Vol. 428: 49–61, 2011
doi: 10.3354/meps09052

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 3

# Trophic dynamics in a relatively pristine subtropical fringing mangrove community

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ABSTRACT: Mangroves provide important habitats for many species throughout the tropics and subtropics. But the direct contribution of mangrove productivity to associated food webs through trophic interactions varies depending on site-specific context. We used stable isotopes to examine trophic structure among major habitat types associated with 2 fringing mangrove areas in Shark Bay, Western Australia, a nearly pristine ecosystem. The only mangrove species, *Avicennia marina*, had a distinctive $\delta^{13}C$ isotopic value, which allowed direct testing of the hypothesis that consumers relied on mangrove-derived production. We found little evidence to support this hypothesis in isotope values of invertebrates or fish from 4 different feeding guilds. Within the species of fish we were able to sample, variation in $\delta^{13}C$ and $\delta^{15}N$ stable isotope values occurred over spatial scales of hundreds of meters. Some of this variation is consistent with the spatial mosaics of seagrass, sand flat and mangrove habitats available to fish. In a nearly pristine system, fish captured in mangrove systems show fine scale variability in stable isotope values, but we found no indication that mangrove productivity directly supported local fish populations through the trophic web.

KEY WORDS: Energy flow · Fish · Food web · Seagrass · Stable isotope analysis · Australia



## INTRODUCTION

Habitats at terrestrial–ocean boundaries can influence nearby marine ecosystems more than might be predicted based on their size alone. Mangroves, in particular, are thought to affect both primary and secondary productivity well beyond intertidal zones (Duffy 2006, Nagelkerken et al. 2008, Nagelkerken 2009). Links between mangroves and surrounding marine habitats are driven by active movement of animals and by the exchange of nutrients through currents and tides. Mangrove habitats, however, can vary substantially in their structure and function (Ewel et al. 1998). The importance of mangroves to populations of fish is highly variable among systems (Faunce & Serafy, 2006), which may be due to spatial structure (landscape characteristics), temporal dynamics (hydrodynamics) or species composition (Lugendo et al. 2007, Faunce & Layman 2009).

Mangrove systems are often classified into 3 major categories: 'fringing mangroves', which are typically narrow in extent and occur along embayments, lagoons or sheltered ocean coasts; 'riverine mangroves', which lie along estuarine river banks and are of variable salinity; and 'basin mangroves', which are found behind fringe and riverine mangroves and have variable degrees of tidal flushing (Ewel et al. 1998). In riverine mangroves, mangrove trees with prop roots or pneumatophores add physical structure in the water column that increases protective cover and surface area for epibiota, thereby increasing the diversity and abundance of invertebrates and juvenile fish. Further, riverine and basin mangrove sediments often are rich in organic carbon and favor burrowing benthic invertebrates and infauna (Nagelkerken et al. 2008). In contrast, fringing mangroves often have few of the characteristics that make riverine mangroves so important in supporting high biodiversity and productive fisheries (Ewel et al. 1998).

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Feeding activities of fish is one process linking mangroves to other local habitats. Fish in mangrove habitats can vary their feeding behavior in response to local variation in prey abundance and predation risk (Laegdsgaard & Johnson 2001, Sanchez-Jerez et al. 2002, Unsworth et al. 2007), which may modify cross-habitat linkages. Many species of fish found in fringing mangroves are considered 'opportunistic,' shifting feeding locations and prey items in response to local conditions (Hammerschlag-Peyer & Layman 2010). Such shifts may be particularly pronounced in mangrove systems with low prey availability and, thus, could lead to greater connectivity to non-mangrove food webs.

In this study, we explored food web structure and feeding relationships in fringing mangrove habitats of the relatively pristine ecosystem of Shark Bay, Western Australia. We used patterns of stable isotope variation of invertebrates and fish to infer to what degree mangroves were directly supporting secondary production. We were especially interested in the extent to which fishes with different feeding strategies depend on mangrove-derived primary productivity. We also examined potential sources of variation in fish isotope values with a particular focus on (1) the influence of body size within species and (2) a landscape level variable, i.e. extent (i.e. total size) of mangrove habitats. Food web models in little-impacted ecosystems, like Shark Bay, are very rare (but see Abrantes & Sheaves 2009); thus, this study provides valuable benchmarks for comparison of trophic dynamics with hydrologically comparable systems more impacted by human activity.

## MATERIALS AND METHODS

**Study location.** Shark Bay is a 13 000 km$^2$ subtropical embayment with an average depth of 9 m, located on the central coast of Western Australia. The bay is subdivided by peninsulas and barrier islands into the Eastern and Western Gulfs (see Heithaus 2004). Shark Bay has a pronounced salinity gradient increasing to the south and east and reaching up to 70‰ in Hamelin Pool in the extreme SE corner of the bay (UNEP, World Conservation Monitoring Centre 2008). Designated as a Marine Park and World Heritage Area in 1991, Shark Bay is subject to very low fishing pressure and is one of the world's most pristine remaining seagrass ecosystems.

Habitats of Shark Bay create an interconnected mosaic (Sheaves 2009). This mosaic includes extensive shallow seagrass beds, sandy unvegetated areas, deeper-water mixes of sand and sparse seagrass, fringing mangroves, and intertidal sand flats. The dominant seagrasses *Amphibolus antarctica* and *Posidonia australis*, and a mix of less common tropical seagrass species, cover ~4000 km$^2$ of Shark Bay (Walker, 1990). Mangroves occur along ~30% of coastal fringes of the study area with *Avicennia marina* (gray mangrove) being the single species. Most of this fringe is narrow, consisting of a thin line of trees, but larger, protected bays are scattered through the east bay. These larger bays tend to have compact, hard, gypsum-dominated sediments with low organic content and very little accumulated detritus. Even the bays are marine-dominated, with freshwater input occurring infrequently (e.g. during cyclones).

We selected 2 mangrove systems (Dubaut Creek and Guichenault Point) along the eastern coast of Peron Peninsula and sampled organisms from 3 subsites at each location (Fig. 1). These were selected because they had the largest patches of accessible mangrove. Guichenault Point creates Herald Bight within which the protected southwest and west shores are lined with tidal creeks, mangroves and mud flats (Guichenault Interior; GI). The boundary between the tidal creek and bay was designated Guichenault Mouth (GM). The east side of Guichenault Point is more exposed to the Eastern Gulf, except for a small lagoon (Guichenault Lagoon; GL) that is lined with mangroves and where seagrass detritus creates a permanent flocculent layer over the sandy sediments. Salinity in Herald Bight tends to vary little ~40‰ (Travers & Potter 2002, White & Potter 2004).

Dubaut Creek, ~35 km south south-east of Guichenault, is a tidal creek connected to a birrida (a hypersaline land feature with saltbush, *Salicornia*, and soils dominated by gypsum clay). We sampled in the tidal channel and intertidal flats up to 1200 m from the creek mouth (Dubaut Interior, DI) and at the mouth of the tidal creek (Dubaut Mouth; DM). Southeast of the entrance to Dubaut Creek is a smaller creek with a low density of mangroves (Dubaut Point; DP) and a short (150 m) tidal creek that drains a largely-unvegetated area of gypsum clay. Salinity in Dubaut Creek and near Dubaut Point ranged from 42 to 50‰ in June 2008. We also sampled at sites well removed from potential mangrove influence, including seagrass habitats (SG) and sandy intertidal (MM) near Monkey Mia, 21 km south of Guichenault and 8 km north of Dubaut.

We used geographic systems analysis software (ArcGIS) to calculate areas of aquatic habitat types available to fish near the entrances to each of the 4 mangrove subsites. Habitat polygons were classified as fringing mangrove, channel, sand, seagrass, seagrass-sand mix, or detritus-sand mix, using visual interpretation of a 1 m resolution orthophotograph taken in 2006. Habitat patches were identified within 1 km of the mouth of each subsite, using the shortest path available to fish. The distance of 1 km was

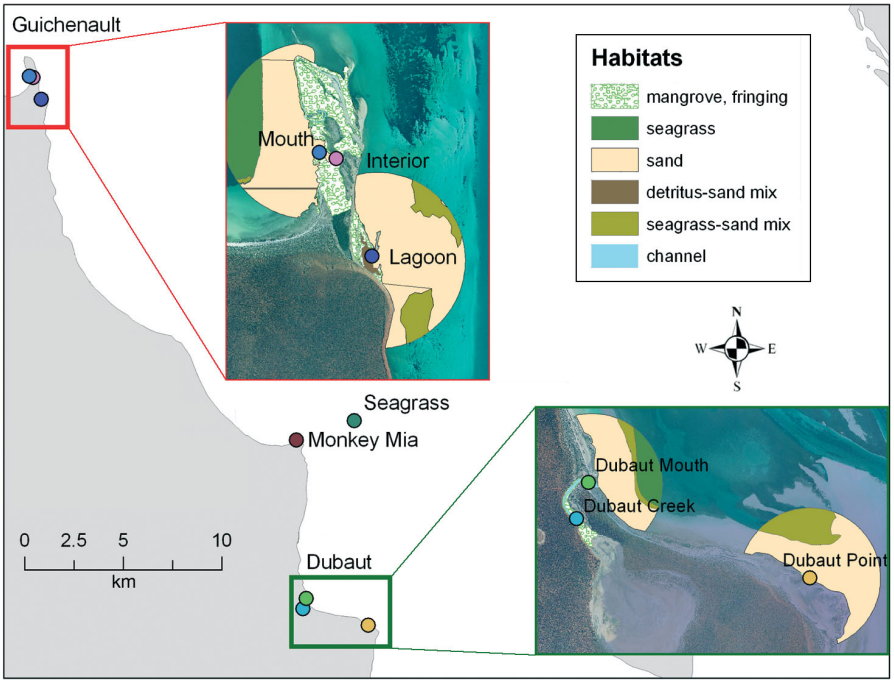


Fig. 1. Eastern Gulf of Shark Bay, Australia (25° 45′ S, 113° 44′ E). Study sites. Insets: detailed locations of Guichenault and Dubaut study sites

selected to encompass habitats that would be reasonably encountered by fish moving with tides between mangrove and deeper habitats. Daily movements with tides are documented in Caribbean and Australian systems, even though precise pathways are difficult to quantify (Meynecke et al. 2008, Luo et al. 2009, Mendoza-Carranza et al. 2010, Sakabe & Lyle 2010) The 'shortest path' was a straight line except when land projected into the area. Areas for habitat patches of each type were then summed.

**Sample collections and processing.** Collections were made between 27 May and 14 July 2008. During this time the water temperature ranged from 17 to 24°C. Fish from mangrove habitats were captured using traps, seines, and dip nets. We sampled from seagrass beds (SG) using fish traps and dip nets (see Heithaus 2004). Four species of fish were collected over sand using a dip net at the intertidal edge at MM. The sampling procedures were designed to obtain individuals from the most common species and was not intended to be a full survey or population estimate of the fish communities. Fish species were assigned to feeding guilds based on examination of stomach contents (authors' unpubl. data), a review of literature about fish in western Australia, and information from FishBase (Froese & Pauly 2009). Identifications were assisted by Hoese et al. (2007).

Captured fish were placed on ice and frozen until processing. Total length was measured and, for individuals >4 cm, the dorsal and lateral muscle was removed, rinsed in distilled water, dried for 24 to 48 h at 60°C and then ground to a fine powder using a mortar and pestle. Smaller fish were rinsed, dried and ground whole. Samples were shipped to the United States in microfuge tubes and stored in a −20°C freezer. Samples were redried at 60°C prior to weighing for isotope analysis.

Invertebrates were collected at each site and frozen until processed. We especially focused on collecting suspension-feeding bivalves and grazing gastropods to represent the invertebrate basal consumers in the mangrove food webs, as recommended by Post (2002), Layman (2007) and Mallela & Harrod (2008). Bivalves were collected by manually sifting the sediments in a 2 m square area at Guichenault Interior and the edge of the channel draining Dubaut Creek. Small shrimp and crabs were collected by disturbing the sediments and sweeping vegetation with a large dip net. For large crabs, a single claw was removed. During processing, mollusks were manually separated from their shells and, when present, opercula were removed. Small crustaceans were dried whole and combined into samples of 10 to 25 organisms. Muscle was isolated from a single claw of large crabs. Tissue was rinsed in distilled water, dried and processed as described for fish.

For primary producers, *Avicennia marina* leaves were sampled directly from at least 5 trees per site. Samples were cut into small pieces to facilitate drying prior to grinding to a fine powder. We collected epibiota growing on pneumatophores of *A. marina* by cutting immersed pneumatophores, and then removing attached organisms by scraping with a razor blade.

Seagrass and algal samples were collected as part of a larger study (D. Burkholder unpubl.). Epiphytes were removed with a razor blade from samples of all larger plants prior to drying and grinding. Seagrass and epiphytes were rinsed in distilled water prior to processing. Scraped samples were placed in aluminum trays and dried in a heated desiccator for at least 72 h. Tissue was ground with mortar and pestle to a fine powder, stored in sealed vials and frozen after shipping to Florida International University (FIU) for processing of samples for stable isotope analysis.

Samples were processed at FIU following Post et al. (2007) for the determination of $\delta^{13}C$ and $\delta^{15}N$. Some crustacean and algal samples required acidification to remove inorganic carbon. To acidify tissue, sample powder was placed in a glass watch glass and then into chamber containing HCl vapor. These samples were then dried 24 h at 60°C before weighing. A separate portion of unacidified sample was retained for $\delta^{15}N$ determination. For all samples 1 ± 0.05 mg of dried powder was placed in tin capsules and sent to the Yale Earth System Center for Stable Isotopic Studies (ISC-SIS) for isotopic analysis. Large amounts of lipid can shift $\delta^{13}C$ independent of diet, so numerical corrections of $\delta^{13}C$ were calculated when the ratio of carbon to nitrogen, C:N > 3.32 as suggested by Post et al. (2007). The correction was used for at least 1 individual in 10% of taxa (Appendix 2) with an average correction of −0.34‰.

Stable isotope values are reported using δ notation:

$$\delta^{13}C \text{ or } \delta^{15}N = 1000[(R_{sample} \times R_{standard}^{-1}) - 1] \quad (1)$$

where $R = {}^{13}C:{}^{12}C$ or ${}^{15}N:{}^{14}N$.

The global standard for measuring $\delta^{13}C$ is PeeDee belemnite and atmospheric N is used for $\delta^{15}N$. Our tissue standard was trout muscle, and at least 10 trout samples were interspersed through each run of 46 wells ($\delta^{13}C_{trout}$ = −28.70‰, SD = 0.106‰, 50.0% C; $\delta^{15}N_{trout}$ = 15.79‰, SD = 0.081‰, 13.1% N; sample size = 42).

**Data analysis.** Descriptive statistics, ANOVA and ANCOVA were run in Minitab. Data were evaluated for normality and homogeneity of variances. Variances of stable isotopes were homogeneous except for *Pelates octolineatus* for $\delta^{13}C$ and *Gerres subfasciatus* for both isotopes. After $\log_{10}$ transformations of length, the assumptions of ANCOVA were met by data distributions for all species except *P. sexlineatus*.

Stable isotopic values often vary with body size (Gu et al. 1996, Shannon et al. 2001, Barnes et al. 2008), so log transformed length was included as a covariate in tests for site differences in $\delta^{13}C$ and $\delta^{15}N$. The interaction between length and site was evaluated, but excluded from final models when $p > 0.10$. Potential patterns in average $\delta^{13}C$–$\delta^{15}N$ stable isotope values between sites were evaluated using circular statistics with Oriana (Schmidt et al. 2007). Such analysis uses Rayleigh's Z statistic. In these analyses, replicates are average stable isotope values for species in common between pairs of sample sites. Circular statistics evaluate hypotheses about trends in shifts of position in a 2-dimensional space: $\delta^{13}C$–$\delta^{15}N$ stable isotope biplots in our study.

## RESULTS

The total amount of mangrove habitat varied among sites with GI >> DI > GL >> DP (Fig. 2). The areas of dense seagrass beds also varied among subsites, with GI again ranking highest.

Thirteen common species of fish were collected from 7 sites, with sample sizes varying from 1 to 45 per site (Appendix 1). The number of species encountered in the mangrove sites was consistent with relative amount of mangrove habitat for each site, with 10 species captured in GI, 6 in DI, 5 in GL and 3 from DP. *Amniataba caudavittata* and *Rhabdosargus sarba* were the most widespread species and each was captured from 5 sites; *Pelates octolineatus* was captured in 4 sites. The sample sizes do not reflect relative abundances of fish in the sampling areas because collections stopped when target numbers were obtained.

Fish taken from traps placed in seagrass beds tended to be larger than individuals captured in traps and nets in mangrove habitats (Appendix 1). On average, *Pelates octolineatus* and *Amniataba caudavittata* were larger than those from the largest mangrove sites by 135 and 36%, respectively; *Rhabdosargus sarba* from seagrass were at least 39% larger than individuals from mangroves. Only *Colurodontis paxmani* were similar in size in seagrass and mangrove sites. Also

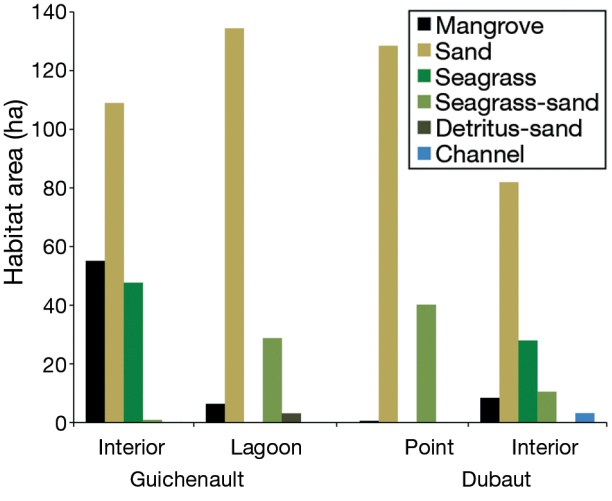


Fig. 2. Proportions of marine habitat types within 1 km of the mouth of the study sites

varying in size among sites were the hardyheads *Atherinomorus vaigiensis* (larger in mangroves than in sandy subtidal) and *Craterocephalus mugiloides* (smaller in mangroves than in sandy subtidal).

### Primary producers from mangroves

*Avicennia marina* leaves had similar $\delta^{13}C$ values at Dubaut and Guichenault (–22.9 ± 2.6‰ at both; Fig. 3), similar to other studies of *A. marina* at other sites in Australia (e.g. Loneragan, et al. 1997, Werry & Lee 2005). Epibiota (mostly algae) growing on the pneumatophores of *A. marina* were also relatively depleted in $^{13}C$ (–21.7‰). Seagrass and seagrass epiphytes were considerably less depleted in $^{13}C$, with $\delta^{13}C$ values ranging from –10.8 to –7.1‰. We observed intermediate levels of $\delta^{13}C$ values among algae collected from seagrass beds (–16.3 to –13.3‰, except for 1 sample of a calcareous red alga with a mean of –21.3‰).

### Carbon sources for basal consumers

It was not possible to directly measure the stable isotope signatures of all primary producers, particularly for benthic microalgae and pelagic phytoplankton. As such, we did not employ a model such as IsoSource (Phillips & Gregg 2003). Instead, we used primary consumers (and invertebrates potentially eaten by fish) as an index of stable isotope values entering the base of the food webs among sites (e.g. Layman 2007). Appendix 2 gives sample sizes, sites and average stable isotope values by taxon.

If *Avicennia marina* or epibiota were important to these trophic pathways, tissue values should be relatively depleted in $^{13}C$. None of the invertebrate taxa displayed $\delta^{13}C$ values that suggested significant reliance on mangrove primary productivity, and these patterns were consistent across mangrove sites and other sites (Fig. 4). The most $^{13}C$ depleted species, a tunicate, was collected from a seagrass bed more than 2 km from the nearest mangrove site. Only 6 invertebrate species were captured in mangrove and at least 1 other habitat, so rigorous statistical analysis was not possible; however, for all 6 of those species, the individuals from the mangrove habitat were less $^{13}C$ depleted than those collected from seagrass beds or sand flats. This is the opposite of the direction hypothesized if mangrove productivity was at the base of the trophic systems. $\delta^{13}C$ values for invertebrates captured in mangroves (between –12 and –14‰) were close to those of algae. The $\delta^{13}C$ values of invertebrates from Monkey Mia were $^{13}C$-enriched, suggesting more reliance on seagrass-based trophic pathways. Organisms from the mangrove sites had isotope values generally similar to those from seagrass sites, except for bivalves, where seagrass-collected individuals were more depleted ($\delta^{13}C$ values of –17‰ versus –12 to –14.5‰), which again, is opposite from the direction predicted by the hypothesis of significant mangrove contribution to trophic webs.

### Carbon sources for fish

Patterns in $\delta^{13}C$ in fish that we were able to sample failed to support a prediction of increased reliance on *Avicennia marina*-based trophic pathways in the interior mangrove sites (DI and GI). Similar to invertebrate consumers, fish species from all feeding guilds (Elliott et al. 2007) were substantially less depleted in $^{13}C$ ($\delta^{13}C$ averages ranged from –11 to –17‰) than *A. marina*

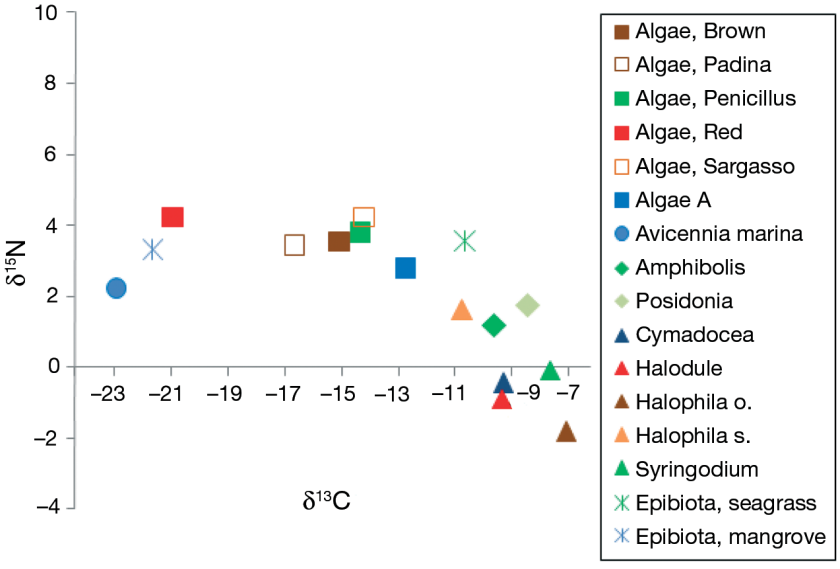


Fig. 3. Stable isotope biplot for primary producers from Shark Bay, Australia. Algae (■): A = unknown calicified green alga, Brown = unknown brown alga, Penicillus = *Penicillus* sp., Red = unknown red alga, and Sargasso = *Sargassum* spp. Mangrove (●): *Avicennia marina*. Temperate seagrasses (◆): Amphibolis = *Amphibolis antarctica*, Posidonia = *Posidonia australis*. Tropical seagrasses (▲): Cymadocea = *Cymodocea angustata*, Halodule = *Halodule uninervis*, Halophila o. = *Halophila ovalis*, Halophila s. = *H. spinulosa*, Syringodium = *Syringodium isoetifolium*. Epibiota (✱): seagrass = epiphytes scraped from seagrass blades, mangrove = epibiota scraped from pneumatophores of *Avicennia marina* in mangrove creeks; SD for $\delta^{13}C$ are omitted for simplicity, but range from 0.8 to 1.8‰

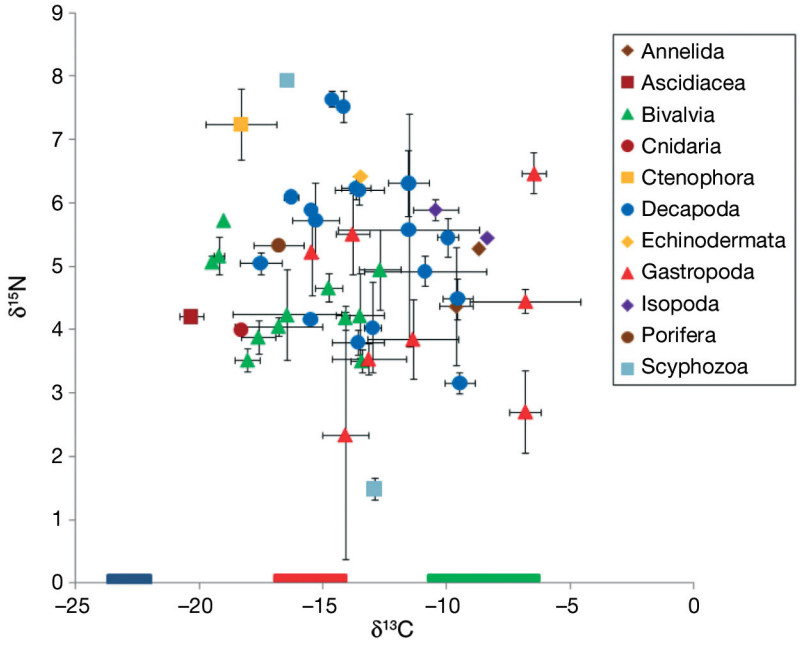


Fig. 4. Stable isotope biplots for invertebrate basal consumers from the study sites in Shark Bay, Australia. Means ± SD. $\delta^{13}C$ ranges: mangrove leaves and epibiota (blue line), marine algae (red line), and seagrass species (green line)

(Fig. 5A–E). This range for fish also exceeded the ranges of $\delta^{13}C$ of most invertebrate basal consumers from mangrove habitats, suggesting some fish were moving across the system boundaries or feeding on imported food sources. Invertebrates from a pristine, tropical estuary in Queensland, Australia, appeared to incorporate productivity from mangrove and microphytobenthos in mangrove; these invertebrates were consumed by some fish (Abrantes & Sheaves 2009). Mangrove habitat and more diverse mangrove species dominated that system; more research will be required to evaluate hypotheses about whether differences in the habitat mosaic or community composition account for apparent differences in trophic structure in Shark Bay.

Length was related to $\delta^{13}C$ for 3 of the focal species of fish (Table 1). The influence of length depended on location for *Atherinomorus vaigiensis*, where the values of $\delta^{13}C$ decreased much faster with increasing size at the sandy intertidal site of Monkey Mia than at GI. Larger *Rhabdosargus sarba* and *Gerres subfasciatus* tended be more enriched in $^{13}C$ when sites were considered together (although there was a suggestion of a decreasing slope for *G. subfasciatus* from DP).

Among-site differences in $\delta^{13}C$ values were significant ($p < 0.05$) for 4 species of fish and marginally significant ($0.05 < p < 0.10$) for 2 others (Table 1). The $\delta^{13}C$ value of *Atherinomorus vaigiensis* was less depleted in the Guichenault mangrove compared to Monkey Mia, with additional variation explained by differences in length as well as an interaction between site and length. $\delta^{13}C$ was more depleted in larger fish at GI, but less depleted with size at Monkey Mia. *Gerres subfasciatus* also varied in $\delta^{13}C$ where fish from the larger GI mangrove site were more $^{13}C$ depleted than the individuals from the smaller DP site. Fish captured in seagrass were not consistently different in $\delta^{13}C$ compared to fish from mangrove sites, which is also inconsistent with a hypothesis of major contributions of *Avicennia marina* to food webs. In summary, several species of fish varied in $\delta^{13}C$ values among sites separated by no more than 20 km, but without consistent pattern among sites in the direction of this variation (Rayleigh's *Z*'s: 0.36 to 2.74, all $p > 0.05$ for 6 pairwise comparisons of sample sites).

Across sites, invertebrate consumers showed narrow ranges of $\delta^{15}N$ values; these varied < 2.5‰ for all invertebrates and by < 1.5‰ for 80% of taxa. Fish were characterized by greater variation in $\delta^{15}N$ values, which differed among sites for all the feeding guilds but were influenced by size in only a few cases (Fig. 5A–E, see Table A1 & A2). The within-species $\delta^{15}N$ values differed among sites for 4 of 8 species of fish and marginal site effects were seen in *Colurodontis paxmani* (Table 2). Within species, the ranges of $\delta^{15}N$ were 1.9‰ (*Pelates octolineatus*), 1.2‰ (*Gerres subfasciatus*), 1.7‰ (*Craterocephalus mugiloides*), and 0.8‰ (*Apogon rueppelli*). *Atherinomorus vaigiensis* lacked site effects independent of differences in length and showed a marginal site-by-length interaction, with larger fish more enriched in $^{15}N$ within GI (a site with a larger range of sizes for this species). Similarly, larger *Amniataba caudavittata* and *C. paxmani* were more enriched with $^{15}N$. Variation in $\delta^{15}N$ among sites for *A. caudavittata* and *A. vaigiensis* were likely due to

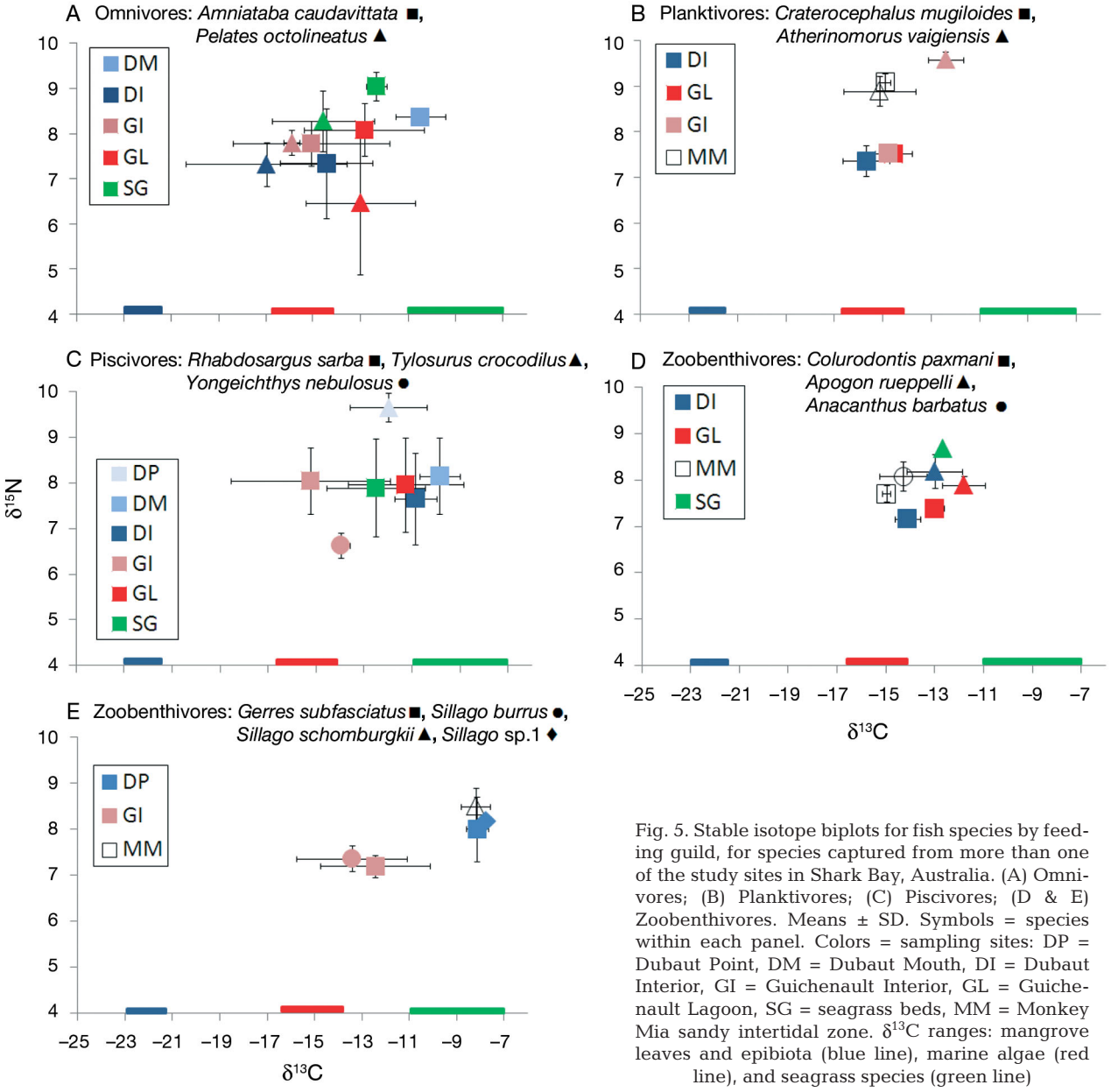


Fig. 5. Stable isotope biplots for fish species by feeding guild, for species captured from more than one of the study sites in Shark Bay, Australia. (A) Omnivores; (B) Planktivores; (C) Piscivores; (D & E) Zoobenthivores. Means ± SD. Symbols = species within each panel. Colors = sampling sites: DP = Dubaut Point, DM = Dubaut Mouth, DI = Dubaut Interior, GI = Guichenault Interior, GL = Guichenault Lagoon, SG = seagrass beds, MM = Monkey Mia sandy intertidal zone. $\delta^{13}C$ ranges: mangrove leaves and epibiota (blue line), marine algae (red line), and seagrass species (green line)

Table 1. Site and length effects on $\delta^{13}C$ for species of fish found in 2 or more sites in Shark Bay, Australia, using ANCOVA. Site by length interaction was initially specified, but the interaction was dropped in reanalysis if the interaction was not significant ($p > 0.10$). Slope of length-$\delta^{13}C$ regression: indicated by β for significant length effects. Two values of β indicate slopes that varied with site. Data in **bold** indicate statistically significant parameters

| Species | N | $F_{Site}$ | $p_{Site}$ | $F_{Length}$ | $p_{Length}$ | β | $F_{Site×Length}$ | $p_{Site×Length}$ | $R^2$ (%) |
|---|---|---|---|---|---|---|---|---|---|
| *Amniataba caudavittata* | 47 | 1.86 | 0.135 | 0.35 | 0.555 | | NS | NS | 17.5 |
| *Apogon rueppelli* | 14 | 2.04 | 0.181 | 0.06 | 0.812 | | NS | NS | 9.0 |
| *Atherinomorus vaigiensis* | 19 | **5.14** | **0.039** | **10.48** | **0.005** | 15.0, –11.4 | **6.14** | **0.026** | 83.4 |
| *Colurodontis paxmani* | 10 | **12.68** | **0.007** | 1.06 | 0.343 | | NS | NS | 72.3 |
| *Craterocephalus mugiloides* | 19 | 2.72 | 0.085 | 0.04 | 0.851 | | NS | NS | 18.8 |
| *Gerres subfasciatus* | 24 | **15.81** | **0.001** | **4.87** | **0.039** | 12.8 | NS | NS | 64.2 |
| *Pelates octolineatus* | 65 | 2.59 | 0.061 | 0.27 | 0.605 | | NS | NS | 11.5 |
| *Rhabdosargus sarba* | 44 | **8.02** | **<0.001** | **4.82** | **0.034** | –10.8 | NS | NS | 39.5 |

Table 2. Site and length effects on $\delta^{15}N$ for species of fish found in 2 or more sites in Shark Bay, Australia, using ANCOVA. Site by length interaction was initially specified, but the interaction was dropped in reanalysis if the interaction was not significant ($p > 0.10$). Slope of the length-$\delta^{13}C$ regression is indicated by β for significant length effects. Data in **bold** indicate statistically significant parameters

| Species | N | $F_{Site}$ | $p_{Site}$ | $F_{Length}$ | $p_{Length}$ | β | $F_{Site\times Length}$ | $p_{Site\times Length}$ | $R^2$ (%) |
|---|---|---|---|---|---|---|---|---|---|
| *Amniataba caudavittata* | 47 | 1.56 | 0.203 | **19.15** | **0.000** | 3.0 | NS | NS | 51.6 |
| *Apogon rueppelli* | 14 | **4.76** | **0.035** | 0.39 | 0.546 | | NS | NS | 39.6 |
| *Atherinomorus vaigiensis* | 19 | 1.40 | 0.255 | **6.55** | **0.022** | –3.1 | 3.32 | 0.089 | 80.1 |
| *Colurodontis paxmani* | 10 | 3.52 | 0.097 | 5.55 | 0.057 | | NS | NS | 41.1 |
| *Craterocephalus mugiloides* | 19 | **6.05** | **0.007** | 0.72 | 0.411 | | NS | NS | 90.2 |
| *Gerres subfasciatus* | 24 | **11.15** | **0.003** | 0.02 | 0.877 | | NS | NS | 36.3 |
| *Pelates octolineatus* | 65 | **6.57** | **0.001** | 0.49 | 0.488 | | NS | NS | 31.8 |
| *Rhabdosargus sarba* | 44 | 0.30 | 0.876 | 0.18 | 0.676 | | NS | NS | 0.0 |

differences in sizes among sites. Comparing sites, the range of $\delta^{15}N$ values for all fish was narrow at 1.46‰ ($F = 9.40$, $p < 0.01$, $R^2 = 15.2\%$).

## DISCUSSION

Two major patterns emerge from our results. Stable isotope values of carbon suggest minor contributions, at most, from mangrove trees to secondary productivity of small fish using fringing mangrove habitat in Shark Bay. Also, within species of fish, stable isotope values can vary over spatial scales as localized as hundreds of meters. We structure our discussion around these 2 themes.

### Mangrove contributions to fish productivity

Although fish and invertebrates inhabit the fringing mangrove habitat, they are not deriving a substantial proportion of their biomass from *Avicennia marina*-based trophic pathways or its pneumatophores-associated epibiota. This interpretation is consistent with findings in other systems that have pointed out the relatively low consumer reliance on mangrove productivity (Fry & Ewel 2003, Layman 2007). In the almost pristine ecosystem of Shark Bay, invertebrates (–15.7 to –9.34‰) and fish (–14.9 to –7.8‰) tend to have $\delta^{13}C$ values that are more consistent with those of algae and/or seagrass. Blaber (2007) suggested that fish might benefit from mangrove habitats by feeding on mangrove-associated epiphytes rather than on mangrove-derived production, but in our study epiphytes tended to have the same signature as mangrove leaves. Other potential sources of primary productivity in fringing mangroves are benthic microalgae (especially diatoms), pelagic phytoplankton, macroalgae, and detritus from seagrass beds imported with tides. Although our study was not designed to distinguish which of these form the base of fish trophic systems, our results clearly support the hypothesis that fish rely on mangroves for a reason or reasons other than direct feeding pathways.

Numerous fish species inhabiting mangroves migrate between mangrove and adjacent habitats (Nagelkerken & van der Velde 2004, Sheaves 2005, Hammerschlag-Peyer & Layman 2010). In Shark Bay, most species of fish caught in fringing mangrove habitats also inhabit seagrass and sand flat habitats suggesting that individual fishes studied herein may move frequently between habitats in this system (Black et al. 1990, Linke et al. 2001, Travers & Potter 2002, Heithaus 2004). Alternatively, basal resource pools can be readily transported among habitat types in coastal systems (Melville & Connolly 2003, Connolly et al. 2005), and fish may remain within mangrove-dominated habitats and feed on imported resources.

The expected direction of nutrient movement in mangrove-seagrass complexes has been somewhat controversial. The 'outwelling hypothesis' (Odum & Heald 1975) proposed that carbon from mangrove productivity would be exported from these coastal systems to adjacent offshore systems, but most tests of the hypothesis have found the opposite; nutrients tend to be transported from seagrass beds in to mangrove habitats (Lee 1995, Bouillon et al. 2008, Kristensen et al. 2008, but see Sheaves & Molony 2000). Some riverine and basin mangroves may substantially support the food webs of adjacent habitats (Thimdee et al. 2008), but fringing mangroves are much less likely to provide such a major carbon subsidy (Faunce & Layman 2009). This is particularly true for Shark Bay, where fringing mangroves are small in stature, represent a small fraction of the total habitat, and fish have access to rich feeding opportunities in adjacent seagrass beds.

If food from the most common primary producers is not a major benefit of occupying these fringing mangroves, why are so many fish in this habitat? The most

obvious explanation is protection from larger predators, as fringing mangroves also provide the benefit of predator avoidance (Meynecke et al. 2007, Platell et al. 2007). Recent studies have provided multiple lines of evidence that mangroves are critical for predator protection, instead of the commonly held belief that they also provide additional food resources (Grol et al. 2008, Dorenbosch et al. 2009). The potential impact of fringing mangroves is illustrated by comparing the density of juvenile sharks from seagrass and unvegetated nursery areas that are either close or far from the Guichenault site; nurseries close to mangroves had 2- to 10-fold more sharks (White & Potter 2004). Protective benefits were observed for fish moving in and out of mangrove creeks in Queensland, Australia (Meynecke et al. 2008), and for *Acanthopagrus latus* in Shark Bay, Australia (Platell et al. 2007). These observations support additional studies on differences in predation rates among habitats.

### Variation in stable isotope values

We observed differences in stable isotopic values within and between species, between habitats, and between sample sites for the same habitat. Hypotheses for ecological mechanisms accounting for such variation include body size (within species), different feeding niches (within or between species), variation in basal resource values (between sample sites), and landscape variation (the extent of mangrove in the local habitat mosaic).

The small influence of body size on stable isotopic values for most species of fish was consistent with recent findings that some coastal fish vary in habitat use independent of body size (Hammerschlag-Peyer & Layman 2010 and references therein). Many studies suggested widespread correlations between fish size and habitat use and feeding (e.g. Minns 1995, Gu et al. 1996, Shannon et al. 2001, Barnes et al. 2008, Chassot et al. 2008), but fish size was not a major influence in our study. The influence of size may decline with increasing complexity of food webs where body size of primary consumer taxa is highly variable (Layman et al. 2005). Additionally, when fish can choose among several alternative habitat types and food resources, individual variation in behavior may mask the population-level influences of body size (Hammerschlag-Peyer & Layman 2010).

Spatial variation in diet was suggested by differences in $\delta^{13}C$ among sites that were statistically detectable for areas just hundreds of meters apart. In parallel with our observations of fine-scale variation in stable isotope values, studies of *Pelates octolineatus*' stomach contents by Sanchez-Jerez et al. (2002) indicated variation in diet within scales of hundreds of meters that reflected differences in the abundance of prey among the studied seagrass habitats. For *Amniataba caudavittata* at Dubaut Creek, the $\delta^{13}C$ value was different at the mouth of the creek, compared to interior sampling locations. These patterns are also consistent with variation in primary consumer isotope variation across a scale of hundreds of meters in coastal systems of the Bahamas, a similar marine-dominated, oligotrophic, coastal system (Hammerschlag-Peyer & Layman 2010).

In general, we did not observe consistent patterns of variation in carbon sources associated with differences in the habitat mosaic; $\delta^{13}C$ did not vary systematically with different mangrove habitat size or the proportions of the habitat mosaics that were seagrass and mangroves. Further studies would be required to determine whether fine-scale variation in habitat mosaics lead to predictable differences in trophic structure. The low contribution of mangroves and their epibiota to trophic webs, however, suggests that in restricted fringing mangrove systems like those of Shark Bay there may be relatively little variation across a range of habitat mosaics. In addition, any subtle variation in isotope values based on habitat mix may be minimized by the localized spatial variation in diets observed for species.

Much has been written about non-ecological sources of variation in stable isotope values. Differences in fractionation within individuals among tissues, and between individuals within the same environments can cause variation in stable isotopic values (Barnes et al. 2008, Martínez del Rio et al. 2009), as can changes in the structure of the food web beneath a consumer of interest (Post 2002, Layman et al. 2007). Within a population, laboratory studies show that even individuals consuming exactly the same food can vary in stable isotope values; for $\delta^{15}N$, laboratory-reared wild bass showed coefficients of variation (CV) of 2.6%, which was equivalent to the CV for some wild-caught bass populations (Barnes et al. 2008). In their study, the CV for $\delta^{13}C$ for equilibrated laboratory-reared bass was 1.2% while wild-caught populations CV was 14% overall. In our study, CV's ranged from 5.0 to 26.3% (mean: 13.8%) for $\delta^{13}C$ and 3.3 to 11.6% (mean: 6.7%) for $\delta^{15}N$, greatly exceeding variability expected from internal mechanisms. Further, we minimized differences from non-trophic sources by using only muscle tissue from fish and by sampling within a narrow interval of time.

In conclusion, even though vegetation density suggests high primary productivity in mangrove communities, on a local scale there is little evidence of mangroves directly supporting secondary production of consumers. We also provide additional data that

emphasize the multiple spatial scales at which consumer isotope values can vary: a source of variation that must be accounted for in coastal marine systems.

*Acknowledgements.* R. Black and A. Brearley (University of Western Australia) helped with identifications of invertebrates. We thank S. Morrison (Western Australian Museum) for assistance in identifying fish. We thank the staff of CALM at Monkey Mia for their logistic support. This research was supported by grants from the National Science Foundation (OCE0526065, OCE0620409, OCE0745606, OCE0746164, and by funding from Kenyon College to E.R.H. This is contribution #46 from the Shark Bay Ecosystem Research Project.

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**Appendix 1.** Table A1. Lengths and sample sizes for fish used for stable isotope analysis from Shark Bay, Western Australia. Sites: DP = Dubaut Point, DM = Dubaut Mouth, DI = Dubaut Interior, GL = Guichenault Lagoon, GI = Guichenault Interior, SG = subtidal seagrass beds, MM = intertidal sandy fringe at Monkey Mia. Sample size for each cell indicated within parentheses. ***ANOVA $p < 0.001$, **$p < 0.01$, *$p < 0.05$; NS = $p > 0.10$. Comparisons of length are based on Tukey 95% simultaneous confidence intervals (the null hypothesis cannot be rejected for sites sharing a superscript)

| Species | | Site: Length (mm) ± SE (n) | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Common name | DP | DM | DI | GL | GI | SG | MM |
| *Amniataba caudavittata* | Yellowtail trumpeter *** | | 104.0 ± 4.3 (3)$^{a,b}$ | 75.3 ± 4.6 (13)$^{a}$ | 137.2 ± 10.1 (12)$^{a}$ | 83.3 ± 4.0 (12)$^{a,b}$ | 186.6 ± 11.1 (7)$^{c}$ | |
| *Apogon rueppelli* | Gobbleguts NS | | | 61.2 ± 7.87 (4) | 59.0 ± 2.52 (9) | | 70.0 (1) | |
| *Atherinomorus vaigiensis* | Ogilby's hardyhead *** | | | | | 136.3 ± 3.1 (10)$^{b}$ | | 78.1 ± 3.1 (10)$^{a}$ |
| *Colurodontis paxmani* | Paxman's leather-jacket NS | | | 51.0 ± 5.0 (2) | | 49.5 ± 4.5 (2) | 55.7 ± 0.3 (6) | |
| *Craterocephalus mugiloides* | Spotted hardyhead *** | | | 36.1 ± 2.1 (5)$^{a}$ | 33.5 ± 0.7 (5)$^{a}$ | 35.6 ± 0.5 (5)$^{a}$ | | 57.5 ± 2.0 (4)$^{b}$ |
| *Gerres subfasciatus* | Roach*** | 79.8 ± 3.5 (10)$^{b}$ | | | | 66.57 ± 2.5 (14)$^{a}$ | | |
| *Pelates octolineatus* | Striped trumpeter*** | | | 64.8 ± 6.4 (6)$^{b}$ | 92.2 ± 14.8 (4)$^{c}$ | 37.7 ± 1.2 (10)$^{a}$ | 216.4 ± 4.4 (45)$^{d}$ | |
| *Rhabdosargus sarba* | Tarwhine *** | | 115.2 ± 13.2 (5)$^{a}$ | 103.8 ± 7.2 (5)$^{a}$ | 107.2 ± 4.1 (19)$^{a}$ | 101.1 ± 5.7 (11)$^{a}$ | 160.0 ± 7.1 (4)$^{b}$ | |
| *Sillago burrus* | Western trumpeter Whiting NA | | | | | 94.7 ± 1.3 (10) | | |
| *Sillago schomburgkii* | Yellowfin whiting NA | | | | | | | 97.0 ± 11.0 (2) |
| *Sillago* sp. | Whiting sp. NA | 97.4 ± 9.5 (10) | | | | | | |
| *Tylosurus crocodilus* | Slender longtom NA | 279.7 ± 2.3 (3) | | | | 259.0 (1) | | |
| *Yongeichthys nebulosus* | Shadow goby NA | | | | | 52.6 ± 2.3 (9) | | |

**Appendix 2.** Table A2. Taxa and sample sizes (N) for invertebrates contributing to stable isotope values for primary consumers (see Fig. 4). N: number of individuals; In parentheses: number of independent measures of stable isotope values where individuals were aggregated to obtain sufficient tissue for analysis. Sites: DI = Dubaut Interior, GL = Guichenault Lagoon, GI = Guichenault Interior, SG = subtidal seagrass beds, MM = intertidal sandy fringe at Monkey Mia

| Taxon | Taxon species/morphospecies | N | Mean δC | Mean δN | Sites |
|---|---|---|---|---|---|
| Annelida | Tube worm sp 1 | 4 | –8.43 | 4.37 | SG |
| Annelida | Tube worm sp 2 | 20 (1) | –7.86 | 6.21 | SG |
| Annelida | Tube worm sp 3 | 40 (2) | –8.20 | 5.27 | SG |
| Ascidiacea | Ascidian sp 1 | 2 | –20.33 | 4.21 | SG |
| Bivalvia | *Anomalocardia squamosa* | 7 | –14.09 | 4.19 | GI |
| Bivalvia | *Brachiodontus ustulatus* | 10 | –13.43 | 3.51 | DI |
| Bivalvia | *Callista impar* | 3 | –14.77 | 4.66 | SG |
| Bivalvia | *Chlamys asperrima* | 6 | –19.21 | 5.17 | SG |
| Bivalvia | *Modiolus* sp. | 10 | –18.04 | 3.81 | SG |
| Bivalvia | Pectinidae sp 1 | 3 | –19.48 | 5.07 | SG |
| Bivalvia | Pennatulacea sp 1 | 1 | –19.01 | 5.73 | SG |
| Bivalvia | *Pinna* cf. *mundula* | 10 | –16.79 | 4.05 | GL, SG |
| Bivalvia | *Pitar citrina* | 20 | –13.51 | 4.22 | DI, GI, MM |
| Bivalvia | *Placamen berryi* | 11 | –12.69 | 4.95 | DI, GL, MM |
| Bivalvia | *Saccostrea* ?*commercialis* | 28 | –16.45 | 4.24 | GI, GM, SG |
| Bivalvia | *Strombus* sp | 3 | –13.94 | 2.33 | SG |
| Decapoda | *Callinectes* sp 1 | 3 | –12.97 | 6.22 | MM |
| Decapoda | *Callinectes* sp 2, adult | 6 | –10.42 | 5.25 | MM, SG |
| Decapoda | *Callinectes* sp 2, juvenile | 5 | –9.96 | 5.45 | MM |
| Decapoda | *Clibanarius* sp. | 6 | –10.87 | 4.92 | GI, GL |
| Decapoda | Eurybrachyura sp 1 | 3 | –13.58 | 3.80 | GL |
| Decapoda | *Gafrarium intermedium* | 12 | –12.99 | 4.03 | DI, GI |
| Decapoda | Gallitheid sp A | 3 | –17.53 | 5.05 | SG |
| Decapoda | Gallitheid sp B | 4 | –15.50 | 4.16 | SG |
| Decapoda | Malacostraca sp 1 | 75 (3) | –15.3 | 5.72 | SG |
| Decapoda | Malacostraca sp 2 | (6) | –13.53 | 6.21 | DI, GI |
| Decapoda | Malacostraca sp 3 | (3) | –15.48 | 5.89 | SG |
| Decapoda | Malacostraca sp 4 | (3) | –15.71 | 5.89 | SG |
| Decapoda | Malacostraca sp 5 | (3) | –14.17 | 7.52 | SG |
| Decapoda | *Mictrys* ?*longicarpus* | 3 | –9.47 | 6.47 | MM |
| Decapoda | Palaeomonetid sp 1 | 3 | –9.55 | 4.49 | SG |
| Decapoda | Palaeomonetid sp 2 | 3 | –13.66 | 6.23 | GL |
| Decapoda | *Scylla* sp | 10 | –11.54 | 6.31 | MM |
| Echinodermata | Asteroidea sp 1 | 1 | –13.48 | 6.42 | SG |
| Gastropoda | *Calthalotia* cf. *mudulata* | 5 | –13.80 | 5.51 | SG |
| Gastropoda | *Clypeomorus bifasciata* | 3 | –13.15 | 3.53 | GI |
| Gastropoda | *Nassarius clarus* | 5 | –6.47 | 6.47 | MM |
| Gastropoda | *Philine angasi* | 5 | –6.82 | 4.44 | MM |
| Gastropoda | *Pyrene bidentata* | 50 (5) | –15.46 | 5.22 | GL, SG |
| Gastropoda | *Terebralia semistriata* | 25 | –11.36 | 3.81 | DI, DM, GI |
| Isopoda | Isopod sp 1 | 5 (1) | –8.36 | 5.44 | SG |
| Isopoda | Isopod sp 2 | 15 (3) | –10.44 | 5.90 | MM |
| Planktotroph Ctenophora | Ctenophore spp | 17 | –18.31 | 7.24 | SG |
| Porifera | Porifera sp 1 | 1 | –16.79 | 5.33 | SG |
| Scyphozoa | *Aurelia anrita* | 1 | –16.45 | 7.93 | SG |
| Scyphozoa | Phyllorhiza punctata | 3 | –12.92 | 1.48 | SG |

*Editorial responsibility: Ivan Nagelkerken, Nijmegen, Netherlands*

*Submitted: November 3, 2009; Accepted: January 21, 2011*
*Proofs received from author(s): April 2, 1011*