


# Lanternfish larvae (Teleostei: Myctophidae) feeding ecology in the continental slope and off oceanic islands in the tropical Atlantic

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## ABSTRACT

Abstract Myctophids are central in ocean food webs, yet knowledge of the ecology of larval stages is sparse. We investigated if larval feeding ecology is different in continental shelf break waters compared to waters off oceanic islands in the western Tropical Atlantic. The larvae were collected through diurnal and nocturnal oblique hauls using a Bongo net and stomach contents were analyzed. The larvae ranged between 2.27 and 16.5 mm in standard length. Diet composition was different in the slope and islands (Permutational Multivariate Analysis of Variance (PERMANOVA),  $P < 0.001$ ). Diatoms (mainly *Thalassiosira* spp. and fragments of diatoms) were numerically important in the diet at the slope site (69% of relative importance). Copepods were the most relevant prey (71% of relative importance) near the islands. Copepods were the biomass-dominant dietary item at both areas, alongside ostracods near the islands. Smaller prey items were more important for smaller larvae, particularly those measuring up to 4 mm. Larger prey became relatively more important as the larvae grew to at least 8 mm. Larvae fed mostly during the daytime regardless of their size class.

**KEYWORDS:** Ichthyoplankton; fish larvae stomach content; fish early stages diet composition; Ichthyoplankton size classes and diet composition; feeding incidence

## INTRODUCTION

Mesopelagic organisms are found in oceanic waters globally, ranging from the surface to a depth of 1000 m, where they are a prevalent biological component (Sassa et al., 2002; Catul et al., 2011; Irigoien et al., 2014). Among them, myctophids (lanternfishes) stand out in terms of number of species, abundance and consequently biomass (Sassa et al., 2002; Franco et al., 2006; Catul et al., 2011; Katsuragawa et al., 2014; Eduardo et al., 2021). Their ability to undertake large diel vertical migrations makes them key players in the carbon flux between the surface and deep waters (Belcher et al. 2019). Additionally, myctophids play an important role in the open oceanic waters where they are prey for higher predators (e.g. marine birds; Connan et al. 2007) as they prey secondary producers (e.g. copepods, ostracods and, euphausiids; Contreras et al., 2015; Saunders et al., 2018), therefore establishing a link between distant trophic levels. In upper oceanic waters, Myctophid biomass, represented by

larvae and/or juveniles, accounts for 75% of mesopelagic fish biomass caught by trawling (see Catul et al., 2011).

The concentration of larval stages of myctophids in the upper 200 m of the water column has been confirmed in several studies (Moser and Smith, 1993; Olivar et al., 2018). In addition, other studies have been showing the dominance of myctophid larvae over other taxa in oligotrophic surface waters of tropical and subtropical regions (Nonaka et al., 2000; Franco et al. 2006; Katsuragawa et al. 2014, Olivar et al. 2018; Santana et al., 2020a and 2020b). The dynamics of the tropical oceanic regions are completely different from the typical annual production cycles of temperate regions, which are characterized by two productivity peaks throughout the year—spring and autumn blooms. The tropical regions are markedly oligotrophic resulting from constant water column stratification (Olivar et al., 2018). Fish larvae must be able to find and capture adequate food once vitelline reserves are depleted and nutrition becomes exogenous

(Nunn et al. 2012). The mortality rate of larval fish, in general, during particular this stage is very high (i.e. Hjort, 1914), because of the low feeding performance of the larvae during their first days of existence, even if the environment is rich in prey (China and Holzman, 2014). Therefore, the maintenance of myctophid assemblages in tropical/subtropical oligotrophic oceanic waters constitutes a challenge and an intriguing matter since at no time of the year will there be a typically higher biological production and the survival of the larvae will not be associated with the concept of “match/mismatch” (Cushing, 1990) so important in higher latitude regions (Kristiansen et al., 2011).

Feeding ecology studies on fish larvae and juveniles are scarce (Nunn et al., 2012). Regarding myctophids, investigations on larval feeding ecology were conducted in many different oceanographic regions such Central Atlantic (Conley and Hopkins, 2004), Pacific (Sassa and Kawaguchi, 2005; Rodríguez-Graña et al., 2005; Sassa, 2010; Zavala-Muños, 2019), Western Mediterranean (Bernal et al., 2013; Bernal et al., 2020; Contreras et al., 2015), Southern Ocean (Nirazuka et al., 2021) and Southwest Atlantic Ocean, where only one recent study (Contreras et al., 2019) contributed to reduce this relevant knowledge gap.

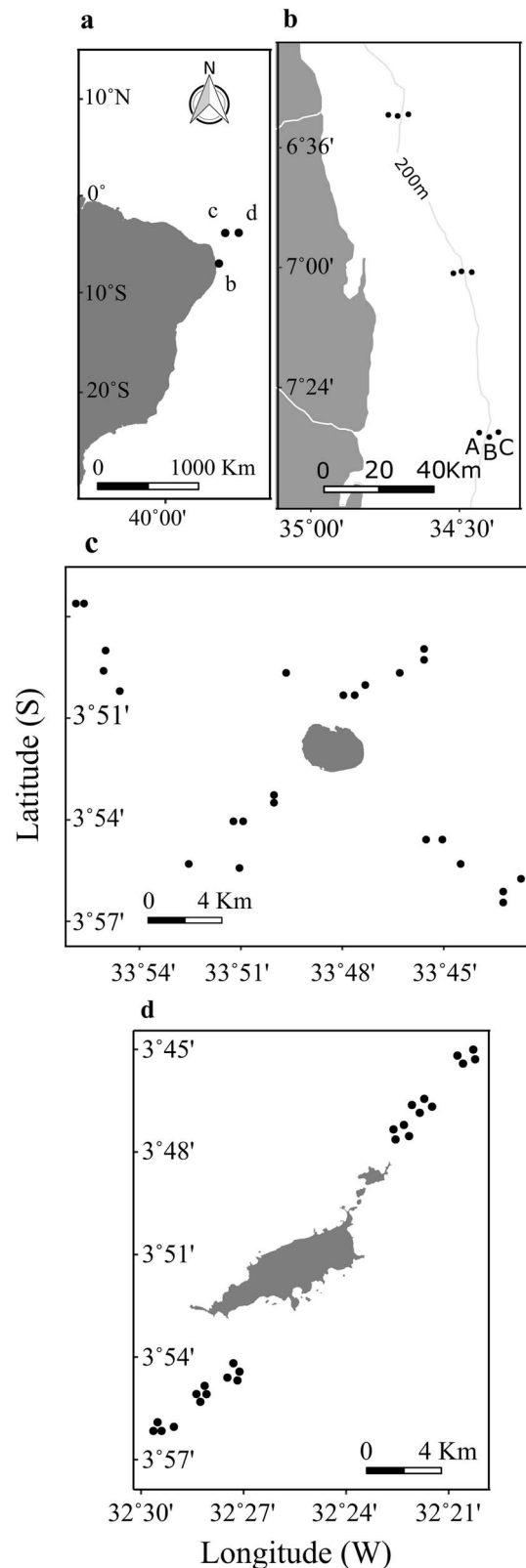
We investigated the hypothesis that myctophid feeding ecology is different when larvae dwelling in the waters off the continental shelf of northeastern Brazil are compared to larvae dwelling off oceanic islands, where there is the possibility of breaking the typical tropical structure because of possible interactions between the ocean circulation and the bathymetry around the islands. Stomach contents of myctophid larvae collected in areas close to the continental shelf break in northeastern Brazil and in areas surrounding oceanic islands in the tropical Atlantic were analyzed. The goal was to investigate the potential difference in the feeding habits of myctophid larvae occurring in the shelf break area and around oceanic islands, and the ontogenetic variability in the feeding habits of myctophid larvae in the western tropical Atlantic.

## METHOD

### Larvae sampling and laboratorial procedures

Two oceanographic expeditions were conducted during 2010 and 2012 on board *RV Cruzeiro do Sul* of the Brazilian Navy, in areas of the continental shelf break (CSB) off northeastern Brazil and around oceanic islands (ISL) in the western Tropical Atlantic (Fernando de Noronha Archipelago and Rocas Atoll; Fig. 1). The ichthyoplankton was collected through oblique hauls carried out from a maximum depth of 200 m to the surface, using a 60 cm diameter Bongo net equipped with a 500  $\mu\text{m}$  mesh. The samplings were carried out during the daytime (5:00 am–5:00 pm) and nighttime (5:00 pm–05:00 am). The larvae were fixed in borax-buffered formaldehyde at a final concentration of 4%.

The myctophids were identified to the lowest taxonomic level through specialized literature (e.g. Richards, 2006). From these, 630 individuals were separated to have their stomach content analyzed (47% from the CSB and 53% from the ISL). Of all individuals, 64% were collected during nighttime samplings, while 36% were collected during daytime samplings. Morphometric measurements of the upper jaw length (UJL), standard length (SL), and body height (BL), in addition to the extraction,



**Fig. 1.** (a) Location in the western South Atlantic of the studied areas; (b) positioning of the oceanographic stations over the continental shelf break (CSB) off northeastern Brazil; (c) positioning of the oceanographic stations in the region surrounding the Rocas Atoll; and (d) positioning of the oceanographic stations in the regions around the Fernando de Noronha archipelago (FN).

quantification, measurement of linear dimensions and volume estimation of the stomach and intestine contents were performed.

The intestine of each larva was extracted and opened longitudinally through a cut made with the aid of a fine needle. The content was transferred and spread over the surface of a common slide and analyzed under microscopy. The maximum length and width of each food item were measured, and the volume of each food item was estimated using stereometric formulae (e.g. Sun and Liu, 2003). Each food item was identified to the lowest taxonomic level. Preys in advanced degree of digestion were classified as unidentified organic matter.

### Data analysis

The relation between SL and UJL, and between UJL and food size (as the maximum width) were investigated through linear regression models for the most representative genera (*Diaphus*, *Ceratoscopelus*, *Lampadena* and *Lepidophanes*). The fitted regression models were compared between species through an one-way Analysis of Covariance (one-way ANCOVA), using SL as covariate.

The feeding incidence (FI) was calculated as the proportion of larvae with any stomach content in comparison to the total number of examined larvae. This calculation was performed for the myctophids in general, as well as for each of the four most representative genera. The independence of the FI concerning time and area was tested through a Cochran–Mantel–Haenszel  $\chi^2$  test for *Diaphus* and myctophids in general. A  $\chi^2$  test was used to test for independence among FI and time for the remaining genera (*Ceratoscopelus*, *Lepidophanes* and *Lampadena*). A Cochran–Mantel–Haenszel  $\chi^2$  test was also used to test for independence of the FI concerning the time and the genus being considered. The coefficient phi was used to estimate the strength of the relation when the null hypothesis of independence was rejected ( $P < 0.05$ ).

FI was estimated for larvae grouped into 0.5 mm size classes to investigate a potential variability with the increase in larvae length. The size classes ranged from 2 to 17 mm for the family in general, and from 3.5 to 9.5 mm for the most representative genera. Comparisons were made through the analysis of contingency tables using the  $\chi^2$  tests.

The myctophid larvae were grouped into three size classes (< 4 mm, 4–8 mm, and 8–12 mm) to investigate the diet. The diet was described by the preys' frequency of occurrence (FO), the proportion of the total counts (PT), proportion of volume (PV) in comparison to the total volume, and by the relative importance index (RII), calculated as  $(PT + PV) * FO$  (e.g. Landaeta et al., 2015; Landaeta et al., 2011), and expressed as percentages to allow direct comparisons between different preys (Cortés, 1997). These estimates were calculated considering the area (CSB and ISL) and larval size classes. The diet composition was compared between areas and size classes by PERMANOVA models based on the Hellinger distance matrix calculated from the numerical matrix of preys and from the matrix of preys' volume.

The feeding success of larvae was estimated by measuring the number of prey items per gut (stomach and intestine content; NG), maximum prey width (MW), and total volume of prey

items per gut (stomach and intestine content; VG). A Spearman non-parametric correlation test was conducted to investigate whether feeding success affected larval growth.

All analyses were conducted using the R language (version 4.05) within the RStudio IDE (version 1.4) using the following packages: base (R Core Team 2021), vegan (Oksanen et al., 2020), tidyverse (Wickham et al., 2019) and in Python language (version 3.9) within the PyCharm CE free community IDE (version 2021.1.1), using the following libraries: matplotlib (Hunter, 2007) and pandas (Pandas Development Team, 2024).

## RESULTS

### Morphometric relationships

A total of 27 taxa were identified (Table I). The larvae ranged between 2.3 and 16.5 mm in SL and between 0.16 and 3.5 mm in upper jaw length UJL. The genera with the highest number of analyzed specimens were *Diaphus* ( $n = 337$  individuals), *Lampadena* ( $n = 43$  individuals), *Ceratoscopelus* ( $n = 41$  individuals), and *Lepidophanes* ( $n = 40$  individuals). *Diaphus* specimens exhibited the greatest range of variation in linear measurements, varying between 2.3 and 16.5 mm of SL and between 0.16 and 3.5 mm of UJL. *Lampadena* individuals varied between 2.6 and 13 mm of SL and 0.24 and 2 mm of UJL. *Ceratoscopelus* individuals varied between 3.8 and 10.6 mm of SL and 0.32 and 1.2 mm of UJL, while for *Lepidophanes* the variation was between 3.2 and 9.2 mm of SL and 0.24 and 1.28 mm of UJL.

SL and UJL were positively correlated in the four genera (Fig. 2; Pearson's correlation test,  $P < 0.001$ ). For *Lampadena*, *Lepidophanes*, and *Ceratoscopelus*, the variability was higher than in *Diaphus* (lower  $R^2$  values; Fig. 2). The rate of increase in the UJL with the increase in SL is similar in *Diaphus*, *Ceratoscopelus* and *Lepidophanes*, and slightly lower in *Lampadena* (ANCOVA,  $P < 0.05$ ).

### Feeding incidence

The feeding incidence in myctophid larvae was higher during the daytime in both the continental shelf break and off the islands (Cochran–Mantel–Haenszel,  $P < 0.001$ ; Table II). Also, the relationship between feeding incidence and time was moderate in the continental shelf break ( $\phi$  coefficient values  $> 0.3$ ; Table II), and weak off the islands for *Diaphus* and myctophids in general. It was not possible to consider the different areas in the comparison for *Ceratoscopelus*, *Lampadena* and *Lepidophanes*, due to the lower number of individuals. *Lepidophanes* also had a significantly higher feeding incidence during the day ( $\chi^2$  test,  $P < 0.05$ ). Feeding incidence was statistically independent in relation to the time of day for *Ceratoscopelus* and *Lampadena*, although a general trend of higher feeding incidence during the daytime was observed. No relationship between feeding incidence and larvae size classes was observed ( $\chi^2$  test;  $P > 0.05$ ; Fig. 3).

### Diet composition

The diet composition of the myctophid larvae at the slope showed a higher number of distinct prey taxa in relation to the islands (36 and 20, respectively; Table III). The most common prey taxa at the slope were remnants of meso- and macroplanktonic organisms in advanced stage of digestion (60%), centric

**Table I:** List of the identified taxa in the continental shelf break (CSB) and around the oceanic islands of Rocas Atoll (RA) and Fernando de Noronha archipelago (FN)

Species	<i>n</i>	SL range	UJL range	CSB	RA	FN
<i>Benthoema suborbitale</i>	10	3.2–4.4	0.4–1.2		•	•
<i>Bolinichthys</i> sp.	7	5.0–9.2	0.6–1.6			•
<i>Ceratoscopelus maderensis</i>	17	4.8–9.6	0.5–1.2		•	•
<i>Ceratoscopelus warmingii</i>	23	3.8–10.6	0.3–1.2	•	•	•
<i>Ceratoscopelus</i> sp.	1	4.8	0.5			•
<i>Diaphus brachycephalus</i>	22	3.2–8.2	0.2–1.6		•	•
<i>Diaphus mollis</i>	8	3.4–11.0	0.4–1.9	•	•	•
<i>Diaphus</i> spp. <sup>a</sup>	307	2.3–16.5	0.2–3.5	•	•	•
<i>Diogenichthys atlanticus</i>	8	4.0–5.6	0.2–1.5		•	•
<i>Electrona risso</i>	2	4.0–5.4	0.3–0.8		•	
<i>Hygophum taaningi</i>	18	2.4–8.0	0.2–1.0		•	•
<i>Hygophum</i> sp.	4	4.4–5.6	0.3–1.0		•	•
<i>Lampadena luminosa</i>	2	4.4–5.2	0.6–0.6		•	•
<i>Lampadena atlantica</i>	2	4.6–4.8	0.4–0.6			•
<i>Lampadena</i> spp. <sup>b</sup>	39	2.6–13.0	0.2–2.0	•	•	•
<i>Lampanyctus alatus</i>	1	3.2	0.6		•	
<i>Lampanyctus nobilis</i>	25	3.6–7.6	0.4–2.4		•	•
<i>Lampanyctus</i> sp.	4	4.8–10.0	1.0–2.0			•
<i>Lepidophanes gaussi</i>	3	7.4–9.2	0.8–1.3		•	•
<i>Lepidophanes guentheri</i>	34	3.2–7.6	0.2–0.8		•	•
<i>Lepidophanes</i> sp.	3	6.4–7.2	0.6–1.1			•
<i>Myctophum asperum</i>	13	3.2–6.7	0.2–1.6		•	•
<i>Myctophum nitidulum</i>	5	4.0–10.0	0.4–2.4		•	•
<i>Myctophum obtusirostre</i>	5	3.7–6.4	0.4–1.0		•	•
<i>Myctophum</i> spp. <sup>b</sup>	9	3.2–5.0	0.2–0.8		•	•
<i>Nannobranchium</i> sp.	6	3.4–6.1	0.6–2.4		•	•
<i>Notoscopelus</i> sp.	1	3.2	0.6		•	

*n*—number of analyzed individuals <sup>a</sup>six morphotypes; <sup>b</sup>three morphotypes. The • character marks the occurrence of the species in the studied areas.

**Table II:** Feeding incidence (in %) of the myctophids and *Diaphus* larvae in the region of the continental shelf break (CSB) and oceanic islands (ISL) during different times (day and night), and feeding incidence for the genera *Ceratoscopelus*, *Lampadena* and *Lepidophanes* during different times

	Day		Night		<i>P</i>	$\phi$	
	CSB	ISL	CSB	ISL		CSB	ISL
Myctophids	88.62	68.93	56.32	45.22	<0.001	0.35	0.22
<i>Diaphus</i>	90.09	64.29	53.85	47.62	<0.001	0.39	0.16
<i>Ceratoscopelus</i>	50		38.71		n.s.	–	
<i>Lampadena</i>	85		70		n.s.	–	
<i>Lepidophanes</i>	86		39		<0.05	0.35	

$\phi$ —strength of the dependence between compared variables; *P*—*P* values of the  $\chi^2$  test

diatoms of the genus *Thalassiosira* (31%), and fragments of digested diatoms (22%). The most frequent preys near the islands were fragments of micro-, meso- and macroplanktonic organisms in advanced stage of digestion, representing 80% of the preys found in the stomach/intestine content.

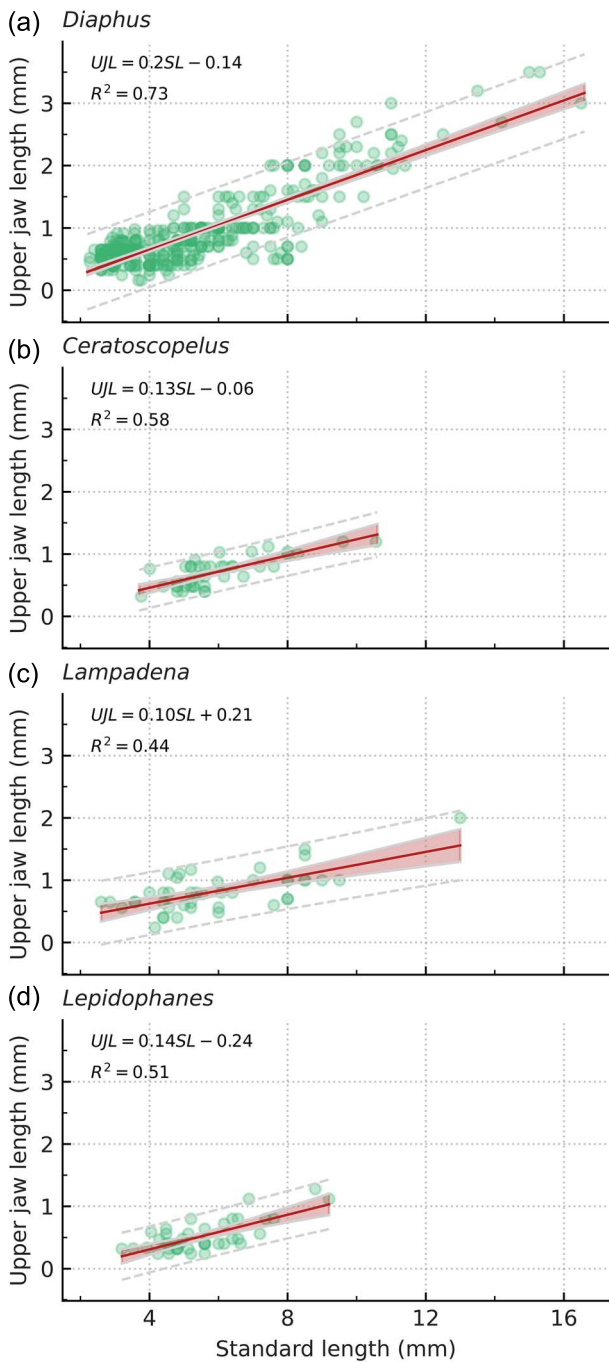
There was evidence that diet composition was different in the CSB and ISL regions, both in terms of the number of preys, and in terms of the volume of preys (PERMANOVA, *P* < 0.001). Diatoms (mainly *Thalassiosira* spp. and diatom fragments) proved to be numerically important in the diet composition at the CSB region (RII of 69%; Table III; Fig. 4a). Copepods were the most relevant preys at the ISL region (RII of 71%; Table III; Fig. 4a) and proved to be the biomass-dominant dietary item both in the CSB and in the ISL region. Ostracods were also relevant in the ISL region.

A clear change in the diet of the myctophid larvae was evidenced when different size classes were compared, both numerically and in terms of volume (Table IV; PERMANOVA, *P* < 0.001). Likewise, a clear change was observed in the relative importance of food item classes between larvae size classes. Smaller preys, such as microplanktonic organisms (e.g. diatoms, dinoflagellates and ciliates) were much more important for the smaller larvae (up to 4 mm of SL). Larger preys, such as copepods, increased in relative importance especially in larvae from at least 8 mm of SL (Fig. 4b).

### Feeding success

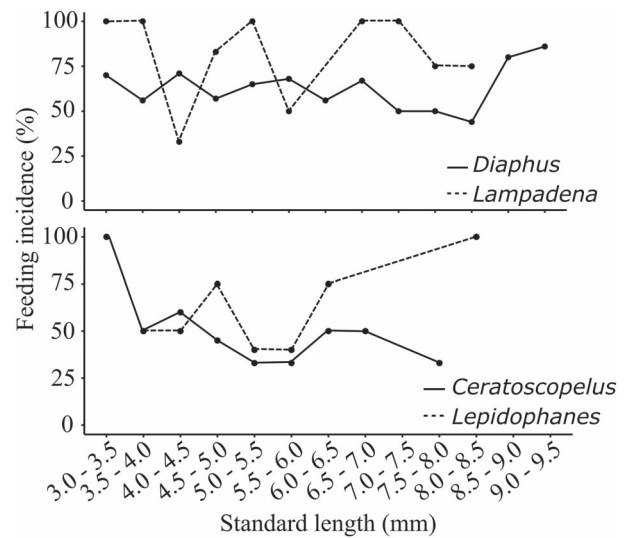
The number of preys per gut (NG) varied between 1 and 20 (3.3 ± 3.1). No relationship between NG and SL was observed (Spearman correlation test, *P* > 0.05; Fig. 5a). The total volume





**Fig. 2.** Relationship between the standard length (SL) and upper jaw length (UJL) of *Diaphus* (a), *Ceratoscopelus* (b), *Lampadena* (c) and *Lepidophanes* (d) larvae of the family Myctophidae in the oceanic region of the western Tropical Atlantic. Filled area—confidence interval of the linear regression model; Dashed lines—prediction interval for the linear regression model; Straight line—fitted values for the linear regression model.

of preys per gut (VG) varied between  $1.097 \times 10^{-6}$  and  $2.824 \times 10^{-1} \text{ mm}^3$  ( $6.9 \times 10^{-6} \pm 0.24 \times 10^{-3}$ ) and correlated positively with the SL (Spearman correlation test,  $P < 0.001$ ; Fig. 5b). The maximum prey width (MW) varied between 6.6 and 586.2  $\mu\text{m}$  ( $80.6 \pm 79.7$ ) and correlated positively with the SL (Spearman



**Fig. 3.** Feeding incidence throughout larvae development in *Diaphus*, *Lampadena*, *Ceratoscopelus*, and *Lepidophanes*.

correlation test,  $P < 0.001$ ; Fig. 5c). Therefore, the lanternfish larvae from the Tropical Atlantic ingested larger volume and bigger prey as they grow.

## DISCUSSION

Myctophids had a higher feeding incidence during the daytime than at nighttime in both the continental slope and off the islands, and *Diaphus* larvae contributed greatly to this result. Among the studied genera in the present study, *Lepidophanes* larvae were daytime feeders, while *Ceratoscopelus* and *Lampadena* larvae fed regardless the time of day. Daytime foraging is a typical behavior that has been observed in different regions of the world (e.g. Sassa and Kawaguchi, 2005; Sassa, 2010; Bernal et al., 2013; Contreras et al., 2015 and 2019). The feeding peak for several species of myctophids in the larval stage occurs in the middle of the day (Conley and Hopkins, 2004). The fact that these larvae are visual predators (Hunter, 1981) makes the availability of light an important factor influencing their feeding. Studies have evidenced differences in feeding behavior among ontogenetic stages of myctophids, with larvae being characterized mostly as daytime feeders and adults as night feeders (Bernal et al., 2013).

Myctophid larvae presented feeding incidence values varying between 38.7% in *Ceratoscopelus* and 90.1% in *Diaphus* from CSB, at night and day, respectively. Most values observed for both regions were like those found in many different high productive oceanographic areas of the Pacific (Sassa and Kawaguchi, 2005; Rodríguez-Graña et al., 2005; Sassa, 2010) and the Western Mediterranean (Sabatés et al., 2003; Bernal et al., 2013; Bernal et al., 2020; Contreras et al., 2015). In contrast, feeding incidence values observed in the present study were overall higher than those found by Contreras et al. (2019) for myctophid larvae from equatorial and tropical Atlantic, including oceanic Brazilian waters. However, the feeding incidence for *Diaphus* transformation stages (measuring between 10.0 and 14.0 mm) at day and night times (87.2 and 92.1%, respectively) from these regions

**Table III:** Myctophid larvae diet composition in the Continental Shelf Break (CSB) and around the Fernando de Noronha archipelago and Rocas Atoll (ISL) regions

Prey	CSB				ISL			
	FO	PT	PV	RII	FO	PT	PV	RII
<i>Trichodesmium</i> spp.	0.49	0.21	0.05	0.01	–	–	–	–
<i>Coscinodiscus</i> spp.	9.71	4.63	0.18	2.29	6.29	5.61	0.09	2.23
<i>Thalassiosira</i> spp.	31.55	25.26	0.69	40.11	15.43	22.45	0.25	21.75
<i>Fragilaria</i> sp.	0.49	0.63	0.00	0.02	–	–	–	–
<i>Nitzschia</i> spp.	14.56	7.79	0.09	5.62	6.86	6.63	0.02	2.83
Pennate diatom	7.77	4.42	0.07	1.71	1.14	1.02	0.01	0.07
Diatom fragment	22.33	16.63	0.36	18.59	1.71	1.53	0.01	0.16
<i>Gonyaulax birostris</i>	0.49	0.21	0.01	0.01	–	–	–	–
<i>Podolampas spinifera</i>	0.49	0.21	0.00	0.01	–	–	–	–
<i>Tripes kofoidii</i>	0.49	0.21	0.00	0.01	–	–	–	–
Dinoflagellata n.i.	13.11	6.95	0.14	4.55	0.57	0.51	0.00	0.02
Ciliophora n.i.	0.97	0.42	0.03	0.02	–	–	–	–
Oligotrichia n.i.	0.49	0.21	0.00	0.01	–	–	–	–
<i>Eutimninus</i> sp.	3.4	1.47	0.04	0.25	0.57	0.51	0.01	0.02
<i>Tintinnopsis campanula</i>	0.97	0.42	0.06	0.02	–	–	–	–
<i>Tintinnopsis carajacensis</i>	0.49	0.21	0.05	0.01	–	–	–	–
<i>Tintinnopsis</i> sp.	3.88	1.89	0.23	0.40	1.71	1.53	0.02	0.16
<i>Undella claparedei</i>	0.97	0.42	0.03	0.02	0.57	0.51	0.01	0.02
<i>Undella</i> sp.	0.97	0.42	0.01	0.02	–	–	–	–
Tintinnina (cyst)	0.49	0.21	0.04	0.01	–	–	–	–
Tintinnina n.i.	5.34	2.32	0.06	0.62	–	–	–	–
Foraminifera n.i.	–	–	–	–	0.57	0.51	0.00	0.02
Cyst n.i.	0.49	0.21	0.03	0.01	–	–	–	–
Microplankton (ad)	5.83	–	–	–	22.29	–	–	–
Polychaeta	0.49	6.95	4.43	0.27	0.57	0.51	0.15	0.02
<i>Euterpina</i> sp.	0.49	0.21	6.56	0.16	–	–	–	–
<i>Oithona</i> sp.	0.49	0.21	0.10	0.01	–	–	–	–
<i>Clausocalanus</i> sp.	0.49	0.21	5.87	0.15	–	–	–	–
Copepod fragment	2.91	2.53	8.57	1.58	12.57	32.14	43.12	58.76
Copepod legs	3.88	2.11	0.73	0.54	10.29	14.8	0.49	9.77
Copepod antennae	0.49	0.42	0.04	0.01	1.71	4.08	0.20	0.45
Copepoda n.i.	5.83	9.26	70.90	22.90	2.29	4.59	7.20	1.68
Copepod eggs	0.49	0.21	0.14	0.01	1.14	1.02	0.50	0.11
Copepod nauplii	–	–	–	–	1.71	1.53	0.65	0.23
Chaetognatha hooks	0.49	1.68	0.07	0.04	–	–	–	–
Chaetognatha n.i.	0.49	0.21	0.06	0.01	–	–	–	–
Echinodermata larvae	0.49	0.63	0.37	0.02	–	–	–	–
Ostracod	–	–	–	–	0.57	0.51	47.26	1.69
Meso-, macroplankton (ad)	59.71	–	–	–	57.71	–	–	–

n.i. – non identified; ad – advanced digestion. FO—frequency of occurrence (%); PT—proportion to the total number of preys (%); PV—proportion to the total volume of preys (%); RII—relative importance index (%)

were similar to the feeding incidence observed in *Diaphus* spp. at daytime (90.1%), in the present study.

An increase in the ability of the larvae to find prey could be expected as they grow since their locomotion speed, the distance of perception and capture success rate are positively correlated with the age or size of the larvae (Hunter, 1981). However, feeding incidence was not influenced by the size of the larvae within the size range analyzed in our study, although bigger prey was ingested by bigger larvae. The independence of feeding incidence in relation to the size of the larvae could be associated with the oligotrophic nature of the studied region, which hampers the capture of food particles for larvae in all size classes. Although other authors have observed an increase in feeding incidence with the increase in size of some species of myctophids (Sassa and Kawaguchi, 2005; Sassa, 2010), in some cases this

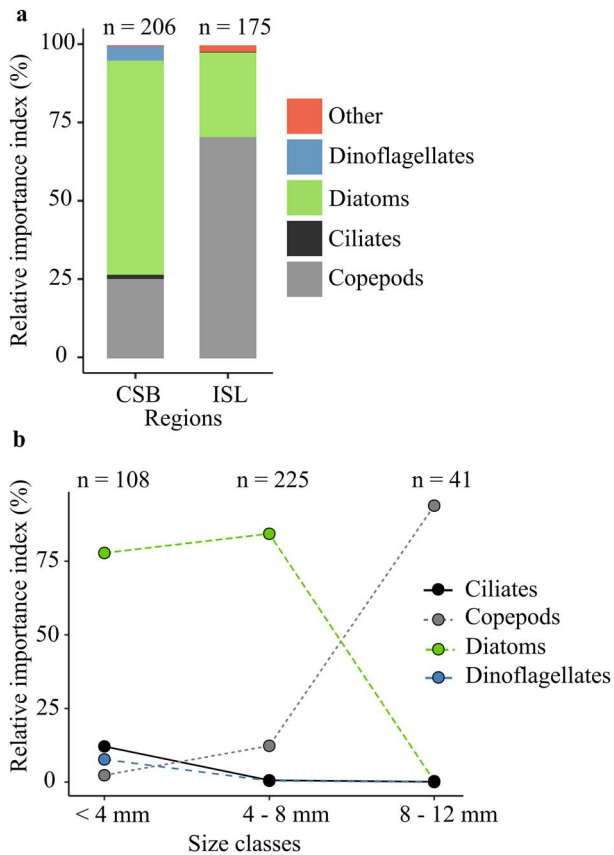
increase was not observed within the size range analyzed in the present work, starting to occur from 12 mm (Sassa, 2010). For other families, both increase (e.g. Carangidae) and decrease (e.g. Scombridae) have been observed in the feeding incidence throughout the increase in larvae size, even within the size range analyzed in this work (Sassa et al., 2008). Patterns of no increase in the feeding incidence with the increase in larvae size have also been observed in environments of high biological productivity (Vera-Duarte and Landaeta, 2016).

High rates of feeding incidence are associated with a decrease in larval mortality caused by starvation (Sassa et al., 2008). The natural challenge imposed on the larvae by the oligotrophic nature of the waters in the studied areas may be offset by a change in the relative importance of the prey taxa that are captured by the myctophid larvae throughout early development. The

**Table IV:** Diet composition throughout myctophid larval development in tropical Atlantic regions

Prey	< 4 mm (n = 108)				4–8 mm (n = 225)				8–12 mm (n = 41)			
	FO	PT	PV	RII	FO	PT	PV	RII	FO	PT	PV	RII
<i>Trichodesmium</i> spp.	0.9	0.4	0.6	0.03	–	–	–	–	–	–	–	–
Centric diatom	43.5	31.7	5.03	45.0	27.6	39.4	0.9	69.2	29.3	22.5	0.3	16.8
Pennate diatom	30.6	18.9	1.6	17.6	11.11	12.5	0.1	8.75	2.4	0.8	0.0	0.05
Diatom fragment	22.2	21.4	2.7	15.1	9.3	10.8	0.2	6.4	9.8	4.2	0.03	1.03
Dinoflagellata	20.4	11.9	1.5	7.7	2.7	2.6	0.04	0.4	4.9	1.7	0.01	0.2
Ciliophora	23.1	13.2	5.4	12.1	3.1	3.03	0.1	0.6	9.8	3.3	0.1	0.8
Foraminifera	–	–	–	–	0.4	0.4	–	0.01	–	–	–	–
Microplankton a.d.	6.5	–	–	–	16.4	–	–	–	17.1	–	–	–
Cyst n.i.	0.9	0.4	0.4	0.02	–	–	–	–	–	–	–	–
Polychaeta	–	–	–	0	0.4	0.4	0.2	0.02	2.4	27.5	5.7	2.04
Copepoda	0.9	0.4	79.2	2.1	3.1	6.9	18.6	5.0	24.4	32.5	92.7	77.0
Copepod eggs	0.9	0.4	2.9	0.1	0.4	0.4	0.5	0.02	2.4	0.8	0.2	0.1
Copepod nauplii	–	–	–	–	1.3	1.3	1.05	0.2	–	–	–	–
Copepod legs	2.8	1.2	0.8	0.2	8	13.0	0.7	6.8	12.2	5	0.9	1.8
Copepod antennae	–	–	–	–	1.3	3.5	0.3	0.3	2.4	1.7	0.05	0.1
Chaetognatha n.i.	–	–	–	–	0.4	0.4	0.1	0.01	–	–	–	–
Chaetognatha hooks	–	–	–	–	0.4	3.5	0.1	0.1	–	–	–	–
Echinodermata larvae	–	–	–	–	0.4	1.3	0.52	0.05	–	–	–	–
Ostracoda	–	–	–	–	0.4	0.4	76.6	2.1	–	–	–	–
Meso-, macroplankton a.d.	56.5	–	–	–	58.2	–	–	–	61.0	–	–	–

FO – frequency of occurrence (%); PT – proportion in comparison to the total number of preys (%); PV – proportion in comparison to the total volume of preys (%); RII – relative importance index (%); n – number of analyzed guts; a.d. – advanced digestion; n.i. – non identified

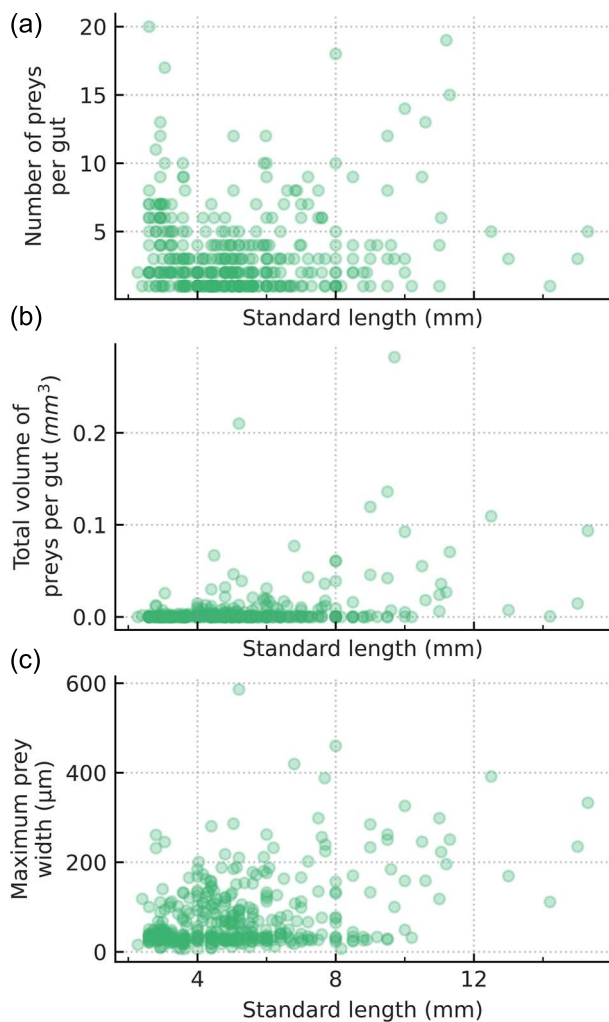


**Fig. 4.** Relative importance index (RII) of the most relevant food item classes in the intestine content of myctophid larvae in the continental shelf break (CSB) and around the Fernando de Noronha archipelago and Rocas Atoll (ISL) (a). Changes in the RII of the most relevant food item classes in the intestine content throughout myctophid larval development (b).

feeding preference of 3–8 mm larvae towards the less motile microplanktonic organisms, such as diatoms, and of larvae >8 mm—when they already have higher locomotion capacity (Fisher, 2005)—towards larger preys, may be an adaptation to the oligotrophic nature of the studied areas. Many species start exogenous feeding by capturing abundant nano- and microplanktonic organisms in the environment, such as diatoms, ciliates, and dinoflagellates among others (Nakagawa et al., 2007; van der Meeren, 1991).

The higher intake of diatoms on the slope in comparison to off the islands may be associated with the fact that the availability of microalgae is higher close to the more productive waters of the continental shelf, and therefore, their occurrence in the stomach contents is more frequent and in greater quantity than off the islands. The less motile nature of microalgae associated with their higher abundance than larger zooplanktonic organisms facilitate their capture and ingestion by larvae of smaller size classes.

The increase in the ingested volume and prey maximum width with the increase in larval length has been described in several regions and is not exclusive to myctophids (e.g. Sassa and Kawaguchi, 2005; Sassa, 2010; Vera-Duarte and Landaeta, 2016; Vera-Duarte and Landaeta, 2017). With the increase in the size of the larvae, their mouth opening is also increased, and this makes it possible to ingest larger preys. Despite the importance of the relationship between larval mouth gape and the dimensions of the ingested prey, the larval growth is not the only factor influencing the selectivity of prey. Behavioral and physiological aspects are also important (Rodríguez-Graña et al., 2005). One of the most important consequences of this change in the larvae diet is that not only the size of the food item can be changed, but its taxa as well, as observed for larvae of several myctophids from a range of habitats (Sassa, 2010; Contreras et al., 2015; Contreras et al., 2019; Bernal et al., 2020; Sabatés et al., 2003).



**Fig. 5.** (a) Relationship between the number of preys per gut (NG) and larval standard length (SL). (b) Relationship between preys' volume per gut (VG) and standard length (SL). (c) Relationship between prey's maximum width (MW) and standard length (SL) of myctophid larvae.

In the studied areas, a drastic change in diet was observed, with a considerable decrease in the relative importance of diatoms and an increase in the importance of copepods and ostracods, with the increase in the larvae length, especially after reaching 8 mm in SL. Similar results were observed for *Diaphus vanhoeffeni*, *Hygophum macrochir*, and *Myctophum affine* from oceanic waters of the equatorial and tropical Atlantic (Contreras et al., 2019), *Ceratoscopelus maderensis*, *Hygophum benoiti* (Contreras et al., 2015), *Benthosema glaciale* and *Myctophum punctatum* (Sabatés et al., 2003) from western Mediterranean. In these species, there has been a shift in diet from preflexion towards more developed stages (postflexion and transforming stages), with an increased importance of ostracods (Contreras et al., 2019), as observed in the present study. Conley and Hopkins (2004) studied the diet composition of larvae of 14 myctophid species from the oceanic waters of the eastern Gulf of Mexico. They found that ostracods dominated the diet of most Myctophinae larvae. According to the authors, ostracods are more preferred by Myctophinae over other

abundant crustacean prey (e.g. copepods) due to a combination of factors such as larval eye morphology that increases visual ability, relatively larger gape, ostracod pellucidity, and escape response. This explanation provides a reasonable account for the increased importance of ostracods in the larger daytime myctophid feeders studied here.

In areas of high productivity, the prey preference generally transitions with myctophid size from copepod nauplii at small predator sizes to a diet based on larger organisms, such as juvenile and adult copepods (Sassa et al., 2008; Sassa, 2010; Bernal et al., 2013), ostracods (Sassa and Kawaguchi, 2005), or appendicularians (Sassa et al., 2008) at larger predator sizes. Therefore, the increase in the total volume of prey that is observed with the increase in larvae length is not always accompanied by an increase in the number of captured prey. Such a quantitative increase in captured prey was not observed, as in several other regions with similar or completely different environmental characteristics (Bernal-Durán and Landaeta, 2017; Sassa and Kawaguchi, 2005). However, this relationship is species-specific, since an increase in the number of preys in association with the size of the larvae have already been observed for some species from different families, including Myctophidae (Sassa and Kawaguchi, 2005; Sassa and Tsukamoto, 2012).

## CONCLUSIONS

The information generated from this investigation contributes to fill the gap in the knowledge on the feeding ecology of myctophid larvae in western tropical Atlantic areas. Myctophid larvae fed mainly during daytime and presented a shift from smaller and more numerous preys to bigger and fewer preys with their increase in size. This pattern is in agreement with what is observed in other oceanic areas worldwide.

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There is no data archiving associated with this research.

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