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Comparative Feeding Ecology of Cardinalfishes (Apogonidae) at Toliara Reef, Madagascar

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Bruno Frédérich, Loïc N. Michel, Esther Zaeytydt, Roger Lingofo Bolaya, Thierry Lavitra, Eric Parmentier, and Gilles Lepoint (2017) Despite their importance in coral reef ecosystem function and trophodynamics, the trophic ecology of nocturnal fishes (*e.g.* Apogonidae, Holocentridae, Pempheridae) is by far less studied than diurnal ones. The Apogonidae (cardinalfishes) include mostly carnivorous species and evidence of trophic niche partitioning among sympatric cardinalfishes is still limited. The present study combines stomach contents and stable isotope analyses to investigate the feeding ecology of an assemblage of eight cardinalfishes from the Great Reef of Toliara (SW Madagascar). $\delta^{13}C$ and $\delta^{15}N$ of fishes ranged between -17.49‰ and -10.03‰ and between 6.28‰ and 10.74‰, respectively. Both stomach contents and stable isotopes showed that they feed on planktonic and benthic animal prey in various proportions. Previous studies were able to group apogonids in different trophic categories but such a discrimination is not obvious here. Large intra-specific variation in the stomach contents and temporal variation in the relative contribution of prey to diet support that all apogonids should be considered as generalist, carnivorous fishes. However the exploration of the isotopic space revealed a clear segregation of isotopic niches among species, suggesting a high level of resource partitioning within the assemblage. According to low inter-specific variation in stomach content compositions, we argue that the differences in isotopic niches could be driven by variation in foraging locations (*i.e.* microhabitat segregation) and physiology among species. Our temporal datasets demonstrate that the trophic niche partitioning among cardinalfishes and the breadth of their isotopic niches are dynamic and change across time. Factors driving this temporal variation need to be investigated in further studies.

Key words: Apogonids, Stable isotopes, Isotopic niche, Diet, Western Indian Ocean.

BACKGROUND

Trophic niche partitioning is a major axis of ecological diversification in reef fishes (Wainwright and Bellwood 2002). Trophic ecology of reef fishes has been broadly studied but, to date, most studies have focused on diurnal taxa (*e.g.* Pratchett 2005; Frédérich et al. 2009). Abundant nocturnal reef fishes include bullseyes (Pempheridae), soldier- and squirrelfishes (Holocentridae), and cardinalfishes (Apogonidae) (Hobson 1965; Hobson 1972). Despite their importance for coral reef ecosystem function and trophodynamics (Harmelin-Vivien 2002), these groups remain less studied than other reef fish families.

Diurnal fishes show a high level of trophic diversity including herbivores, corallivores, detritivores, durophagous fishes, zooplankton

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feeders, fish predators, and omnivores (Randall 1967; Wainwright and Bellwood 2002). This variety contrasts the limited trophic diversity of nocturnal fishes, which are mainly carnivorous. Common prey items of nocturnal fishes are restricted to fish, zooplankton and mobile benthic invertebrates (Gladfelter and Johnson 1983; Marnane and Bellwood 2002; Wainwright and Bellwood 2002). Despite this apparent similarity of diet preferences, differences in the feeding ecology of nocturnal fishes can be highlighted. Food might be partitioned by taxon and prey size. For example, some holocentrids consume predominantly shrimps when others mainly eat crabs (Gladfelter and Johnson 1983). Variation in the timing of foraging and spatial niche partitioning has also been reported (Marnane and Bellwood 2002; Annese and Kingsford 2005).

Cardinalfishes (Apogonidae) comprise 347 valid species (Eschmeyer et al. 2016), widely distributed in all tropical and warm temperate seas. They usually occur in coral and rocky reefs while some species inhabit seagrass meadows, soft bottoms and estuaries. Apogonids form a major component of reef fish assemblages, both in terms of species diversity and numerical abundance (Wainwright and Bellwood 2002). Most apogonids are carnivorous species feeding on benthic organisms, plankton and small fish (Vivien 1975; Chave 1978; Barnett et al. 2006; Marnane and Bellwood 2002). They can be segregated into two trophic groups: piscivores and generalists that feed on a range of benthic and planktonic crustaceans (Barnett et al. 2006). Stomach content analysis suggested overlap in many apogonids' diet, and most studies failed to identify clear sub-groups of planktonic and benthic feeders based on stomach contents (Barnett et al. 2006). However, Marnane and Bellwood (2002) found that some species foraged high in the water column at night, suggesting a diet relying more on planktonic prey.

To date, most studies about trophic diversity of apogonids are based on stomach content analyses (Vivien 1975; Marnane and Bellwood 2002; Barnett et al. 2006). This method allows identification of prey with high resolution. However, it only gives a snapshot of the diet at sampling time (Hyslop 1980), while trophic processes can show high temporal variation. Gut content examination can also lead to over-estimation of poorly palatable and/or digestible items as it focuses on ingested food, but gives no information about whether this food is actually assimilated and exploited by consumers or not.

These limitations reinforce the importance of trophic markers, such as the use of stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$). Stable isotope analysis has emerged as a powerful tool for tracing dietary sources, as the isotope ratios of a consumer are mostly driven by those of its food (Peterson and Fry 1987; Layman et al. 2012). This method provides an integrated measure of the dietary components over a much longer period of time than do gut contents. Although stable isotope analysis does not provide a detailed picture of dietary preferences, it gives an average estimate of an organism's preferred diet that is much less subject to temporal bias (Layman et al. 2012). Recently, stable isotope compositions were also revealed as a powerful tool for assessing the trophic niche width of species and for identifying trophic specialists from generalists (Bearhop et al. 2004; Jackson et al. 2011).

In the present study, our main objective was to compare the feeding ecology of eight species of Apogonidae at the Toliara Great Reef (SW Madagascar). Since these apogonids co-occur in the inner reef, we expected some degree of trophic partitioning among species to reduce competition (Schoener 1974). Specifically, we aimed (1) to characterize their diet; (2) to estimate their trophic niche size and potential overlap among trophic niches; (3) to study interannual variation in their feeding ecology. To achieve these goals, we combined stomach contents and stable isotope analyses. This dual approach was motivated by the complementarity between the two techniques and the potential of each one to compensate for the other technique's caveats. Joint use of these techniques has already proven valuable to delineate feeding strategies among numerous consumers, including coral reef fishes (*e.g.* Frédérich et al. 2009; Layman and Allgeier 2012; Lepoint et al. 2016). To ensure robust quantitative estimates of isotopic niches, data were explored using advanced Bayesian tools such as the SIBER niche metrics (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011).

MATERIALS AND METHODS

Sampling

Fishes were collected on the Great Reef of Toliara (SW Madagascar – 23.36°S, 43.66°E) during June 2011, July 2012 and July 2014. Every year, fishes were captured within the same area

along the inner reef slope. A total of 182 specimens (Table 1) were sampled by scuba diving at depths ranging from 2 to 10 m after being anesthetized by a solution of clove oil. During the field campaigns conducted in 2011 and 2012, fishes were captured during the morning (*i.e.* between 7 and 9 a.m.) while fishes from 2014 were collected at dawn. After their capture, the fishes were brought to the surface and killed as quickly as possible by overdose immersion in MS-222. They were then placed on ice.

Each fish was weighed and its standard length (SL) was measured to the nearest millimeter. Samples (± 1 cm^3) of lateral muscle tissue of each fish were used for stable isotope analysis. The digestive tract was removed and conserved in 70% ethanol for stomach content analysis. Potential fish food items (*i.e.* zooplankton and benthic invertebrates) were taken from the fish collection site. The protocol for sampling food sources is fully detailed in Frédérich et al. (2009). In brief, mesozooplankton was sampled with a 250 mm mesh size net every sampling year, and small benthic invertebrates (*e.g.* amphipods, isopods, annelids…) were trapped using small light traps made by plastic bottles containing glow sticks (Michel et al. 2010) in 2011 and 2014 only. Sample sizes of these food sources and their mean isotopic values are provided as supplementary material (Table S1).

Stomach content analysis

After dissection, stomachs were opened and all dietary constituents were dispersed onto individual glass slides. All food items were identified using a Wild M10 binocular microscope. Animal prey were identified to the phylum, class or family and assigned to the planktonic or the benthic environment. Plant items were classified as either phytoplankton or fragments of benthic algae. Amorphous material (*i.e.* items lacking any identifiable features) was classified as unrecognized. In order to define the diet of every apogonid, we quantified food items as a percentage of occurrences and as a mean percent composition of each item in the stomach content (Hyslop 1980).

Stable isotope analysis

Samples of lateral muscle tissue and potential food sources were dehydrated for at least 48 h at 50°C before being ground into a homogenous powder using mortar and pestle. Inorganic carbon present in samples can be a source of bias for C stable isotope ratio analysis. Therefore, after grinding, samples containing carbonates (zoobenthos) were placed for 24 h under a glass bell with fuming HCl (37%; Merck, for analysis quality) to eliminate calcareous material. Measurements were performed using an IsoPrime100 isotope ratio mass spectrometer (Isoprime, UK) coupled to a vario MICRO cube C-N-S elemental analyzer (Elementar Analysensysteme GMBH, Italy) for sample transformation and automated analysis. Isotopic ratios were expressed using the δ notation (‰) (Coplen 2011). Certified Reference Materials (CRM) were IAEA-N1 (ammonium sulphate, $\delta^{15}N$ = 0.4 ± 0.2‰; mean ± SD) for nitrogen and IAEA-C6 (sucrose; $\delta^{13}C$ = -10.8 ± 0.5‰; mean ±

Table 1. List of the studied species. N, number of specimens; SL, standard length. The percentage of specimens in which stomach was empty is provided

Year	Species	N	Size range (SL, mm)	Empty stomach (%)
2011	*Ostorhinchus cookii*	9	47.1 – 69.5	66.7
	Ostorhinchus cyanosoma	15	37.5 – 46.8	60
	Pristiapogon fraenatus	15	52.4 – 68.3	20
	Pristiapogon kallopterus	5	46.1 – 57	0
2012	*Ostorhinchus cookii*	14	48 – 79	28.6
	Cheilodipterus quinquelineatus	2	52 – 69	50
2014	*Ostorhinchus aureus*	25	54.1 – 91.2	24
	Ostorhinchus cyanosoma	18	41.9 – 49.9	22.2
	Pristiapogon fraenatus	27	53.7 – 89.6	55.6
	Pristiapogon kallopterus	15	62.6 – 93.8	26.7
	Taeniamia fucata	25	65.2 – 76.7	24
	Zoramia leptacantha	12	34.5 – 39	0

SD) for carbon. Both CRM are calibrated against the international references Vienna Pee Dee Belemnite and atmospheric air for carbon and nitrogen, respectively. Standard deviations on replicate measurements of a randomly selected fish muscle sample (one replicate measurement every 15 analyses) were less than 0.3‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Data treatment and statistics

To determine whether apogonids differed in their diet composition, Bray-Curtis similarity coefficients between individuals were computed using relative stomach content composition (percentage) data. These coefficients were subsequently used to perform hierarchical clustering. The non-parametric ANOSIM test (analysis of similarity) was then used to statistically test differences in stomach contents among species. This test provides an output R-value and a P-value stating about its significance. R-value is supposed to vary between 0 and 1, and R-value > 0.5 suggests divergence between groups (Clarke and Warwick 2001). Additionally, the null hypothesis of no difference in global foraging tactics (expressed as the percentage of planktonic or benthic animal prey found in stomach contents) among species was tested using a one-way ANOVA followed by post-hoc multiple comparison tests (Tukey test). The percentages were arcsine-square root transformed before the analysis to meet the normality assumption (Shapiro-Wilk's test, after transformation).

When relevant, interspecific and/or interannual differences in $\delta^{13}C$ and $\delta^{15}N$ were tested using hypothesis-based comparison procedures. D'Agostino & Pearson normality tests revealed that several datasets did not follow a Gaussian distribution. Non-parametric procedures (Mann-Whitney U test when 2 groups were compared, Kruskal-Wallis one-way analysis of variance followed by Dunn's post-hoc test when 3 groups or more were compared) were therefore applied. Linear regressions were applied to examine trends of stable isotope composition with fish size (SL) and with stomach contents (% of zooplankton) (Frédérich et al. 2010). The ANOSIM, ANOVA, Mann-Whitney U test, Kruskal-Wallis test and associated post-hoc tests, and linear regressions were performed using the statistical software PAST (Hammer et al. 2001).

For fish groups with N ≥ 5, isotopic niche parameters were computed using the SIBER package (Version 2.0; Jackson et al. 2011) for R (R Development Core Team 2015). SIBER was used to generate bivariate standard ellipses that represent core isotopic niches of consumers. Areas of these ellipses were estimated using correction for small sample size (SEA_C, Jackson et al. 2011). Areas of the ellipses associated to each species were also estimated using Bayesian modelling (SEA_B, 10^6 iterations), and direct pairwise comparisons of SEA_B were performed. Model solutions were presented using credibility intervals of probability density function distributions. Pairwise comparisons were considered meaningful when probability of occurrence exceeded 95%.

RESULTS

Stomach contents

A large proportion of the 182 examined stomachs were found to be empty (N = 55; Table 1). For the five species captured in 2011 and 2012, the numbers of stomachs containing prey were very low. Moreover, very little prey material was found in the non-empty stomachs. Therefore, only frequency of occurrences of all dietary categories was investigated for species sampled in 2011 and 2012 (Table 2). On the other hand, both frequency of occurrences and percentages of composition for each prey category were calculated for species collected in 2014, where sufficient amounts of prey material were observed (Tables 2 and 3).

Generally speaking, apogonids showed a carnivorous diet. The eight species mainly fed on zooplankton (copepods, crustacean larvae, polychaete larvae and chaetognaths) and small benthic invertebrates (amphipods, small decapods and harpacticoid copepods; Table 2). A significant amount of unrecognized prey items was present in all studied species. Planktonic copepods and decapods were the most recurrent prey found in stomachs. Algae were never ingested, except by few individuals (N = 3) of *Ostorhinchus aureus* in 2014. Small fishes were observed in the stomach of *Pristiapogon kallopterus* in both 2011 and 2014. Temporal variation in the type of prey selected was observed. For example, *O. cyanosoma*, *P. fraenatus* and *P. kallopterus* were used to feed on harpacticoids in 2014 but not in 2011. Planktonic copepods were largely encountered in the stomachs of *P. fraenatus* in 2014 only.

The ANOSIM test performed on percentage composition of stomach contents of fishes

sampled in 2014 was significant ($P < 0.001$), suggesting that interspecific differences were present in stomach content composition. However the ANOSIM R statistic was very low ($R = 0.23$), suggesting that the "species" factor was not a major driver of stomach content similarity because the composition of stomach contents greatly varied within each apogonid species (Table 3). The ANOVAs revealed different feeding strategies among apogonids (zooplankton: $F = 6.313$, *d.f.* = 5,81, $P < 0.001$; zoobenthos: $F = 3.089$, *d.f.* = 5,81, $P = 0.013$). *Pristiapogon kallopterus* consumed significantly less planktonic prey than the other species. *Zoramia leptacantha* foraged less in the

Table 2. Frequency of occurrence (%) of all dietary categories in the eight studied species of apogonids. For species collected during different sampling campaigns, results are shown for every year. *C.* = *Cheilodipterus*, *O.* = *Ostorhinchus*, *P.* = *Pristiapogon*, *T.* = *Taeniamia*, *Z.* = *Zoramia*

	C. quinquelineatus	*O. aureus*	*O. cookii*		*O. cyanosoma*		*P. fraenatus*		*P. kallopterus*		*T. fucata*	*Z. leptacantha*
Prey category	2012	2014	2011	2012	2011	2014	2011	2014	2011	2014	2014	2014
Planktonic animal preys												
Copepods	0	79	0	0	33.3	71.4	0	58.3	0	18.2	31.6	100
Crustacean larvae	0	26.3	0	0	0	28.6	7.7	8.3	0	0	57.9	91.7
Polychaete larvae	100	0	0	18.2	33.3	0	0	0	0	0	0	0
Chaetognaths	0	5.3	0	0	0	0	0	0	0	0	0	0
Benthic animal preys												
Harpacticoid copepods	0	36.8	0	0	0	35.7	0	16.7	0	9.09	0	83.3
Amphipods	0	10.5	0	0	16.7	21.4	7.7	16.7	0	0	5.3	0
Ostracods	0	21.1	0	0	0	0	0	0	16.7	0	0	0
Decapods	100	26.3	100	81.8	66.7	28.6	84.6	66.7	100	90.9	63.2	16.7
Gastropods	0	5.3	0	0	0	0	0	0	0	0	0	8.3
Polychaetes	0	0	0	0	0	0	0	16.7	0	0	0	0
Algae	0	15.8	0	0	0	0	0	0	0	0	0	0
Fish	0	0	0	0	0	0	0	0	0	9.1	0	0
Fish scales	0	5.3	0	9.1	0	0	0	0	16.7	0	5.3	0
Eggs	0	0	0	0	0	7.1	0	16.7	0	9.1	0	0
Unrecognized	100	100	100	100	100	100	100	100	100	90.9	100	83.3

Table 3. Mean percent composition of all dietary categories in the six species of apogonids collected in 2014. Results are presented as Mean (%) ± SD. *O.* = *Ostorhinchus*, *P.* = *Pristiapogon*, *T.* = *Taeniamia*, *Z.* = *Zoramia*

Prey category	*O. aureus*	*O. cyanosoma*	*P. fraenatus*	*P. kallopterus*	*T. fucata*	*Z. leptacantha*
Planktonic animal preys	53.3 ± 33.5	57.9 ± 38.0	28.8 ± 32.9	11.6 ± 26.6	59.3 ± 39.2	82.8 ± 13.3
Copepods	35.7 ± 31.9	43.0 ± 37.2	27.4 ± 33.1	11.6 ± 26.6	16.3 ± 29.2	54.0 ± 22.9
Crustacean larvae	16.7 ± 30.9	14.8 ± 25.3	1.4 ± 4.8	0.0	43.0 ± 41.6	28.8 ± 21.9
Polychaete larvae	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognaths	0.9 ± 3.8	0.0	0.0	0.0	0.0	0.0
Benthic animal preys	40.2 ± 33.3	35.0 ± 35.6	63.5 ± 34.3	70.2 ± 43.3	39.0 ± 40.3	17.2 ± 13.3
Harpacticoid copepods	19.2 ± 32.8	11.3 ± 18.9	5.6 ± 14.8	3.0 ± 10.1	0.0	16.3 ± 13.8
Amphipods	6.3 ± 23.1	10.2 ± 27.4	10.4 ± 29.1	0.0	1.1 ± 4.6	0.0
Ostracods	8.5 ± 18.9	0.0	0.0	0.0	0.0	0.0
Decapods	5.6 ± 11.0	13.5 ± 28.8	44.7 ± 41.4	67.2 ± 42.2	37.9 ± 40.0	0.7 ± 1.7
Gastropods	0.6 ± 2.5	0.0	0.0	0.0	0.0	0.3 ± 0.9
Polychaetes	0.0	0.0	2.8 ± 6.5	0.0	0.0	0.0
Algae	4.3 ± 10.5	0.0	0.0	0.0	0.0	0.0
Fish	0.0	0.0	0.0	9.1 ± 30.2	0.0	0.0
Fish scales	2.3 ± 9.8	0.0	0.0	0.0	1.8 ± 7.6	0.0
Eggs	0.0	7.1 ± 26.7	7.8 ± 19.0	9.1 ± 30.2	0.0	0.0

benthic compartment than *P. kallopterus* and *P. fraenatus* (Tables 3 and 4). No significant variation was shown for the other species (Table 4).

Stable isotopes

Zooplankton $\delta^{13}C$ was comparable in 2011 and 2012, but less negative in 2014 (Fig. 1A). Carbon isotopic composition of zoobenthos was variable according to sampling year (Fig. 1A), but it was more ^{13}C-enriched than zooplankton in both 2011 and 2014. The difference between mean $\delta^{13}C$ of the two food items varied drastically according to sampling year, as it was 5.73‰ in 2011 but only 0.97‰ in 2014. $\delta^{15}N$ of food items did not seem to follow a consistent temporal variation pattern, and was quite comparable for both food items in every sampling year (Fig. 1A).

Carbon isotopic composition of cardinalfishes was spread over a large interval (Fig. 1A), with values ranging from -11.14 ± 0.45‰ (*Ostorhinchus cookii* in 2011; mean ± SD) to -16.97 ± 0.37‰ (*Taeniamia fucata* in 2014; mean ± SD). Nitrogen isotopic composition also showed considerable dispersion (Fig. 1A), as values ranged from 6.61 ± 0.19‰ (*O. cookii* in 2011; mean ± SD) to 10.14 ± 0.61‰ (*P. kallopterus* in 2014; mean ± SD). This isotopic variability was partly related to the sampling year, as $\delta^{13}C$ and $\delta^{15}N$ seemed to shift towards more negative and higher values throughout time, respectively. However, species-specific trends were also present. For example, $\delta^{15}N$ of *P. kallopterus* and *P. fraenatus* were identical in 2011 (Mann-Whitney test: $U = 19$, $P = 0.113$; Fig. 1A), but *P. kallopterus* showed significantly higher $\delta^{15}N$ than *P. fraenatus* in 2014 (Mann-Whitney test: $U = 72.5$, $P < 0.001$; Fig. 1A). In 2011, $\delta^{13}C$ of fishes showed significant interspecific variation (Kruskal-Wallis test: $H = 34.12$, $P < 0.001$). Post-hoc multiple comparisons (Dunn's test) showed that two groups were present (Fig. 1A): one composed of *P. fraenatus* and *O. cookii*, and another composed of *P. kallopterus* and *O. cyanosoma*. The latter group had more negative $\delta^{13}C$ than the former, suggesting that, in 2011, zooplankton was more important in the diet of *P. kallopterus* and *O. cyanosoma* than in the diet of *P. fraenatus* and *O. cookii*. In 2014, significant variation in $\delta^{13}C$ was also present (Kruskal-Wallis test: $H = 109.9$, $P < 0.001$). Three groups were present (Dunn's multiple comparison tests: $P < 0.05$ in each case): one composed of both species of *Pristiapogon* (*P. fraenatus* and *P. kallopterus*), one composed of both species of *Ostorhinchus* (*O. cookii* and *O. aureus*), and one composed of *T. fucata* and *Z. leptacantha* (Fig. 1A). $\delta^{13}C$ decreased, and contribution of zooplankton to diet therefore presumably increased, when going from the first to the third group (Fig. 1A).

Bivariate standard ellipses of all fish groups were markedly separated (Fig. 1B). This suggests that all cardinalfishes occupy distinct isotopic niches. The only niche overlap found was between *P. fraenatus* and *P. kallopterus* in 2014, and it was very small (0.04‰^{2}, *i.e.* 8.46% of the SEA_C of *P. fraenatus* and 5.05% of the SEA_C of *P. kallopterus*; Fig. 1B). Moreover, there was no overlap between standard ellipses associated with different years for fishes sampled in more than one period (*O. cookii*, *O. cyanosoma*, *P. fraenatus* and *P. kallopterus*; Fig. 1B). Isotopic niche width was quite variable, with SEA_C values ranging from 0.13‰^{2} (*P. kallopterus* in 2011) to 0.89‰^{2} (*P. kallopterus* in 2014; Fig. 2). Pairwise comparisons of model-estimated ellipse areas (SEA_B) suggested niche width differences among species were robust, as many relative probabilities exceeded 95% (Table 5). Trends for species sampled in successive years were not consistent. Standard ellipse area of *P. kallopterus* showed a drastic increase from 2011

Table 4. Results from Tukey multiple comparisons tests when using data on planktonic (below the diagonal) and benthic animal preys (above the diagonal). Significant results are highlighted in italics and marked with an asterisk. *O.* = *Ostorhinchus*, *P.* = *Pristiapogon*, *T.* = *Taeniamia*, *Z.* = *Zoramia*

	O. aureus	*O. cyanosoma*	*P. fraenatus*	*P. kallopterus*	*T. fucata*	*Z. leptacantha*
O. aureus		0.999	0.602	0.239	0.999	0.747
O. cyanosoma	0.999		0.357	0.106	1	0.925
P. fraenatus	0.466	0.303		0.989	0.467	*0.045**
P. kallopterus	*0.012**	*0.005**	0.587		0.158	*0.007**
T. fucata	0.984	0.999	0.140	*0.001**		0.856
Z. leptacantha	0.402	0.579	*0.005**	*< 0.001**	0.818	

to 2014 ($SEA_{B,\ 2011} < SEA_{B,\ 2014}$ in 99.94% of model solutions; Fig. 2 and Table 5). On the other hand, the isotopic niche of *O. cyanosoma* showed a width decrease from 2011 to 2014 ($SEA_{B,\ 2014} < SEA_{B,\ 2011}$ in 100% of model solutions; Fig. 2 and Table 5). Probabilities of standard ellipse area differences in *O. cookii* ($SEA_{B,\ 2011} < SEA_{B,\ 2012}$ in 87.58% of model solutions) and *P. fraenatus* ($SEA_{B,\ 2011} < SEA_{B,\ 2014}$ in 11.21% of model solutions; Fig. 2 and Table 5) were inferior to 95%, suggesting no meaningful temporal trend in niche width in these taxa. Finally, there was no relation between SEA_C and the size range of sampled fishes (linear regression analysis, $R^2 = 0.15$, $P = 0.24$), suggesting that the

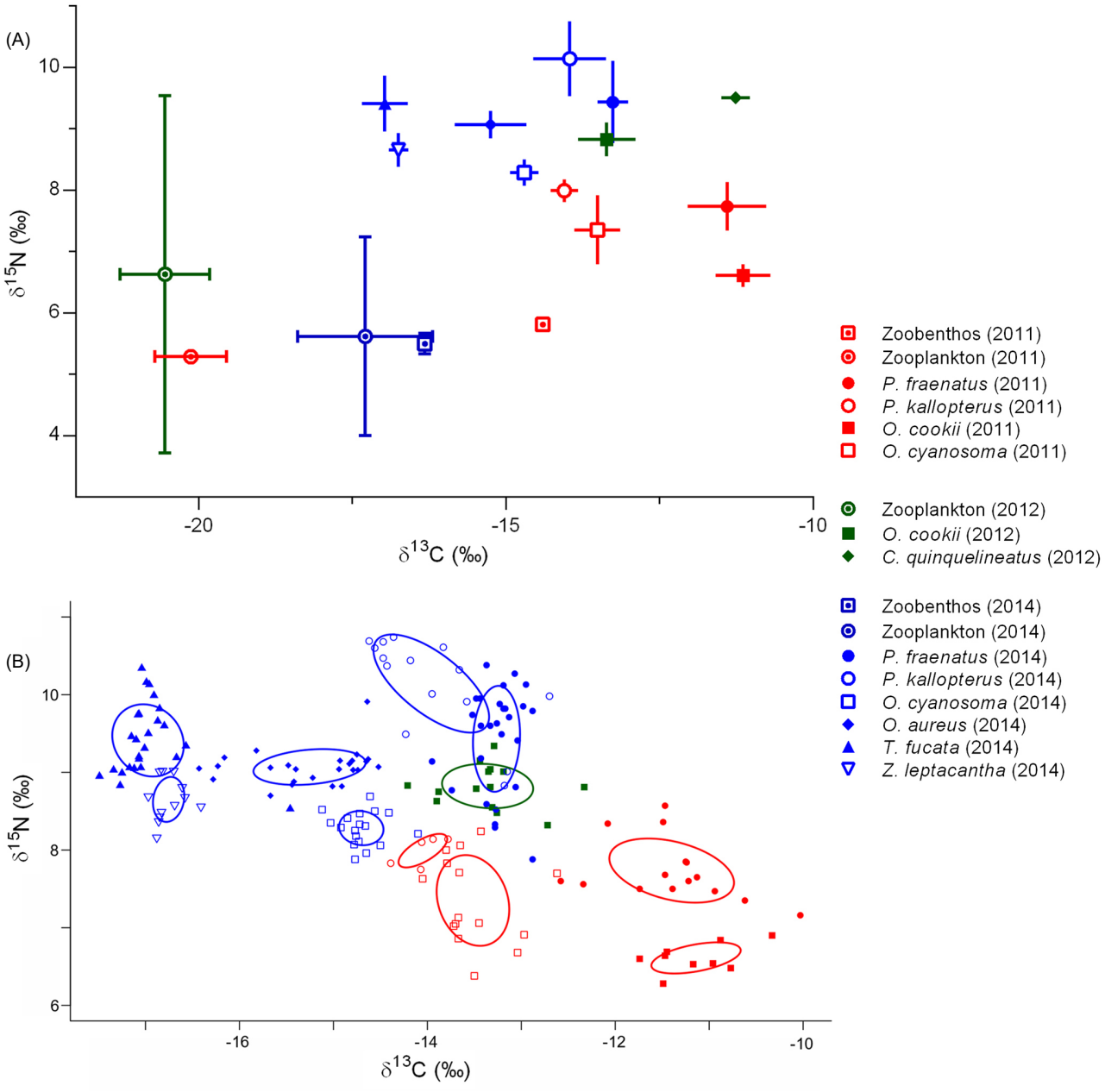

Fig. 1. (A) Mean values (± SD) of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) of cardinalfishes. (B) Isotopic niches of cardinalfishes. Points are individual measurements, and solid lines represent the bivariate standard ellipses associated to each group Species and sampling years are represented by different symbols and colors, respectively.

isotopic niche size was not related to variation in size ranges of the studied species (Table 1).

Linear regression analyses revealed that the variation of carbon or nitrogen isotopic compositions was size-related in most of the apogonids ($0.22 \leq R^2 \leq 0.90$; Fig. 3). However, size range varied greatly among species samples (Table 1) and that could have impacted the results of linear models. For example, *Z. leptacantha* was the only species for which the isotopic compositions were unexplained by body size but its size range was the smallest from all studied species (size range = 5.5 mm; Table 1). In *P. fraenatus*, *P. kallopterus* and *T. fucata*, there was a strong,

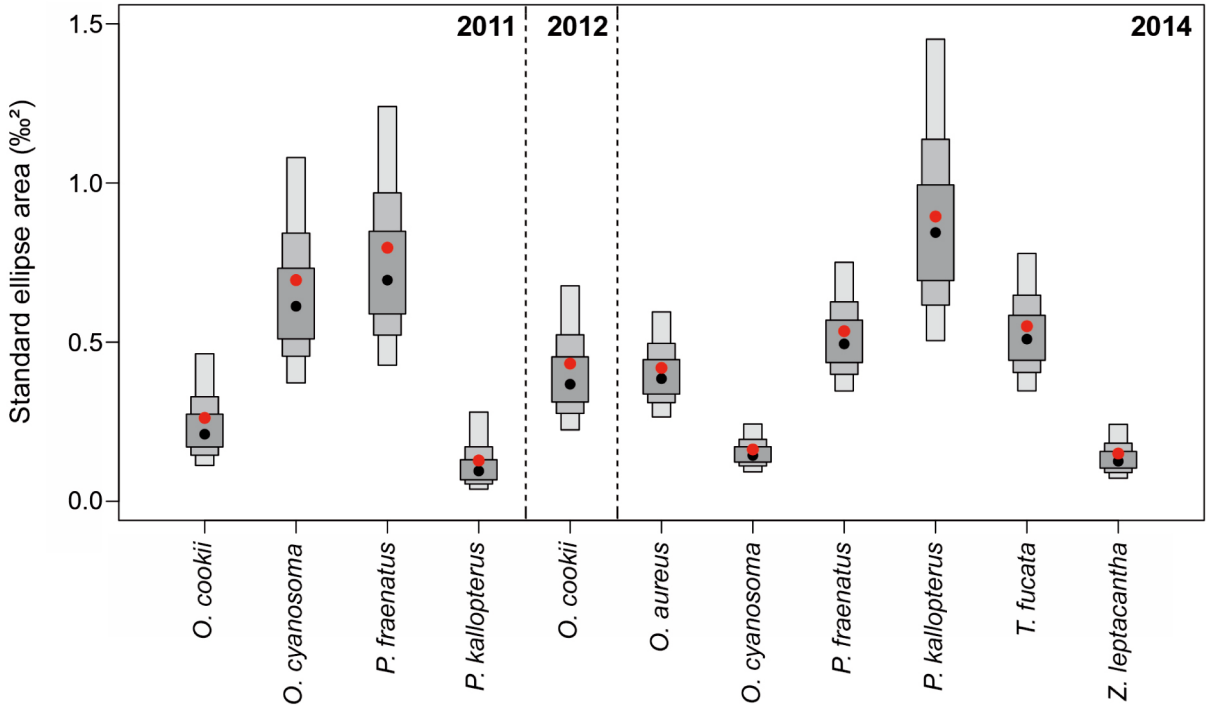

Fig. 2. Boxplots of model-estimated bivariate standard ellipse area (SEA_B). Dark, median and light grey boxes are respectively the 50%, 75% and 95% credibility intervals of the probability of density function distributions of the model solutions, and black dots are the modes of these distributions. Red dots represent the standard ellipse areas computed using a frequentist algorithm adapted for small sample sizes (SEA_C).

Table 5. Pairwise comparisons of standard ellipses areas of cardinalfishes estimated through Bayesian modeling (SEA_B). Each cell contains the relative probability (%) that the standard ellipse of the fish group listed as line is smaller than the standard ellipse of the fish group listed as column, based on 10^6 model runs. Values highlighted in italics and marked with an asterisk are probabilities higher than 95%. *O.* = *Ostorhinchus*, *P.* = *Pristiapogon*, *T.* = *Taeniamia*, *Z.* = *Zoramia*

	O. cookii 2011	*O. cyanosoma* 2011	*P. fraenatus* 2011	*P. kallopterus* 2011	*O. cookii* 2012	*O. aureus* 2014	*O. cyanosoma* 2014	*P. fraenatus* 2014	*P. kallopterus* 2014	*T. fucata* 2014	*Z. leptacantha* 2014
O. cookii 2011	-	*98.67**	*99.38**	10.89	87.58	89.28	13.04	*96.53**	*99.77**	*96.83**	10.35
O. cyanosoma 2011	1.33	-	65.45	0.25	10.10	6.62	0.00	22.31	79.16	25.28	0.00
P. fraenatus 2011	0.62	34.55	-	0.14	5.12	2.50	0.00	11.21	66.24	13.17	0.00
P. kallopterus 2011	89.11	*99.75**	*99.86**	-	*98.21**	*98.51**	70.07	*99.46**	*99.94**	*99.48**	62.31
O. cookii 2012	12.42	89.90	*94.88**	1.79	-	49.78	0.40	76.20	*97.96**	78.48	0.46
O. aureus 2014	10.72	93.38	*97.50**	1.49	50.22	-	0.15	80.83	*99.25**	82.73	0.27
O. cyanosoma 2014	86.96	*100.00**	*100.00**	29.93	*99.60**	*99.85**	-	*99.99**	*100.00**	*100.00**	39.16
P. fraenatus 2014	3.47	77.69	88.79	0.54	23.80	19.17	0.01	-	*95.63**	53.85	0.00
P. kallopterus 2014	0.23	20.84	33.76	0.06	2.04	0.75	0.00	4.37	-	5.38	0.00
T. fucata 2014	3.17	74.72	86.83	0.52	2.04	17.27	0.00	46.15	94.62	-	0.03
Z. leptacantha 2014	89.65	*100.00**	*100.00**	37.69	*99.54**	*99.73**	60.84	*100.00**	*100.00**	*99.97**	-

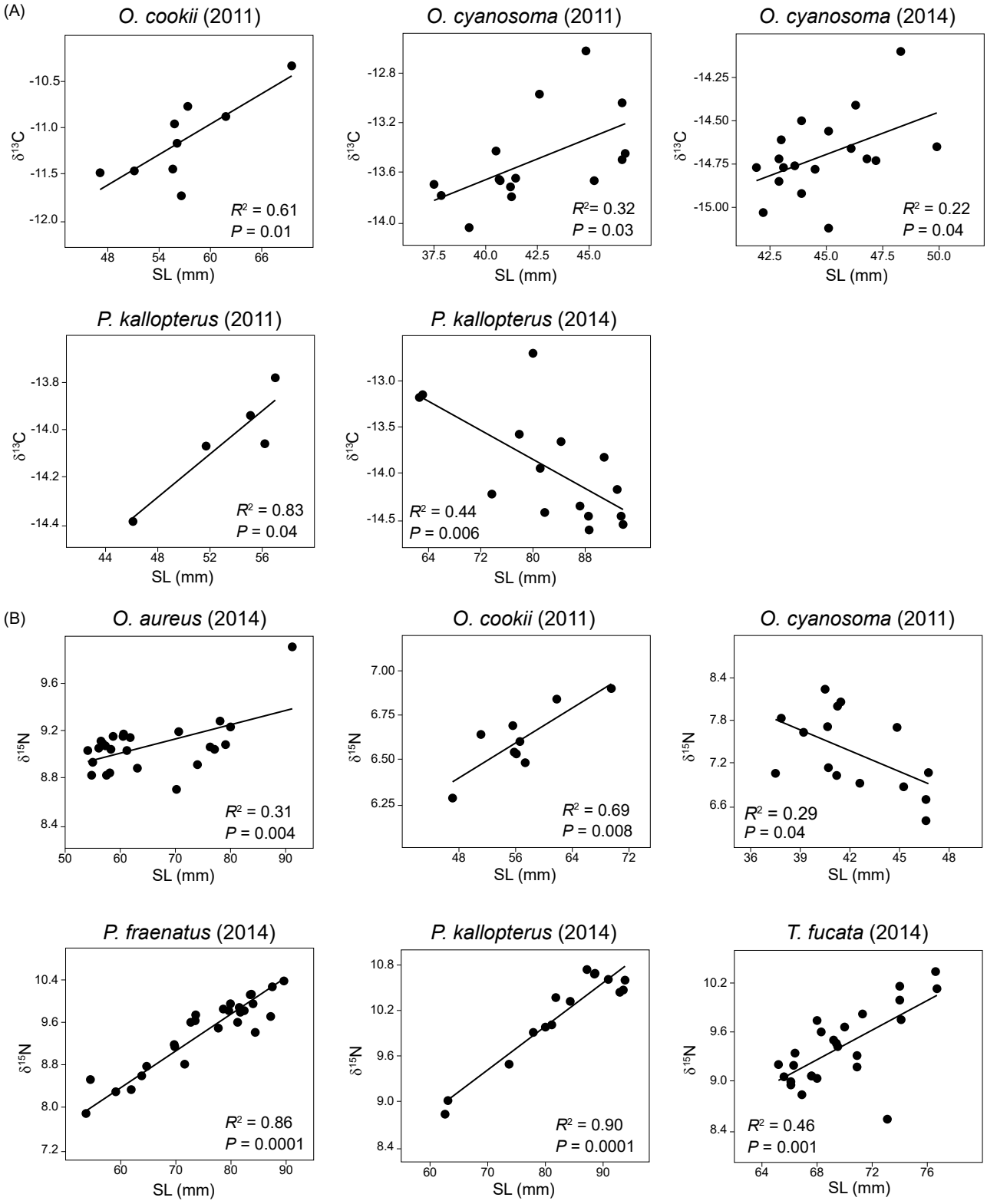

Fig. 3. Relationship between body size (SL, mm) and isotopic values (A: $\delta^{13}C$; B: $\delta^{15}N$) in studied apogonids. Only significant relationships are illustrated.

significant positive relationship between fish size and $\delta^{15}N$ (Fig. 3). Possibilities of comparisons between sampling years were limited but, in *P. kallopterus*, the positive relationship between fish size and $\delta^{13}C$ observed in 2011 shifted to a negative one in 2014 (Fig. 3). In the great majority of species, the $\delta^{13}C$ and the $\delta^{15}N$ values were unrelated to the proportion of zooplankton found in stomach contents (Linear regressions: $R^2 \leq 0.21$, $P > 0.05$; data not shown). Only in *P. kallopterus* from 2014 was the percentage of zooplankton slightly related to $\delta^{13}C$ values ($R^2 = 0.37$, $P = 0.04$).

DISCUSSION

Stomach content analyses show that cardinalfishes from Toliara lagoon have somehow similar carnivorous diets. On the other hand, the stable isotope analyses provide some evidences for fine-scale niche partitioning in apogonids, because no overlap among species was observed in the isotopic space. Size-related variation in stable isotope composition of fishes also suggests niche partitioning within some species.

Both stomach contents and isotope data show that cardinalfishes feed on planktonic and benthic animal prey in various proportions, which is in agreement with previous studies (Vivien 1975; Marnane and Bellwood 2002; Barnett et al. 2006). Except some small fishes encountered in the stomachs of *Pristiapogon kallopterus*, we found low evidence of piscivory in the studied species. Vivien (1975) was able to delineate three trophic groups: strict planktivorous species, strict benthic feeders, and species eating both types of animal prey. This discrimination is not obvious in the present study and we argue in favor of generalist, carnivorous diets in cardinalfishes with some feeding preferences (see also Marnane and Bellwood 2002; Barnett et al. 2006). For example, stable isotope ratios suggest that *Pristiapogon fraenatus* and *P. kallopterus* mainly forage on benthic prey but zooplankton or even small fishes were found in their stomachs (Fig. 1A; Table 2).

Large intra-specific variation in the stomach contents (Table 3) and temporal variation in the relative contribution of prey to diet (Fig. 1) are further arguments to characterize the feeding ecology of apogonids as generalist, carnivorous fishes. To date, relatively few studies have illustrated temporal variation in the diet of coral reef fishes and most of them focused on diurnal fishes (*e.g.* Letourneur et al. 1997; Frédérich et al. 2016). Stomach contents provide information on the most recent meal only, making this method much more sensitive to temporal variation (Hyslop 1980). Here, frequency of occurrence of dietary categories suggested that *Ostorhinchus cookii* consumed a larger proportion of planktonic prey in 2012 than in 2011. This trend was confirmed by isotopic compositions, revealing that this variation in feeding habits might persist for longer periods. At the Great Reef of Toliara (GRT), Vivien (1975) classified *Ostorhinchus cyanosoma* as a zooplankton specialist while Marnane and Bellwood (2002) found that zoobenthos may account for a large proportion of its diet at One Tree Island (Australia). Our data suggest that, at the Toliara Reef, *O. cyanosoma* has a mixed diet (*e.g.* intermediate $\delta^{13}C$ values in 2014; Fig. 1A) and feeds on both zoobenthos and zooplankton. The diet of apogonids may vary at smaller spatial scales. Indeed, Vivien (1975) illustrated considerable variations in the diet of *Ostorhinchus endekataenia* and *P. kallopterus* living in different biotopes from the GRT. For example, *P. kallopterus* ingests a large proportion of isopods in seagrass beds when it feeds largely on shrimps on the reef slopes (Vivien 1975). All these examples of temporal and spatial variation in the feeding preferences clearly demonstrate opportunism and diet plasticity in cardinalfishes.

Nevertheless, the present study is the first, to our knowledge, that illustrates a segregation of isotopic niches in an assemblage of cardinalfishes. For each sampling year, fish $\delta^{13}C$ values were scattered over a ~4‰ range. Carbon stable isotope ratios are mostly influenced by consumer preferences in prey type or foraging habitat. Indeed, as illustrated in previous studies on the trophic ecology of damselfishes from the GRT (Frédérich et al. 2009, 2010; Lepoint et al. 2016), the $\delta^{13}C$ axis represents a continuum of food sources from plankton (the most negative values) to zoobenthos (the least negative values; Fig. 1A). Differences in the C isotopic values were also demonstrated for fish species living in different areas (Frédérich et al. 2012; Letourneur et al. 2013) or different micro-habitats (Lepoint et al. 2016) of the same coral reef. $\delta^{15}N$ is well known for showing a stepwise increase with increasing trophic level (DeNiro and Epstein 1981) and this second niche axis is therefore related to trophic position. Here, $\delta^{15}N$ values varied within a ~2-3‰ interval among apogonids of each sampling year. As evidenced by the lack of overlap of standard ellipses (Fig. 1B), all the cardinalfish

species showed distinct isotopic niches that differ by at least one of the two niche axes. This suggests ecological niche segregation within the assemblage. Differences in these isotopic niches may be related to different diet (*i.e.* varied prey species) but also to different trophic behavior (*e.g.* pelagic vs. benthic), different foraging habitat (*e.g.* water column, coral boulders, sandy areas) or different foraging location in the same habitat, as stable isotope composition may vary spatially. Relatively high similarity in the composition of stomach contents among species (Tables 2 and 3) does not support that the variation in isotopic niches is mainly related to strong short-term differences in the type of prey selected. Nevertheless, we cannot reject the possibility that an analysis of stomach contents with higher resolution (*i.e.* identification of prey to lower taxonomic levels – *e.g.* family or species) could help to refine such an assumption. On the other hand, we argue that differences in isotopic niches reflect a partitioning of foraging locations and/or behaviors among species. Indeed, isotopic niche variability is also determined by isotopic variability of sources (so-called baseline shifts; Boecklen et al. 2011), that could in turn be related to spatial variability (Flaherty and Ben-David 2010). Thus, species differ significantly in their isotopic niches because the isotopic composition of their food sources differs spatially. This hypothesis is in total agreement with the visual surveys of Marnane and Bellwood (2002) revealing that different apogonid species share restricted resting habitats by day but they segregate spatially at night, both horizontally and vertically in the water column. By reporting different foraging locations in six species of Hawaiian cardinalfishes at night, the observations of Chave (1978) strengthen our statement. Thus, apogonids may forage in the water column, over horizontal substrates, over vertical substrates or near holes in isolated coral heads. In the same habitat, apogonids may segregate spatially, feeding on the same food resource but in various places.

The ecological niche (*sensu* Hutchinson 1957) of a species is defined as a n-dimensional hypervolume whose axes represent environmental and/or resource requirements of this organism. The isotopic niche must be seen as a proxy of this ecological niche, integrating two of its axes subsets, *i.e.* both trophic and habitat-related information (Flaherty and Ben-David 2010). Here, isotopic niche width (*i.e.* standard ellipse area) was quite variable among species and also varied temporally. No major interspecific differences in stomach content compositions of apogonids suggest that the breadth of isotopic niches could be more related to the diversity of foraging locations (*i.e.* microhabitat segregation) than to diversity of consumed prey species. Species showing small standard ellipse areas (*e.g. Z. leptacantha* and *O. cyanosoma* [2014]) could be considered as specialists in their foraging areas, when others are feeding on prey dispersed on various locations (*e.g. T. fucata*, *P. fraenatus*, *P. kallopterus*). Although there were considerable differences in the size ranges of sampled fishes for each species, the lack of relation between size ranges and standard ellipse areas suggest that potential sampling biases related to fish size are unlikely.

Hutchinson (1957) distinguished the fundamental and realized ecological niches. The fundamental niche of a species may be assessed when the effects of biotic interactions (competition and predation) are excluded. Conversely, the realized niche is obtained when the biotic interactions are included in the calculation of the niche. The realized niche is typically a smaller volume than the fundamental region within a multidimensional hyperspace (Kearney 2006). The fundamental trophic niche of most cardinalfishes is a carnivorous diet made of small pelagic and benthic animal prey. The niche differentiation in the isotopic space conceptualizes their realized niche. Segregation is likely to operate through a combination of different factors, including morphological, physiological and behavioral adaptations. To date, ecomorphological studies did not find morphological traits explaining dietary segregation in apogonids (Barnett et al. 2006) but behavioral adaptations might certainly support it (Chave 1978; Marnane and Bellwood 2002). Our temporal datasets demonstrate that the realized trophic niche of cardinalfishes is dynamic both spatially and temporally, and contextualized. Indeed, the relative position of every species in the isotopic space varied across time and sampled populations. For example, in 2011, *P. kallopterus* was significantly more ^{13}C-depleted than *P. fraenatus*, while in 2014 the two species showed statistically identical δ^{13}C values. Conversely, the δ^{15}N of these two species were identical in 2011, but different in 2014 (Fig. 1A). In addition, the isotopic niche width of one species may greatly vary between two time periods. Accordingly, *O. cyanosoma* showed one of the smallest standard ellipse areas in 2014 when it had the largest one

alongside *P. fraenatus* in 2011. Inter-specific and inter-guild competition, food abundance and habitat structural complexity are probably main factors shaping resource segregation and associated feeding ecology of cardinalfishes on the Great Reef of Toliara.

The majority of studied apogonids showed size-related variation of isotopic compositions. These relationships may be interpreted as diet shift (Frédérich et al. 2010), habitat shift (Frédérich et al. 2012) or temporal variability of food sources (Matthews and Mazumder 2005). Linear models revealed that the variation in isotopic compositions is often poorly related to diet changes in the type of prey but we argue that the variation of $\delta^{15}N$ could be at least related to changes in the size of prey (Frédérich et al. 2010). Size-variation of the isotopic values could be an evidence of some partitioning in foraging locations among individuals of the same species. On the other hand, we also need to be cautious about the ecological interpretation of these variations. In some species, the isotopic compositions varied less than 1-1.5‰ across body size range (*e.g. O. cookii* 2011, *O. cyanosoma* 2014, *P. kallopterus* 2011; Fig. 3) and such variation could be influenced by age-related variability in diet-tissue fractionation and/or physiology (Sweeting et al. 2007a, b; Gajdzik et al. 2015).

To conclude, the present study provides some evidence of niche partitioning in an assemblage of Apogonidae. All species feed on small benthic and planktonic animal prey in variable proportions but the isotopic data suggest a segregation of their foraging locations. The trophic niche partitioning among cardinalfishes is dynamic, changing across time and it is shaped by various factors determining a niche segregation context. Further studies are needed to explore the drivers of feeding ecology in Apogonidae and to question the redundancy of their functional roles in coral reef ecosystems.

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Supplementary Material

Table S1. Isotopic compositions of food sources. (download)