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$\delta^{13}C$ and $\delta^{15}N$ reveal significant differences in the coastal foodwebs of the seas surrounding Trinidad and Tobago

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ABSTRACT: This study assessed nearshore, marine ecosystem function around Trinidad and Tobago (TT). The coastline of TT is highly complex, bordered by the Atlantic Ocean, the Caribbean Sea, the Gulf of Paria and the Columbus Channel, and subject to local terrestrial runoff and regional riverine inputs (e.g. the Orinoco and Amazon rivers). Coastal organisms can assimilate energy from allochthonous and autochthonous sources. We assessed whether stable isotopes $\delta^{13}C$ and $\delta^{15}N$ could be used to provide a rapid assessment of trophic interactions in primary consumers around the islands. Filter-feeding (bivalves and barnacles) and grazing organisms (gastropods and chitons) were collected from 40 marine sites during the wet season. The flesh of organisms was analysed for $\delta^{13}C$ and $\delta^{15}N$. Results indicate significant variation in primary consumers (by feeding guild and sampling zone). This variation was linked to different energy sources being assimilated by consumers. Results suggest that offshore production is fuelling intertidal foodwebs; for example, a depleted $\delta^{13}C$ signature in grazers from the Gulf of Paria, Columbus Channel and the Caribbean and Atlantic coastline of Tobago indicates that carbon with an offshore origin (e.g. phytoplankton and dissolved organic matter) is more important than benthic or littoral algae during the wet season. Results also confirm findings from other studies indicating that much of the coastline is subject to cultural eutrophication. This study revealed that ecosystem function is spatially variable around the coastline of TT. This has clear implications for marine resource management, as a single management approach is unlikely to be successful at a national level.

KEY WORDS: Stable isotope · Trophic · Energetic subsidy · Filter-feeder · Grazer · Marine · Orinoco

INTRODUCTION

Marine foodwebs have sometimes been considered to be relatively simple; however, it has become increasingly clear that trophic relationships in coastal marine ecosystems can be highly complex (reviewed by Pomeroy 1974, Azam et al. 1983, Yokoyama et al. 2005, Vander Zanden & Fetzer 2007, Williams et al. 2007). For instance, organisms inhabiting near-shore habitats can potentially assimilate energy and nutrients originating from a diverse range of marine and terrestrial sources. Depending on location, such sources may include primary producers (and the detritus and nutrients released during their decomposition or digestion) from both autochthonous (seagrass, macroalgae, benthic and planktonic algae) and allochthonous (freshwater and estuarine phytoplankton, macrophytes, terrestrial leaf litter, terrestrial sediments) sources (Pomeroy 1974, Fry & Sherr 1984). An understanding of energy flow into a system and the trophic interactions between different groups of consumers is necessary in order to understand how an ecosystem func-

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tions. Clearly, such knowledge is required for informed management and conservation of essential goods and services (e.g. fisheries, nutrient recycling). Here, we apply a stable isotope approach to provide a rapid assessment of how primary consumers around the coasts of Trinidad and Tobago (TT) vary in terms of their carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values and how this reveals extreme spatial variation at the base of coastal foodwebs around this twin island country.

The analysis of consumer stable isotope ratios relies on their utility as a means to record long-term patterns of the assimilation of energy and nutrients (McCutchan et al. 2003). Different primary production modes have distinct and characteristic carbon stable isotope ($\delta^{13}C$) values: cf. mangrove trees (–27‰), marine phytoplankton (–22‰) and benthic algae (–17‰) (reviewed by France 1995, Muzuka & Shunula 2006). Hence, $\delta^{13}C$ provides a useful means by which to trace sources of energy utilised by consumers in a particular ecosystem (Fry & Sherr 1984, Peterson & Fry 1987). Carbon trophic fractionation is low between consumers and their food, with a mean (±SD) value in coastal and estuarine taxa of 0.6 (±2.5) (Yokoyama et al. 2005, their Table 4). This permits the flow of energy from different sources to be traced through an ecosystem, and previous studies have used differences in the $\delta^{13}C$ signature of terrestrial plants and marine organic matter to distinguish the source of carbon in marine systems and to determine the degree of terrestrial input (Leblanc et al. 1989, Risk et al. 1994). Stable isotope ratios of nitrogen ($\delta^{15}N$) are typically used as a means to assess consumer trophic level as consumers exhibit a stepwise enrichment of $\delta^{15}N$ by 3 to 5‰ relative to their prey (Minagawa & Wada 1984, Peterson & Fry 1987). However, $\delta^{15}N$ can also provide information on the source of nitrogen. Primary producers utilising atmospheric N have a $\delta^{15}N$ signature close to zero, whereas those obtaining N from animal or human wastes tend to have enriched $\delta^{15}N$ values (≥5‰), allowing the assessment of terrestrial runoff in marine producers via measurement of $\delta^{15}N$ (Mendes et al. 1997, Gartner et al. 2002).

In order to capture long-term basal variation between particular ecosystems or to compare areas within an ecosystem, researchers often examine stable isotope ratios collected from long-lived primary consumers. In aquatic ecosystems, it has become common to use molluscs as temporal isotopic integrators of pelagic (suspension-feeding bivalves) and littoral/benthic (grazing gastropods) primary production (Post 2002, Jennings & Warr 2003, Nadon & Himmelman 2006). In this study we compared isotope ratios in grazing and filter-feeding invertebrates (Post 2002) to assess isotopic variation at the base of coastal foodwebs around TT.

Due largely to their location, the islands of TT are characterised by highly complex coastal marine systems. The coastal zones include 4 distinct marine systems: the Atlantic Ocean, the Caribbean Sea, the Gulf of Paria and the Columbus channel (Fig. 1). Apart from the potential influence of these distinct marine systems, biological production and community structure is also influenced by runoff from local (e.g. rivers, sewage) and regional (e.g. from neighbouring Venezuela) sources. The largest influence is the combined discharge from 2 of the world's largest rivers, the Amazon and the Orinoco. Together, these rivers account for approximately 20% of freshwater discharge into the World's oceans and TT are located directly in the path of their discharge. Most freshwater and sediment runoff from these rivers enters the near-shore environment during the wet season (June to December). Riverine inputs from the Orinoco and Amazon represent the principal hydrographic influence on the near-shore coastal zones of TT during the wet season, i.e. local

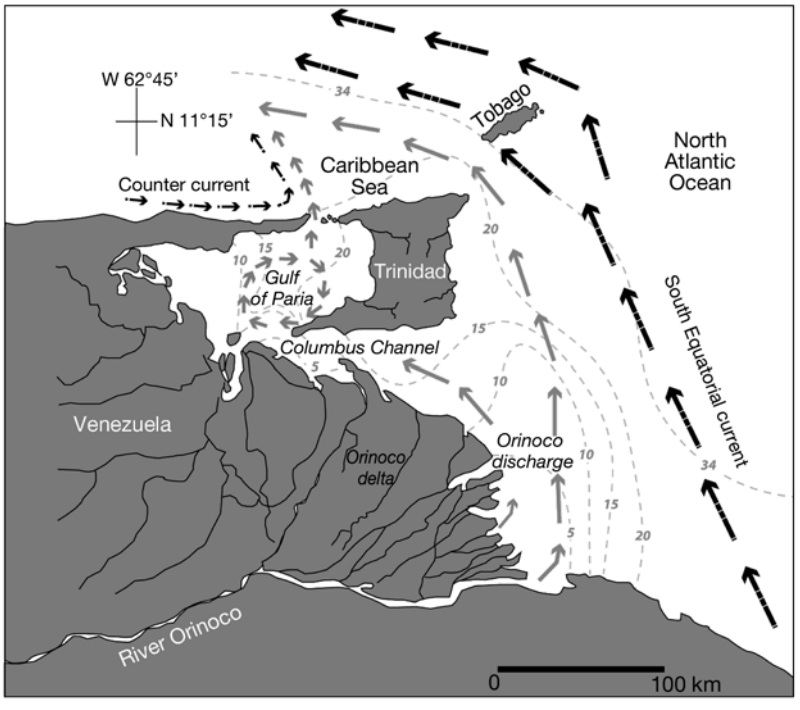

Fig. 1. Location of Trinidad and Tobago relative to the South American mainland. Arrows indicate the principle currents distributing freshwater (and associated nutrients, organic matter and sediments) from the River Orinoco and River Amazon (via the South Equatorial current) to the waters around Trinidad and Tobago. Dashed lines indicate surface salinity values

runoff has a much reduced influence. For instance, during the peak wet season, the islands are typically surrounded by turbid riverine runoff from the Orinoco and to a lesser degree the Amazon. During these periods, coastal waters are characterised by high sediment and nutrient loads. Freshwater inputs can be so high that surface salinities can fall to as low as 20 at the mouth of the Gulf of Paria located between Southern Trinidad and Venezuela (see Fig. 1) (Agard & Gobin 2000). The influence of organic inputs (dissolved and particulate organic matter) on coastal productivity is particularly marked in the shallow Gulf of Paria. Here, biological productivity is elevated and is dominated by detrital pathways (Manickchand-Heileman et al. 2004). The locations of the remaining coasts of the twin island republic are such that they are likely to exist along a gradient of influence from the combined Orinoco/Amazon discharge. The northern coasts of TT are located in the typically oligotrophic Caribbean Sea, and, whilst influenced by westward flowing Atlantic water masses, they are potentially most distant from the influence of this discharge. The eastern coast of Trinidad and the southern coast of Tobago are both located in the North Atlantic Ocean (Fig. 1). Although these ecosystems here are undoubtedly influenced by seasonal runoff from the Orinoco and Amazon, the degree of influence is probably less than that in the shallow Gulf of Paria. The coastal zones of TT are clearly potentially heterogeneous due to a complex combination of geographical (location, bathymetry) and hydrographic (residence times, local currents) factors.

Like other island nations, TT is particularly reliant on coastal ecosystems for a series of ecological goods and services, including fisheries and particularly in Tobago, marine ecotourism. As scientists and managers from local universities, national governmental agencies and non-governmental organisations (NGOs) attempt to develop sustainable means of resource use, there is a pressing need for basic information regarding ecosystem processes and function in these areas (CARSEA 2007).

The key objectives of this study were to: (1) examine isotopic ($\delta^{13}C$ and $\delta^{15}N$) variation in 2 distinct feeding guilds (filter-feeders and grazers) to provide baseline information in order to evaluate foodweb structure and trophic level of marine organisms around TT, (2) assess levels of spatial variability in $\delta^{13}C$ and $\delta^{15}N$ across the islands, and (3) determine whether isotopic values collected from marine invertebrates could be used as a rapid assessment method to determine sources of primary production around the islands.

MATERIALS AND METHODS

In order to assess the spatial variation in $\delta^{13}C$ and $\delta^{15}N$ in nearshore marine waters around the islands of TT, filter-feeding (e.g. bivalves, barnacles) and grazing (gastropods, chitons) invertebrates were collected from 40 sites around TT (Fig. 2). All sampling was conducted during the wet season (November 2006 to January 2007). Organisms were collected from the intertidal zone during low tide and from the ropes of surface marker buoys while snorkelling (collection depth <1 m). Following collection, some individuals were identified as secondary consumers (e.g. *Thais haemastoma floridana* and *Purpura patula*) and were discounted from subsequent analyses. Where possible, repeated samples within a taxon were size-matched to minimise any effects of ontogenetic dietary shifts (Rossi et al. 2004).

Once collected, samples were placed on ice and subsequently frozen until the somatic tissues could be removed from shells. All shells and carapaces were dis-

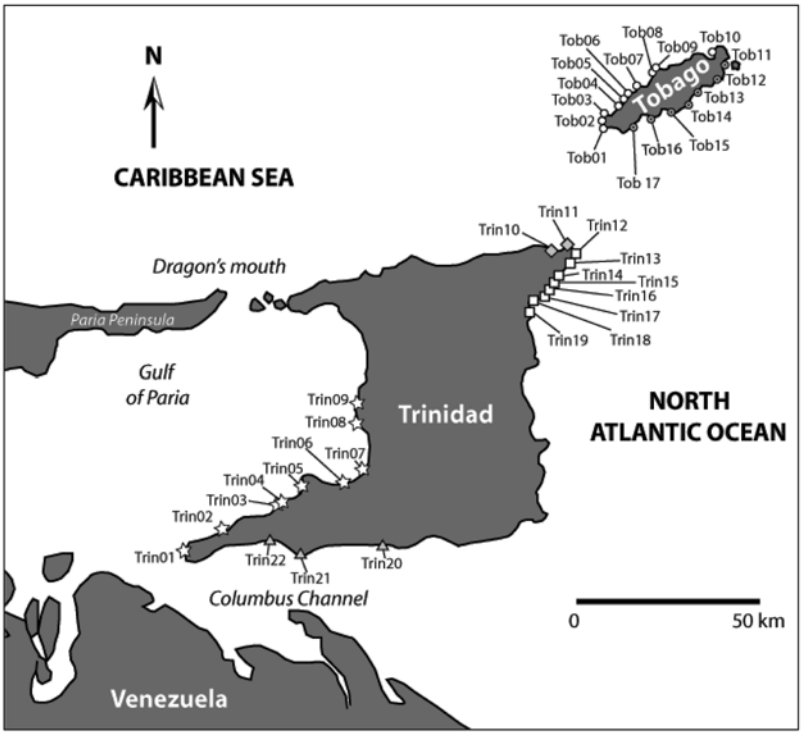

Fig. 2. Location of sites sampled. Different regions are represented by the following markers: ☆ = sites in the Gulf of Paria; ◇ = Caribbean coast of Trinidad; □ = Atlantic coast of Trinidad; △ = Columbus Channel, Trinidad; ○ = Caribbean coast of Tobago; ◉ = Atlantic coast of Tobago

carded. Specimens were washed in distilled water prior to dissection. Stomachs (and contents) were removed to limit any influence on isotopic values. For consistency, where possible, soft muscle tissue was preferentially selected for isotope analyses (Risk & Erdmann 2000, Yokoyama et al. 2005). Samples were then macerated, placed into vials and oven-dried at 60°C for 48 h. Dried samples were subsequently transported to the Max Planck Institute for Limnology, Germany, where they were ground to a fine powder using an agate pestle and mortar. Prior to stable isotope analyses, samples were weighed (ca. 0.55 mg) and loaded into tin cups prior to combustion in a Eurovector elemental analyser coupled to a Micromass Isoprime continuous-flow isotope-ratio mass spectrometer. Ratios of heavy to light isotopes are given using the δ notation expressed in units of per mille (‰), using the equation: δ (‰) = $[(R_{sample} / R_{standard}) - 1] \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ in the sample (R_{sample}) or reference standard ($R_{standard}$). Reference materials were secondary standards of known relation to the international standards of Vienna PeeDee Belemnite (VPDB) (for carbon) and atmospheric N_2 (for nitrogen). Repeated analyses of internal standards inserted after every 6 samples resulted in a precision (SD) of <0.1‰ (carbon) and <0.3‰ (nitrogen).

Statistical analysis. Data analyses focused on testing for isotopic variation between feeding guilds and sampling zone (Fig. 2). Mean $\delta^{13}C$ and $\delta^{15}N$ values were compared between putative feeding guilds (filter-feeders and grazers) and the 6 sampling areas (Fig. 2: Gulf of Paria, Caribbean coast of Trinidad, Atlantic coast of Trinidad; Columbus Channel, Trinidad; Caribbean coast of Tobago and Atlantic coast of Tobago) using *t*-tests and 2-way ANOVA with sampling zone (Sea) and feeding guild (Guild) as factors (SYSTAT 11.00.01). Statistical tests were conducted on $\log_{10}$-transformed data to improve normality and balance variances. $\delta^{13}C$ data, which were all negative, were transformed as $\log_{10}(x + 50)$. Although statistical comparisons were conducted on transformed data, non-transformed values (e.g. means ± SD) are reported throughout for clarity.

Unfortunately, we were unable to collect identical taxa at all 40 study sites. However, we statistically compared the taxonomic composition of samples from each of the sampling zones using the analysis of similarities (ANOSIM) routine of PRIMER 6.1.5 (Bray-Curtis similarities of square-root-transformed, species presence/absence data, 10 000 permutations).

Mean pooled $\delta^{13}C$ and $\delta^{15}N$ values for grazing and filter-feeding consumers collected around TT were compared with typical values collated from $\delta^{13}C$ and $\delta^{15}N$ analyses of energy sources and consumers studied from tropical marine ecosystems (Fry et al. 1982, Minagawa & Wada 1984, Smith et al. 1985, Keegan & DeNiro 1988, Yamamuro et al. 1992, Yamamuro & Kayanne 1995, Achituv et al. 1997, Heikoop et al. 2000). Data were classified as: organic matter fractions (particulate organic matter, benthic organic matter, sediment organic fraction), primary producers (green algae, blue-green algae, brown algae, phytoplankton, red algae, seagrass and foraminifera), coral (tissue and tissue complete with zooxanthellae), or consumers (filter-feeding invertebrates, grazing invertebrates, fish, omnivorous invertebrates and zooplankton).

RESULTS

$\delta^{13}C$

$\delta^{13}C$ values varied considerably between different intertidal primary consumers, ranging between –19.7 and –11.6‰. However, the bulk of the variation in $\delta^{13}C$ values could be attributed to the large difference (2-way ANOVA: Guild $F_{1,326} = 241.2$, $p < 0.001$; Fig. 3a, Table 1) between $\delta^{13}C$ values in filter-feeding (mean ± SD = –17.1 ± 1.5‰, n = 202) and grazing (mean ± SD = –12.2 ± 3.1‰, n = 136) invertebrates. The results of the 2-way ANOVA also indicated significant variation in mean $\delta^{13}C$ values by sampling area (Sea $F_{5,326} = 24.2$, $p < 0.001$). The significance of the interaction term (Guild × Sea $F_{5,326} = 16.5$, $p < 0.001$) indicated that differences in $\delta^{13}C$ values between grazers and filter-feeders were not consistent between seas (Table 1). Subsequent analyses were restricted to comparisons within the different feeding guilds (1-way ANOVA) or to differences between guilds in each of the seas (2 sample *t*-tests adjusted for separate variances; see Tables 1 to 3).

Variation in $\delta^{13}C$ between sampling zones

Grazers

Grazer $\delta^{13}C$ varied between –23‰ (from Site Trin21 in the Columbus Channel) and –6.3‰ (Site Trin17, Atlantic coast of Trinidad). A 1-way ANOVA on $\log_{10}(x + 50)$-transformed $\delta^{13}C$ data showed significant differences in mean $\delta^{13}C$ between the different sampling zones ($F_{5,130} = 13.04$, $p < 0.001$; Table 1a). Grazers from the Caribbean coast of Trinidad were most enriched in ^{13}C (mean ± SD = –8.1 ± 1.3‰), moderately enriched from the Atlantic coast of Trinidad (–10.5 ± 2.49‰), close to the overall grazer mean on the Caribbean coast of Tobago (–12.6 ± 1.9‰) and increasingly ^{13}C-depleted from the Gulf of Paria (–13.9 ± 2.4‰), the Atlantic coast of Tobago (–14.1 ± 1.1‰) and the Columbus Channel (–14.9 ± 5.4‰). Bonferroni-corrected post hoc comparisons indicated that sam-

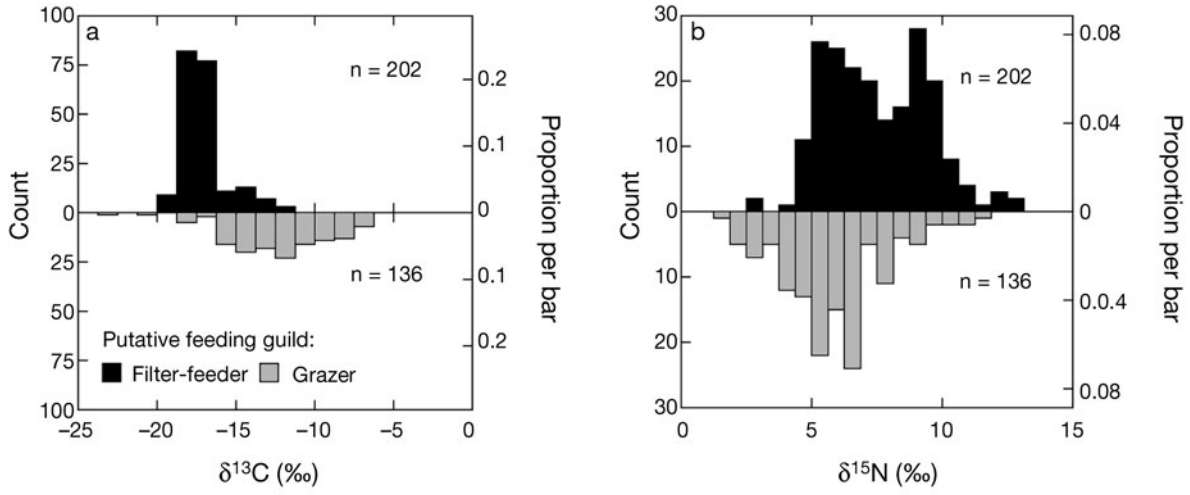

Fig. 3. Distribution of (a) $\delta^{13}C$ and (b) $\delta^{15}N$ values in putative filter-feeding and grazing invertebrates collected in the intertidal zones of Trinidad and Tobago

Table 1. Isotopic variation in (a) grazing and (b) filter-feeding intertidal invertebrates. Letters indicate statistical similarities (Sim.) between sampling areas following Bonferroni-corrected post hoc comparisons

Site	$\delta^{13}C$ (‰)				$\delta^{15}N$ (‰)			
	Mean	SD	n	Sim.	Mean	SD	n	Sim.
(a) Grazers								
Tobago Atlantic	−14.1	2.2	21	a	6.3	1.6	21	A,C,D,E
Tobago Caribbean	−12.6	1.9	36	a	4.4	1.9	36	B
Trinidad Atlantic	−10.5	2.5	49	b	5.7	1.2	49	A,C
Trinidad Caribbean	−8.1	1.3	6	b	5.6	0.5	6	A,B,D,E
Trinidad Columbus Channel	−14.9	5.4	10	a	7.0	1.9	10	A,C,D,E
Trinidad Gulf of Paria	−13.9	2.4	14	a	8.5	2.2	14	A,D
All sites pooled	**−12.2**	**3.1**	**136**		**5.8**	**2.0**	**136**	
(b) Filter-feeders								
Tobago Atlantic	−17.3	1.1	33	s,t,u,v,x,y	6.6	1.6	33	S,T
Tobago Caribbean	−16.4	1.7	19	s,t,x	6.4	1.3	19	S,T
Trinidad Atlantic	−17.7	1.1	69	s,u,y	7.1	1.9	69	S,T
Trinidad Caribbean	−13.1	0.5	11	v	7.5	1.8	11	S,T,U
Trinidad Columbus Channel	−16.7	1.2	14	s,t,x,y	7.5	1.6	14	S,T,U
Trinidad Gulf of Paria	−17.4	0.7	56	s,u,v,x,y	9.0	1.7	56	S,U
All sites pooled	**−17.1**	**1.5**	**202**		**7.5**	**2.0**	**202**	

pling areas fell into 2 groups in terms of overlap in $\delta^{13}C$ ($p = 0.07–1$), an enriched group from the Atlantic and Caribbean coasts of Trinidad, and a depleted group from the remaining sampling zones, namely the Atlantic and Caribbean coasts of Tobago, the Gulf of Paria and the Columbus channel.

Filter-feeders

Filter-feeder $\delta^{13}C$ values were ^{13}C-depleted and displayed less variation (Table 1b) relative to grazing invertebrates, ranging between −19.7‰ (from Site Trin15 on the Atlantic Coast of Trinidad) to −11.6‰ (Site Tob16 on the Caribbean coast of Tobago). A 1-way ANOVA (on $\log_{10}(x+50)$-transformed data) showed significant differences in mean $\delta^{13}C$ between the different sampling zones ($F_{5,196} = 33.96$, $p < 0.001$; Table 1b). Samples of filter-feeding invertebrates collected from the Caribbean coast of Trinidad were particularly ^{13}C-enriched (13.1 ± 0.5‰) with no statistical overlap with other sites (Bonferroni-adjusted $p < 0.001$). When data from this area were removed from the analysis, the differences between the various sampling areas was reduced considerably ($F_{4,186} = 5.7$, $p < 0.001$). Differences between mean $\delta^{13}C$ values from other sampling zones ranged between −16.4 ± 1.7‰ from the Caribbean coast of Tobago to −17.7 ± 1.1‰ on the Atlantic coast of Trinidad. The statis-

tical differences between the remaining sampling zones were less distinct than those shown between grazers.

Variation in $\delta^{13}C$ within sampling zones

Due to the significant interaction between feeding guild and site, $\delta^{13}C$ values were compared between grazer and filter-feeding invertebrates individually for each sampling zone using 2 sample *t*-tests adjusted for separate variances (see Table 2 for results of *t*-tests). In all but 1 comparison (Trinidad Columbus Channel) grazer invertebrates were significantly enriched in ^{13}C relative to filter-feeding invertebrates collected in the same sampling zone (Tables 1 & 2). There was a relatively strong positive relationship between mean filter-feeder and grazer $\delta^{13}C$ values in each of the sampling areas, but this was not statistically significant (r = 0.71, n = 6, p = 0.11).

$\delta^{15}N$

Invertebrate $\delta^{15}N$ values varied between 1.5 and 13‰ (Fig. 3b), an equivalent of ca. 3.5 trophic levels using typical values of $\Delta^{15}N$ (Post 2002, Yokoyama et al. 2005). A 2-way ANOVA on $\log_{10}$-transformed $\delta^{15}N$ data revealed a substantial effect of feeding mode on mean $\delta^{15}N$ (Guild $F_{1,326}$ = 23.0, p < 0.001). Grazing invertebrates were significantly depleted in ^{15}N (5.8 ± 2.0‰) relative to filter-feeders (7.5 ± 2‰). Mean $\delta^{15}N$ varied between different sampling zones (Sea $F_{5,326}$ = 19.6, p < 0.001), and there was a small but statistically significant interaction between feeding mode and sampling area (Guild × Sea $F_{5,326}$ = 3.8, p = 0.003). Due to the positive interaction between putative feeding guild and sampling zone, further comparisons were restricted to 1-way ANOVAs comparing mean $\log_{10}$-transformed $\delta^{15}N$ across the different sampling areas within each of the putative feeding guilds, and *t*-tests comparing mean $\log_{10}$-$\delta^{15}N$ between the feeding modes within each sampling zone.

Table 2. Results of *t*-tests (separate variance) comparing mean $\delta^{13}C$ and $\delta^{15}N$ in grazing and filter-feeding intertidal invertebrates (see Table 1 for mean values)

	$\delta^{13}C$			$\delta^{15}N$		
	t	df	p	*t*	df	p
Tobago Atlantic	−6.43	28.5	<0.001	0.47	28.5	0.63
Tobago Caribbean	−7.57	36.1	<0.001	5.04	52.8	<0.001
Trinidad Atlantic	−19.79	67.8	<0.001	4.52	107.3	<0.001
Trinidad Caribbean	−9.47	6.2	<0.001	−3.07	13.6	0.008
Trinidad Columbus Channel	−0.85	9.7	0.414	0.68	16.7	0.506
Trinidad Gulf of Paria	−5.48	13.7	<0.001	0.92	16.2	0.37

Variation in $\delta^{15}N$ between sampling zones

Grazers

Individual grazer $\delta^{15}N$ values ranged between 1.5‰ (from Site Tob14 on the Caribbean coast of Tobago) and 11.7‰ (collected at Site Trin03 in the Gulf of Paria). A 1-way ANOVA showed a significant difference in mean $\delta^{15}N$ values (range 4.4 to 8.5‰) between the different sampling areas ($F_{5,130}$ = 13.6, p < 0.001; see Table 1). Post hoc comparisons revealed considerable overlap in $\delta^{15}N$ across sampling sites (see Table 1a) and that mean $\delta^{15}N$ was significantly depleted in grazers from the Caribbean coast of Tobago (4.4 ± 1.9‰). Differences between the other sampling zones were complex (compare values in Table 1a); however, $\delta^{15}N$ values were particularly enriched in the Gulf of Paria (8.5 ± 2.2‰) and the Columbus Channel (7 ± 1.9‰).

Filter-feeders

Individual $\delta^{15}N$ values from putative filter-feeders varied between 2.7‰ (from Site Tob06 on the Atlantic coast of Tobago) and 13‰ (collected at Site Trin06 in the Gulf of Paria). As noted above, mean $\delta^{15}N$ values were generally enriched relative to grazing invertebrates. Comparisons across the different sampling zones showed significant differences in mean grazer $\delta^{15}N$ ($F_{5,196}$ = 12.2, p < 0.001); however, overlap was considerable between most sampling zones (Table 1b). Bonferroni-adjusted post hoc comparisons indicated that filter-feeder $\delta^{15}N$ was particularly enriched in the Gulf of Paria (9.0 ± 1.7).

Variation in $\delta^{15}N$ within sampling zones

Due to the significant interaction between feeding guild and site, we compared grazer and filter-feeding $\delta^{15}N$ values within each sampling area using 2 sample *t*-tests adjusted for separate variances (see Table 2 for results of *t*-tests). In half of the comparisons (Tobago Atlantic, Columbus Channel and Gulf of Paria) there were no significant differences between grazer and filter-feeder mean $\delta^{15}N$ (Tables 1 & 2). Comparison of the patterns across the different sampling areas revealed a positive correlation between mean filter-feeder and grazer $\delta^{15}N$ values within each sampling zone (r = 0.86, n = 6, p = 0.027).

Sample structure and ANOSIM

The considerable isotopic differences we have demonstrated between sampling areas could potentially reflect a taxonomic effect, e.g. species-specific feeding strategies. The species structure of samples analysed during the study differed between sampling zones (R = 0.33, p < 0.001). However, Bonferroni-adjusted pairwise comparisons indicated that this effect was likely to be small, and that in only 2 cases did species composition differ significantly between sampling zones (Table 3).

Comparison of results with literature values

We used members of 2 putative feeding guilds (filter-feeder and grazing invertebrates) as indicators of the energy sources available to marine consumers in the marine waters of TT. Comparisons with mean $\delta^{13}C$ values from studies of coral reef ecosystems conducted worldwide indicate that our choice of these 2 putative feeding guilds is robust (Fig. 4). Including a typical $\Delta^{13}C$ value of 1‰, it is apparent that the mean filter-feeder $\delta^{13}C$ values from the coasts around TT overlap with literature data for various putative energy sources indicative of a likely pelagic marine (particulate organic matter, phytoplankton, dissolved organic matter) or terrestrial (terrestrial sediments) source. Conversely, our estimates of mean grazer $\delta^{13}C$ values display an apparent overlap with benthic energy sources collected from the coral reef literature (benthic organic matter, blue-green algae and brown algae).

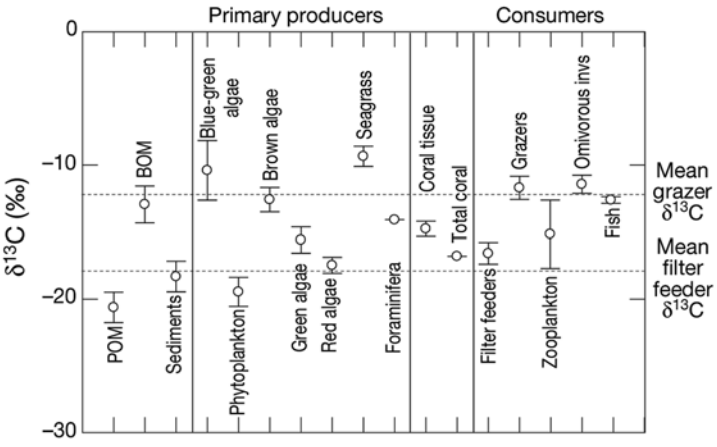

Fig. 4. Comparison of mean (±1 SE) reef organism $\delta^{13}C$ values from the coral reef literature with mean values for putative filter-feeders and grazers collected during the present study. POM = particulate organic matter, BOM = benthic organic matter

DISCUSSION

Our results have revealed: (1) significant isotopic variation in primary consumers (filter-feeders and grazers) collected from the coastal zone of TT, (2) that ecosystem function is spatially variable around the islands, and (3) that marine invertebrates can be used to rapidly assess nearshore marine primary production. On average intertidal filter-feeding invertebrates were $\delta^{13}C$-depleted relative to grazers (mean ± 95% CI difference = 4.9 ± 0.56‰). This difference is statistically indistinguishable from the difference in mean $\delta^{13}C$ values for marine pelagic and benthic algae (5‰) estimated by France (1995) for marine coastal areas. This provides indirect evidence that our approach of sampling intertidal grazing and filter-feeding invertebrates (following Post 2002) effectively distinguishes between coastal pelagic and benthic foodwebs. However, comparisons of temporal isotopic variation from these consumer guilds and their putative food sources are required to fully establish the veracity of our approach.

Our analyses revealed significant variation in $\delta^{13}C$ and $\delta^{15}N$ at both the level of feeding guild and sampling area. However, significant ANOVA interaction terms (most marked in $\delta^{13}C$ analysis) indicated that foodwebs differed across coastal zones, but also that differences between the 2 putative feeding guilds

Table 3. Analysis of similarities (ANOSIM) R values (shown below the diagonal) with associated Bonferroni-adjusted p-values (above the diagonal) for comparisons between sampling zones (no. of comparisons = 15, adjusted p = 0.003). Note that the species composition of samples collected in the different coastal areas only differed significantly in 2 of 15 comparisons (**bold**)

	Tobago Atlantic	Tobago Caribbean	Trinidad Atlantic	Trinidad Caribbean	Trinidad Gulf of Paria	Trinidad Columbus Channel
Tobago Atlantic	–	p = 0.3	p = 0.3	p = 1.0	p = 0.88	p = 0.54
Tobago Caribbean	R = 0.29	–	**p = 0.013**	p = 1.0	p = 0.07	p = 1.0
Trinidad Atlantic	R = 0.38	***R* = 0.34**	–	p = 1.0	**p = 0.015**	p = 0.09
Trinidad Caribbean	R = 0.11	R = 0.21	R = 0.20	–	p = 1.0	p = 1.0
Trinidad Gulf of Paria	R = 0.14	R = 0.36	***R* = 0.45**	R = 0.27	–	p = 0.09
Trinidad Columbus Channel	R = 0.25	R = 0.23	R = 0.53	R = 0.79	R = 0.46	–

were not consistent. We suggest that these differences relate to variation in the sources of energy assimilated by consumers between the different coastal zones, which furthermore indicates that ecosystem function is spatially variable in these areas.

Initial analyses indicated an increased level of variation in filter-feeder $\delta^{13}C$, but this was influenced by the inclusion of enriched filter-feeders from the Trinidad Caribbean coast (probably reflecting utilisation of seagrass-derived detritus). If these data are discounted, the differences between sites became less clear, suggesting that although there are significant differences in filter-feeder $\delta^{13}C$ (and therefore the likely source of their food) around the islands, the differences are far less clear than that shown in grazing macroinvertebrates. Mean filter-feeder $\delta^{13}C$ values were depleted (mean = –17.1‰) and overlapped with estimates of $\delta^{13}C$ values for terrestrial sediments, phytoplankton and particulate organic matter collected from tropical coastal ecosystems (Fig. 4). Mean (±SD) filter-feeder $\delta^{13}C$ values (–17.1 ± 1.5‰) were enriched by ca. 4‰ compared to organic matter collected off the sediments at the mouth of the Orinoco (mean ± SD = –21.0 ± 0.91‰) by Medina et al. (2005). Although there may be some interannual variation in $\delta^{13}C$ values for sediments discharged by the Orinoco, it seems unlikely that filter-feeding organisms collected from intertidal areas around TT are assimilating organic carbon directly from Orinoco sediments.

Even though individuals of both putative feeding guilds were collected from identical areas (often <30 cm apart), the significantly depleted $\delta^{13}C$ values in grazers at some sites (e.g. Gulf of Paria, Columbus Channel, Tobago Caribbean and Tobago Atlantic) are perhaps indicative of increased assimilation of energy originating from offshore sources, e.g. phytoplankton or dissolved organic matter, which is typically enriched ($\delta^{13}C$ > –18‰) when compared to benthic algae or terrestrial sources (Gagan & Sandstrom 1987). This indicates that in some areas, local production of benthic/littoral algae is overwhelmed by carbon with an offshore origin and hence offshore production may also fuel benthic/littoral foodwebs. Fisheries production is high in the Gulf of Paria (Manickchand-Heileman et al. 2004), reflecting the high primary productivity and nutrient inputs from Orinoco River (Agard & Gobin 2000). Interestingly, using a model based on estimates of trophic level, Manickchand-Heileman et al. (2004) suggested that the Gulf of Paria foodweb was dominated by a detrital energy pathway, with very little of the available phytoplankton being grazed before it joined the detritus pool.

Our results have demonstrated that spatial variation in $\delta^{15}N$ values from consumers belonging to a single putative trophic level was of a magnitude typically seen in consumers 3.5 trophic levels apart. Although the literature indicates that all taxa analysed were primary consumers, there is clearly the potential that some individuals may be functional omnivores (e.g. feeding at >1 trophic level). However, most variation in $\delta^{15}N$ reflected differences between sampling areas. Although some of this variation might reflect the extremely complex local geology and subsequent influences on inorganic N, it is more likely to be driven by spatial variation in nutrient enrichment. This may reflect inputs of ^{15}N-enriched domestic sewage (Agard & Gobin 2000), the upwelling of nutrients from river-derived currents (Muller-Karger & Castro 1994) or even nutrient recycling (Michener & Schell 1994). The most ^{15}N-enriched area was the Gulf of Paria, which is highly productive, receiving nutrient-rich waters from the Orinoco as well as effluent from major settlements, agriculture and industry located in central Trinidad (Agard & Gobin 2000, Manickchand-Heileman et al. 2004, Marion et al. 2005). The Gulf of Paria is shallow, and has a relatively long hydrological residence time (Hall 1989). These factors may lead to increased $\delta^{15}N$ values at the base of the foodweb due to nutrient recycling (Michener & Schell 1994).

Although the present study has shown clear differences between grazer and filter-feeder $\delta^{13}C$ values, differences in $\delta^{15}N$ between members of the 2 putative feeding guilds were less distinct, but statistically significant. However, when $\delta^{15}N$ values were compared within each sampling zone, differences became less obvious, with half of all comparisons between filter-feeders and grazers failing to meet conventional levels of statistical significance. All areas showing overlap in $\delta^{15}N$ values between the 2 feeding guilds (the Gulf of Paria, Columbus channel and the Atlantic coast of Tobago) also displayed enriched grazer $\delta^{13}C$ values. The convergence in $\delta^{13}C$ and $\delta^{15}N$ values in these areas provides further evidence that grazer and filter-feeding taxa in these areas are both assimilating energy and nutrients with an offshore origin.

Grazing and filter-feeding invertebrates collected from the Caribbean coast of Trinidad were particularly enriched in ^{13}C. Enriched $\delta^{13}C$ values are commonly considered indicative of assimilation of epilithic algae if comparisons are made along a simple pelagic-littoral/benthic axis. However, it is likely that in this case the enriched $\delta^{13}C$ values reflected assimilation of carbon originating from the seagrass beds found adjacent to the sample sites (IMA 2004).

The present study aimed to provide a rapid assessment of coastal ecosystem processes in the hydrologically diverse coastal areas of TT during a single season. Our approach has successfully revealed the level of complex variation across the different coastal zones of TT. However, there are minor flaws that in future we

aim to resolve in order to provide a quantitative estimate of the relative amount of energy and nutrients assimilated from different potential sources.

Our approach was constrained by an inability to repeatedly sample the same species at each site. This reflects logistical difficulties (boat time and access to habitats) as well as differences in community structure around the coasts of TT. However, our analyses indicated that our samples were largely taxonomically similar and only differed significantly in 2 sampling zones. It is likely that future studies will require more resources and time in order to gather more taxonomically balanced samples. One possible approach would be to follow a bioassay approach, e.g. to plant suitable local species (Costanzo et al. 2005).

Following the work of others (e.g. Post 2002) we followed a functional rather than taxonomical approach to assess general patterns at the base of coastal foodwebs. Our simple assumption that individuals were primary consumers and could be further classified as either grazers or filter-feeders may have added error into our results. Some isotope studies have revealed that members of putative feeding guilds can and do shift between feeding modes to reflect access and profitability of different feeding strategies (Eggers & Jones 2000).

The present study confirms the utility of stable isotope analysis as a means of rapid assessment of ecological variation at a whole-ecosystem level (France 1995, 1997, Post et al. 2000, Post 2002, Vander Zanden & Fetzer 2007). Our results also suggest that Post's (2002) bivalve/gastropod model developed to examine isotopic variation between pelagic and littoral production in freshwater lakes has considerable potential for studies of coastal marine systems.

Cultural eutrophication is defined here as any anthropogenic activity that introduces nutrients into the coastal zone. Lapointe (2003) examined isotopic variation in macroalgae in Tobago and showed evidence of cultural eutrophication. Although it is difficult to partition the possible influences of nutrient recycling, long retention times and riverine inputs on the patterns in our data, our wide-scale study confirms earlier work (Agard & Gobin 2000, Lapointe 2003, Burke & Maidens 2004, CARSEA 2007) that showed that much of the coast of TT is subject to cultural eutrophication. Our results and the approach used here may allow interested governmental agencies and NGOs, which are generally aware of the problem, the opportunity to target particular problem areas.

Future studies should employ a multidisciplinary approach to examine the clearly complex marine ecology of TT and possible influence of riverine inputs from the Orinoco and Amazon rivers. Future isotopic research could include the collection of putative basal resources, e.g. suspended/benthic sediments, phytoplankton, particulate organic matter, dissolved organic carbon, and benthic algae in inshore and offshore habitats around TT. Ideally sample collection would coincide with the temporal patterns in discharge from these large rivers, i.e. by covering both wet and dry seasons (Lewis & Saunders 1989). We purposely focused on primary consumers, but future work should also include more trophic levels, including primary producers (benthic algae and phytoplankton), and higher trophic levels, including those consumers important to ecosystem function and to human consumption (fish, cephalopods, etc.). Although our approach was limited to intertidal habitats, it is likely that this has effectively captured much of the variation between pelagic (filter-feeders) and benthic (grazers) production (France 1995). However, future sampling in deeper water will provide information more relevant for fisheries management in the region (Manickchand-Heileman et al. 2004). Due to riverine inputs (e.g. sediment) from the Orinoco, the local distribution of coral reefs is largely restricted to the Atlantic and Caribbean coastline of Tobago. Future studies will also examine whether the relative contribution of autotrophy or heterotrophy in corals is variable in Tobago, and whether reefal production is subsidised by offshore production or riverine inputs.

CONCLUSIONS

The present study has demonstrated significant spatial isotopic variation in basal consumers around the coasts of TT, and provides evidence that marine ecosystems can vary significantly even at this relatively small spatial scale. Although this probably partly reflects the particular geographical location of the 2 islands, it suggests that an assumption that seemingly similar, closely located ecosystems will function in the same way is flawed.

Our study has established a $\delta^{13}C$ and $\delta^{15}N$ baseline which can be used to compare findings from other studies in TT and across greater spatial scales. Post's (2002) freshwater lake study showed a mean difference in littoral and pelagic $\delta^{13}C$ values of 6.7‰. Our results from coastal marine ecosystems showed a slightly less distinct difference (4.9‰). However, our values were statistically indistinguishable from that shown by France (1995). This not only provides evidence for differences between marine and freshwater systems, but provides indirect support for our approach as a means of rapid assessment of coastal foodwebs with potential for application elsewhere.

Our results have revealed marked isotopic variation in different coastal areas of TT, and we suggest that

this difference has ecological implications, especially regarding variation in energy flow and foodweb structure in these areas. If so, it is clear that any attempt to develop and apply a single management approach to the different coastal areas of TT is unlikely to be successful. We suggest that our methods provide a means of rapid assessment suitable for regions reliant on marine ecosystem goods and services, and may be particularly suitable for other small island nations.

Some tropical regions are characterised by distinct seasonal weather patterns such as the Caribbean wet and dry seasons, and our work in TT needs to consider the dry season. Current climate change predictions suggest that the wet seasons are likely to become wetter regionally (Singh 1997, CARSEA 2007). This is likely to result in increased river discharge during the wet season. The implications of any such shifts in riverine discharge for coastal productivity in the region is currently unknown, but we suggest that our approach offers a means by which changes can be monitored.

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