Ecological niche of an abundant teleost *Pelates octolineatus* in a subtropical seagrass ecosystem

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ABSTRACT: This study used primary producer abundance surveys, stomach content analysis, stable isotope analysis, and mixing models to investigate the ecological niche of western striped trumpeters *Pelates octolineatus* in the subtropical seagrass ecosystem of Shark Bay, Australia. The percent cover of seagrass and macroalgae in the study area was 35.9 ± 4.3 and 28.59 ± 3.8 % (mean ± SE), respectively. Of the 2 dominant seagrass species, *Amphibolis antarctica* was present at a higher number of stations than *Posidonia australia*, and although fast-growing, smaller-bodied seagrass species occurred infrequently, only 3 stations surveyed did not contain seagrass. Algae also occurred at the majority of stations (47 of 49 stations). *P. octolineatus* stomach contents consisted mainly of primary producers (87.7 %). The mean relative amount of seagrass and algae in *P. octolineatus* stomachs was similar (43.7 ± 44.1 and 44.0 ± 43.8 %, respectively), although there was considerable variation among individuals. There was a positive relationship between fish length and percentage of seagrass consumed. Stable isotope values suggested that algae contributed a larger portion of assimilated food rather than seagrass, but predictions from mixing models more closely coincided with stomach content analysis when the standard deviation of potential food sources was increased. *P. octolineatus* exhibited a similar, but smaller, isotopic niche space to sympatric, largely herbivorous, green turtles *Chelonia mydas* (27.3 and 62.4 units, respectively). These data suggest that *P. octolineatus* function as herbivores in this subtropical seagrass system, thereby having the potential to structure primary producer communities and facilitate the transfer of primary production to higher trophic levels.

KEY WORDS: Stomach content analysis · Stable isotope analysis · Mixing models · Primary producer · Herbivory

INTRODUCTION

Herbivores play a critical role in food web dynamics by transferring primary production to higher trophic levels, yet the importance of teleost herbivory in seagrass ecosystems not associated with reefs has generally been considered low (Thayer et al. 1984, White et al. 2011, Poore et al. 2012). Some studies, however, have challenged this view (Heck & Valentine 2006, Valentine & Duffy 2006). Indeed, herbivorous fish can consume substantial proportions of seagrass production, e.g. 80 % in the Florida

Keys (Kirsch et al. 200) and 73 % off the northeast coast of Spain (Tomas et al. 2005), and may modify plant traits that indirectly affect other species (Pages et al. 2012). Understanding the role of teleost consumption in seagrass ecosystems is important because seagrasses (1) are the foundation of highly productive ecosystems that provide critical habitat in the form of shelter and foraging sites (Connolly 1994, Heck et al. 2003), (2) are an important carbon store (Fourqurean et al. 2012), and (3) are now among the most threatened ecosystems on earth (Waycott et al. 2009).

A critical first step in understanding the effects of teleost consumption on primary producers in seagrass communities is to identify herbivorous species and quantify their diets. While stomach content analysis is the most common method for elucidating teleost diets and can provide detailed information on taxa that are consumed, it provides only a snapshot of an individual's diet (Hyslop 1980). Complementary insights into trophic interactions of species can be obtained using stable isotope analysis (SIA) (Peterson & Fry 1987, Layman et al. 2012). SIA provides insights into relative trophic level using $\delta^{15}N$ values and the sources of carbon supporting diets using $\delta^{13}C$ values (Peterson & Fry 1987, Layman et al. 2012).

Shark Bay, Western Australia, offers a model system for investigating teleost consumption of primary producers in a seagrass system; it is one of the largest seagrass ecosystems in the world and features large populations of teleosts, as well as large-bodied herbivores, piscivores, and top predators (Heithaus et al. 2012). The western striped trumpeter *Pelates octolineatus* (Jenyns, 1840) of the Family Terapontidae is a medium-sized teleost (max. length = 28 cm) that has been observed consuming seagrasses (Burkholder et al. 2012). It is the most abundant medium-sized teleost in the study site by an order of magnitude (Heithaus 2004) and, therefore, could substantially impact seagrass and algal communities. In addition, Shark Bay has been the site of multiple studies investigating the trophic interactions of a variety of species, including megagrazers such as green turtles *Chelonia mydas* (Burkholder et al. 2011) and dugongs *Dugong dugon* (Wirsing et al. 2007), facilitating a community-level understanding of trophic interactions. This study used a combination of primary producer surveys, stomach content, and SIA to investigate the ecological niche of *P. octolineatus* and to compare their isotopic niche with another sympatric herbivore, the green turtle *C. mydas*, in the Shark Bay system.

MATERIALS AND METHODS

Study site

Shark Bay (25° 45' S, 113° 44' E) is a ca. 13 000 km^2 subtropical embayment featuring ~4000 km^2 of seagrass beds, located along the central coast of Western Australia. The study site was in the Eastern Gulf, offshore of Monkey Mia, where water temperatures are generally high (>20°C) during September to May (warm season) and drop to as low as 12°C during June to August (cold season) (Heithaus et al. 2012). The study site consists of shallow seagrass banks (1.5–4.5 m depth) with the occasional sand patch (Burkholder et al. 2013a). The community is dominated by 2 slow-growing and large-bodied seagrass species (*Amphibolis antarctica* and *Posidonia australis*), with fast-growing, small-bodied seagrass species (*Cymodocea angustata*, *Cymodocea serrulata*, *Halodule uninervis*, *Halophila ovalis*, *Halophila spinulosa*, and *Syringodium isoetifolium*) (Walker et al. 1988, Burkholder et al. 2013a) occurring less frequently. Benthic communities in Shark Bay also host ca. 160 taxa of macroalgae (Kendrick et al. 1990). Epiphytic red algae (Rhodophyta) are most speciose but green algae (Chlorophyta) are the most conspicuous (Kendrick et al. 1990). The brown alga *Dictyota furcellata* (Heterokontophyta) is also common.

Fish communities inside the study area are dominated by the western striped trumpeter *Pelates octolineatus*, previously referred to as *P. sexlineatus* (Heithaus 2004). This demersal species is commonly found in estuaries, lagoons, and seagrass/algae beds around the southwestern coast of Australia, from Broome to eastern South Australia (Gomon et al. 1994). They reach a maximum length of approximately 28.0 cm (Gomon et al. 1994) and are reportedly omnivores (Paxton et al. 1989). Beyond observations of *P. octolineatus* consuming uprooted primary producers (Burkholder et al. 2012) however, the importance of primary producers in their diets is unexplored.

Primary producer surveys

To estimate the relative abundance of seagrass and macroalgae within the study location, 49 stations were surveyed across 3 offshore banks between 24 March and 30 July 2012. The survey focused on the most commonly occurring species: 5 seagrass species (Magnoliophyta: *Amphibolis antarctica*, *Posidonia australis*, *Cymodocea angustata*, *Halodule uninervis*, *Halophila ovalis*), 2 red algae species (Rhodophyta: *Laurencia* sp., *Haliptilon roseum*), and 2 brown algae species (Heterokontophyta: *Dictyota furcellata*, *Sargassum* sp.). Specific stations were determined by stopping the vessel every 400 m along pre-established transects (Heithaus & Dill 2006) of each bank and surveyed using snorkel or hookah diving. Percent cover was estimated by an observer using a 60 × 60 cm quadrat dropped haphazardly 3 times at the station. The average percent cover was calculated for seagrass and algae from the 3 quadrat drops at each station. It is important to note that primary producer

surveys were conducted after a 'marine heat wave', in which unprecedented water temperatures exceeded 3°C above the long-term average over an extended area of Shark Bay during February and March 2011 (Pearce et al. 2011) impacting seagrass, as well as potentially impacting macroalgal communities (Thomson et al. 2015).

Samples of seagrass and algae were collected by hand at each site for SIA. Three specimens per species per station were collected if available. Sampling was supplemented by haphazardly collecting species that were observed in the study area but not encountered within quadrat samples. All samples were stored on ice and frozen upon return to shore.

Pelates octolineatus were collected from seagrass banks during both the warm (February to May) and cold seasons (June to August) of 2011 and the warm season of 2012 using rectangular fish traps (34 × 24 × 21 cm, with 10 cm conical entrances that tapered from a 6 cm to 4 cm diameter opening, mesh size = 1.2 × 1.3 cm) baited with 100 g of squid and deployed for less than 4 h. Bait bags prevented the ingestion of bait by fish to avoid biasing stomach content analysis. Captured fish were euthanized (pithed), stored on ice and immediately frozen upon return to shore until the fish could be processed. Fork length and wet weight were recorded for euthanized individuals and stomach content analyses were conducted. Muscle samples, collected from just below the dorsal fin, were retained for SIA.

Stomach content analysis

For each fish, wet weight was determined for stomach contents alone. Excess water was removed by blotting until dry. The contents were leveled in a petri dish, observed under a dissecting microscope, and the contribution of each prey category (seagrass, algae, and animal matter) were estimated as a proportion of the total mass of the stomach contents. These methods provided an estimate of the relative amount of each prey category and were selected to maximize the number of fish stomachs analyzed. In addition, to evaluate the effectiveness of our visual estimation method, we analyzed a subsample of haphazardly chosen fish stomachs (n = 32) using specific mass methods. For each subsample, we weighed the mass of the total stomach content, as well as the mass of algae, seagrass, or animal matter contained within the stomach. This allowed us to determine the actual proportion of seagrass, algae and animal matter in the stomach by dividing the weight of each prey cat-

egory by the total stomach weight. We then used non-parametric sign-ranked tests to determine if the category proportion from our visual estimates were statistically different than our category proportions obtained by weight. There was no significant difference between our visual estimation and weight methods for proportion of seagrass (Wilcoxon test; W = 514, p = 0.98), algae (W = 495, p = 0.82) or animal matter (W = 536, p = 0.71) observed in fish stomachs (see Table 2). To provide an error for our visual estimation method, we used the maximum difference between the visual and weighed proportion of prey categories for each subsample, and then used these maximum differences to determine the mean ± SD (4.4 ± 6.8%). Each prey category for all fish sampled were quantified using frequency of occurrence and estimated relative amount of total contents (Bowen 1996, Jobling et al. 2001).

All available stomachs were used to determine the identity of primary producers consumed by *P. octolineatus* to the lowest taxonomic group possible. Not all prey fragments could be identified due to either state of digestion or inability to identify any distinguishing characteristics.

Stable isotope analysis

All seagrass, algae and fish tissue samples were rinsed in deionized water, dried in a food dehydrator (Ezidri Ultra FD 1000) at 60°C for a minimum of 24 h, and then ground to a fine powder. For all seagrass samples, a razorblade was used to scrape epiphyte/epibiota from leaves prior to rinsing. A subsample of ~6 specimens of seagrass and algae from different sites was used to obtain a general overview of their isotopic signature in the study area during the course of the present study. These data were supplemented with data obtained in previous years (2005–2009) (Burkholder et al. 2011, M. R. Heithaus unpubl. data), which included isotopic data of potential invertebrate prey items, to account for inter-annual and seasonal variability in stable isotope values. Carbon isotopic signatures were analyzed both with and without acidification procedures for all algal samples; previous studies showed that acidification was not necessary for seagrass (Burkholder et al. 2011). Acidified $\delta^{13}C$ values were used for a taxon when acidification resulted in changes in carbon isotopic values of more than 0.3‰. Acidification required placing dried powder samples in petri dishes placed in an open chamber of hydrochloric acid for a minimum of 5 d, after

which time the samples were again dehydrated and powdered.

No lipid extractions were performed on fish samples because C:N ratios in fish muscle tissue (3.4 ± 0.3, mean ± SD) indicated that lipid corrections were unnecessary (i.e. C:N <3.5) (Post et al. 2007).

For SIA, 0.4–0.7 mg of powdered samples were weighted into tin capsules and analyzed at the Florida International University Stable Isotope Laboratory (SD of analysis = ±0.03 and ±0.09‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively). Linear regression was used to investigate the relationship between stable isotope values and fish length, and a $\delta^{15}N$–$\delta^{13}C$ stable isotope biplot and descriptive statistics were used to summarize the isotopic values of *P. octolineatus* and their potential prey items.

To explore the relative contributions of seagrasses, algae and animal matter to the assimilated diets of *P. octolineatus*, a Bayesian isotope mixing model was used based on a Gaussian likelihood with a mixture Dirichlet-distributed prior on the mean (500 000 iterations with a burn in of 50 000) (Inger et al. 2013). Source data for diets were categorized as seagrass, algae, and animal matter and all available stable isotope data within each group were used to determine a mean and standard deviation for each source group. Since trophic enrichment factors (TEF) are not available for *P. octolineatus*, 2 different TEFs from the literature were used: (1) TEFs for herbivorous fish ($\Delta^{15}N$: 4.8 ± 1.3‰ [Mill et al. 2007], and $\Delta^{13}C$: 0.5 ± 0.7‰ [Wyatt et al. 2010]), and (2) average TEFs calculated using the diet-dependent discrimination factors for fish muscle tissue (n = 166, $\Delta^{15}N$: 3.5 ± 0.2‰, $\Delta^{13}C$: 0.5 ± 0.6‰) (Caut et al. 2009). Additionally, sea-grass stable isotope values can vary seasonally for a species within a single location by up to 5‰ for both $\delta^{15}N$ and $\delta^{13}C$ (Anderson & Fourqurean 2003, Hyndes et al. 2013), but the seasonal variation in stable isotope values for both primary producers and animal prey in this study site is currently unknown. Therefore, a second set of mixing models was run using a conservative standard deviations of 5.0‰ for both $\delta^{15}N$ and $\delta^{13}C$ for each prey category.

To investigate how the isotopic niche of *P. octolineatus* relates to that of green turtles *Chelonia mydas*— a largely herbivorous megagrazer in Shark Bay (Burkholder et al. 2011)—we compared the total areas of the convex hull encompassing all isotopic values (Layman et al. 2007) for *P. octolineatus* in this study to that of sympatric green turtles. Similar to the data for *P. octolineatus*, green turtle data, previously published in Burkholder et al. (2011), were collected across multiple years and seasons. Although dugongs are another known herbivore in Shark Bay, sufficient stable isotope data from dugongs in the study area were not available.

All statistical analyses were run using R version 2.14.0 (R Development Core Team 2011).

RESULTS

Primary producer survey

Across the 49 stations surveyed, the percent cover of seagrass and macroalgae was 35.9 ± 4.3% (mean ± SE) and 28.59 ± 3.8%, respectively (Fig. 1). Seagrass *Amphibolis antarctica* was present at 36 stations,
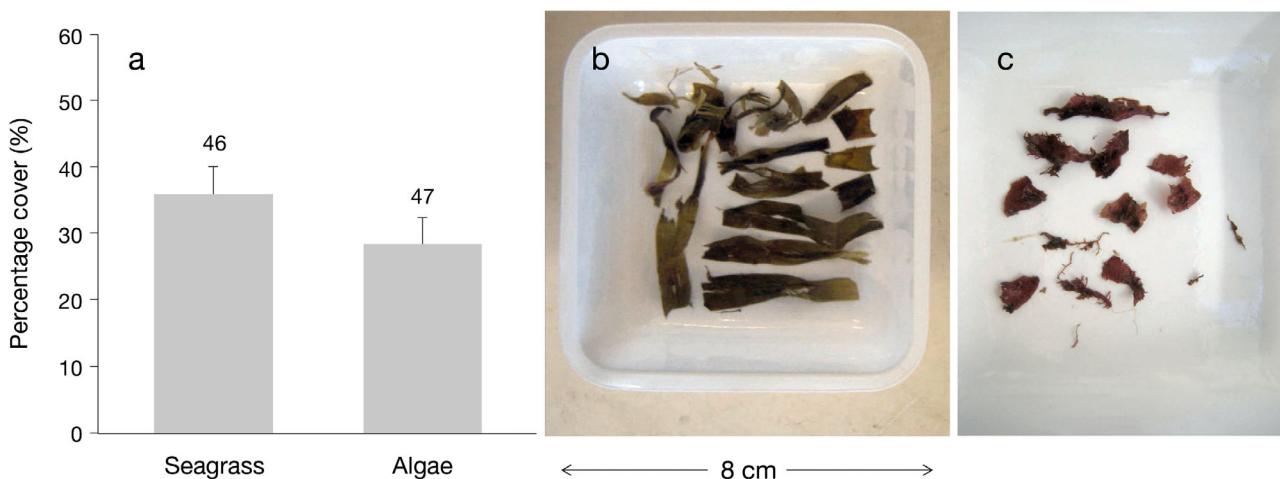

Fig. 1. (a) Mean percent cover of seagrass and algae at 49 surveyed stations. Error bars represent ±SE, and values above error bars indicate the number of sites where seagrass or algae were present. (b) Segments of the seagrass *Amphibolis antarctica* contained in the stomach contents of *Pelates octolineatus*. (c) Segments of algae contained in stomach contents of *P. octolineatus*

and had a higher occurrence than *Posidonia australis* (present at 14 stations), and although the fast-growing, smaller-bodied seagrass species occurred infrequently, only 3 stations surveyed did not contain seagrass. Algal species surveyed occurred at the majority of stations (47 of 49 stations).

Stomach content analysis

In total, 94 individual fish were collected for stomach content analysis, of which only 1 stomach was empty and another contained matter that could not be identified into prey categories. Our analyses were conducted on the remaining 92 fish (Table 1). All seagrass (with the exception of *P. australis*) and algal species observed during the primary producer survey were also found in the stomach contents of analyzed fish. In addition, other Rhodophyta (*Acanthophora* sp., *Ceramium* sp., *Gracilaria* sp., *Jania* sp., *Metagoniolithon* sp., *Polysiphonia* sp.), and Chlorophyta (*Penicillus* sp.) that were not included in the primary producer survey were also found. Interestingly, seagrass segments contained within the stomachs were not merely small bites but could be long segments of seagrass, often in excess of 3.5 cm (Fig. 1b), whereas algal matter was more often observed in discreet bite-sized pieces (Fig. 1c). Animal matter accounted for only 12.3% (Table 2) of stomach contents and consisted of unidentified animal matter, small snails, crustacean appendages and fish scales. Primary producers made up the vast majority

(87.7%) of *Pelates octolineatus* stomach content (Table 2). The percentage of animal matter consumed was not significantly different between years (Kruskal-Wallis; $\chi^2 = 1.89$, df = 1, p = 0.17). A positive relationship existed between fish length and the percentage of seagrass consumed, but year was not a significant predictor between consecutive warm seasons (Table 3).

Stable isotope analysis

P. octolineatus isotope values varied considerably (Fig. 2). A total of 116 isotopic values with corresponding fish length, season and year information were available for analysis, with a further 50 isotopic values available from previous years. For fish collected from 2011–2012, $\delta^{15}N$ ranged from 6.1 to 9.6‰ with a mean of 8.5 ± 0.6‰ (±SD), and $\delta^{13}C$ ranged from −21.3 to −10.5‰ with a mean of −16.6 ± 2.5‰. The range in isotopic values increased only slightly when available data from previous years were included ($\delta^{15}N$ = 5.5 to 9.6‰, $\delta^{13}C$ = −21.3 to −9.8‰) (Fig. 2). No significant effect of fish length, year, or season was detected for $\delta^{15}N$ values (Table 4), but fish length was positively correlated to $\delta^{13}C$ values, with a significant interaction in fork length by year.

Seagrasses were relatively more depleted in $\delta^{15}N$ and enriched in $\delta^{13}C$ compared to algae (Fig. 2). Among algal species, red algae were the most en-

Table 1. Number and size of *Pelates octolineatus* used for stomach content analysis from each year and season

Year	Season	Sample size (n)	Size Mean ± SD (cm)	Range (cm)
2011	Warm	35	17.7 ± 2.0	13.7–21.8
2011	Cold	13	18.0 ± 1.6	16.3–21.7
2012	Warm	44	17.3 ± 1.8	12.5–21.7

Table 3. ANOVA of fish length in relation to percentage of seagrass consumed between consecutive warm seasons

	df	SS	MS	*F* value	p-value
Percent seagrass consumed	1	27.85	27.85	8.11	<0.01
Year	1	3.96	3.96	1.15	0.29
Percent seagrass consumed × year	1	0.28	0.28	0.08	0.78
Residuals	74	254.17			

Table 2. Estimates of *Pelates octolineatus* stomach contents, showing the frequency of occurrence (%) and percentage of contents (mean ± SD) of each food category. Parentheses: no. of occurrences/no. of samples

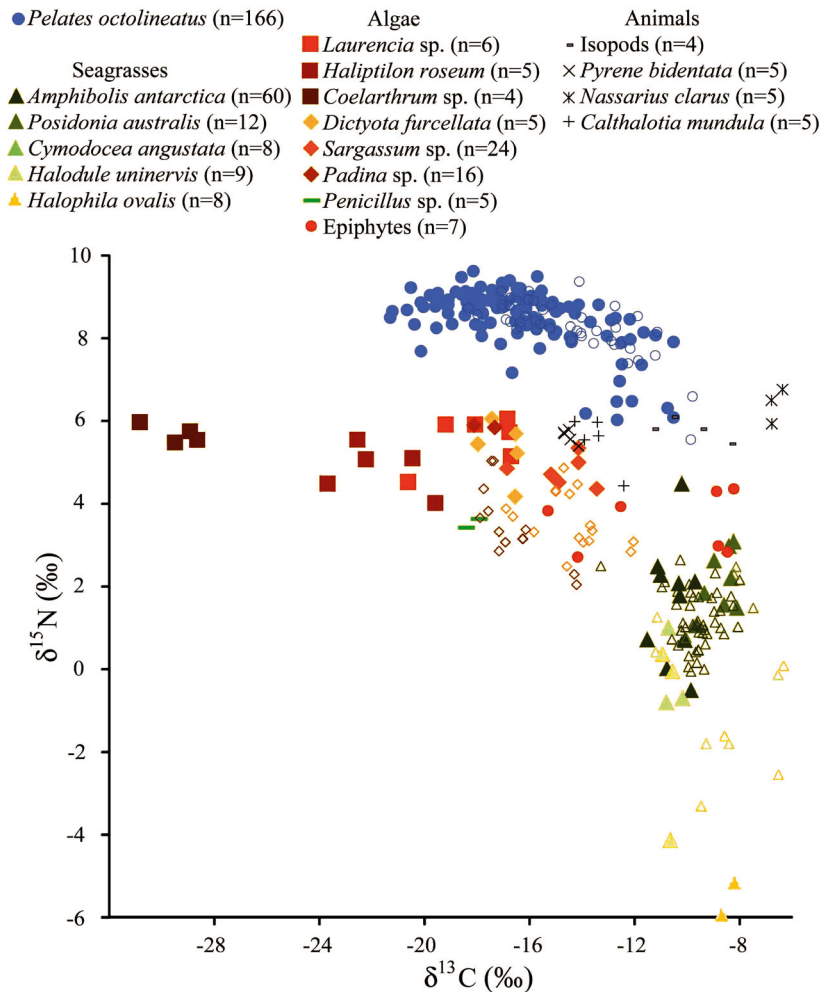|	Stomach content by visual estimation				Stomach content by weight	
	All samples (n = 92)		Subsample (n = 32)		Subsample (n = 32)	
	Frequency of occurrence	Percentage of contents	Frequency of occurrence	Percentage of contents	Frequency of occurrence	Percentage of contents
Seagrass	62.0 (57/92)	43.7 ± 44.1	62.5 (20/32)	45.8 ± 45.6	65.6 (21/32)	44.6 ± 45.6
Algae	68.5 (63/92)	44.0 ± 43.8	62.5 (20/32)	38.7 ± 43.7	68.8 (22/32)	40.5 ± 43.8
Animal matter	29.3 (27/92)	12.3 ± 25.9	34.4 (11/32)	15.5 ± 27.9	31.3 (10/32)	14.9 ± 28.5

Fig. 2. Isotopic values of *Pelates octolineatus* and their potential diet items by food category (seagrass, algae, and animals). Closed symbols = data from 2010–2012. Open symbols = data from 2005–2009 derived from Burkholder et al. (2011) and M. R. Heithaus (unpubl. data)

riched in δ^{15}N and the most depleted in δ^{13}C. Seagrasses had an overall range of 11.2 and 8.7‰ in δ^{15}N and δ^{13}C, respectively. The overall range in δ^{15}N and δ^{13}C was, respectively, 2.0 and 14.1‰ for red algae, 4.0 and 6.1‰ for brown algae, and 0.5 and 4.7‰ for green algae, and 1.6 and 7.1‰ for epiphytes. Animals were more enriched in δ^{15}N compared to seagrasses and some algae species.

Stable isotope mixing models predicted greater contributions of algae and animal matter to assimilated diets than seagrasses (Fig. 3). The TEFs used for fishes had relatively little impact on predicted dietary contributions. Based on TEFs for herbivorous fish and prey category standard deviations calculated from the present study, the mean predicted proportion of seagrass, algae and animal matter in fish diets was 0.20, 0.50, and 0.30, respectively (Fig. 3a).

The mean predicted proportion of seagrass decreased to 0.11 when the trophic enrichment values were determined using the methods proposed by Caut et al. (2009). The maximum upper limit for the 95% CI of seagrass contribution to *P. octolineatus* diets was ≤0.42 regardless of TEF used.

Stable isotope mixing models run with increased standard deviations for the prey categories resulted in increased dietary contribution of seagrass, where the mean predicted proportion of seagrass, algae and animal matter in fish diets was 0.29, 0.40, and 0.31, respectively, based on TEFs for herbivorous fish (Fig. 3b). The relative predicted contribution of seagrass, algae and animal matter was similar (0.27, 0.41, and 0.32, respectively) (Fig. 3b) when TEFs were calculated using the values proposed by Caut et al. (2009). In these cases, the maximum upper limit for the 95% CI of seagrass contribution to *P. octolineatus* diets was ≤0.57.

P. octolineatus exhibited a similar, but smaller, isotopic niche than *Chelonia mydas* (27.3 and 62.4 units, respectively) (Fig. 4). The increased isotopic niche for *C. mydas* compared to *P. octolineatus* was driven by greater ranges in isotopic values for both δ^{15}N (6.18 compared to 4.08‰, respectively) and δ^{13}C (14.33 compared to 11.51‰, respectively). The total area of the convex hull constructed for *P. octolineatus* displayed considerable overlap with *C. mydas*. Only 1.2% (2 of 166) of individual isotopic values for *P. octolineatus* fell outside the total area of *C. mydas*, while 37.0% (30 of 81) of individual isotopic values for *C. mydas* fell outside the total area of *P. octolineatus*.

DISCUSSION

The results of the present study indicate that the vast majority (87.7%) of *Pelates octolineatus* diets consist of primary producers, with seagrass comprising a large proportion of observed stomach content. The high proportion of primary producers in the diets of *P. octolineatus* suggests that this teleost species

Table 4. ANOVA for nitrogen and carbon isotopic values in relation to fish length, year, and season

	df	SS	MS	F-value	p-value
Nitrogen					
Fork length	1	0.44	0.44	0.85	0.36
Year	1	0.03	0.03	0.06	0.8
Season	1	0.47	0.47	0.91	0.34
Fork length × year	1	0.64	0.64	1.24	0.27
Fork length × season	1	0.02	0.02	0.04	0.85
Residuals	110	57.02			
Carbon					
Fork length	1	69.5	69.49	13.6	<0.001
Year	1	14.1	14.11	2.77	0.1
Season	1	0	0.04	0.01	0.93
Fork length × year	1	23.7	23.67	4.64	0.04
Fork length × season	1	1.5	1.48	0.29	0.59
Residuals	110	560.5	5.1		

Fig. 4. Total isotopic areas of consumers, green turtle *Chelonia mydas* and teleost *Pelates octolineatus*, and mean (±SD) of potential prey items by category (animals, algae, and seagrass)
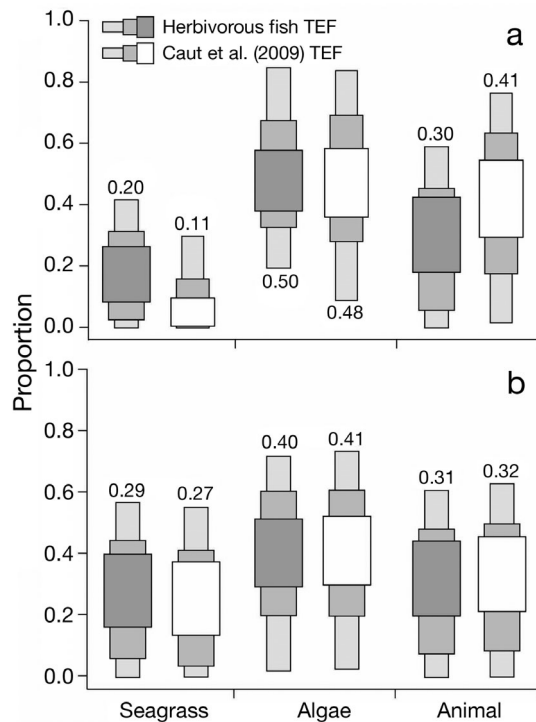

Fig. 3. Results of stable isotope mixing models for *Pelates octolineatus* using, firstly, published trophic enrichment factors (TEF) for herbivorous fishes, denoted by darkest central boxes (Mill et al. 2007, Wyatt et al. 2010), and secondly, using TEFs for fish muscle from Caut et al. (2009) (open central boxes). Models in (a) used prey category standard deviations based on empirical data from this study. Models in (b) used prey category standard deviations of 5.0‰ for both $\delta^{15}N$ and $\delta^{13}C$ to account for unknown seasonal variability. Shading represents 95% (lightest), 75% (medium), and 25% (darkest and no shading) credibility intervals, with the mean predicted contribution for each prey category provided above or below each bar
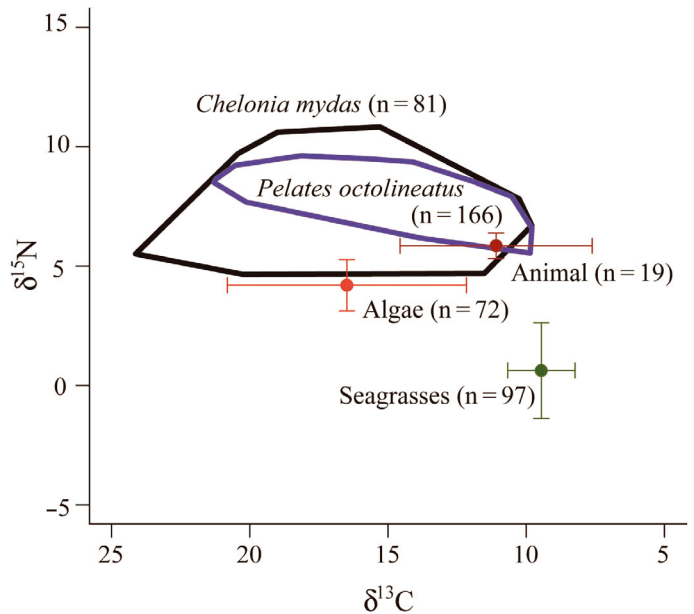
functions as a herbivore in the Shark Bay subtropical seagrass ecosystem. The consumption of primary producers by *P. octolineatus* may play a more important role in facilitating the transfer of primary production to higher trophic levels than was previously appreciated. Indeed, *P. octolineatus* is prey for a variety of predators in the bay (Bessey & Heithaus 2013).

In the present study, less than 1% of fish had empty stomachs, as would be expected for a herbivore (Arrington et al. 2002), and most fish had a large amount of food in their stomach (~2% of body weight, back-transformed). This pattern is likely driven by the generally lower protein content of some primary producers compared to animal matter (Bowen et al. 1995), as well as the difficulty in digesting cellulose. Although the digestion of some primary producers, such as seagrass, presents a challenge, complex gut alimentary may assist *P. octolineatus* in the processing of seagrass matter. Terapontid fishes display complex looping of the intestine during ontogeny, and the negative correlation between intestinal length and proportion of animal prey consumed is widely accepted (Davis et al. 2013). Indeed, a positive relationship existed between fish length and percentage of seagrass consumed. Interspecific differences in intestinal length can explain a large proportion (~65%) of the variability of animal matter consumed in terapontid diets. These interspecific differences in intestinal length during ontogenetic

development may be the mechanism enabling this family of fishes to adopt diverse modes of feeding, including carnivory, invertivory, omnivory, detritivory, and herbivory (Davis et al. 2013).

Stable isotope mixing models suggested that algal contributions to assimilated biomass were higher than both seagrass and animal matter. Macroalgae may have a higher nutritional value compared to seagrass species (Smit et al. 2006), allowing for easier assimilation of energy from macroalgal sources. Interestingly, Poore et al. (2012) suggested that producer traits (such as algal identity) explain more variation in herbivore impacts than consumer identity. Indeed, macroalgae and epiphyte-covered seagrasses have been identified as important food sources for herbivorous fishes in other coastal systems, e.g. Mississippi salt marsh (Sullivan & Moncreiff 1990), subtropical lagoon in Bermuda (McGlathery 1995), and temperate seagrass meadow in Western Australia (Smit et al. 2006). Both red and brown algae are commonly consumed by herbivorous fish (Bell et al. 1978, Conacher et al. 1979), and these taxa were frequently encountered in the stomach contents of *P. octolineatus*. Further studies into algal and seagrass nutritional value and palatability, as well as more explicit studies investigating the role of grazers in structuring seagrass and algal dynamics, could increase our understanding of herbivory in Shark Bay and other seagrass ecosystems.

The combination of gut contents and stable isotope analyses suggests that while algae may make up a greater portion of assimilated biomass than would be expected, herbivore consumption of seagrasses is greater than would be predicted by stable isotopic data alone. Indeed, despite roughly similar proportions of algae and seagrass in the stomachs of fishes, $\delta^{13}C$ values of *P. octolineatus* were more similar to those of algae compared to seagrasses. Stable isotope mixing models using increased standard deviations for prey categories predicted the mean proportional contribution of seagrass and algae in fish diets to be 0.29 and 0.40, respectively. Comparatively, the mean proportional contribution of seagrass and algae to fish diets observed in stomach content analysis were both 0.44. Therefore, diet studies based on stable isotope data alone may not adequately describe the potential functional role of herbivores in seagrass ecosystems. The mismatch between views of trophic interactions based on isotopes and gut contents has important implications for understanding the ecological role of herbivores in seagrass ecosystems. For example, the total isotopic niche space of *P. octolineatus* fell almost entirely within that of green turtles.

Mixing models suggested that these turtles were assimilating a large proportion of nutrients from algae, some from gelatinous macroplankton, and, with the exception of a few individuals, relatively little from seagrasses (Burkholder et al. 2011). Results from the present study suggest that these isotopic results could underestimate the functional impacts of turtles on seagrass communities. This hypothesis is supported by results of exclosure experiments in Shark Bay where the exclusion of large herbivores (turtles and dugongs) resulted in increased leaf length for 2 species of seagrass, with the shoot density of one species nearly tripling (Burkholder et al. 2013b).

Seagrass beds are threatened by myriad human-induced impacts, necessitating an understanding of the processes that affect seagrass ecosystem structure and function (Waycott et al. 2009, Adam et al. 2011). The present study suggests that fish have the potential to play an important role in the dynamics of seagrass communities. Therefore, further studies that directly measure the top-down impacts of herbivorous teleosts will assist in effective management of these ecosystems, and could enhance the ability to predict community trajectories under scenarios of climate change and other anthropogenic impacts.

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