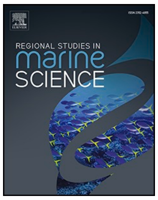
Regional Studies in Marine Science 75 (2024) 103563

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma



Variability of trophic ecology in two teleost species associated with lagoonal habitats (Great Reef of Toliara, SW Madagascar)

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ARTICLE INFO

Keywords:
Siganidae
Gobiidae
Lagoon
Stomach contents
Stable isotopes
Trophic diversity

ABSTRACT

Since the pioneering work in 70', relatively few studies looked at the trophic niches of teleost reef fishes in Madagascar. The lagoon of Toliara (SW Madagascar) is facing threat from the use of mosquito net trawls, often practiced in seagrass and fringing reef habitats. These practices have the potential to induce alterations in the ecological dynamics of the species and in their feeding behaviors. The primary objective of this study is to investigate the dietary preferences and their potential interannual and spatial variation in two teleost fish species frequently found in mosquito net trawl: the rabbitfish *Siganus sutor* as juveniles and the goby *Oplopomus oplopomus* as adults. Sampling was conducted at two distinct sites, Ankilibe and Sarodrano, over a two-year period, in December of both 2017 and 2018. The diet composition of these two species was assessed through the examination of their stomach contents and the analysis of stable isotopes (δ^{13}C and δ^{15}N) from a sample of 40 individuals during each field campaign. A total of 22 different food items were identified in the stomach of young *S. sutor*, with seagrass and benthic mobile prey items being predominant. In adult *O. oplopomus*, 21 food items were identified, with a high representation of mobile benthic prey and zooplankton. Analyses of stomach contents and stable isotopes revealed significant variations in diet composition across different years and spatial locations. In addition, the results indicated a significant variation in diet according to the size of the individuals studied. The present study is one of the few documenting trophic variations in reef fishes, highlighting some feeding plasticity which could be highly valuable for a rapid adaptation in changing environments.

1. Introduction

The Great Reef of Toliara (GRT) is a great barrier reef in the South-West of Madagascar in front of the city of Toliara. This barrier reef is 18 km long and 980–3000 m wide separated by a turbid lagoon reaching 2 km wide (Pichon, 1978). Vezo people, the largest ethnic group in Toliara, depends essentially on the resources of the GRT for their small-scale fisheries' activity (Andréfouët et al., 2013). Backreef habitats and lagoon habitats (e.g. seagrass beds, sandy areas, coral and macroalgae patches just behind the reef flat) are specially targeted by fishermen using mosquito net trawl (Bush et al., 2017; Behivoke et al., 2021; Jaonalison et al., 2022). These post reef areas shelter resident fish fauna but also numerous fishes at juvenile stage which will colonize other reef habitats later during their ontogeny (Nagelkerken et al., 2002;

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https://doi.org/10.1016/j.rsma.2024.103563
Received 27 November 2023; Received in revised form 29 April 2024; Accepted 29 April 2024
Available online 3 May 2024
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Raharinaivo et al., 2020; Jaonalison et al., 2022; Ranaivomanana et al., 2023).

The GRT is highly degraded due to high fishing and gleaning pressure and trampling at low tide (Pichon, 1978; Andréfouët et al., 2013; Chevalier et al., 2015; Ranaivomanana et al., 2023). Small-scale fisheries and dependence on natural resources are critical in coastal communities of West Indian Ocean countries by contributing to food security and daily income (De la Torre-Castro et al., 2014). Fishing pressure is well known to cause changes in fish community structure (Russ and Alcala, 1989; Campbell and Pardede, 2006) but it might also be expected that the ecological niche of fish species varies with changes in the taxonomic and the functional diversity of communities (Villamor and Becerro, 2012).

Study of the trophic ecology helps to understand the energy dynamics within ecosystems and to decipher the interactions between consumers and food sources (Manko, 2016). It also provides insights to the trophic partitioning among cohabiting species (Frédérich et al., 2009; Gajdzik et al., 2016; Schalk et al., 2017). The combination of stomach contents with stable isotope analyses is actually a very effective tool to study the feeding of an organism and to understand the food web (Hyslop, 1980; Mantel et al., 2004; Parkyn et al., 2001). Stomach contents provide valuable information mainly related to fish feeding habits. This method allows the identification of the ingested food at a time before sampling and the determination of the frequently consumed prey (Dinh et al., 2017; Manko, 2016). Stomach contents give precise information about the composition of diets and the interactions between predator and prey, which is relevant for studying complex systems where species may consume a large diversity of prey items (Layman et al., 2012).

Analyses of stable isotopes can provide time and space integrated insights into trophic relationships among organisms (Zieman et al., 1984; Jardine et al., 2003; Bouillon, 2011). It presents the advantage of providing a temporally integrated information for weeks to months, and this information reflects the dietary habits and the foods that are usually assimilated by the consumer (Caut et al., 2010). Carbon and nitrogen stable isotope ratios have been successfully used to understand the trophic relationships, their dynamics as well as trophic partitioning which operate in marine ecosystems (Lee, 2000; Davenport and Bax, 2002). Carbon isotope composition of an organism essentially reflects the origin of assimilated carbon (Sweeting et al., 2007) when nitrogen isotope ratio permits to estimate the trophic level of organisms and the origin of its dietary nitrogen (Post, 2002; Sweeting et al., 2007).

Spatial and seasonal fluctuations in food availability dictate the dynamics of biological communities (Yang et al., 2008). Those fluctuations may affect variation in species diet (Behrens and Lafferty, 2012; Dinh et al., 2017). At a large spatial scale, Chen et al. (2019) revealed the existence of a geographical variation in the diet of *Dascyllus abudafur* between populations from Red Sea and Madagascar, and hypothesized this variation is driven by environmental conditions. Frédérich et al. (2017) have showed a temporal variation in diet of apogonids in the GRT. By combining stomach content and stable isotope analyses, they revealed that the degree of planktivory of the cook's cardinalfish varied between two years.

Temporal diet variation is especially well-known in fishes living in temperate regions. For example, the sand goby *Pomatoschistus minutus* has a food composition strongly influenced by the seasons. This species mainly ingests chironomids in spring, amphipods in summer and ostracods in autumn in the northern Baltic Archipelago (Aarnio and Bonsdorff, 1993). Another species of goby, *Mesogobius batrachocephalus* from the Romanian Black Sea (Bulgaria) has a food composition dominated by bivalves in summer and isopods in autumn (Roşca and Mânzu, 2011). Mendes et al. (2009) have shown a spatial variability in the diet of the blenny *Scartella cristata* in Rio de Janeiro, Brazil. Detritus was the most abundant in gut contents of individuals from Ponta da Cabec, which is directly affected by the upwelling. On the second site, Fortaleza, which is protected from the upwelling and influenced most of the time by coastal, warm waters, algae were the most abundant in the fish gut content.

Since the pioneering work of Harmelin-Vivien (1981) about the trophic relationships of Toliara reef fishes, relatively few studies looked at the trophic niches of teleost reef fishes in Madagascar. For fish assemblages on the GRT, the studies are limited to the trophic diversity of few families like Pomacentridae (Frédérich et al., 2009) and Apogonidae (Frédérich et al., 2017). Some authors have discussed specific topics like intraspecific competition (Frédérich et al., 2010) and trophic diversity in herbivorous damselfishes (Lepoint et al., 2016). Beyond this, the trophic ecology of most fishes from the GRT remains understudied and studies exploring the spatial and temporal variation of trophic ecology of coastal fishes from tropical and subtropical regions is clearly limited.

The study of trophic variation across time and space is critically important to document trophic plasticity and improve our understanding of fish adaptation in changing environments. The present work aims to estimate diet variation in teleost fish species associated with seagrass beds and sandy areas at Toliara reef. We targeted here two species commonly found in the nets of Vezo fishermen. The first one is the herbivorous spinefoot rabbitfish *Siganus sutor* (Valenciennes, 1835). Juveniles of this species are among the most dominant fish species captured by mosquito net trawl in Toliara lagoon on warm season (Jaonalison et al., 2020a, 2020b). They colonize shallow coastal habitats including seagrass beds and mangroves. At the adult stage, their home range increases and they inhabit seagrass areas and coral reefs (Geets and Ollevier, 1996). The second species is the carnivorous spinecheek goby *Oplopomus oplopomus* (Valenciennes, 1837), which is highly represented on the catch of mosquito net trawl in Toliara lagoon (Jaonalison, 2019). This species lives as adult in solitary or in pair on the silty bottoms of inner lagoons and bays (Syms and Jones, 2004).

2. Materials and methods

2.1. Study area

This study was carried out in the lagoon of the GRT (SW of Madagascar, Mozambique Channel), just behind the reef flat of the reef barrier. This lagoon harbours large areas of seagrass meadows (Lepoint et al., 2008; Wallner-Hahn et al., 2022). Fishes were collected in areas in front of two fishermen villages: Ankilibe (23°25'43'S, 43°44'27'E) and Sarodrano (23°31'04'S, 43°44'07'E). The first sampling site, located in front of Ankilibe village, is characterized by large seagrass beds between the fringing reef and the barrier reef (Fig. 1). Sampling was operated in the seagrass beds and on the fringing reef. The second sampling site, near the Sarodrano village, is located near the mouth of the river Onilahy and the southern extremity of the GRT. There, sampling was operated in seagrass beds.

2.2. Sampling

The two targeted fish species, *Siganus sutor* (Siganidae) and *Oplopomus oplopomus* (Gobiidae), were collected in collaboration with two local fishermen using mosquito net trawls. We operated three campaigns: in Ankilibe from December 1–6 2017, in Ankilibe and in Sarodrano from December 6–8 2018. The comparison of campaign between Ankilibe in 2017 and in 2018 allowed us to know the possible inter-annual trophic variation. We studied spatial variation by comparing the two campaigns in Ankilibe and Sarodrano in 2018. Catches of fishermen were recovered and placed into cooler with ice during the transport to the laboratory at "Institut Halieutique et des Sciences Marines" (IH.SM). At the laboratory, fishes were sorted and separated by morphospecies. For each sampling, 40 individuals of *S. sutor* and of *O. oplopomus* were randomly selected to represent the entire size range of the catch. Their standard length (SL) was measured to the nearest 1 mm using a calliper and specimens were then dissected. Samples (0.5–1 cm^3) of lateral muscle tissue of each fish were used for stable

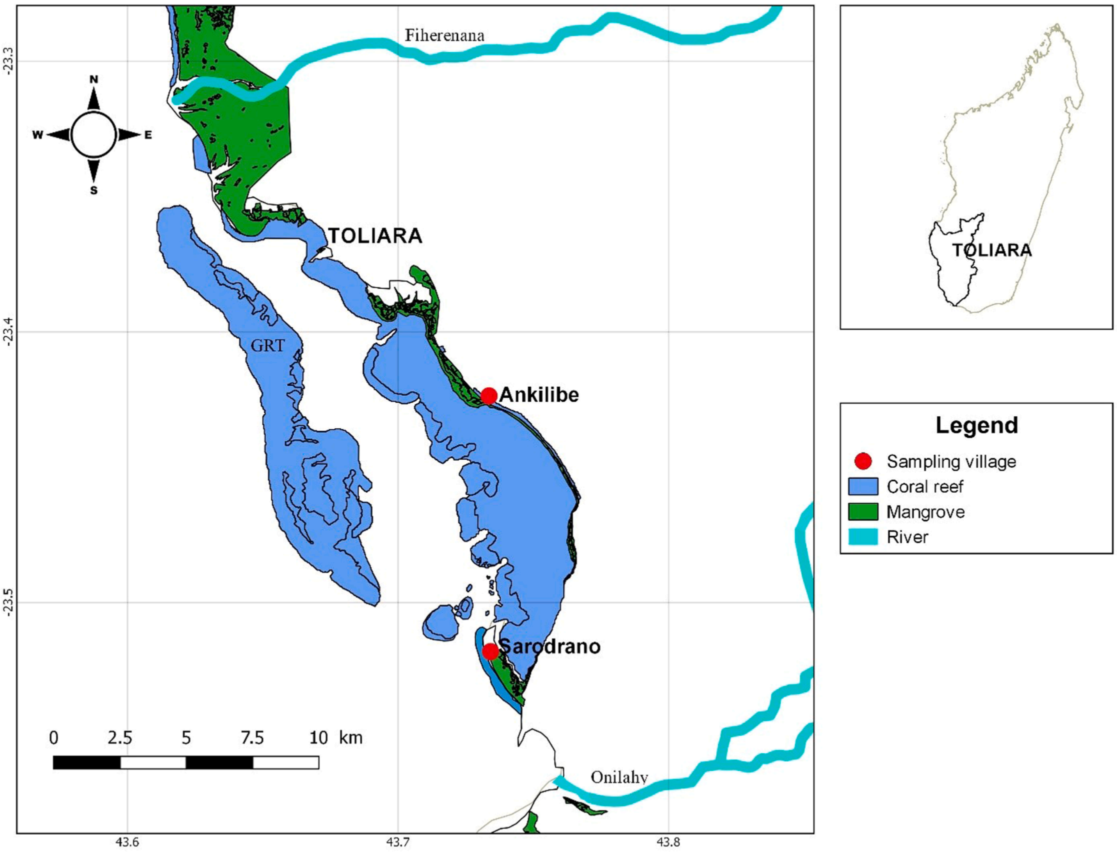


Fig. 1. Localisation of the sampling area close to Ankilibe and Sarodrano villages.

isotope analysis. Muscle samples were dried for 72 h at 40°C and then ground into a homogenous powder with a mortar and a pestle. The digestive tract (i.e. from the oesophagus to the rectum) was removed and conserved in 70% ethanol to analyze its content.

2.3. Stomach content analysis

After dissection, the stomach contents were spread into a petri dish for an examination under a binocular microscope. A 15 ×15 square grid of 5 ×5 mm were placed under the petri dish to count the food item according to the methodology developed by Wilson and Bellwood (1997). The dominant item in the 50 randomly marked grid was identified to the taxonomic level of class or order and then counted. The prey items were then classified into seven food categories as phytoplankton, macroalgae, seagrass, zooplankton, mobile benthic prey, sessile benthic prey and a category "others" for rubble and undetermined food items. In order to explore diet variation in both fish species, we quantified food items as percentages of occurrence and abundance of each item in stomach contents (Hyslop, 1980).

2.4. Stable isotope analysis

Stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were measured at the Laboratory of Trophic and Isotopic Ecology of the University of Liège in Belgium using an isotope ratio mass spectrometer (IsoPrime 100, Elementar UK, United Kingdom) coupled to an elemental analyser (microVario, Elementar, Germany). Stable isotope ratios were expressed in δ notation according to the following formula:

δX (‰) = [(R sample - R standard)/ R standard] x 1000

X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for samples or standards.

Certified materials were IAEA-N1 ($\delta^{15}N = +0.4 \pm 0.2$‰) and IAEA C-6 (sucrose) ($\delta^{13}C = -10.8 \pm 0.2$‰). Glycine was placed every 15 samples as secondary reference material (in lab reference) with $\delta^{15}N = +2.25 \pm 0.3$‰ and $\delta^{13}C = -47.5 \pm 0.3$‰. The standard deviations for replicated measurements (0.3‰ for both $\delta^{13}C$ and $\delta^{15}N$) were measured on an in-house standard (seabass muscle) placed every 15 samples in each batch.

2.5. Statistical analysis

The variation in the size of individuals from each species across the three campaigns was tested using an ANOVA. To vizualize whether the diet of the two species vary in space and time, a Non-Metric Multidimensional Scaling (NMDS) based on the presence or absence of the food type was performed using Jaccard index (Salako et al., 2013). A Bray-Curtis matrix was generated to quantify the compositional dissimilarity in the abundance of food types, which was then subjected to a Hellinger data transformation and represented using multidimensional scaling (MDS) (Mardia et al., 1979). Ellipses representing the dispersion of data points for each campaign to a 95% confidence level were generated using the vegan CovEllipse function (Mair et al., 2022). Analysis of similarity (ANOSIM) was used to test the spatial and temporal similarity of frequency and abundance of food item based on the four more represented food categories (namely macroalgae, seagrass, zooplankton and benthic mobile prey). ANOSIM is a test of the significance of similarities between/among groups where an R-value, the ratio of the between groups variation to the within group variation, is calculated. Thus, in addition to the information provided by the p-value, a $R > 0.5$ suggests that the between-group variation is higher than the within-group variation. When significant differences were found, a SIMPER analysis (similarity percentage) was conducted to find the contribution of item to the dissimilarity between compared fish groups. This test highlights which food categories are primarily responsible for an observed difference between campaigns (Iglesias and Kastner, 2013). The correlation between the abundance of the main food categories and the size of the fish was tested using linear regression models.

Similarly, we aimed to compare stable isotopic values among years and sampling sites. The variation of the isotopic values according to the length of the individuals was tested using linear regression models. Normality and homogeneity of stable isotope values were tested respectively with Kolmogorov-Smirnov and Levene tests. Then a T-test or a Wilcoxon test was used to compare the average values of $\delta^{13}C$ and $\delta^{15}N$. Spatial and temporal variation of the isotopic niche parameters were also tested by using SIBER (Stable Isotope Bayesian Ellipses in R) from the R-package SIAR (Jackson et al., 2011). Bivariate standard ellipses representing core isotopic sample niches were generated. Standard ellipse areas (SEA_B) associated to each temporal and spatial group were computed using Bayesian modelling (10^6 iterations). We used the posterior estimates of the ellipses for each group to generate a boxplot representing a model-estimated SEA_B. And then, a two-by-two comparison of posterior draws for both campaigns allowed to test whether one group's ellipse is smaller or larger than another (Jackson et al., 2011).

3. Results

Studied individuals of *S. sutor* sized from 23.3 to 120.8 mm of standard length (SL), with an average SL of 42.6 ± 23.1 mm. The individuals caught in 2018 stand out for the presence of few larger sizes (Fig. 2) (with a maximum SL of 52.6 mm in Ankilibe in 2017, 120.8 and 95.2 mm in Ankilibe and Sarodrano in 2018, respectively). The size of *O. oplopomus* ranged between 37.7 and 70.5 mm, with an average SL of 53.9 ± 8.9 mm. The size range for *S. sutor* was relatively large in Ankilibe 2018 when it was relatively small and similar between Ankilibe 2017 and Sarodrano 2018. The variation of size range was lower for *O. oplopomus*. Samples of both species varied significantly in size between years (ANOVA: $p<0.05$). Accordingly, we conducted all the next analyses when including all the individuals on one hand and by subsampling 38 specimens in each campaign from the same size range (excluding the largest fish) on the other hand. No variation in our results was observed and we thus can conclude the size variation existing among the three compared campaigns did not influence our main conclusions. Hereafter, results from all the individuals are represented on this study.

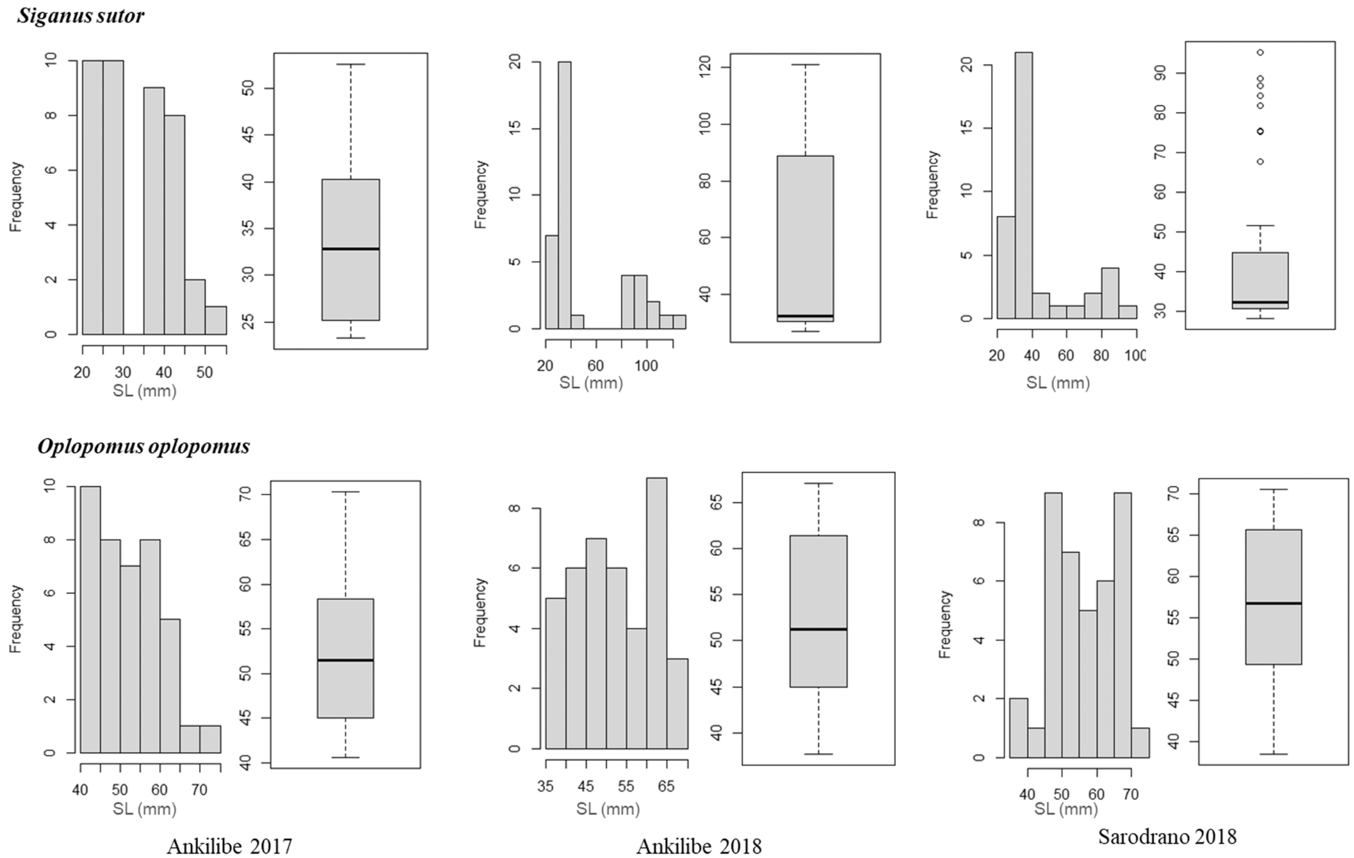
4. Stomach contents analyses

4.1. *Frequency of food categories*

Gut content of 240 individuals from the two species were analysed. Of these, only three individuals had an empty stomach. Seven main food categories had all been represented in *S. sutor* with a total of 22 different food items (Table 1). Fragments of seagrass are the most frequent item found in their stomach. Five main food categories were observed in *O. oplopomus* with a domination of mobile benthic prey. A total of 21 types of food items were identified in their stomach (Table 1).

A qualitative inspection of NMDS plots revealed that the diet of *S. sutor* caught in Ankilibe 2017 (lowest values along the first axis) differed from individuals caught in 2018 (higher values along the first axis). Variation in the diet of *O. oplopomus* seems less obvious (Fig. 3).

The analysis of similarities showed a significant difference between the diet composition of *S. sutor* from the three campaigns (ANOSIM: $R=0.59$, $p<0.05$). ANOSIM also revealed a significant difference of diet composition between years ($R=0.59$, $p<0.05$). SIMPER analysis exhibited that this temporal variation was mainly contributed by the algae where the mean frequency was very low (2.56%) in 2017 against 84.62% in 2018 (Table 2). A significant spatial variation was also



Siganus sutor

Oplopomus oplopomus

Ankilibe 2017

Ankilibe 2018

Sarodrano 2018

Fig. 2. Size (standard length, mm) range of collected individuals for *Siganus sutor* and *Oplopomus oplopomus* at the two sites and years.

Table 1
Percentage of occurrence (%F) of all dietary categories in the three compared campaigns per species. Ankilibe and Sarodrano are abbreviated by Ank. and Sar., respectively.

		Siganus sutor			***Oplopomus oplopomus***		
		Ank. 2017	**Ank. 2018**	**Sar. 2018**	**Ank. 2017**	**Ank. 2018**	**Sar. 2018**
Analyzed individual		40	40	40	40	40	40
Empty stomach		1	1	0	1	0	0
Food items	**Phylum**						
Phytoplankton		30.77	35.90	17.5	0	0	0
Macroalgae		2.56	84.62	75	2.5	2.5	0
Seagrass		76.92	92.31	67.5	40	12.5	17.5
Zooplankton							
Chaetognaths	Chaetognatha	0	0	0	2.5	0	0
Radiolarian	Retaria	20.51	30.77	20	2.5	2.5	0
Jellyfish	Cnidaria	5.13	0	0	0	0	0
Siphonophorae	Cnidaria	5.13	15.38	0	2.5	7.5	0
Copepoda	Arthropoda	25.64	35.9	25	65	35	27.5
Decapod larvae	Arthropoda	0	0	0	2	0	4
Pelagic Ascidiacea	Chordata	5.13	2.56	0	2.5	2.5	22.5
Fish larvae	Chordata	2.56	0	0	0	0	0
Fish	Chordata	0	2.56	0	0	5	12.5
Mobile benthic prey							
Foraminifera	Foraminifera	48.72	66.67	60	70	47.5	52.5
Polychaeta	Annelida	5.13	0	0	10	0	2.5
Ophioleucida	Echinodermata	0	2.56	0	2.5	0	0
Gastropoda	Mollusca	35.9	35.9	22.5	67.5	42.5	20
Bivalvia	Mollusca	12.82	15.38	2.5	12.5	22.5	10
Ostracoda	Arthropoda	10.26	10.26	22.5	27.5	5	12.5
Isopoda	Arthropoda	15.38	0	20	25	7.5	0
Decapod	Arthropoda	15.38	43.59	15	62.5	72.5	90
Amphipoda	Arthropoda	12.82	23.08	0	17.5	35	35
Cladoceran	Arthropoda	2.56	0	0	2.5	2.5	0
Hydracarinida	Arthropoda	0	7.69	0	0	2.5	0
Tanaidacea	Arthropoda	0	0	0	0	7.5	7.5
Sessile benthic prey							
Scleractinia	Cnidaria	0	5.13	0	0	0	0
Tunicata	Chordata	0	7.69	0	0	0	0
Others							
Operculum		64.10	41.03	12.5	0	0	0
Egg		12.82	0	0	2.5	0	0
Spicules		0	2.56	0	0	0	0
Fish scale		5.13	0	10	0	0	0
Unrecognized		5.13	35.90	10	2.5	0	0

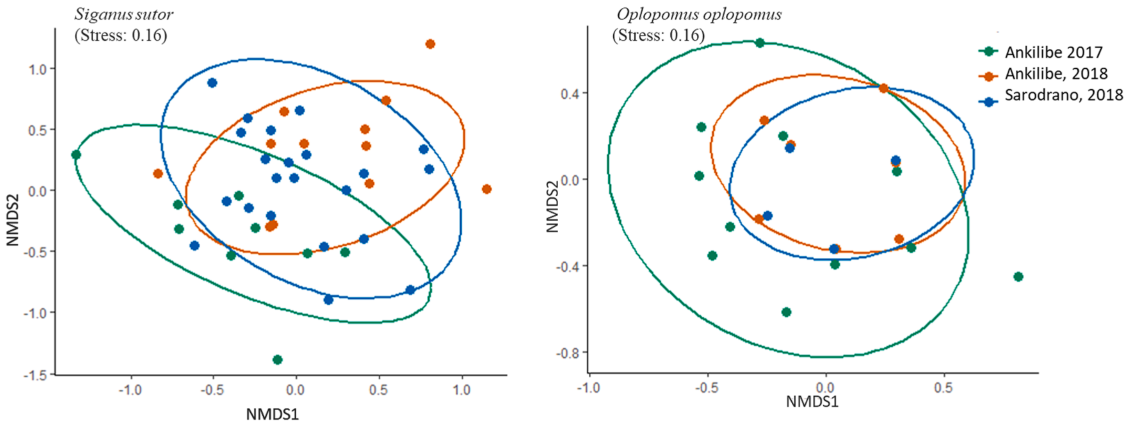


Fig. 3. Non-metric Multidimensional scaling (NMDS) plot generated from Bray-Curtis similarity index based on the presence or absence of food type on stomach of *Siganus sutor* and *Oplopomus oplopomus* for the two study sites and years (n = 40 per sampling event). Ellipses represent 95% confidence level. The low number of points shown in the figure is due to the overlap of the plots.

detected (ANOSIM: R=0.42, p<0.05), due to the high value of zooplankton and seagrass in the stomach content of *S. sutor* in Ankilibe 2018 compared to those from Sarodrano 2018. Similarly, the frequency of food types varied among the samples of *O. oplopomus* from the three campaigns (ANOSIM: R=0.68, p<0.05). ANOSIM showed a significant difference of diet composition between year (ANOSIM: R=0.6, p<0.05). The difference is due to the high occurrence of zooplankton and seagrass in fish from Ankilibe 2017. The significant spatial variation (ANOSIM: R=0.65, p<0.05) is caused by a high occurrence of zooplankton in fish samples from Ankilibe 2018.

4.2. *Abundance of food categories*

Mobile benthic prey, seagrass and algae are the most abundant prey

Table 2
Results from SIMPER analyses applied on the frequencies of food items explaining the dissimilarities among groups. Cumulative contribution of food categories is provided. Av.a and Av.b refer to the frequency of food category for the two compared groups.

		Food category	Av.a	Av.b	Cumulative contribution
S. sutor	Av.a: 2017	Macroalgae	2.56	84.62	27
	Av.b: 2018	Other	69.23	51.28	44
		Zooplankton	38.46	48.71	60
	Av.a: Ankilibe	Other	51.28	60	20
	Av.b: Sarodrano	Zooplankton	48.71	25	39
		Seagrass	92.3	67.5	56
O. oplopomus	Av.a: 2017	Zooplankton	66.66	52.5	40
	Av.b: 2018	Seagrass	40	12.5	68
	Av.a: Ankilibe	Zooplankton	52.5	30	63
	Av. b: Sarodrano				

found in the stomach of *S. sutor* (Fig. 4). Mobile benthic prey largely dominated the diet of *O. oplopomus* in term of item abundance. The second most abundant item was Zooplankton. MDS plots suggested that the diet of fishes from Ankilibe 2017 differed from the others, in both species (variation along the second axis, Fig. 5).

Siganus sutor showed significant difference among the three tested campaigns (ANOSIM: R=0.46, $p<0.05$). According to R values, it seems that temporal variation (ANOSIM: R=0.48, $p<0.05$) is overriding relatively to spatial variation (ANOSIM: R=0.35, $p<0.05$). SIMPER analysis showed that the low value of algae in campaign in Ankilibe 2017 (mean 0.02 fragment/individual) is responsible for 27% of the significant temporal variation (Table 3). On the other hand, individuals from Ankilibe 2018 fed mainly macroalgae (mean 4.07/individual) and on seagrasses (mean 5.1/individual). The difference of abundance of seagrass and macroalgae and mobile benthic prey was responsible of 67% of the difference between the two sites (Table 3).

In *O. oplopomus*, the difference between the two years (ANOSIM: R=0.25, $p<0.05$) and the two sites (ANOSIM: R=0.22, $p<0.05$) was less obvious. Differences were mainly driven by the abundance of mobile benthic prey and zooplankton (Table 3).

We detected some significant variation in the abundance of food category ingested related to the body size of the two species (Fig. 6). On one hand, a positive relationship was observed between *S. sutor* body size (SL) and vegetal food (algae, seagrass). On the other hand, large *S. sutor* consumed less quantity of animal prey (zooplankton and mobile benthic prey). In *O. oplopomus* from Ankilibe in 2018, a significant negative relationship between the percentage of zooplankton and fish size was observed. Accordingly, it seems that larger *O. oplopomus* consumed less zooplankton than smaller individuals.

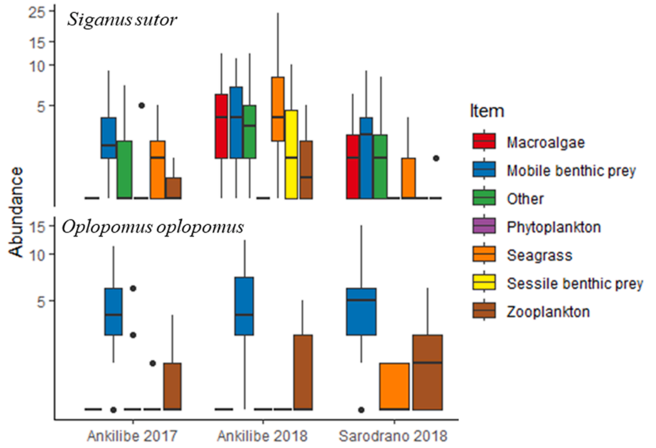


Fig. 4. Abundance, based of stomach content analysis of the dietary categories in samples of *Siganus sutor* and *Oplopomus oplopomus* from the three campaigns.

4.3. Stable isotopes

The position of *S. sutor* and *O. oplopomus* differed in the isotopic space defined by $\delta^{13}C$ and $\delta^{15}N$. In *S. sutor*, the $\delta^{13}C$ values varied from −20.7‰ to −12.6‰ with an average value of −16.7 ± 1.3‰ (Fig. 7). The $\delta^{15}N$ values ranged from 5.9‰ to 9.2‰ with an average value of 7.6 ± 0.7‰. In *O. oplopomus*, the $\delta^{13}C$ values were between −13.6‰ and −10.5‰ with an average value of −12.1 ± 0.7‰. Their $\delta^{15}N$ values varied from 6.7‰ to 8.3‰ for an average value of 7.4 ± 0.3‰. Sample of both species from the three campaigns overlapped in the isotopic space but some variations were also observed. *S. sutor* and *O. oplopomus* sampled in Ankilibe 2018 differed remarkably from the two others, having higher $\delta^{13}C$ values. Individuals of *S. sutor* from Ankilibe 2017 significantly differed from the one of Ankilibe 2018 regarding $\delta^{13}C$ (T-test, $p<0.05$) when no variation was observed between Ankilibe 2018 and Sarodrano 2018. The three campaigns of *S. sutor* did not differ along the $\delta^{15}N$ axis. In *O. oplopomus*, the isotopic ratios of $\delta^{13}C$ and $\delta^{15}N$ varied significantly between campaigns in the two years and the two sites (T-test and Wilcoxon test, $p<0.05$).

The respective area of the ellipses defining the trophic niche of each campaign provided information on the existence of trophic variation across time and space (Fig. 8). The area of the standard ellipse of *S. sutor* captured at Ankilibe in 2017 is bigger than those of the two others (Table 4). For the second year of sampling (2018), campaign in Ankilibe had a slightly larger area than the campaign in Sarodrano. The isotopic diversity was largely lower in *O. oplopomus* than in *S. sutor*, with the largest area at Ankilibe in 2018 followed by Ankilibe 2017 and then Sarodrano in 2018. The comparison of group's posterior distributions revealed that only the *S. sutor* from Ankilibe 2017 had an ellipse area significantly bigger than the ellipses of the two other campaign (proportion<0.05). For *O. oplopomus*, no significant difference was found.

Stable isotope values varied also with fish body size. Indeed, a significant positive relationship between SL and $\delta^{13}C$ was detected for all campaigns of *S. sutor* and for *O. oplopomus* in Ankilibe 2017 (Fig. 9). Interestingly, this relationship was significantly negative for the campaign of *O. oplopomus* in Sarodrano 2018. On the other hand, there was a significant negative relationship between $\delta^{15}N$ values and the SL of *S sutor* from Ankilibe 2017 and Sarodrano 2018, while this relationship was positive for *O. oplopomus* from Sarodrano 2018.

5. Discussion

According to the study of Kamukuru (2009) at Dar es Salaam, Tanzania, the size at first sexual maturity of *S. sutor* would be comprised between 215 and 230 mm TL for male and female, respectively. Therefore, the individuals of *S. sutor* in our study were all juveniles with a size varying from 23.3 to 120.8 mm. On the other hand, the majority of *O. oplopomus* individuals (37.7–70.5 mm) probably reached adulthood as the maximum size is 100 mm (Kuiter and Tonozuka, 2001).

The capture of the fish having been carried out in the morning, data

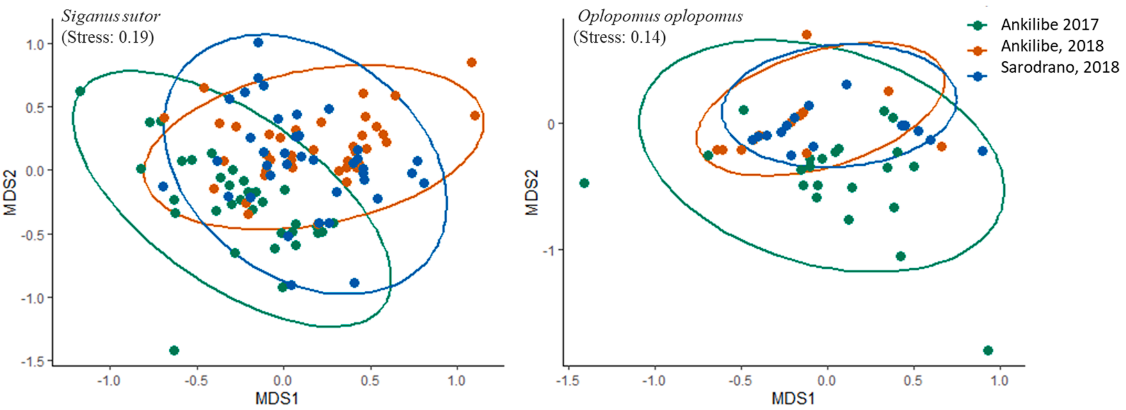


Fig. 5. Multidimensional Scaling (MDS) plots of food type abundance on stomach of *Siganus sutor* and *Oplopomus oplopomus* for the two study site and years. Ellipses represent 95% confidence level.

Table 3
Results from SIMPER analyses applied on the abundance of food categories explaining the dissimilarities among groups. Cumulative contribution of food categories is provided. Av.a and Av.b refer to the frequency of food category for the two compared groups.

		Food category	Av.a	Av.b	Cumulative contribution
	Av.a: 2017 /	Macroalgae	0.02	4.07	27
S. sutor	Av.b: 2018	Seagrass	1.58	5.1	50
	Av.a: Ankilibe /	Seagrass	5.1	1.075	25
	Av. b: Sarodrano	Macroalgae	4.07	1.9	49
		Mobile benthic prey	3.8	2.7	67
O. oplopomus	Av.a: 2017 /	Mobile benthic prey	4.17	4.57	47
	Av. b: 2018	Zooplankton	1.1	0.95	66
	Av. a: Ankilibe /	Mobile benthic prey	4.57	5.22	55
	Av. b: Sarodrano				

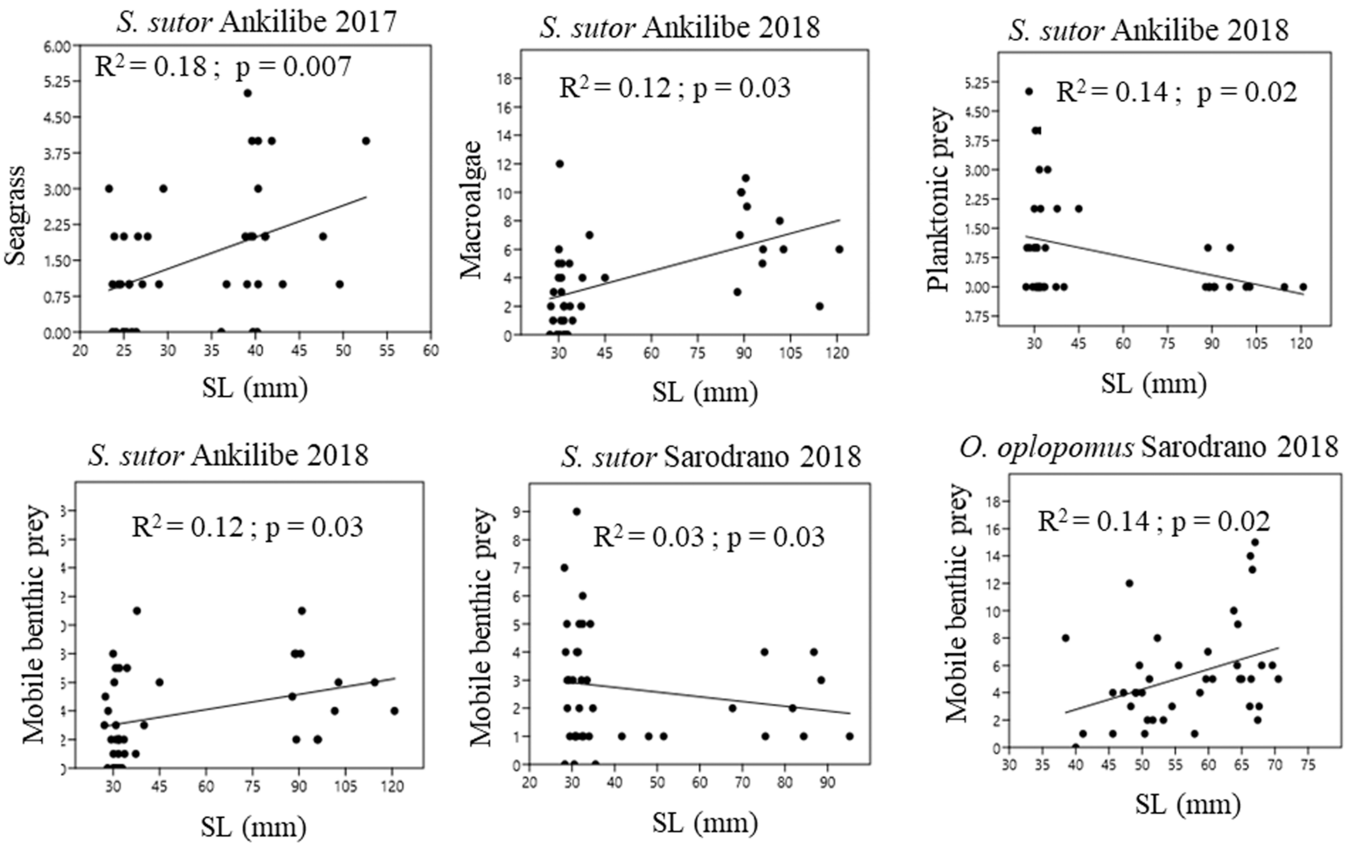


Fig. 6. Relationship between body size (SL) and abundance of principal food categories in *Siganus sutor* and *Oplopomus oplopomus*. Only significant relationships are illustrated.

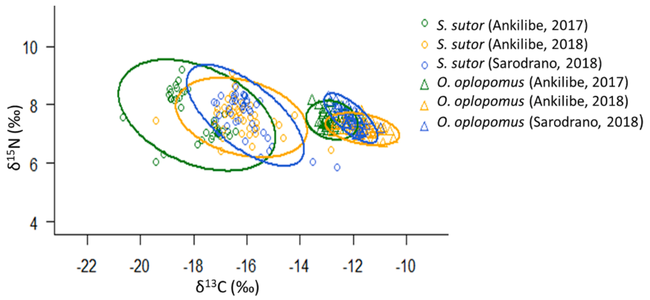


Fig. 7. Individual values of δ^{13}C and δ^{15}N (in ‰) of *Siganus sutor* and *Oplopomus oplopomus*. Species and campaigns are represented by different symbols and colours, respectively and solid lines represent the bivariate standard ellipses associated to each campaign.

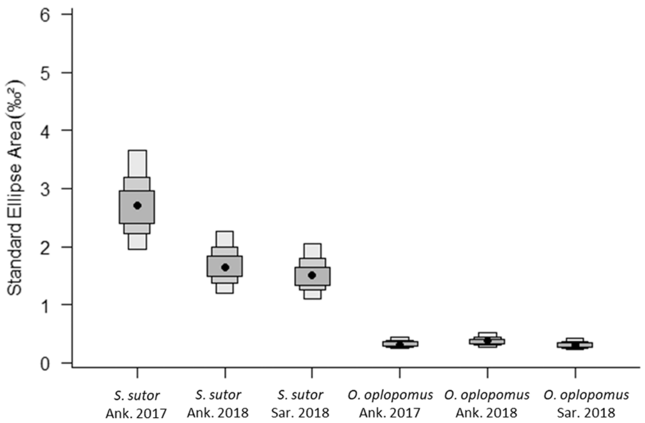


Fig. 8. Boxplots illustrating model-estimated bivariate Standard Ellipse Areas (SEA_B) across campaigns, with dark, median and light grey boxes indicating respectively 50%, 75% and 95% credibility intervals and dots signifying distribution modes. Ank and Sar refer to Ankilibe and Sarodrano, respectively.

from stomach contents strongly suggest that these two species have a diurnal activity (Harmelin-Vivien, 1981; Fox et al., 2009). A set of 22 food types divided into seven food categories were found in the stomach contents of *S. sutor* with a dominance in terms of abundance of benthic prey, seagrass and algae. In *O. oplopomus*, 21 food items grouped in five food categories have been identified, of which the benthic animal prey are the most strongly represented. It has been shown that the frequency of occurrence and the abundance of these food categories vary significantly depending on the site or the year of sampling. These variations are also reflected in the isotopic values, strengthening the hypothesis of the presence of trophic plasticity in both species. Indeed, the difference is reflected by the variation of the size of standard ellipses between site and year. Both methods also revealed that the feeding habits of *S. sutor* and *O. oplopomus* varied during growth.

5.1. Trophic ecology of Siganus sutor and Oplopomus oplopomus

The Siganidae fish family mainly groups herbivorous species (Undermann et al., 1983; Duray and Southeast Asian Fisheries Development Center, 1998). Our study demonstrates a general preference for plants (algae and seagrasses) in *S. sutor*, especially the largest specimens (Fig. 6). Nevertheless, various animal prey such as small mobile benthic organisms were found in large quantities in their stomach, particularly in the smallest individual. The consumption of animal prey is certainly necessary for juvenile whose growth requires a diet rich in protein (Pitt, 1997; Campbell et al., 2011). This could be also related to the morphological change needed to become herbivorous. For example, researchers have shown that herbivorous fishes have generally longer gut than predatory fish (Al-Hussaini, 1949; Montgomery, 1977; Montgomery and Pollak, 1988; Motta, 1988) and it have been confirmed by recent studies (Elliott and Bellwood, 2003; German and Horn, 2006; Berumen et al., 2011) that time is needed for morphological and physiological adaptations along the ontogenetic diet shift. Indeed, most larvae and post-larvae of herbivorous fish living in coral reefs are zooplanktivorous before gradually becoming omnivorous during their early juvenile phase, to finally become later herbivorous (Frédérich et al., 2012; Dromard et al., 2015). Our data suggested that *S. sutor* becomes relatively rapidly herbivorous as sub-adults already display gut contents dominated by plants.

The diversity of food items found in the stomach of *S. sutor* is translated to a wider isotopic niche in comparison with *O. oplopomus* (Fig. 7). Indeed, it is possible that the large variation of isotopic ratios of carbon and nitrogen reflects the diversity of consumed food items but several other factors can influence this isotopic diversity. Among others, the diversity of feeding areas can also explain the isotopic variance in *S. sutor*. It is also obvious that the large isotopic niche of *S. sutor* observed in the present study is strongly influenced by the ontogenetic diet shift. Indeed, we provided evidence that the larger specimens consume more plant matters than small ones (Fig. 6). The most negative values of δ^{13}C correspond to small individuals who depend or who still recently depended on zooplankton (Guo et al., 2014) which has very low δ^{13}C values and high δ^{15}N values (Frédérich et al., 2009, 2010; Lepoint et al., 2016). Benthic invertebrates (e.g. harpacticoid copepods), plants (algae and seagrass) have a less negative value of δ^{13}C than zooplankton on Toliara reef system (Lepoint et al., 2008; Frédérich et al., 2010). It is therefore evident that as they grow up, *S. sutor* becomes omnivorous as demonstrated by stomach contents and an increase of δ^{13}C values, and then become more herbivorous. Accordingly, the positive linear relationship between fish body size and δ^{13}C and the negative relationship between size and δ^{15}N in *S. sutor* support the hypothesis of an ontogenetic shift from planktivory to herbivory.

A large majority of gobies have preferences for benthic animal prey (Guo et al., 2014) and some species show a strict carnivorous diet as observed in the genus *Pomatoschistus* (Salgado et al., 2004). The high frequency and abundance of benthic prey, especially small crustaceans and molluscs, found in the stomach of *O. oplopomus* confirms a rather carnivorous diet (Harmelin-Vivien, 1981). Nevertheless, plant fragments are frequently found in gut content. However, they were rarely abundant. Indeed, only small fragments of seagrass have been found in reduced numbers, which can be explained by the proximity of seagrass beds in their habitat but also the presence of seagrass detritus laying on the sand (Syms and Jones, 2004). The presence of zooplankton in the stomach of *O. oplopomus* indicates that this species is not satisfied solely with prey living near the seabed. This species also feed on prey living in the water column such as copepods, siphonophores and ascidian larvae. This is probably linked to the strong tidal current on this area, transporting everyday zooplankton from ocean to the lagoon. For the gobies,

Table 4
Area of the standard ellipses of the isotopic values for each campaign of both species.

Species	*Siganus sutor*			*Oplopomus oplopomus*		
Campaigns	Ankilibe 2017	Ankilibe 2018	Sarodrano 2018	Ankilibe 2017	Ankilibe 2018	Sarodrano 2018
SEA_B (‰^{2})	2.7	1.67	1.49	0.33	0.37	0.31
Mode	2.69	1.6	1.5	0.33	0.36	0.3
95% interval	[1.93–3.64]	[1.2–2.29]	[1.06–2.08]	[0.23–0.45]	[0.27–0.52]	[0.23–0.42]

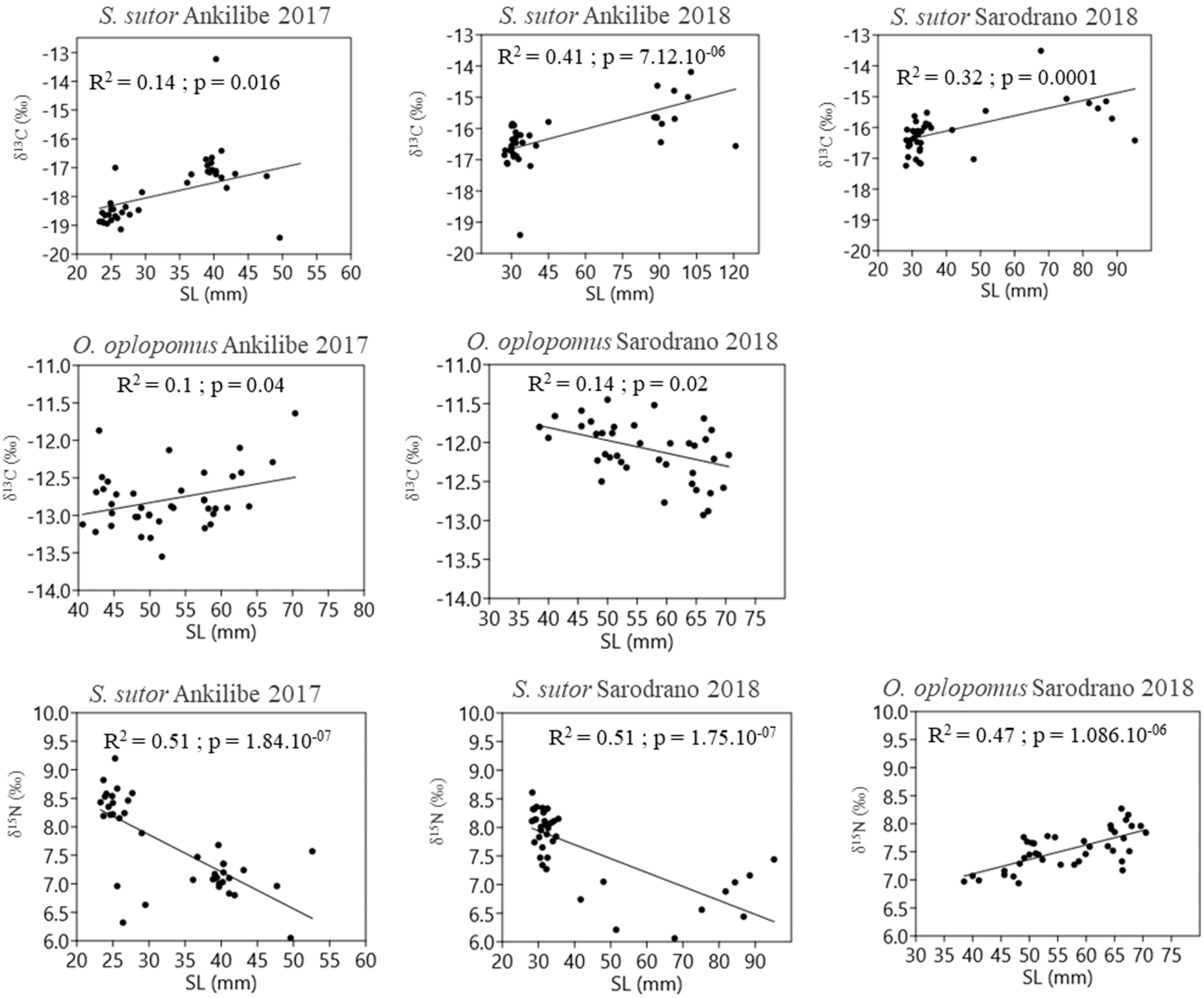


Fig. 9. Relationship between body size (SL) and stable isotope values in individuals of *Siganus sutor* and *Oplopomus oplopomus* from the three campaigns. Only significant relationships are illustrated.

food selection is highly influenced by the availability of the prey, their density and the visibility (Aarnio and Bonsdorff, 1993; Guo et al., 2014). The mobility of prey can also play a role on food preference (Magnhagen and Wiederholm, 1982).

As O. oplopomus feed essentially on benthic animal prey, it has a higher δ^{13}C value than *S. sutor*. *Oplopomus oplopomus* has a very low isotopic variance (Fig. 6) suggesting that individuals have very similar feeding habits within restricted areas. Conversely to *S. sutor*, specimens of *O. oplopomus* are almost all adults with an isotopic equilibrium, explaining the low variation in the isotopic values. The small area of the standard ellipses may result from more restricted feeding areas and a smaller variation in body size within the studied populations in comparison with *S. sutor*. Accordingly, we did not detect any variation of the diet with fish body size. The positive relationship between fish size and δ^{15}N values may be interpreted as a variation of the trophic level of individuals who tend to consume more and more larger prey with their increasing size, without any shift of prey type (Frédérich et al., 2010).

5.2. *Variation of the trophic niches across time and space*

The present work is one of the few documenting interannual and small-scale spatial variation in the trophic ecology of reef-associated fishes in East Africa and Madagascar. The temporal variation in the diet of *S. sutor* does not reflect a drastic change in food type, but rather is related to changes in the proportions of food ingested. This is a size-related variation as well. This type of diet variation has also been observed in herbivorous blenny *Scartella cristata* in the south-eastern Brazilian coast (Mendes et al., 2009). *Siganus sutor* captured in December 2018 ate significantly more algae than those in December 2017 which consumed more mobile benthic prey. Their values of δ^{13}C also show a variation with time, strengthening the hypothesis of temporal trophic variation. The diet of *S. sutor* seemed to vary between sites, difference being expressed in terms of the variation in the diversity of the item captured. Seagrass materials were more abundant in fish captured at Ankilibe 2018 and they are less numerous in the individuals from Sarodrano 2018. In terms of food item frequency, individuals from Ankilibe are more diverse than those from Sarodrano. However, this spatial variation highlighted by stomach contents is not translated in the values of the isotopic ratios. This apparent discrepancy between trophic methods might suggest opportunistic diet shift not related as a long-term general trend (Salgado et al., 2004; Dinh et al., 2017).

In *O. oplopomus*, temporal variation is also observed via the frequency and abundance of items consumed. Individuals from Ankilibe 2017 had ingested a greater diversity of item compared to those from

Ankilibe 2018. This difference is generated by the high frequency rate and abundance of zooplankton item, directly in relation with tidal cycle and current which bring zooplankton from ocean in the lagoon. This temporal variation is also reflected in the values of the isotopic ratios. Indeed, variations in the isotopic ratio of C and N are observed in the two consecutive years. The trend is the same at both sampling sites. Indeed, a small difference is observed on the abundance of the food type. In addition, a greater richness in the frequency of item is observed in individuals captured at Ankilibe 2018. Unlike *S. sutor*, this spatial variation is also reflected in the isotopic values of either C or N. As zooplanktonic production may vary between year, this also reflect the opportunistic behaviour of this species, able to exploit a water column food source when it is present. This underlines the important coupling between water column and benthic compartment in trophic ecology of numerous reef fishes (Magnhagen and Wiederholm, 1982; Frédérich et al., 2010; Dinh et al., 2017).

The feeding strategy may vary depending on the food source composition of the environment (Magnhagen and Wiederholm, 1982; Carman et al., 2006; Behrens and Lafferty, 2012; Ebrahim et al., 2020). In this study, the temporal variation in the diet of the two species may be due to their adaptation to the variation in the food availability of the environment (Kerschner et al., 1985; Dinh et al., 2017) (Sampaio et al., 2010). This was proven by a similar study carried out on 28 fish species in *Posidonia* meadows in the Gulf of Naples, Italy (Zupo and Stübing, 2010). The spatial variation may result from varied biotic factors such as a difference in the composition of food sources between sites and a difference in competitive interactions among fish species (Guo et al., 2014). The Sarodrano village is located near to Onilahy, a river mouth. Then, the supply of organic carbon from the river can enrich the local sediment leading to varied primary production (Plotieau et al., 2014). In a context of overfishing, we cannot exclude the impact of a change in community structure leading to these trophic variations. Some authors have proved that the use of bottom-fishing gear like the mosquito net can have in the long term an effect on continental shelves that cause reductions in benthic biodiversity, abundance, and biomass, and changes in species composition (Tillin et al., 2006; Svane et al., 2009). Few studies worldwide have examined the secondary effects, such as altered predator–prey dynamics focusing on change in food web (De Juan et al., 2007; Fanelli et al., 2009; Henriques et al., 2014).

Harmelin-Vivien (1981) have shown that the feeding behaviours of some reef fishes from the GRT may vary depending on the size of the individuals, time and the surrounding marine life. The present study provides new information about the variation of the trophic ecology across time and space in additional fish species at two different ontogenetic stages. The spatial and temporal variations demonstrate an opportunistic feeding habit of the fish (Aarnio and Bonsdorff, 1993; Dinh et al., 2017; Schalk et al., 2017). Feeding opportunism, or trophic plasticity, can be highly adaptive in systems under anthropogenic pressures. The link between allometric diet variation and trophic plasticity should be further investigated to better understand if ecological adaptation is mainly driven by young or adult stages, or both. Future works should certainly continue to quantify the trophic variation of reef fish species and test if this ecological plasticity help them when facing anthropogenic threats such as overfishing and eutrophication. Unfortunately, the GRT is threatened (Andréfouët et al. 2013) but it provides an interesting system to study the responses of fish communities and fish populations facing overfishing.

CRediT authorship contribution statement

Helga Berjulie Ravelohasina: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Richard Rasolofonirina:** Writing – review & editing, Visualization, Validation, Supervision, Project administration. **Henitsoa Jaonalison:** Writing – review & editing, Supervision, Methodology. **Jamal Angelot Mahafina:** Writing – review & editing, Validation, Resources, Project administration. **Gilles Lepoint:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis. **Dominique Ponton:** Writing – review & editing, Validation. **Bruno Frédérich:** Writing – review & editing, Visualization, Validation, Supervision.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests Helga Ravelohasina reports financial support was provided by Western Indian Ocean Marine Science Association. Helga Ravelohasina reports financial support was provided by African Union. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgement

Authors wish to thank the technicians and the local fishermen for their help during field sampling. This study was financially supported by the Western Indian Ocean Marine Science Association (WIOMSA) « MArine Research Grant I » (MARG I, Contract 7/2018), the WIOMSA mobility grant (MARG II, Contract 2/2019) and the African Union « Mwalimu Nyerere, Master Scholarship ».

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