Running Head: Carbon flow in tropical seascapes

Tracing carbon flow through coral reef food webs using a compound-specific stable isotope approach

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ABSTRACT

Coral reefs support spectacularly productive and diverse communities in tropical and sub-tropical waters throughout the world's oceans. Debate continues, however, on the degree to which reef biomass is supported by new water column production, benthic primary production, and recycled detrital carbon. We coupled compound-specific $\delta^{13}C$ analyses with Bayesian mixing models to quantify carbon flow from primary producers to coral reef fishes across multiple feeding guilds and trophic positions in the Red Sea. Analyses of reef fishes with putative diets composed primarily of zooplankton (*Amblyglyphidodon indicus*), benthic macroalgae (*Stegastes nigricans*), reef-associated detritus (*Ctenochaetus striatus*), and coral tissue (*Chaetodon trifascialis*) confirmed that $\delta^{13}C$ values of essential amino acids from all baseline carbon sources were both isotopically diagnostic and accurately recorded in consumer tissues. While all four source end-members contributed to the production of coral reef fishes in our study, a single source end-member often dominated dietary carbon assimilation of a given species, even for highly mobile, generalist top predators. Microbially-reworked detritus was an important secondary carbon source for most species. Seascape configuration played an important role in structuring resource utilization patterns. For instance, *L. ehrenbergii*, showed a significant shift from a benthic macroalgal food web on shelf reefs (71 ± 13% of dietary carbon) to a phytoplankton-based food web (72 ± 11%) on oceanic reefs. Our work provides insights into the roles that diverse carbon sources play in the structure and function of coral reef ecosystems and illustrates a powerful fingerprinting method to develop and test nutritional frameworks for understanding resource utilization.

Key words: amino acids; Bayesian mixing model, diet, fish; Red Sea

INTRODUCTION

Coral reefs represent some of the most productive and biologically diverse ecosystems on Earth (Odum and Odum 1955; Ryther 1969; Connell 1978; Hughes et al. 2002). Yet this observation remains enigmatic given that many coral reefs occur at latitudes characterized by significant nutrient limitation (Muscatine 1973; Hallock and Schlager 1986). More than a century ago, Darwin (1842) posed the question of how coral reefs were so productive and diverse in oligotrophic ocean waters – a question that we have yet to satisfactorily answer. One hypothesis proposes that reef-associated planktivores act as a "wall of mouths" that captures significant amounts of carbon fixed in the water column by phytoplankton (Emery 1973; Hamner et al. 1988; Genin et al. 2009; Wyatt et al. 2010). Other ideas have linked high productivity on coral reefs to mechanisms that efficiently recycle carbon and nutrients within the system, through symbioses (Muscatine and Porter 1977; Cowen 1988), remineralization pathways (Richter et al. 2001; Wild et al. 2004; Wyatt et al. 2012a; de Goeij et al. 2013), and microbially-reworked detrital pathways (Alongi et al. 1988; Gast et al. 1998; Ferrier-Pages and Gattuso 1998). Distinguishing among these competing hypotheses is important to understanding the mechanisms that underlie coral reef function and resilience as well as the species responsible for maintaining these processes in the face of global climate change and anthropogenic disturbance (Pandolfi et al 2003; Cote et al 2005; Hughes et al 2007).

The structure and function of coral reefs are intricately tied to the sources and pathways of carbon flow through reef food webs (Lindeman 1942; Moore et al. 2004). However, accurate estimates of carbon flow are challenging to obtain in systems characterized by complex food webs. Stable isotope analysis (SIA) provides a method for tracing carbon flow that avoids many

of the challenges associated with constructing food webs from conventional gut content analysis and feeding observations (Deb 1997; Bearhop et al. 2004). However, coral reefs remain challenging systems to examine with SIA due to difficulties characterizing multiple end-members at the base of the food web (hereafter source end-members) and interpreting shifts in diet, trophic position, and baseline isotope values ($\delta^{13}C_{baseline}$) in highly dynamic systems (Post 2002). Bulk SIA has, therefore, seen limited use in coral reef systems, with most studies either forced to rely on trends of increasing $\delta^{15}N$ values and decreasing $\delta^{13}C$ values as indicative of increased reliance on oceanic productivity or suffering from underdetermined mixing models and uncertainty regarding trophic fractionation in complex food webs (Carassou et al. 2008; Greenwood et al. 2010; Wyatt et al. 2012b; Hilting et al. 2013; Letourneur et al. 2013).

Recent work has highlighted opportunities to enhance studies of carbon flow in ocean environments by analyzing $\delta^{13}C$ values of specific biochemical compounds, particularly amino acids (AAs) (reviewed in McMahon et al. 2013). Metabolic diversity in essential AA synthesis pathways and isotope effects generates unique isotopic signatures or "fingerprints" among diverse source end-members (Hayes 2001; Scott et al. 2006; Larsen et al. 2009, 2013) that are robust to many of the factors affecting bulk $\delta^{13}C$ values (Larsen et al. 2015). While primary producers and bacteria can synthesize essential AAs *de novo*, most animals do not possess the necessary enzymatic pathways to synthesize these AAs at a rate sufficient for normal growth (Borman et al. 1946; Reeds 2000) and therefore must incorporate essential AAs directly from their diet with minimal trophic fractionation (Hare et al. 1991; Howland et al. 2003; Jim et al. 2006; McMahon et al 2010). Essential AA $\delta^{13}C$ signatures propagate through food webs virtually unmodified (Arthur et al. 2014; Schiff et al. 2014; McMahon et al. 2015), which avoids the complications of variable and poorly characterized trophic fractionation factors in mixing models

(Bond and Diamond 2011). Furthermore, this compound-specific stable isotope analysis (CSIA) approach typically provides five or more essential AAs with independent synthesis pathways in a single analysis, allowing for better constraint of source end-member signatures while avoiding the biases common to underdetermined mixing models using poorly resolved dual isotope approaches in systems with multiple end-members (Fry 2013; Brett 2014).

In this study we coupled CSIA with a Bayesian isotope mixing model approach to determine the sources of carbon assimilated by seven species of coral reef fishes spanning a wide range of feeding guilds and trophic positions on Saudi Arabian reefs in the Red Sea. We initially determined if $\delta^{13}C$ values in essential AAs differed among four distinct end-members (phytoplankton, benthic macroalgae, corals, and detritus) and between reef locations. We then addressed the following specific questions: 1. Which carbon sources supported our focal reef fish species? 2. Does carbon source use vary spatially between shelf and oceanic reefs? Earlier studies by Emery (1973) and Hamner et al. (1988) hypothesized that water column production contributed significantly to the carbon sequestered in fish biomass on coral reefs, while more recent studies have suggested recycling pathways may play significant roles in reef production (Richter et al. 2001; Wild et al. 2004; de Goeij et al. 2013). As reefs globally face increasing pressures from climate change and anthropogenic disturbances (e.g. Polovina 1984; Arias-Gonzalez et al. 2004; Hilting et al. 2013), understanding carbon flow in reef systems will become even more important to their long term conservation and management.

METHODS

Study site

We sampled four source end-members (96 samples total) and seven coral reef fish species (260 samples total) from isolated coral reefs located on the continental shelf (shelf reefs, n = 4) and in oceanic waters beyond the shelf (oceanic reefs, n = 4) near Al-Lith on the Saudi Arabian coast of the Red Sea in March 2009 and June 2010 (Fig. 1). The oceanic reefs were steep-walled pinnacles rising rapidly from deep water (>300 m). Shelf reefs were situated on the continental shelf in water not exceeding 60 m depth. Shelf reefs were characterized by water with visibility usually less than 25 m. Conversely, the oceanic reefs were steep-walled pinnacles rising rapidly from deep water (>300 m) with visibility often exceeding 40 m. Saudi reefs in the Red Sea are characterized by relatively little structural complexity at the habitat level (Shepherd and Shepherd 1991), and none of our study reefs had lagoon or back-reef environments.

We characterized carbon isotope signatures of four distinct source end-members at the base of the food web on each reef: 1) phytoplankton, 2) macroalgae, 3) coral, and 4) detritus. We collected calanoid copepods that feed on phytoplankton, dinoflagellates, and protists within pelagic food webs (e.g. Kleppel 1993) using a 1 m diameter, 333 μm mesh net towed in the water column around the perimeter of each reef (n = 3 tows per reef). Given that essential AAs show virtually no fractionation between diet and consumer (McMahon et al. 2010, 2013), the essential AA $\delta^{13}C$ values of pelagic copepods provided a faithful proxy for pelagic phytoplankton. We collected a filamentous macroalga (*Womersleyella setacea*) that is farmed by the dusky farmerfish (*Stegastes nigricans*, Lacepede 1802) (Hata and Kato 2002) from each reef (n = 3 sites collected throughout each reef). We selected a species of staghorn coral, *Acropora pharaonis*, that is targeted by corallivores (e.g., Berumen and Pratchett 2008) to represent carbon fixed by autotrophic zooxanthellae and heterotrophic feeding by corals (n = 3 coral tables collected throughout each reef). Given the challenges in isolating the detrital end-member, we

selected the detritivorous black sea cucumber, *Holothuria atra*, as a proxy for detritus (Moriarty 1982; Uthicke 1999) (n = 3 individuals collected throughout each reef).

We collected adult individuals from seven species of reef fishes, representing a suite of feeding guilds from detritivores to top predators. There were no significant differences in total length between individuals collected on shelf and oceanic reefs for any species (Online Resource 1). Feeding ecology of each species was classified according to Sommer et al. (1996) and Lieske and Myers (2004). Lined bristletooths, *Ctenochaetus striatus* (Quoy and Gaimard 1825), are common detritivorous surgeonfish that typically ingest sediments to target detritus, blue-green algae, and benthic diatoms. Bullethead parrotfish, *Chlorurus sordidus* (Forsskål 1775), feed on benthic algae and detritus. We sampled two species of damselfish that occupy different feeding guilds. Pale damselfish, *Amblyglyphidodon indicus* (Allen and Randall 2002), feed primarily on zooplankton, while dusky farmerfish, *S. nigricans*, feed almost exclusively on farmed filamentous macroalgae, such as *W. setacea*. Chevron butterflyfish, *Chaetodon trifascialis* (Quoy and Gaimard 1825), are obligate corallivores that feed on the polyps and mucus of corals, most commonly in the genus *Acropora.* Ehrenberg's snapper, *Lutjanus ehrenbergii* (Peters 1869), are mesopredators that feed primarily on benthic invertebrates and small fishes. Giant moray eels, *Gymnothorax javanicus* (Bleeker 1859), were selected as resident top piscivores at each reef. Due to the small size of the reefs, we were able to effectively sample individuals from the entire perimeter of each reef (n = 5 individuals per reef, except *G. javanicus* where two or three individuals were collected per reef).

Sample preparation and analysis

Several calanoid copepods were isolated and then homogenized from each plankton tow. Macroalgae samples were cleaned of epizoic fauna and homogenized. Coral tissue was removed

161 from the skeleton with an air pick and represented a consortium of coral tissue, coral mucus, and
162 the associated microbial community. For the detritus end-member, we used homogenized dermal
163 tissue from *H. atra*. Morays eels were captured in baited fish traps and biopsied with a small
164 hand biopsy tool, while the remaining fish species were collected by spear gun. White muscle
165 samples from all individual fishes were frozen on the boat and transported to an on-shore
166 laboratory for further processing. Samples were frozen at -20°C and then lyophilized (freeze-
167 dried) for 48 hrs prior to homogenization with a mortar and pestle.
168 We acid hydrolyzed and derivatized samples prior to CSIA according to McMahon et al.
169 (2011). Briefly, each sample underwent an acid-catalyzed esterification followed by acylation
170 with trifluoroacetic anhydride (TFAA) and dichloromethane (DCM) under an atmosphere of N_2.
171 Samples were brought up in DCM and injected on column in splitless mode at 260°C and
172 separated on a forte SolGel-1ms column (60 m length, 0.25 mm inner diameter, and 0.25 μm
173 film thickness; SGE Analytical Science, Sydney, Australia) in a Agilent 6890N Gas
174 Chromatograph (GC) at the Woods Hole Oceanographic Institution, Woods Hole, MA, USA.
175 The separated AA peaks were combusted online in a Finnigan gas chromatography-combustion
176 continuous flow interface at 1030°C, then measured as CO_2 on a Thermo Finnigan Mat 253 irm-
177 MS. Standardization of runs was achieved using intermittent pulses of a CO_2 reference gas of
178 known isotopic composition. All CSIA samples were analyzed in duplicate along with AA
179 standards of known isotopic composition from Sigma-Aldrich (mean reproducibility for all
180 individual standard AAs was ± 0.2‰) to correct for the introduction of exogenous carbon and
181 kinetic fractionation associated with derivitization (Silfer et al. 1991). We focused on five
182 essential AAs (threonine, isoleucine, valine, phenylalanine, and leucine) with sufficient peak size

183 and baseline GC separation for accurate CSIA (mean reproducibility for all individuals AAs
184 from a long term lab fish muscle standard was ± 0.6‰).
185
186 *Data analysis*
187 We characterized unique isotope signatures for the four source end-members on shelf and
188 oceanic reefs based on the $\delta^{13}C$ values of five essential AAs; threonine, valine, isoleucine,
189 phenylalanine, and leucine. We tested for variations in the $\delta^{13}C$ values of individual essential
190 AAs using a mixed-model analysis of variance (ANOVA) with end-member (n = 4) and location
191 (shelf or oceanic) as fixed factors and reefs nested within location as a random factor. Tukey's
192 honest significant difference (HSD) tests were used for multiple pairwise comparisons of
193 significant effects identified by the ANOVAs. We then visualized the multivariate signatures of
194 essential AA $\delta^{13}C$ values from source end-members and reef fish species with principal
195 component analysis (PCA) using the covariance matrix.
196 To quantify the relative contributions of the four source end-members to the seven fish
197 species on shelf and oceanic reefs, we used a fully Bayesian stable isotope mixing model
198 approach (sensu Ward et al. 2010) within the Stable Isotope Analysis in R (SIAR) package
199 (Parnell et al. 2010; R development core team 2013, ver. 3.0.2). We used the $\delta^{13}C$ values of five
200 essential AAs (threonine, isoleucine, valine, phenylalanine, and leucine) to identify unique
201 isotopic signatures for each source end-member on each reef (n = 3 samples per end-member per
202 reef). We used a small non-zero trophic discrimination factor in the model (0.1 ± 0.1‰) that
203 reflected the minimal trophic fractionation of essential AAs between diet and consumer
204 (McMahon et al. 2010). For the consumer data, we used essential AA $\delta^{13}C$ values from
205 individual samples. We conducted separate models for each species and reef using reef specific

end-member essential AA $\delta^{13}C$ values with the siarsolomcmcv4 function within SIAR (500,000 iterations and an initial discard of the first 50,000 iterations as burn-in). We tested for differences in the relative contribution of the dominant source end-member between shelf and oceanic locations for each species with two-sample t-tests (n = 20 individuals per location).

The resulting data (proportions of each of four end-members) were used to examine variability in carbon source use among focal species and across the seascape. We used a multivariate cluster analysis framework to visualize associations among individual samples and their respective end-member compositions. A k-means strategy identified the most parsimonious number of clusters within the multivariate data set, and then a constellation plot visualized sample associations within these clusters. All univariate, PCA, and cluster analyses were performed in the JMP statistical environment (JMP 2013, ver.11).

RESULTS

We quantified $\delta^{13}C$ values of five essential AAs from a total of 96 end-member samples and 260 fish muscle samples from our eight study reefs (Online Resource 2). Using separate mixed-model univariate ANOVAs of source end-member $\delta^{13}C$ values for each essential AA, we found a significant location*end-member interaction for Val only (Table 1). Location effects were identified for Thr and Val, while end-members differed significantly for all essential AA values. For Thr and Ile, the coral end-member differed significantly from detritus, which was in turn significantly different from phytoplankton and macroalgae (Tukey's HSD). For Phe, the detritus end-member differed significantly from coral and macroalgae, which were in turn significantly different from phytoplankton. Finally, all four end-members were significantly different for Leu $\delta^{13}C$ values.

229 We used a PCA of the essential AA $\delta^{13}C$ values to visualize patterns in the multivariate
230 end-member signatures (Fig. 2). The first two principal components (PCs) of the PCA explained
231 93% of the total variability in the system (PC1 = 70%, PC2 = 23%, Table 2). The loadings for
232 PC1 were all negative and of similar magnitude. Isoleucine was the most important loading for
233 PC2, followed by valine, albeit of opposite sign. The PCA confirmed the relative importance of
234 location and end-members from the univariate ANOVAs above. We found that phytoplankton,
235 macroalgae, coral, and detritus were all clearly separated with non-overlapping 95% density
236 ellipses for almost all end-members from both shelf and oceanic locations in multivariate space
237 (Fig. 2). We detected no obvious effect of location on the multivariate signatures based on the
238 density ellipses for any of the end-members.

239 We then added essential AA $\delta^{13}C$ data from the seven fish species to the PCA model with
240 the end-member signatures (Table 3) to visualize potential associations between carbon end-
241 members at the base of the reef food webs and upper trophic level consumers (Fig. 3). We found
242 good agreement between end-members and their putative consumers. The herbivorous
243 damselfish, *S. nigricans*, always grouped near the macroalgal end-member, *C. striatus* were
244 grouped with the detritus end-member, and *C. trifascialis* were grouped with the coral end-
245 member. The putative planktivore, *A. indicus*, grouped with the phytoplankton end-member on
246 oceanic reefs, however, individuals on shelf reefs fell between phytoplankton and macroalgae.
247 Individuals from the remaining fish species generally fell in the multivariate space between the
248 end-members, indicating that we had adequately constrained the carbon sources at the base of the
249 food web for all of the focal species.

250 The excellent separation of source end-members in multivariate space, good agreement
251 between essential AA $\delta^{13}C$ values of end-members and their primary consumers, and the lack of

252 trophic fractionation of essential AAs provided strong justification for the use of an isotope
253 mixing model to quantify the relative contributions of source end-members to reef fish
254 consumers. The Bayesian isotope mixing model revealed significant variability in the relative
255 contributions of source end-members to upper trophic level consumers (Fig. 4). Variance in
256 model output after 500,000 iterations of the SIAR mixing model was small (5 ± 3%; Online
257 Resource 3).

258 Each of the four source end-members contributed the majority of the carbon assimilated
259 by at least one of the seven fish species across the seascape (Fig. 4). Carbon sources for our
260 primary end-member consumers were generally dominated by their putative diet. Detritus,
261 macroalgae, and coral were the dominant source end-members for *C. striatus* (shelf = 76 ± 8%,
262 oceanic = 70 ± 10%), *S. nigrigans* (shelf = 78 ± 10%, oceanic = 72 ± 11%), and *C. trifascialis*
263 (shelf = 83 ± 4%, oceanic = 79 ± 5%), respectively. There was no effect of location on primary
264 carbon source contribution for any of the three species (samples pooled across reefs within
265 location, two sample t-test, $p > 0.05$). Phytoplankton production contributed 57 ± 7% to our
266 putative planktivore, *A. indicus*, on shelf reefs but that proportion increased significantly to 87 ±
267 5% on oceanic reefs (two sample t-test, $t_{38} = -15.49$, $p < 0.0001$). Detritus (shelf = 49 ± 14%,
268 oceanic = 44 ± 10%) and macroalgae (shelf 36 ± 16%, oceanic = 34 ± 12%) were both major
269 contributors to the diet of *C. sordidus*, with no significant differences between locations for
270 either carbon source. However, carbon source contributions for both *L. ehrenbergii* and *G.*
271 *javanicus* showed significant differences between shelf and oceanic reefs. Macroalgal carbon
272 contributed the majority (71 ± 13%) of the carbon to *L. ehrenbergii* on shelf reefs, but only 17 ±
273 10% on oceanic reefs (two sample t-test, $t_{38} = 14.4$, $p < 0.0001$). Phytoplankton was the
274 dominant end-member (72 ± 11%) for *L. ehrenbergii* on the oceanic reefs. While phytoplankton

was the dominant end-member for *G. javanicus* across locations, contributions were significantly higher on oceanic reefs (79 ± 9%) than on shelf reefs (64 ± 10%) (two sample t-test, $t_{38} = -3.66$, $p = 0.002$).

We used cluster analysis of end-member utilization followed by a constellation plot to help visualize patterns of carbon flow from source end-members to focal consumers. A k-means cluster analyses identified six clusters as the most parsimonious grouping of multivariate end-member proportions. The resulting constellation plot revealed that each of the individual carbon source end-members dominated one of the six clusters (Fig. 5). Cluster A consisted of individuals with high proportions (mean ± SD) of the macroalgal end-member (75 ± 9%), and included *S. nigricans* (Sni) from both shelf and oceanic reefs as well as *L. ehrenbergii* (Leh) from shelf reefs. Samples in Cluster B contained relatively high proportions of both detritus (45 ± 10%) and macroalgae (36 ± 10%) and were dominated taxonomically by *C. sordidus* (Sor), but also contained several individuals of *C. striatus* (Cst), *L. ehrenbergii*, and *S. nigricans*. Cluster C was composed predominantly of *C. striatus* samples with high proportions of detritus (74 ± 8%), while Cluster D consisted exclusively of *C. trifascialis* (Ctr) individuals and the coral end-member (75 ± 9%). Cluster E contained the phytoplankton end-member (79 ± 9%) and contained a taxonomically diverse representation of *A. indicus* (Ain) and *L. ehrenbergii* samples from oceanic reefs, and *G. javanicus* (Gja) samples from both oceanic and shelf locations. Finally, Cluster F consisted almost entirely of *A. indicus* and *L. ehrenbergii* individuals from shelf reefs that were characterized by approximately equal proportions of phytoplankton (55 ± 7%) and macroalgal (38 ± 7%) end-members.

DISCUSSION

298 Identifying important carbon sources supporting coral reef food webs remains a
299 significant and ongoing challenge to ocean ecologists (Wyatt et al. 2012b; Hilting et al. 2013;
300 Letourneur et al. 2013). However, the CSIA fingerprinting approach that we outline here has
301 considerable potential to provide a more comprehensive assessment of carbon flow through reef
302 food webs than was previously possible. We found excellent separation in the $\delta^{13}C$ values of
303 essential AAs among four important source end-members (phytoplankton, macroalgae, coral,
304 and detritus) on the study reefs. We were then able to use Bayesian isotope mixing models to
305 determine relative contributions of each of the end-members to a group of reef fishes spanning
306 multiple feeding guilds and trophic positions. The method provided an alternative to
307 conventional dual-isotope (carbon and nitrogen) approaches that are often under-determined in
308 complex food webs with multiple end-members (Fry 2013; Brett 2014). Moreover, by using
309 essential AAs that exhibit minimal fractionation across trophic levels this method avoids
310 complications of variable and poorly characterized trophic fractionation factors in mixing models
311 (Bond and Diamond 2011). The CSIA fingerprinting approach therefore affords the ability to test
312 hypotheses concerning the response of carbon flow through reef food webs to processes
313 including both natural and anthropogenic disturbances and climate change.
314 We tested the CSIA fingerprinting approach used here by estimating carbon source
315 contributions for several species of coral reef fishes with well-constrained diets. For instance, we
316 estimated that the obligate corralivorous butterflyfish, *C. trifascialis*, received 81 ± 5% of its
317 carbon from coral-fixed carbon. Similarly, the farming damselfish, *S. nigricans*, received 75 ±
318 11% of its dietary carbon from macroalgae. Macroalgae were also important carbon sources for a
319 number of other species in our study, including the roaming herbivore (*C. sordidus*) on oceanic
320 and shelf reefs, and the mesopredator (*L. ehrenbergii*) and the planktivorous damselfish (*A.*

321 *indicus*) on shelf reefs only. Microbially-reworked detritus dominated the sources of essential
322 AAs to *C. striatus*, as we predicted. Interestingly, a recent study has suggested that despite its
323 dental morphology, *C. striatus* can remove more algal turf per hour than the common
324 herbivorous grazer *Acanthurus nigrofuscus* (Marshell and Mumby 2012). We found some
325 support for the functional role of *C. striatus* as an algal grazer, with macroalgae providing an
326 average of 14 ± 7% (upwards of 30% for some individuals) of the carbon consumed and
327 assimilated by individuals across the seascape.
328 Water column primary production represents a significant source of energy and nutrients
329 for coral reefs, as well as an important link between oceanic and reef ecosystems (Emery 1973;
330 Hamner et al. 1988; Richter et al. 2001; Genin et al 2002). Three of the seven species in our
331 study, the planktivorous damselfish *A. indicus*, the mesopredator *L. ehrenbergii*, and the top
332 predator *G. javanicus*, received significant amounts of carbon fixed by phytoplankton (60 ±
333 28%). Interestingly, two dominantly herbivorous fishes, *C. sordidus* and *S. nigricians*, showed
334 moderate reliance on phytoplankton-based carbon (13 ± 6%, reaching 30% for some individuals)
335 on oceanic reefs. Previous studies have found that nominal herbivores such as *Stegastes spp.*
336 assimilated at least some carbon from oceanic sources based on bulk SIA (Wyatt et al. 2012b;
337 Letourneur et al. 2013). Both Wyatt et al. (2012b) and Letourneur et al. (2013) hypothesized that
338 the link between the oceanic production signal and herbivores was through changes in nutrient
339 sources supporting macroalgal production associated with oceanographic forcing, such as
340 upwelling of nutrients (Wyatt et al. 2012a). We were able to directly attribute the oceanic
341 production signal in the herbivorous *S. nigricans* and *C. sordidus* in our study to assimilation of
342 phytoplankton production. Herbivores often consume significant numbers of demersal
343 crustaceans that live in benthic reef habitats (Kramer et al. 2013), either incidentally or as a

complimentary feeding strategy to cope with low protein, plant-based diets (Cruz-Rivera and Hay 2000; Raubenheimer et al. 2009). Many of these crustaceans move up into the water column at night to feed on phytoplankton and particulate organic matter, thereby providing another mechanism for transferring carbon fixed in the water column to herbivorous reef fishes. Alternatively, we cannot rule out the possibility that these consumers were feeding on benthic diatoms, as the amino acid fingerprints of benthic diatoms have not been explicitly tested. Certainly, more detailed studies will be needed to fully resolve the processes that link phytoplankton production with reef food webs.

Detritus represents a major carbon pool in coral reef systems (Crossman et al. 2001), yet decomposition processes are not well understood as they are generally more diverse and difficult to measure than production processes (Alongi 1988; Moore et al. 2004). The CSIA fingerprinting approach outlined here provides a method for identifying microbial processing of organic material (McCarthy et al. 2004; Larsen et al. 2013), and therefore has the potential to improve our understanding of the role that detrital organic material plays in coral reef trophic dynamics and productivity. Sampling the detrital end-member, however, is often difficult in reef environments (e.g. Hilting et al. 2013). We used a detritivorous sea cucumber (Moriarty 1982; Uthicke 1999), *H. atra*, to constrain the isotopic end-member for carbon that had been reprocessed by microbial activity through detrital pathways. The essential AA $\delta^{13}C$ signatures of *H. atra* matched closely to the heterotrophic bacteria end-member of Larsen et al. (2013), suggesting that the sea cucumbers were feeding on a food source that had undergone substantial microbial reworking (Online Resource 4). In addition, our analyses found that detritus was the primary source end-member (73 ± 9%) for the surgeonfish *C. striatus* across the entire system. Previous work indicates that *C. striatus* feeds extensively on detritus based on dental

morphology and feeding observations (Choat et al. 2002, 2004**)**. Taken together, these results suggest that while a combination of new reef and water column production may have been the original source of organic matter to reef detritus, the essential AA $\delta^{13}C$ signature of *H. atra* adequately constrained the isotopic signature of the detrital end-member that is distinct from newly-fixed phytoplankton, macroalgae, and coral carbon.

Detritus was an important source of essential AAs for several focal species, particularly on shelf reefs. For instance, we found that *C. sordidus* received nearly half of its dietary carbon from a detrital end-member with the remaining carbon coming largely from macroalgae. Despite being one of the most abundant coral reef fishes in the Red Sea, the feeding ecology of *C. sordidus* has been challenging to define. Some studies have described *C. sordidus* as a roaming herbivore (Chen 2002; Ledlie et al. 2007; Lecchini and Poignonec 2009), while others have suggested that *C. sordidus* is better described as a detritivore (Choat et al. 2002, 2004). Our results indicated that *C. sordidus* relied on both new reef-derived macroalgal production and microbially-reworked detritus, exhibiting significant dietary plasticity at the individual level. Several upper trophic level consumers, including the mesopredator *L. ehrenbergii* and the top predator *G. javanicus*, received an average of 14 ± 10% (reaching 45% for some individuals) of their dietary carbon from detritus on shelf reefs. These results support the findings of a previous study using bacteria-specific fatty acid profiles and bulk SIA that highlighted the importance of detrital organic matter to the production of the mesopredator *Lethrinus nebulosus* in Australia (Wyatt et al. 2012b). Overall, these results suggest conventional methods of assessing resource utilization of coral reef fishes likely underestimate the importance of microbially-recycled carbon fueling coral reef food webs.

389 While all four source end-members contributed to the production of upper trophic level
390 coral reef fishes in our study, we found that a single source end-member often dominated dietary
391 carbon assimilation in several focal species. This is perhaps not surprising for primary or even
392 secondary consumers, such as the obligate coralivore *C. trifascialis*, the farming herbivore *S.*
393 *nigricans*, and the detritivore *C. striatus*, that are closely linked to their respective end-members
394 at the base of the food web. It has been far more challenging to determine if upper trophic level
395 consumers are similarly linked to a single source end-member at the base of the food web.
396 Conventional diet and bulk isotope approaches typically require extensive characterization of all
397 dietary linkages within a food web to accurately determine the relative contribution of source
398 end-members to top predators. The amino acid isotope fingerprinting approach that we used to
399 track carbon assimilation patterns, on the other hand, does not require reconstruction of entire
400 food web to accurately identify baseline carbon sources for top predators. We found that high
401 trophic level predators in our study system, *L. ehrenbergii* and *G. javanicus*, received the vast
402 majority (>70%) of their carbon from a single end-member, indicating the presence of tightly
403 linked food chains on coral reefs. This result was surprising given that these predators and their
404 typical prey are all highly mobile generalists with the ability to mix diets across multiple food
405 webs (Sommer et al. 1996; Lieske and Myers (2004). These newly discovered tightly-link food
406 webs open new questions about the resilience of top predators to disturbances at the base of the
407 food web.

408 We found significant plasticity in carbon flow patterns of food webs supporting several
409 species in our system as a function of foraging location within the seascape. For instance, when
410 foraging on shallow reefs on the continental shelf, *L. ehrenbergii* relied heavily on reef-derived
411 production from macroalgae and detritus (>85%). Yet when foraging on oceanic reefs

surrounded by deep open water, *L. ehrenbergii* received the majority of their dietary carbon from new water column-based production (>70%), with less than 20% coming from macroalgae and detritus. This pattern of increased reliance on phytoplankton production in oceanic food webs was apparent in several other species as well. The puntative planktivore *A. indicus* always relied on water column-based phytoplankton production for the majority of its dietary carbon; however, individuals residing on shelf reefs also received significant contributions (37 ± 10%) of dietary carbon from macroalgal sources. The mix of phytoplankton and algae in the diet of *A. indicus* on shelf reefs likely reflected higher particulate organic matter loads in the water column of these shallow water shelf reefs, though it is possible that *A. indicus* was directly ingesting macroalgae or macroalgae-consuming invertebrates from the reef surface on the shelf reefs (e.g. Lammens et al. 1985). Yet, as was the case with *L. ehrenbergii*, *A. indicus* residing on oceanic reefs were dominated by carbon from phytoplankton production (87 ± 5%). A similar case was seen in the top predator *G. javanicus*, where the importance of water column-based phytoplankton production was significantly higher on oceanic reefs (79 ± 9%) than it was for individuals on shelf reefs (64 ± 10%). These patterns could not be explained by consumer size, as there were no significant differences in total fish length between individuals collected on shelf and oceanic reefs for any species.

Previous research based on patterns of increasing bulk $\delta^{15}N$ values and decreasing $\delta^{13}C$ values in many coral reef fishes has suggested that the importance of oceanic derived production to coral reef food webs often increases with proximity to the open ocean, perhaps related to the increased access to oceanic nutrients (Wyatt et al. 2012b; Hilting et al. 2013; Letourneur et al. 2013). We directly quantified the increase in relative contribution of water column-based phytoplankton production to a diverse set of upper trophic level coral reef fishes as a function of

435 reef location within the seascape. However, further research is needed to determine whether the
436 observed increase in reliance on water-column production for fishes on oceanic reefs reflected a
437 dietary switch to a more phytoplankton-based food web or an increase in the flow of
438 phytoplankton carbon through the same food webs as on shelf reefs. While our study targeted
439 adult individuals across the entire seascape, previous work has shown that ontogenetic shifts in
440 habitat usage of coral reef fishes can also result in dramatic changes in resource utilization
441 through time and space (McMahon et al. 2012; Cocheret de la Moriniere et al 2013).

442 In conclusion, we found that phytoplankton, macroalgae, coral, and detritus-based carbon
443 sources were all important in supporting the production of a diverse suite of fishes on coral reefs
444 of the Red Sea. However, seascape configuration played an important role in structuring the
445 resource utilization patterns of several species in our study, including a numerically dominant
446 planktivore, a commercially important mesopredator, and a piscivorous top predator. Moreover,
447 carbon utilization in several upper trophic level consumers was dominated by a single end-
448 member, indicating tight links from a single group of primary producers at the base of a food
449 web to top predators. Further work addressing a larger number of species is needed to more
450 comprehensively understand the flow of carbon through entire coral reef food webs. Nonetheless
451 the ability to determine end-member contributions to carbon assimilation in reef fishes using
452 CSIA fingerprinting provides a powerful method to develop and test nutritional frameworks for
453 analyzing resource acquisition and allocation. Understanding these trophodynamic interactions is
454 a key to understanding the spatial resilience of complex ecosystems, such as coral reefs.
455

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465

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Table 1. Results from a mixed-model analysis of variance (ANOVA) to test for variations in source end member $\delta^{13}C$ values of five essential amino acids (AAs) on Red Sea reefs. End-member (EM: plankton, macroalgae, coral, detritus) and location (Loc: shelf, oceanic) were fixed factors, while reef (n = 4) nested within location was a random factor. Bolded *P* values significant at $\alpha = 0.05$

AA	Source	SS	MS	df	F ratio	P < F
Threonine	Location	11.3	11.3	1,6	10.6	**0.017**
	EM	367.9	122.6	3,18	111.6	**<0.0001**
	Loc*EM	5.6	1.86	3,18	1.7	0.203
	Reef(Loc)	6.4	1.05	6,18	0.96	0.477
Isoleucine	Location	0.09	0.09	1,6	0.07	0.799
	EM	215.6	71.6	3,18	53.6	**<0.0001**
	Loc*EM	21.1	7.0	3,18	5.2	**0.009**
	Reef(Loc)	7.9	1.3	6,18	1.0	0.469
Valine	Location	4.8	4.8	1,6	6.4	**0.045**
	EM	392.0	130.7	3,18	246.2	**<0.0001**
	Loc*EM	16.1	5.4	3,18	10.1	**0.0004**
	Reef(Loc)	4.5	0.75	6,18	1.4	0.26
Phenylalanine	Location	2.1	2.1	1,6	1.6	0.254
	EM	194.0	64.7	3,18	60.4	**<0.0001**
	Loc*EM	2.1	0.7	3,18	0.7	0.59
	Reef(Loc)	7.9	1.3	6,18	1.2	0.34
Leucine	Location	0.9	0.9	1,6	0.5	0.487
	EM	441.2	147.1	3,18	196.9	**<0.0001**
	Loc*EM	6.3	2.1	3,18	2.8	0.069
	Reef(Loc)	10.4	1.7	6,18	2.3	0.077

Table 2. Eigenvectors and variance explained (%) for the five principal components (PC) in the principal component analysis of $\delta^{13}C$ values from end member (plankton, macroalgae, coral, and detritus) essential amino acids on shelf and oceanic reefs near Al-Lith, Saudi Arabia in the Red Sea

	PC1	PC2	PC3	PC4	PC5
Threonine	-0.46	0.35	0.68	0.38	-0.23
Isoleucine	-0.33	0.70	-0.24	-0.58	0.07
Valine	-0.42	-0.54	0.12	-0.52	-0.50
Phenylalanine	-0.50	-0.03	-0.67	0.50	-0.21
Leucine	-0.50	-0.31	0.11	-0.03	0.80
Variance	69.5	23.1	3.9	2.5	1.1

Table 3. Eigenvectors and variance explained (%) for the five principal components (PC) in the principal component analysis of end member and fish essential amino acid $\delta^{13}C$ values from shelf and oceanic reefs near Al-Lith, Saudi Arabia in the Red Sea

	PC1		PC2		PC3		PC4		PC5	
	shelf	oceanic	shelf	oceanic	shelf	oceanic	shelf	oceanic	shelf	oceanic
Threonine	0.56	0.44	-0.39	0.50	-0.68	-0.74	0.25	0.06	0.11	0.07
Isoleucine	0.38	0.24	-0.63	0.57	0.56	0.57	-0.35	0.54	0.17	-0.01
Valine	0.41	0.45	0.55	-0.58	0.16	-0.04	0.06	0.54	0.70	0.40
Phenylalanine	0.38	0.43	0.11	0.13	0.42	0.35	0.66	-0.60	-0.47	0.56
Leucine	0.48	0.60	0.38	-0.26	-0.13	0.10	-0.61	-0.23	-0.49	-0.72
Variance (%)	63.3	69.9	28.0	21.9	4.4	4.1	2.9	2.5	1.5	1.4

FIGURES

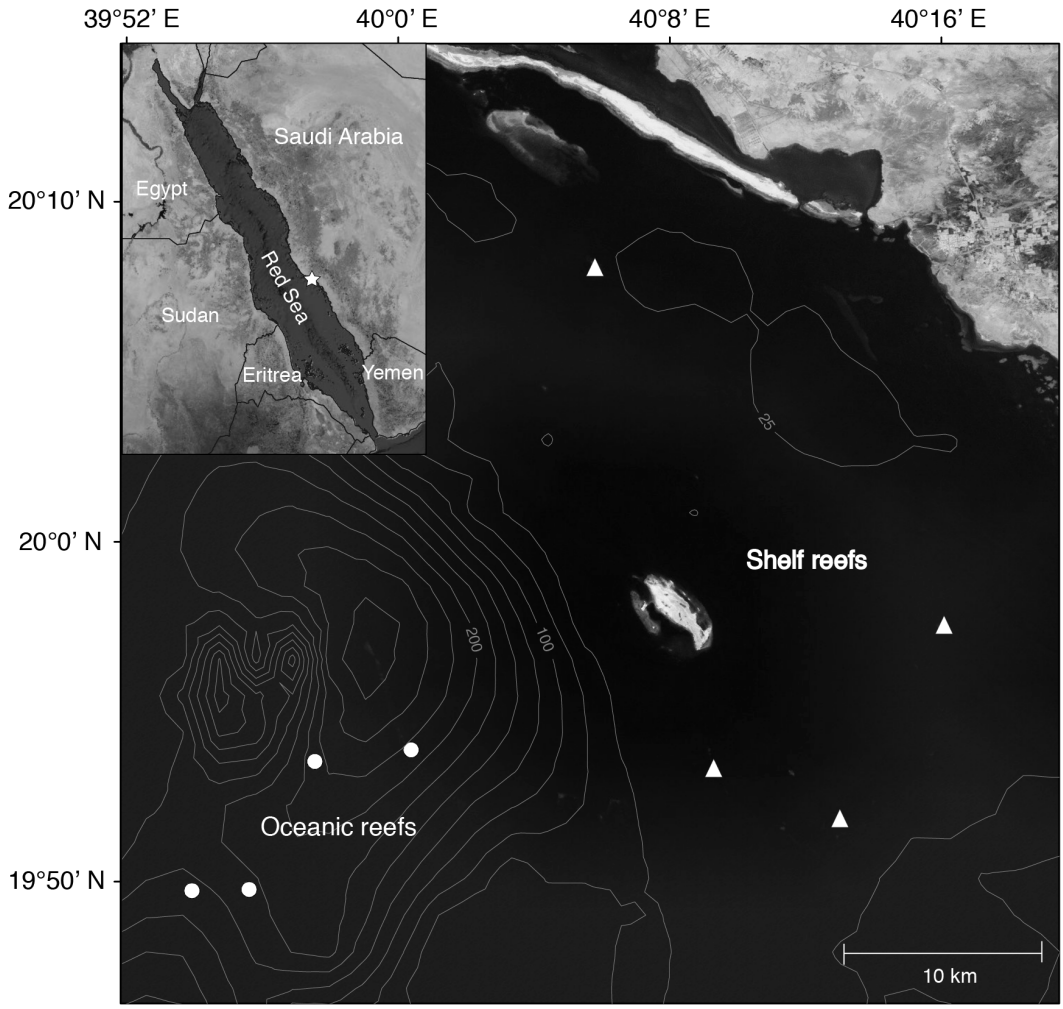
Fig. 1 Map of the collection sites for source end-members and fish species from shelf reefs (triangles) located on the continental shelf and oceanic reefs (circles) located off the continental shelf and surrounded by deep open water (four reefs per location) near Al-Lith (star symbol in inset), Saudi Arabia in the Red Sea. Contour lines indicate 25m isobaths

Fig. 2 Multivariate separation of four source end-members on reefs along the Saudi Arabian coast of the Red Sea visualized as principal component 1 and 2 of a principal component analysis of the $\delta^{13}C$ values of five essential amino acid: threonine, isoleucine, valine, phenylalanine, and leucine. Samples were analyzed from shelf reefs (filled symbols) and oceanic reefs (open symbols) and plotted with 95% confidence ellipses. The four source end-members were: plankton (blue diamonds), macroalgae (green circles), coral (magenta triangles), and detritus (brown squares)

Fig. 3 Multivariate separation of seven reef fish species and four source end-members, visualized as the first 3 principal components of a principal component analysis of the $\delta^{13}C$ values of five essential amino acid: threonine, isoleucine, valine, phenylalanine, and leucine. The four source end-members were plotted as 95% confidence ellipses as follows: plankton (blue), macroalgae (green), coral (magenta), and detritus (brown). Symbols for primary consumers of each of the four end-members were filled in the same color as the 95% confidence ellipses of their diet end-member: *Amblyglyphidodon indicus* (blue diamonds), *Stegastes nigricans* (green circles), *Chaetodon trifascialis* (magenta triangles) and *Ctenochaetus striatus* (brown squares). The remaining species (open symbols) were *Chlorurus sordidus* (red triangles), *Lutjanus ehrenbergii* (purple squares), and *Gymnothorax javanicus* (cyan diamonds) (n = 20 individuals per species per location except *G. javanicus* where n = 10 individuals per location)

Fig. 4 Relative contributions of four source end-members, plankton (blue), macroalgae (green), coral (magenta), and detritus (brown) to the dietary carbon supporting seven fish species, *Stegastes nigricans*, *Chaetodon trifascialis*, *Ctenochaetus striatus*, *Chlorurus sordidus*, *Amblyglyphidodon indicus*, *Lutjanus ehrenbergii*, and *Gymnothorax javanicus*, from a) shelf reefs and b) oceanic reefs near Al-Lith, Saudi Arabia in the Red Sea. Relative contributions were determined from the $\delta^{13}C$ values of five essential amino acids (threonine, isoleucine, valine, phenylalanine, and leucine) of end-members and consumers using a Bayesian stable isotope mixing model (bars represent individuals, n = 20 individuals per species per location except *G. javanicus* where n = 10 individuals per location)

Fig. 5 Constellation plot identifying six clusters (A-F) determined from a k-means cluster analysis of the relative contributions of four source end-members to seven coral reef fish species, *Stegastes nigricans* (Sni), *Amblyglyphidodon indicus* (Ain), *Ctenochaetus striatus* (Cst), *Chlorurus sordidus* (Sor), *Chaetodon trifascialis* (Ctr), *Lutjanus ehrenbergii* (Leh), and *Gymnothorax javanicus* (Gja) collected from shelf reefs (purple labels) and oceanic reefs (cyan labels) along the Saudi Arabian coast of the Red Sea. Points represent individuals (n = 20 individuals per species per location except *G. javanicus* where n = 10 individuals per location). Symbol color shows dominant end-member: phytoplankton (blue symbols), macroalgae (green symbols), coral (magenta symbols), and detritus (brown symbols) for each fish sample


39°52’ E
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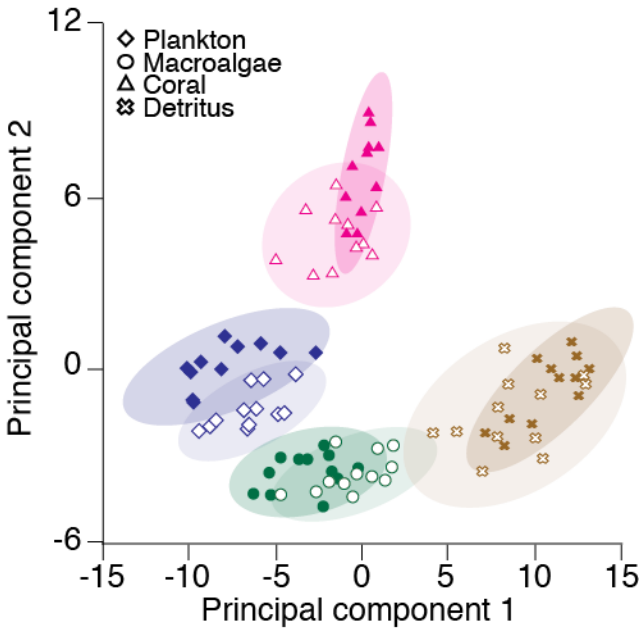
40°16’ E
20°10’ N
20°0’ N
19°50’ N
Saudi Arabia
Egypt
Red Sea
Sudan
Eritrea
Yemen
25
100
200
Shelf reefs
Oceanic reefs
10 km

Figure 1.


Plankton
Macroalgae
Coral
Detritus
Principal component 2
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6
0
-6
-15
-10
-5
0
5
10
15
Principal component 1

Figure 2

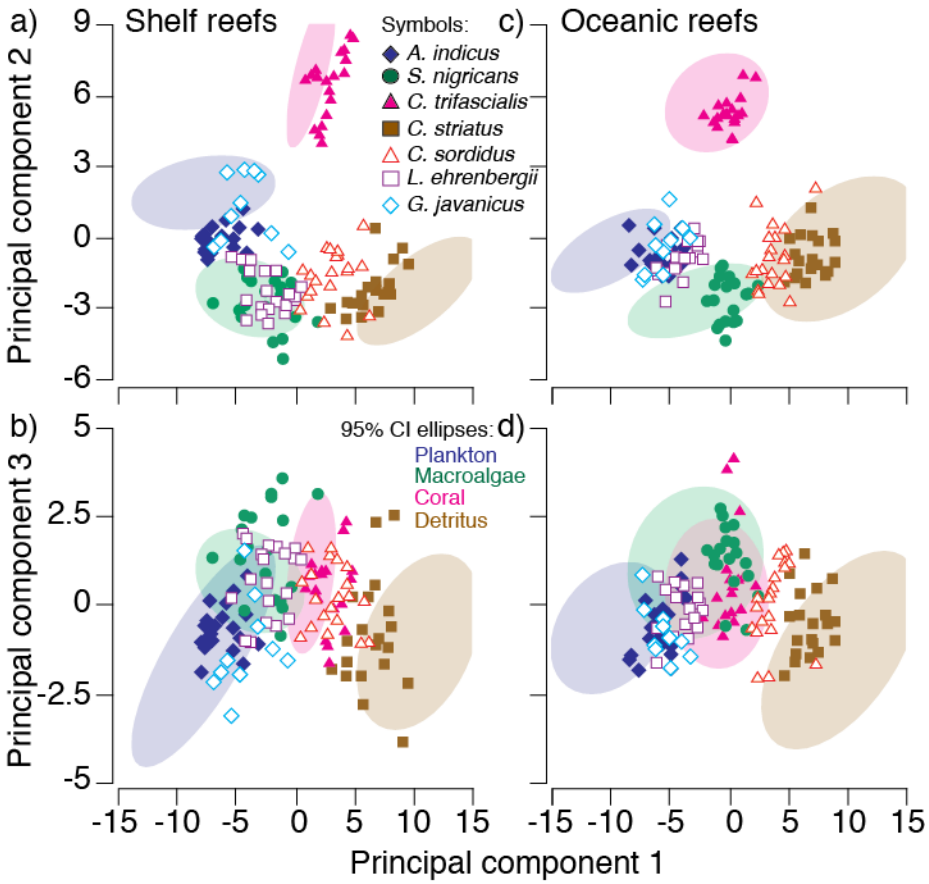
a)
Shelf reefs
c)
Oceanic reefs
Symbols:
A. indicus
S. nigricans
C. trifascialis
C. striatus
C. sordidus
L. ehrenbergii
G. javanicus
b)
d)
95% CI ellipses:
Plankton
Macroalgae
Coral
Detritus
Principal component 2
Principal component 3
Principal component 1
9
6
3
0
-3
-6
5
2.5
0
-2.5
-5
-15 -10 -5 0 5 10 15

Figure 3.

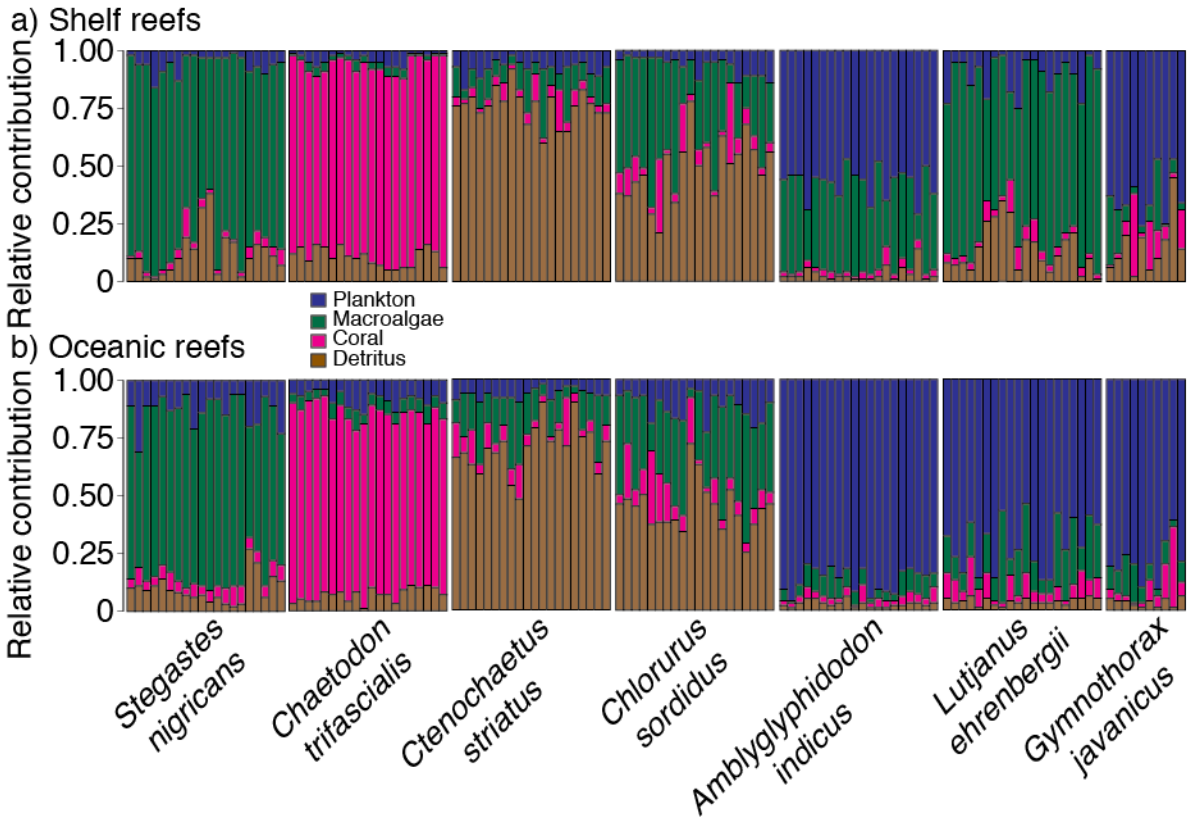
a) Shelf reefs
b) Oceanic reefs
Relative contribution
1.00
0.75
0.50
0.25
0
Plankton
Macroalgae
Coral
Detritus
Stegastes nigricans
Chaetodon trifascialis
Ctenochaetus striatus
Chlorurus sordidus
Amblyglyphidodon indicus
Lutjanus ehrenbergii
Gymnothorax javanicus

Figure 4.

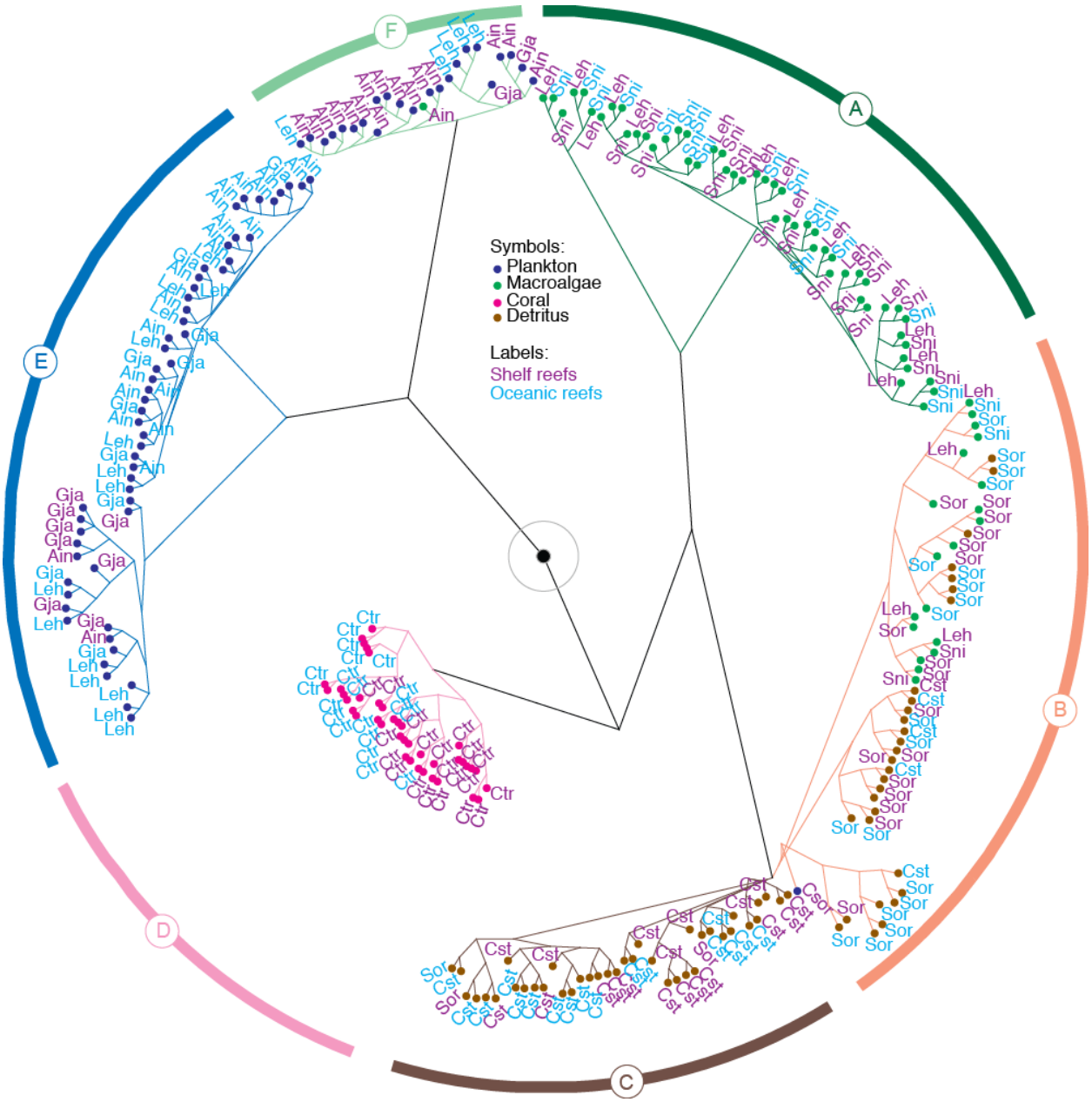
Symbols:
Plankton
Macroalgae
Coral
Detritus
Labels:
Shelf reefs
Oceanic reefs
A
B
C
D
E
F

Figure 5.

Running Head: Carbon flow in tropical seascapes

Tracing carbon flow through coral reef food webs using a compound-specific stable isotope approach

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Declaration of Authorship: KWM, SRT, and MLB conceived of and designed the study, KWM and MLB conducted the fieldwork, KWM and LAH conducted the laboratory analyses, KWM and SRT analyzed the data and wrote the manuscript, MLB and LAH revised and edited the manuscript.

Conflict of Interest: The authors declare that they have no conflict of interest.

Online Resource 1. Total length (mean ± SD measured to the nearest 1mm) of seven species of coral reef fishes analyzed for essential amino acid $\delta^{13}C$ values from shelf and oceanic reefs near Al-Lith, Saudi Arabia in the Red Sea (n = 20 individuals per location). Statistical differences in mean total length were determined by a Welch's unequal variances t-test. Total lengths were not collected for *G. javanicus*, but all individuals were > 1m and considered adults

	Mean Shelf	Mean Oceanic	$T_{df=38}$ (*P* value)
L. ehrenbergii	211 ± 16	208 ± 19	0.57 (*P* = 0.58)
C. striatus	140 ± 17	142 ± 16	-0.37 (*P* = 0.71)
C. sordidus	167 ± 26	174 ± 39	-0.59 (*P* = 0.56)
A. indicus	89 ± 15	91 ± 14	-0.49 (*P* = 0.63)
C. trifascialis	107 ± 11	110 ± 9	-0.87 (*P* = 0.39)
S. nigricans	99 ± 11	93 ± 12	1.48 (*P* = 0.15)
G. javanicus	-	-	-

Online Resource 2. Mean (‰ ± SD) essential amino acid $\delta^{13}C$ values of four source end-members and seven coral reef fish species collected from four shelf reefs and four oceanic reefs (Location: Latitude, Longitude) (n = 3 for all source end-members, 5 for all fish species except *G. javanicus* where n = 2 for Ron's reef, Saut reef, Shi'b Sulaym reef, and Dohra reef, and n = 3 for LJ's reef, Brown reef, Canyon reef, and MarMar reef)

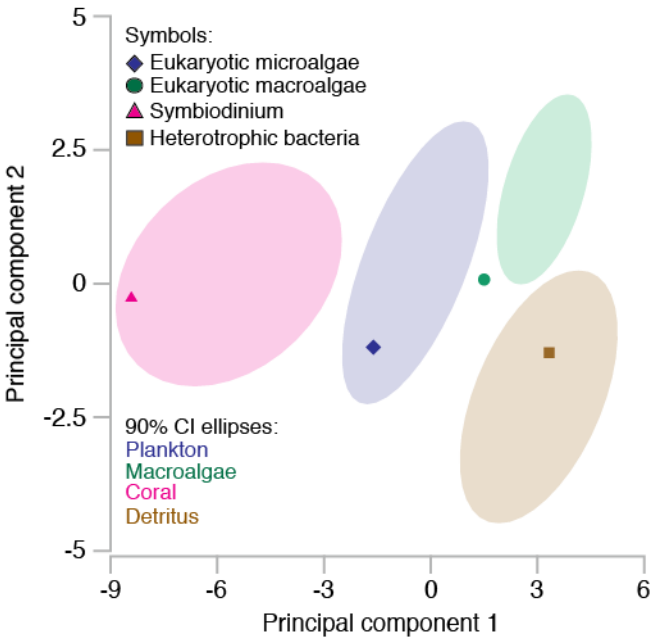
	Threonine	Isoleucine	Valine	Phenylalanine	Leucine
Ron's Reef (Shelf: 20.1348°N, 40.1012°W)					
Plankton	-9.6 ± 0.5	-17.8 ± 0.5	-23.2 ± 0.3	-24.7 ± 0.4	-25.5 ± 0.2
Macroalgae	-9.7 ± 0.8	-16.2 ± 0.9	-18.3 ± 0.8	-21.1 ± 1.0	-22.7 ± 1.1
Coral	-1.8 ± 0.6	-7.8 ± 0.5	-22.1 ± 0.3	-19.3 ± 0.4	-23.3 ± 0.6
Detritus	0.1 ± 1.2	-10.4 ± 0.7	-12. 1 ± 0.7	-16.1 ± 0.4	-13.9 ± 0.7
L. ehrenbergii	-8.7 ± 0.8	-16.7 ± 0.8	-18.9 ± 1.2	-21.1 ± 1.0	-20.8 ± 0.5
C. striatus	-0.6 ± 1.8	-12.6 ± 0.5	-13.9 ± 0.5	-17.7 ± 0.4	-15.6 ± 0.4
C. sordidus	-4.5 ± 1.5	-13.7 ± 0.9	-16.2 ± 1.1	-17.6 ± 0.6	-20.1 ± 0.6
A. indicus	-9.5 ± 0.5	-17.1 ± 0.5	-20.9 ± 0.3	-23.2 ± 0.2	-23.8 ± 0.1
C. trifascialis	-0.3 ± 0.2	-9.6 ± 1.2	-20.8 ± 0.3	-18.7 ± 0.1	-22.3 ± 0.5
S. nigricans	-10.7 ± 0.9	-16.3 ± 1.1	-18.1 ± 1.5	-20.7 ± 0.9	-20.8 ± 1.3
G. javanicus	-8.2 ± 0.1	-17.6 ± 0.3	-21.0 ± 0.1	-23.6 ± 0.4	-23.3 ± 0.1
LJ's Reef (Shelf: 19.9582°N, 40.2673°W)					
Plankton	-8.0 ± 0.2	-17.9 ± 0.4	-23.2 ± 0.3	-24.9 ± 0.2	-26.6 ± 0.3
Macroalgae	-10.7 ± 1.1	-17.0 ± 0.9	-19.4 ± 0.4	-22.2 ± 0.3	-21.7 ± 0.8
Coral	-4.1 ± 0.9	-9.3 ± 1.1	-21.2 ± 0.4	-18.7 ± 0.3	-22.3 ± 0.4
Detritus	-1.2 ± 1.7	-13.8 ± 1.4	-14.3 ± 0.2	-17.1 ± 0.6	-14.5 ± 1.3
L. ehrenbergii	-8.4 ± 1.4	-16.3 ± 0.5	-18.5 ± 1.2	-20.7 ± 1.0	-21.5 ± 0.8
C. striatus	-2.6 ± 0.9	-15.1 ± 1.1	-15.3 ± 0.7	-17.9 ± 0.4	-16.8 ± 0.7
C. sordidus	-6.3 ± 0.6	-14.5 ± 1.1	-17.1 ± 1.4	-19.1 ± 1.0	-18.4 ± 1.3
A. indicus	-9.4 ± 0.4	-17.6 ± 0.3	-21.4 ± 0.3	-23.5 ± 0.3	-24.1 ± 0.3
C. trifascialis	-3.2 ± 0.3	-10.4 ± 0.4	-20.4 ± 0.3	-18.1 ± 0.4	-21.5 ± 0.3
S. nigricans	-9.8 ± 1.1	-15.4 ± 0.6	-18.1 ± 0.6	-21.2 ± 1.0	-21.7 ± 0.6
G. javanicus	-6.4 ± 0.2	-16.3 ± 0.7	-21.8 ± 1.1	-22.8 ± 0.7	-23.6 ± 1.3
Saut Reef (Shelf: 19.8875°N, 40.1565°W)					
Plankton	-7.7 ± 0.4	-14.0 ± 1.1	-21.0 ± 1.1	-23.8 ± 1.0	-23.3 ± 0.9
Macroalgae	-8.7 ± 1.0	-16.7 ± 0.7	-17.6 ± 0.5	-19.3 ± 0.2	-20.3 ± 0.2
Coral	-3.6 ± 0.7	-9.5 ± 1.2	-22.3 ± 0.9	-21.3 ± 1.3	-21.5 ± 0.8
Detritus	0.6 ± 1.6	-11.7 ± 0.8	-12.3 ± 0.4	-16.6 ± 0.9	-14.1 ± 0.9
L. ehrenbergii	-7.9 ± 0.7	-15.1 ± 0.3	-16.8 ± 0.4	-19.0 ± 0.7	-20.1 ± 0.6
C. striatus	-3.3 ± 0.9	-11.6 ± 1.5	-14.0 ± 0.6	-17.2 ± 1.0	-17.4 ± 0.6
C. sordidus	-4.1 ± 1.5	-13.7 ± 1.6	-15.2 ± 1.2	-18.1 ± 0.6	-17.1 ± 1.1
A. indicus	-8.4 ± 1.1	-15.5 ± 0.4	-19.8 ± 0.5	-22.5 ± 0.4	-22.0 ± 0.6
C. trifascialis	-3.3 ± 0.6	-8.0 ± 0.4	-21.5 ± 0.2	-21.5 ± 0.6	-21.2 ± 0.3
S. nigricans	-9.5 ± 1.3	-15.4 ± 1.1	-15.9 ± 0.7	-18.4 ± 0.7	-19.7 ± 0.8
G. javanicus	-6.1 ± 0.1	-14.1 ± 1.5	-19.7 ± 0.5	-22.5 ± 1.2	-22.0 ± 1.2
Brown Reef (Shelf: 19.8556°N, 40.2162°W)					

Plankton	-7.8 ± 0.6	-16.3 ± 0.5	-22.9 ± 0.1	-23.8 ± 0.8	-24.8 ± 0.3
Macroalgae	-7.7 ± 0.8	-17.3 ± 0.8	-18.0 ± 0.6	-19.5 ± 1.0	-22.4 ± 0.4
Coral	-2.1 ± 0.3	-7.9 ± 0.5	-21.3 ± 0.6	-19.3 ± 0.8	-23.1 ± 0.3
Detritus	-0.3 ± 1.2	-11.4 ± 1.7	-12.3 ± 1.7	-16.5 ± 1.3	-15.3 ± 0.7
L. ehrenbergii	-8.0 ± 1.3	-16.3 ± 0.3	-17.6 ± 0.9	-19.3 ± 0.6	-22.1 ± 2.1
C. striatus	-2.9 ± 1.2	-13.9 ± 0.4	-14.3 ± 0.8	-18.3 ± 1.4	-16.4 ± 0.5
C. sordidus	-4.3 ± 1.2	-13.3 ± 0.9	-16.1 ± 1.0	-18.4 ± 0.3	-18.2 ± 0.5
A. indicus	-7.9 ± 0.9	-16.1 ± 0.7	-20.5 ± 0.5	-22.5 ± 0.7	-23.4 ± 0.6
C. trifascialis	-1.0 ± 0.7	-6.7 ± 1.0	-20.0 ± 0.6	-19.0 ± 0.5	-22.3 ± 0.4
S. nigricans	-6.5 ± 0.4	-16.2 ± 0.7	-17.0 ± 0.5	-19.2 ± 0.6	-21.9 ± 0.6
G. javanicus	-7.1 ± 1.4	-13.3 ± 1.2	-20.1 ± 2.1	-22.5 ± 0.7	-21.7 ± 1.8
Canyon Reef (Oceanic: 19.8923°N, 39.9591°W)					
Plankton	-10.4 ± 1.0	-16.6 ± 0.8	-20.5 ± 1.3	-24.1 ± 0.5	-25.3 ± 0.3
Macroalgae	-9.6 ± 1.0	-14.5 ± 1.0	-16.5 ± 1.0	-19.2 ± 1.7	-19.4 ± 0.9
Coral	-5.5 ± 1.3	-12.2 ± 0.9	-22.1 ± 1.2	-18.0 ± 0.4	-22.1 ± 0.8
Detritus	-1.8 ± 1.6	-11.7 ± 0.5	-13.3 ± 1.1	-16.4 ± 1.7	-14.6 ± 1.7
L. ehrenbergii	-9.4 ± 0.5	-16.2 ± 0.9	-19.4 ± 0.5	-22.4 ± 1.0	-24.0 ± 0.4
C. striatus	-3.7 ± 1.0	-12.4 ± 0.8	-14.5 ± 0.5	-17.4 ± 0.4	-16.9 ± 0.8
C. sordidus	-6.0 ± 0.9	-12.7 ± 0.6	-15.7 ± 1.5	-18.0 ± 0.9	-18.0 ± 0.9
A. indicus	-9.7 ± 0.5	-16.5 ± 0.6	-21.4 ± 1.0	-24.5 ± 0.7	-24.3 ± 0.9
C. trifascialis	-5.2 ± 2.0	-7.9 ± 0.2	-20.7 ± 0.6	-19.5 ± 0.4	-21.3 ± 0.1
S. nigricans	-8.9 ± 1.1	-15.1 ± 1.7	-16.7 ± 1.0	-20.7 ± 0.9	-19.0 ± 1.0
G. javanicus	-10.9 ± 1.0	-15.9 ± 0.5	-20.3 ± 1.1	-24.1 ± 0.3	-23.7 ± 0.3
Shi'b Sulaym Reef (Oceanic: 19.8980°N, 40.0062°W)					
Plankton	-9.6 ± 1.0	-16.1 ± 0.2	19.9 ± 0.9	-23.4 ± 0.7	-24.8 ± 0.4
Macroalgae	-10.4 ± 1.2	-15.6 ± 0.7	-17.3 ± 1.3	-20.1 ± 1.3	20.4 ± 0.8
Coral	-3.7 ± 1.4	-11.0 ± 0.5	-22.4 ± 0.6	-18.7 ± 0.5	-21.5 ± 0.6
Detritus	-0.7 ± 0.5	-12.1 ± 1.6	-13.4 ± 0.8	-16.9 ± 1.9	-14.8 ± 1.7
L. ehrenbergii	-10.0 ± 1.0	-15.6 ± 0.6	-19.1 ± 0.5	-22.7 ± 0.5	-23.5 ± 0.7
C. striatus	-3.8 ± 0.9	-13.2 ± 0.4	-15.2 ± 1.0	-17.5 ± 0.7	-15.9 ± 1.1
C. sordidus	-5.0 ± 2.1	-13.6 ± 0.8	-16.4 ± 0.8	-17.8 ± 1.4	-18.8 ± 0.5
A. indicus	-9.2 ± 0.8	-16.0 ± 0.4	-19.2 ± 0.3	-23.2 ± 0.6	-24.0 ± 0.4
C. trifascialis	-4.3 ± 0.5	-11.3 ± 0.3	-21.3 ± 0.4	-19.5 ± 0.8	-21.6 ± 0.5
S. nigricans	-10.3 ± 0.4	-15.3 ± 0.5	-16.9 ± 0.8	-20.4 ± 0.8	-20.1 ± 0.6
G. javanicus	-9.2 ± 0.1	-16.4 ± 0.3	-20.9 ± 1.2	-22.8 ± 1.0	-23.9 ± 0.9
MarMar Reef (Oceanic: 19.8296°N, 39.9267°W)					
Plankton	-8.8 ± 0.5	-15.6 ± 1.4	-19.9 ± 1.1	-22.4 ± 0.4	-24.0 ± 0.8
Macroalgae	-7.8 ± 0.7	-14.6 ± 0.6	-16.6 ± 0.9	-20.5 ± 0.6	-20.7 ± 0.8
Coral	-4.6 ± 1.2	-9.8 ± 0.8	-22.1 ± 0.2	-21.5 ± 0.5	-23.9 ± 0.5
Detritus	-3.5 ± 0.6	-13.8 ± 0.4	-14.4 ± 0.5	-18.4 ± 1.2	-16.7 ± 1.6
L. ehrenbergii	-8.6 ± 0.6	-14.5 ± 0.5	-18.7 ± 0.5	-22.0 ± 0.4	-23.2 ± 1.0
C. striatus	-4.4 ± 0.7	-13.4 ± 1.2	-14.5 ± 0.6	-18.7 ± 0.4	-17.6 ± 0.7
C. sordidus	-5.6 ± 0.5	-14.2 ± 0.8	-15.2 ± 0.6	-19.9 ± 0.7	-19.0 ± 0.8

A. indicus	-9.7 ± 0.8	-16.7 ± 0.5	-21.6 ± 0.7	-22.4 ± 0.3	-23.6 ± 0.2
C. trifascialis	-4.7 ± 0.6	-10.7 ± 0.3	-21.1 ± 0.1	-21.2 ± 0.4	-22.6 ± 0.6
S. nigricans	-9.3 ± 0.5	-13.4 ± 0.5	-16.9 ± 0.5	-20.0 ± 0.5	-20.9 ± 0.2
G. javanicus	-8.1 ± 0.5	-16.0 ± 0.8	-20.7 ± 0.9	-22.2 ± 0.8	-24.0 ± 0.3
Dohra Reef (Oceanic: 19.8289°N, 39.8987°W)					
Plankton	-8.6 ± 0.6	-14.4 ± 0.7	-19.8 ± 1.1	-22.0 ± 0.7	-24.4 ± 0.3
Macroalgae	-8.7 ± 1.2	-14.3 ± 0.9	-16.0 ± 0.9	-19.6 ± 1.1	-19.5 ± 0.8
Coral	-5.5 ± 0.8	-11.1 ± 1.4	-22.1 ± 0.9	-19.0 ± 1.6	-23.1 ± 1.5
Detritus	-2.5 ± 2.1	-12.5 ± 1.9	-13.1 ± 0.5	-15.4 ± 1.0	-14.0 ± 1.7
L. ehrenbergii	-8.4 ± 0.9	-14.9 ± 0.5	-18.7 ± 0.4	-21.2 ± 0.3	-22.7 ± 0.6
C. striatus	-5.5 ± 2.7	-11.2 ± 2.6	-14.0 ± 0.4	-15.9 ± 1.8	-15.0 ± 1.5
C. sordidus	-6.4 ± 0.7	-12.7 ± 0.9	-15.1 ± 0.3	-18.7 ± 0.8	-18.6 ± 1.0
A. indicus	-9.3 ± 0.5	-14.3 ± 0.4	-18.6 ± 0.5	-21.9 ± 0.2	-23.7 ± 0.2
C. trifascialis	-4.8 ± 0.3	-11.3 ± 0.4	-21.0 ± 0.2	-17.7 ± 0.2	-22.5 ± 0.5
S. nigricans	-8.4 ± 1.1	-14.3 ± 0.3	-16.4 ± 0.8	-19.8 ± 0.5	-18.9 ± 0.6
G. javanicus	-7.5 ± 0.2	-15.5 ± 0.3	-20.2 ± 1.1	-21.3 ± 0.3	-24.2 ± 1.4

Online Resource 3. Mean individual variance (‰ ± SD) in SIAR model output of relative contribution of four source end-members to seven coral reef fish species on shelf and oceanic reefs near Al-Lith, Saudi Arabia in the Red Sea (n = 20 individual per location, except *G. javanicus* where n = 10 individuals per location). The standard deviation in relative contribution for each individual was calculated from 500,000 iterations of the model with a 50,000 burn-in discard and then averaged for each location (n = 4 reefs per location, consisting of 5 individuals per reef for all species expect *G. javanicus* where two to three individuals were used per reef)

	Plankton SD		Macroalgae SD		Coral SD		Detritus SD	
	shelf	oceanic	shelf	oceanic	shelf	oceanic	shelf	oceanic
L. ehrenbergii	5.7 ± 2.5	7.9 ± 2.4	8.1 ± 2.9	8.5 ± 2.5	3.1 ± 1.2	5.0 ± 2.1	4.0 ± 1.5	3.1 ± 0.9
C. striatus	4.7 ± 1.4	4.9 ± 1.5	6.5 ± 2.0	8.3 ± 2.6	3.3 ± 1.4	4.3 ± 2.0	4.1 ± 0.9	6.5 ± 1.7
C. sordidus	5.0 ± 2.3	7.5 ± 2.2	7.8 ± 2.5	11.8 ± 3.0	3.7 ± 1.4	5.0 ± 2.1	4.4 ± 0.7	7.7 ± 1.7
A. indicus	5.7 ± 1.5	4.9 ± 1.4	6.3 ± 1.7	4.9 ± 1.8	2.1 ± 1.0	2.8 ± 1.2	1.8 ± 0.9	2.0 ± 0.7
C. trifascialis	2.5 ± 1.6	5.3 ± 1.4	2.1 ± 1.0	4.7 ± 0.9	4.4 ± 1.1	6.1 ± 1.1	3.3 ± 0.5	4.1 ± 1.6
S. nigricans	4.0 ± 2.1	7.8 ± 2.0	6.2 ± 1.9	10.5 ± 3.2	2.6 ± 1.1	4.5 ± 1.0	3.5 ± 1.3	5.4 ± 2.2
G. javanicus	6.3 ± 2.9	7.6 ± 4.2	6.3 ± 3.9	6.2 ± 2.5	3.9 ± 2.7	5.1 ± 4.6	3.2 ± 1.0	2.6 ± 0.9



Online Resource 4. Normalized $\delta^{13}C$ fingerprints of five essential amino acids (threonine, isoleucine, valine, phenylalanine, and leucine) from carbon source end-members visualized using a principal components analysis (PCA). Samples of end-members (n = 24) from reefs near Al-Lith, Saudi Arabia in the Red Sea 90% are displayed as 90% probability ellipses and color-coded as follows: phytoplankton (blue), macroalgae (green), coral (magenta), and detritus (brown). Reference end-members are plotted as filled symbols and include eukaryotic microalgae (blue diamonds), eukaryotic macroalgae (green circles), *Symbiodinium* sp. (magenta triangles), and heterotrophic bacteria (brown squares). The eukaryotic microalgae comprised diatoms, chrysophytes, and chlorophytes from Larsen et al. (2013). The eukaryotic macroalgae comprise Rhodophytes in the same class as the Red Sea macroalgae, Florideophyceae, from Larsen et al. (2013). The *Symbiodinium* sp. samples were isolated from a pure culture at Woods Hole Oceanographic Institution. The heterotrophic bacteria comprise *Rhodococcus spp*. from Larsen et al. (2013)