodon lunulatus* (corallivore), *Chromis xanthura* (planktivore) and *Plectropomus leopardus* (piscivore).

Individuals were collected from two locations in the Ngella Island group (Central Province, Solomon Islands), Tulaghi (location A) and Nagatano (location B) (Fig. 1). Tulaghi has coral reefs extending south from the coastline for up to 5 km, higher human population densities and more intensive land use than Nagatano, a small island on the western tip of the Ngella Island group, which is also surrounded by extensive coral reefs.

Collection of *A. nigrofuscus, C. lunulatus,* and *C. xanthura* was spread across three sampling sites within each location (Fig. 1), to represent hydrographic and habitat variability. Specimens were collected by breathhold spearfishing at depths ranging from 2 to 15 m. Because of lower densities, *P. leopardus* were purchased opportunistically from fishermen at Tulaghi (location A). Individuals were selected to reflect the full length range from landed catch. Total length was recorded for all individuals. All fish were frozen on landing and transported on ice to laboratories of the University of the South Pacific, Honiara, where initial processing was carried out.

The following number of samples and size ranges were obtained: For *A. nigrofuscus* at location A and B, $n = 14$ and 15 with a size range of 45 and 60 mm, respectively. For *C. xanthura,* $n = 15$ at both locations with a size range of 45 mm at location A and 35 mm at location B. For *C. lunulatus,* $n = 15$ and 14 at locations A and B, respectively with both collections having a size range of 20 mm. For *P. leopardus* (collected only at location A), $n = 41$ with a size range of 225 mm.

Sample processing and isotope analysis

Approximately 5 g of lateral muscle were removed from each individual and oven dried at 60°C for 6 h. Dried muscle was stored in plastic tubes and sealed in plastic bags containing silica desiccating gel for transport to the UK where samples were ground, homogenised and 1 mg weighed into 6 mm × 4 mm tin capsules for C and N SIA.

Determination of δ^{15}N, δ^{13}C and % content of C and N was carried out by Elemental Analysis Isotope Ratio Mass Spectrometry by Iso-analytical Ltd (Crewe, UK) using a Europa Scientific elemental analyser coupled to a Europa Continuous Flow Isotope Ratio Mass Spectrometer. Values of δ^{15}N and δ^{13}C were reported relative to N_2 in air and V-PDB, respectively. Calibration and quality control were conducted with an internal reference material traceable to the International Atomic Energy Agency inter-laboratory comparison standards. A blind reference sample of cod muscle ($n = 7$, δ^{13}C: SD = 0.16, δ^{15}N: SD = 0.04) was included, and several samples collected for this study were run as blind duplicates ($n_{\text{duplicates}} = 14$, δ^{13}C: mean SD = 0.17, δ^{15}N: mean SD = 0.21). Duplicates were used to assess precision only and were not included in final analysis.

Statistical analysis

No obvious outliers were detected, so all data were included in the analyses. Length data were converted to weight (g) using length–weight parameters (Goeden 1978; Letourneur et al. 1998; Green et al. 2006; Froese and Pauly 2009). Where specific length–weight relationships were not available genus-wide average values were used (Froese and Pauly 2009). Weight data were $\log_2$ transformed.

Lipids are ^{13}C depleted relative to proteins (Focken and Becker 1998; Sweeting et al. 2006), and variations in lipid content may confound analysis. Lipid-controlled δ^{13}C data

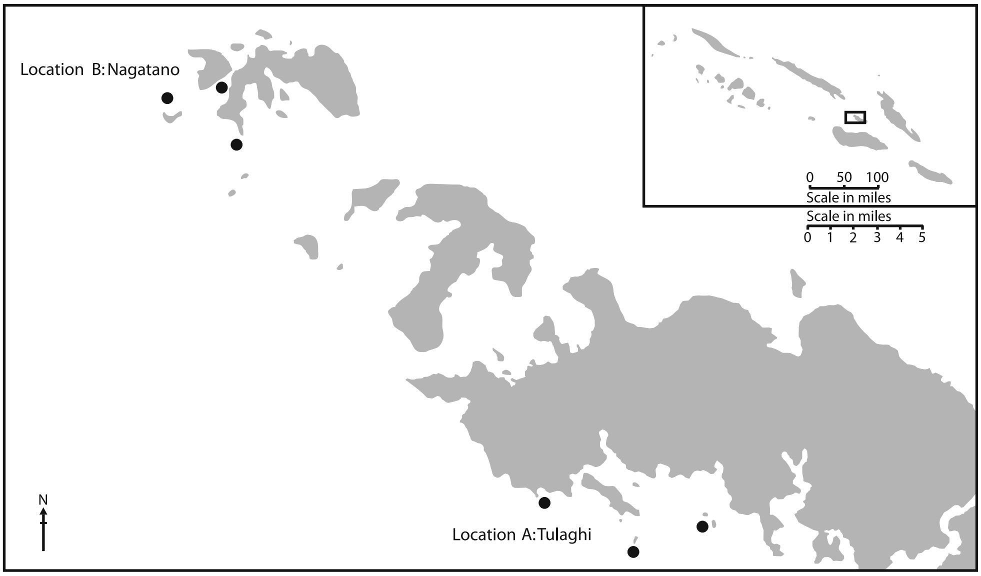

Fig. 1 Map of study locations. *Dots contained within circles* show sample collection sites. *Inset* shows the Solomon Islands

($\delta^{13}C'$) were derived by normalisation of $\delta^{13}C$ following a modified Sweeting et al. (2006) arithmetic correction. In the modification the C:N for pure protein in the arithmetic correction of Sweeting et al. (2006), usually determined by experimental lipid extraction, was replaced with the lowest observed species-specific C:N. This, in effect, normalised $\delta^{13}C$ of each species to the lowest observed lipid content within species. C:N ranges were 3.04–3.47 for *A. nigrofuscus*, 2.97–3.43 for *C. xanthura*, 3.04–3.34 *for C. lunulatus* and 2.98–3.54 for *P. leopardus*. The resultant lipid correction to $\delta^{13}C$ was thus 0.86, 0.93, 0.62 and 1.10‰ or less for each species, respectively. These corrections were independent of size. Normalisation is adequate as analyses of isotopic signature with size were focused principally on changes in slope rather than intercept.

Spatial variation in size-related $\delta^{15}N$ and $\delta^{13}C'$ were assessed using GLM ANCOVA with the interaction term size*location and size as a covariate (Table 1). When size*location effects were significant, location-specific regression parameters were used to describe size-related trends. Where the interaction was not significant, but size was a significant factor pooled regression slopes were given to describe size-related feeding patterns. *P. leopardus* was only obtained from one location; thus, trends in $\delta^{15}N$ and $\delta^{13}C'$ were assessed via least squares linear regression.

Table 1 GLM ANOVA results for *C. xanthura*, *C. lunulatus* and *A. nigrofuscus* $\delta^{15}N$, $\delta^{13}C$, C:N (as % element), and $\delta^{13}C'$ with interaction term Location*Size ($\log_2$ transformed weight)

		A. nigrofuscus		*C. lunulatus*		*C. xanthura*	
		$F_{1,25}$	*p*	$F_{1,25}$	*p*	$F_{1,26}$	*p*
$\delta^{15}N$	Location	0.09	0.765	3.31	0.081	**47.90**	**<0.001**
	Size	0.02	0.876	4.19	0.051	**8.13**	**0.008**
	Location*size	0.31	0.581	3.30	0.082	**6.30**	**0.019**
$\delta^{13}C'$	Location	2.82	0.106	0.01	0.919	0.01	0.907
	Size	0.14	0.716	0.81	0.376	**14.71**	**0.004**
	Location*size	2.41	0.133	0.02	0.886	0.00	0.998

Significant results are highlighted in bold

Residuals of all model fits were used to assess normality and heteroscedasity. On a minority of occasions, residuals were non-normal and no appropriate transformation was found that would induce normality. However given the infrequency of non-normality, the tolerance of tests to this infringement (Underwood 1997) and that analyses all met assumptions of heteroscedasity, GLM outputs were deemed valid. Variance about the mean is given as ± 1SD.

Literature review

To evaluate the ubiquity of ontogenetic or size-related feeding behaviour in tropical fishes, published data on size-related trends in $\delta^{15}N$ or $\delta^{13}C$ were collated from the literature using the ISI literature database (web of knowledge) key word searches. These included combinations of “isotop*”, “trophic”, “size”, “fish*”, “diet”, “coral”, “tropical”, “marine” and forward and backward citation pursuit. The survey covered literature published between January 1977 and April 2009 (Table 2). Criteria for inclusion were all marine and coastal fishes sampled between latitudes 35° north or south.

Results

Species differed in both $\delta^{15}N$ (Kruskal–Wallis $\chi^2 = 110.67$, df = 3, $P < 0.001$) and $\delta^{13}C'$ ($\chi^2 = 96.40$, df = 3, $P < 0.001$) (Fig. 2). Non-parametric pairwise

Table 2 Size-based trends in δ^{15}N and δ^{13}C in tropical fishes

Family	Species	δ^{15}N	δ^{13}C	Guild	Habitat	Author*
Reef fishes						
Acanthuridae	*Acanthurus bahianus*	0	0	H	Coral reef	1
	Acanthurus chirurgus	0	0	H	Coral reef	1
	Acanthurus nigrofuscus	0	0	H	Coral reef	2
	Acanthurus shoal	+	0	H	Coral reef	3
Apogoninae	*Cheilidopterus quinquelineatus*	0	+	P	Coral reef	4
	Cheilodipterus novemstriatus	0	+	Pl	Coral reef	3
Chaetodontidae	*Chaetodon lunulatus*	0	0	Co	Coral reef	2
Haemulidae	*Haemulon flavolineatum*	+	0	C	Coral reef	1
	Haemulon flavolineatum	0	0	C	Coral reef	5
	Haemulon sciurus	+	0	C	Coral reef	1
Lutjanidae	*Lutjanus apodus*	+	−	C	Coral reef	1
	Lutjanus griseus	+	0	C	Coral reef	1
	Ocyurus chrysurus	+	0	C	Coral reef	1
	Ocyurus chrysurus	−	0	C	Coral reef	6
	Ocyurus chrysurus	−	−	C	Coral reef	6
Mullidae	*Parupeneus margaritatus*	+	0	O	Coral reef	3
Nemipteridae	*Scolopsis ghanam*	+	+	I	Coral reef	3
Pomacentridae	*Abudebduf sexfasciatus*	−	+	Pl	Coral reef	4
	Abudebduf vaigiensis	0	0	O	Coral reef	3
	Chromis xanthopterygia	0	0	Pl	Coral reef	3
	Chromis xanthura	+	+	Pl	Coral reef	2
	Stegastes nigricans	+	−	H	Coral reef	4
Scaridae	*Scarus iserti*	0	0	H	Coral reef	1
	Scarus taeniopterus	0	0	H	Coral reef	1
	Cephalopholis hemistiktos	+	0	I	Coral reef	3
	Plectropomus leopardus	+	0	P	Coral reef	2
Synodontidae	*Synodus variegates*	−	0	P	Coral reef	4
Other tropical fishes						
Alepisauridae	*Alepisaurus ferox*	+	…	C	Pelagic	7
Blenniidae	*Ecsenius lineatus*	+	+	O	Rocky reef	8
	Ecsenius namiyei	+	+	O	Rocky reef	8
Hemiramphidae	*Hyporhamphus regularis ardelio*	0	+	O	Seagrass	9
Lutjanidae	*Lutjanus campechanus*	+	+	C	Mixed	10
Mugilidae	*Liza macrolepis*	0	0	D	Mangrove	11
Pomacentridae	*Stegastes fasciolatus*	+	0	H	Rocky reef	8
Scombridae	*Thunnus alalunga*	−	…	C	Pelagic	7
	Thunnus albacares	+	0	C	Pelagic	12
	Thunnus albacares	+	…	P	Pelagic	7
	Thunnus albacares	0	0	P	Pelagic	13
Xiphiidae	*Xiphias gladius*	+	…	P	Pelagic	7
	Xiphias gladius	+	+	P	Pelagic	13

Trends are indicated by symbols (+, positive, 0, none, −, negative, …, no data) for different tropic guilds (*H* herbivore, *P* piscivore, *Pl* planktivore, *Co* coralivore, *C* carnivore, *O* omnivore, *I* invertivore, *D* detritivore). *Cocheret de la Moriniere et al. (2003) (1), this study (2), Mill (2007) (3), Carassou et al. (2008) (4), Nagelkerken et al. (2008) (5), Verweij et al. (2008) (6), Revill et al. (2009) (7), Ho et al. (2007) (8), Carseldine and Tibbets (2005) (9), Wells et al. (2008) (10), Lin et al. (2007) (11), Graham et al. (2007) (12), Ménard et al. (2007) (13)

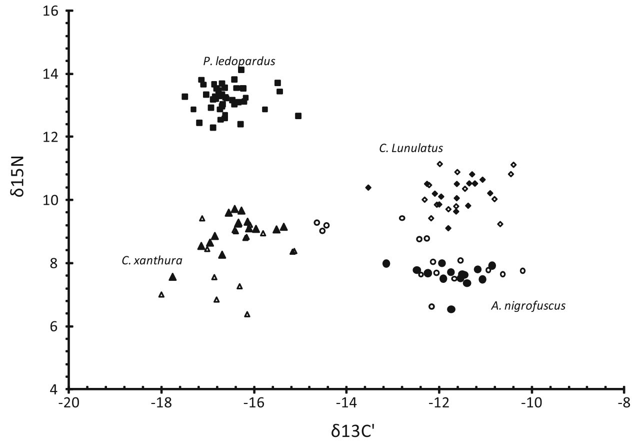

Fig. 2 Isotopic map of sampled populations of the herbivore *Acanthurus nigrofuscus* (*circles*),the corallivore *Chaetodon lunulatus* (*diamonds*), the planktivore *Chromis xanthura* (*triangles*) and the piscavore *Plectropomus leopardus* (*squares*) from Tulaghi (location A) and Nagatano (location B), in the Solomon Islands. *Closed* and *open* shapes represent data from locations A and B, respectively

analysis suggested all species pairs differed in terms of δ^{15}N and δ^{13}C′, except for δ^{13}C′ between *P. leopardus* and *C. xanthura*, and *A. nigrofuscus* and *C. lunulatus*.

For *A. nigrofuscus* δ^{15}N and δ^{13}C′, the location*size interaction was non-significant as were individual factors (Table 1). The pooled regression for δ^{15}N with size irrespective of location was non-significant ($r^2 = 0.002, F_{1,27} = 0.07, P = 0.798$). The pooled regression for δ^{13}C′ was also non-significant ($r^2 = 0.11$, $F_{1,27} = 3.33$, $P = 0.079$).

The location*size interaction for *C. lunulatus* δ^{15}N was marginally non-significant as were both size and location main effects (Table 1). As a small increase in statistical power could tip this result into significance, both pooled and location-specific regressions were investigated. The pooled regression for δ^{15}N was marginally non-significant ($\delta^{15}\text{N} = 6.96 + 0.702 \log_2$ mass, $r^2 = 0.13$, $F_{1,27} = 4.02$, $P = 0.055$). Location-specific regressions were non-significant for location A ($r^2 = 0.002$, $F_{1,13} = 0.03$, $P = 0.865$), but were significant for location B ($\delta^{15}\text{N} = 3.91 + 1.35 \log_2$ mass, $r^2 = 0.36$, $F_{1,13} = 6.75$, $P = 0.023$). δ^{13}C′ was non-significant for all factors (Table 1). The pooled regression of δ^{13}C′ with size irrespective of location was also non-significant ($r^2 = 0.04$, $F_{1,27} = 1.23$, $P = 0.276$).

Chromis xanthura δ^{15}N exhibited a significant location*size interaction (Table 1), with regressions significant at both locations A ($\delta^{15}\text{N} = 5.90 + 0.656 \log_2$ mass, $r^2 = 0.573$, $F_{1,13} = 17.42$, $P = 0.001$) and B ($\delta^{15}\text{N} = 5.346 + 0.635 \log_2$ mass, $r^2 = 0.137$, $F_{1,13} = 29$, $P < 0.001$). In contrast, only size was significant for *C. xanthura* δ^{13}C′ (Table 1) with a significant pooled regression ($\delta^{13}\text{C} = -18.9 + 0.549 \log_2$ mass, $r^2 = 0.261$, $F_{1,28} = 9.89$, $P = 0.004$).

Plectropomus leopardus (collected only from location A) showed a significant positive relationship for δ^{15}N with size ($\delta^{15}\text{N} = 9.75 + 0.367 \log_2$ mass, $r^2 = 0.531$, $F_{1,39} = 44.08$, $P < 0.001$). In contrast, the relationship between δ^{13}C′ and size was non-significant ($r^2 = 0.045$, $F_{1,39} = 1.84$, $P = 0.183$).

Review of size-based isotopic changes

The review generated 27 δ^{15}N- and δ^{13}C-size trends for 24 reef species and a further 13 δ^{15}N-size trends for 10 non-reef species and 10 δ^{13}C-size trends for 8 non-reef species (Table 2). Amongst coral reef fishes, 44.4% of populations studied exhibited positive δ^{15}N-size trends, 40.7% exhibited no trend and 14.8% showed negative trends. In contrast, for δ^{13}C-size trends, 18.5% were positive, 70.4% exhibited no trend and 11.1% exhibited negative trends. Across all tropical populations, the occurrence of positive δ^{15}N-size trends was slightly higher; 52.5% trends were positive, 35.0% were neutral and 12.5% negative, while for δ^{13}C-size trends, neutral trends again dominated (63.9%) with 27.8% exhibiting positive trends and 8.3% recording negative trends.

The data set was not extensive enough to statistically compare the distributions of trends among trophic guilds; however, planktivores, carnivores and piscivores all included examples of all three patterns of δ^{15}N-size trends. Both herbivores and omnivores exhibited only neutral or positive trends in δ^{15}N with body size. Patterns within guilds were less variable for δ^{13}C, with no particular trend in δ^{13}C dominating most guilds with few exceptions. However, both omnivores and planktivores exhibited high frequencies of positive trends in δ^{13}C (60% and 75% of populations, respectively), although the low samples sizes prevented testing of any guild effect on trend type frequencies. Almost 50% of shifts in δ^{15}N dataset were accompanied by shifts in δ^{13}C. Very few shifts in δ^{13}C ($\sim$25%) were observed to occur without associated shifts in δ^{15}N.

Where data sets included the same species from different locations, size-related trends in δ^{15}N frequently contrasted among regions, e.g., *Haemulon flavolineatum*, *Ocyurus chrysurus, Thunnus albacares* (Table 2), with the only exception being *Xiphias gladius*. Comparative data for δ^{13}C were limited to two species, *Haemulon flavolineatum* and *Ocyurus chrysurus*, and these recorded only limited variations with location.

Discussion

Feeding guilds

All four species appeared to occupy isotopically discrete trophic niches, supporting their putative roles in different feeding guilds (Fig. 2). Using $\delta^{15}N$ as a proxy for TrL, and assuming $\Delta\delta^{15}N$ of 3.2‰ (Sweeting et al. 2007b), the highest TrL fish, *P. leopardus* occupied a position two levels above the lowest, *A. nigrofuscus*. The concurrent $\delta^{13}C'$ signatures of *C. xanthura* and *P. leopardus* suggest these species occur within the same food chain; with a difference in $\delta^{15}N$ suggestive of approximately one TrL, supporting gut analysis data indicating that *P. leopardus* feeds heavily on pomacentrid fishes (St John et al. 2001). Unexpectedly, *P. leopardus* appears to derive the majority of its production from planktonic sources, rather than coral or benthic algal production–based food chains, as defined by *C. lunulatus* and *A. nigrofuscus.* This is in contrast to the generalist feeding of many high TrL marine species and provides emphasis for further investigation into energy flows in coral reef systems.

A size invariant $\delta^{13}C'$ for *C. lunulatus* of −10.21‰ suggests an aggregated coral production source $\delta^{13}C$ of around −12‰, typical for coral as reviewed by Heikoop et al. (2000). *A. nigrofuscus* and *C. lunulatus* $\delta^{13}C'$ data did not differentiate, probably as a result of overlapping $\delta^{13}C$ values of coral and algal production sources, rather than overlapping feeding regimes highlighting a weakness in using $\delta^{13}C$ to track production source: the reliance on isotopically discrete production sources. Given that $\delta^{13}C$ ranges for algal (−20‰ to −10‰, Deines 1980), phytoplankton (−35‰ to −14‰ (Descolas-Gros and Fontugne 1990), and coral (−16.9‰ to −8.2‰, Heikoop et al. 2000) production may overlap considerably, distinguishing the relative importance of these sources at a single location may be problematic. Furthermore, consumers' isotopic signatures are aggregates of all dietary items, and so cannot be used to derive a measure of local variability in the $\delta^{13}C$ of related production sources, unless specific feeding regimes are already known.

Ontogenetic trends and location effects

No species varied in $\delta^{13}C'$ between locations, suggesting production sources were consistent among populations. This is in general agreement with $\delta^{15}N$ data for both *A. nigrofuscus* and *C. lunulatus* although in the latter case the location*size interaction was marginal. In contrast, *C. xanthura* $\delta^{15}N$ differed among locations, particularly in small individuals. Size-specific feeding, at location B but not at location A, in *C. lunulatus* appears to have resulted in increasing, although overall non-significant differences between locations with size.

Chromis xanthura exhibited significant positive size-related trends in $\delta^{15}N$ at both locations increasing by the equivalent of ~0.75 TrL at location A and one whole TrL at location B, over the size range sampled (~40–70% of L_{max}). Size-related trends are likely to be a function of both trophic size structuring of zooplankton (Hansen et al. 1994), and size-related prey size selectivity (Coates 1980). Such positive body size-$\delta^{15}N$ relationships have been observed in some (Lindsay et al. 1998), although not all (Carassou et al. 2008) planktivorous fish. The 2.9‰ increase in $\delta^{13}C'$ (a greater change than expected from the magnitude of the concurrent $\delta^{15}N$ change) suggests that trophic shift may be accompanied by a change in planktonic production sources. The literature review showed that positive size $\delta^{13}C'$ relationships were common in studied reef planktivores (Mill 2007; Carassou et al. 2008).

C. lunulatus showed no size $\delta^{13}C'$ relationship, however displayed a positive size $\delta^{15}N$ relationship at location A. *C. lunulatus* is known to show spatially variable feeding preferences, feeding on up to 30 different coral species at a single location (Berumen et al. 2005), and it is possible that a combination of local variability in coral $\delta^{15}N$, (Heikoop et al. 2000) combined with hitherto undocumented size-related shifts in diet caused this result. Very few isotopic data exist for corallivores, especially related to size, and further SIA studies have the potential to elucidate subtle feeding characteristics.

Acanthurus nigrofuscus showed no significant size-related trends with $\delta^{13}C'$ or $\delta^{15}N$, consistent with expectations of obligate herbivory. This appears to be a common pattern in herbivores (Cocheret de la Moriniere et al. 2003), although exceptions exist, e.g., *Acanthurus shoal* (Mill 2007). The lack of any clear relationship with size when diet appears invariant supports assumptions that $\delta^{13}C'$ or $\delta^{15}N$ represent trophic, rather than metabolic, size-related factors (Sweeting et al. 2007a, b).

The positive size TrL relationship reported for *P. leopardus*, corroborates gape size limitation reported by (St John et al. 2001), who reported that as size increased, individuals included an increasingly higher proportion of larger, higher TrL, fish in their diet. This trend was detectable using SIA at even a relatively modest adult size range of ~17–36% of maximum length (Kailola et al. 1993).

Size-based trophodynamic changes generally

Among the collated species, the prevailing pattern was for positive $\delta^{15}N$ size relationships. While collated data contains certain inherent biases, particularly non-random sampling of species, it does suggest that species level size-structured feeding is common in complex systems. Data also suggest that negative TrL size relationships constitute a specialist niche type undertaken by only a few species concurring with observations from temperate systems, for example the North Sea (Jennings et al. 2001).

Despite collating 40 $\delta^{15}N$-size trends, the diversity of feeding behaviours available in tropical habitats precluded quantitative analysis of trends in relation to trophic guilds. Data on certain guilds, e.g., corallivores and detritivores, were virtually absent, although others suggestive predictable patterns, for example positives shifts were common in piscivores, virtually absent in herbivores, while carnivores exhibit a wide range, perhaps reflecting the diversity of prey this category utilises.

It is notable that 50% of δ^{15}N trends are accompanied by δ^{13}C trends and only ~25% of δ^{13}C trends occurred without associated δ^{15}N trends. Although some of these cases may be explained by the trophic fractionation of carbon, this pattern strongly suggests that many size related changes in TrL are accompanied by changes in the source of production. This suggests that two distinct mechanisms drive diet shifts in reef species, occurring in approximately equal proportions, namely *size-based feeding*, resulting from size constraints on feeding, and *ontogenetic dietary shifts*, the result of changing habitat or food sources during ontogeny, during which δ^{15}N shifts may be driven by variation in production source δ^{15}N signatures as well as shifts in TrL. This differs from temperate food webs where feeding is primarily driven by size alone (Jennings 2001). Examination of those species duplicated in the literature review suggests that size-related trends often vary spatially (Nagelkerken et al. 2008; Verwij et al. 2008), even after correcting for artefacts introduced by differences in sampling (e.g., the differences in size range sampled for *Tunnus albacore*, Graham et al. 2007; Ménard et al. 2007).

The frequency of δ^{15}N-sized related tropical feeding behaviour is similar to that of temperate systems, but concurrent δ^{13}C-size shifts indicated a greater role for ontogenetic dietary shift in driving these changes. Given the evidence of both large (oceanic) and small (50 km) scale variability in isotope-body size trends found here, this study highlights a significant degree of plasticity in reef fishes studied. This suggests size-based analysis of reef fishes would provide a productive avenue to identify species potentially vulnerable to reef impacts as a result of constrained trophic behaviour. The small body of existing work also indicates that SIA can provide a range of novel insights into coral reef trophic ecology.

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