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Diet and feeding strategies of myctophids in the Northeast Atlantic

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ABSTRACT: The trophic ecology of myctophids was investigated during spring 2019 in a large geographical span in the Northeast Atlantic (from Cape Verde to northern France), covering oligotrophic open ocean waters off south Iberia to the productive coastal areas of western Morocco. A total of 417 stomachs from 22 different myctophid species were analysed. Myctophids from the southern areas (from 20 to 42° N) mostly fed on copepods, whereas amphipods were the main prey of myctophids collected in the northern stations (from 42 to 48° N). The calanoids *Pleuromamma* spp. and *Candacia* spp., amphipods, euphausiids and decapod larvae were the most positively selected prey by all myctophid species, whenever these prey were present. *Pleuromamma* spp. were the most important prey for most species, with the largest average contribution to dietary carbon (49.6 ± 21.1%), while *Candacia* spp. were the dominant prey of *Lampanyctus ater* (contributing to 40.3% of the estimated dietary carbon), and amphipods were the dominant prey for *Hygophum benoiti* (39.0%), *Myctophum punctatum* (58.4%) and *Symbolophorus veranyi* (56.0%). Results of the present study indicate that myctophids in the Northeast Atlantic are mainly characterized by specialized feeding strategies, although some species showed mixed strategies (*Ceratoscopelus warmingii, Lepidophanes gaussi*, *Lobianchia dofleini* and *Lobianchia gemellarii*) and a few species (*Hygophum hygomii*, *H. benoiti* and *S. veranyi*) showed a generalized feeding strategy. Our data provide key knowledge for food web and ecosystem studies and contribute to determining the trophodynamics of the global mesopelagic fish community.

KEY WORDS: Lanternfishes · Trophic relationships · Micronekton · Mesopelagic fish · Stomach contents

1. INTRODUCTION

The twilight or mesopelagic zone is generally defined as the area of the ocean extending from 200 to 1000 m depth, but a new definition in terms of light intensity has lately been proposed, ranging from 10^{-9} to 10^{-1} µmol quanta m^{-2} s^{-1}(Kaartvedt et al. 2019). This area is dominated by mesopelagic fish. In fact, recent acoustic estimates suggest that mesopelagic fish dominate the world total fish biomass (Irigoien et al. 2014), although these global estimates are still uncertain (Proud et al. 2019). Many species of mesopelagic fish perform diel vertical migrations (DVMs) to feed in the epipelagic zone at night (Clarke 1980, Watanabe et al. 1999, Catul et al. 2011), contributing to the biological pump by actively exporting carbon from the surface layers to the mesopelagic depths (Hidaka et al. 2001, Shreeve et al. 2009, Robinson et al. 2010). Despite their large importance in the marine ecosystems, there is a significant lack of information on the basic biology of many species, including infor-

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mation on the variability of feeding ecology (Aparecido et al. 2023).

The family Myctophidae is one of the most common and abundant families of mesopelagic fish (Catul et al. 2011). Myctophids are prey for a wide range of predators, which include fish (such as Atlantic mackerel), squids, seabirds and marine mammals (Greer Walker & Nichols 1993, Parry 2006, Doksæter et al. 2008, Hedd et al. 2009). As predators, most myctophids mainly prey on copepods (Merrett & Roe 1974, Kawaguchi & Mauchline 1982, Hopkins & Gartner 1992, Podrazhanskaya 1993), but some species are known to feed primarily on other prey groups, such as decapods, amphipods, molluscs and fish (Hopkins & Gartner 1992, Podrazhanskaya 1993, Pusch et al. 2004b). Ontogenetic differences in diet have been reported for several species of myctophids (such as *Benthosema glaciale*, *Hygophum hygomii* and *Ceratoscopelus maderensis*), and prey size increases with increasing fish size (Gjøsæter 1973, Pusch et al. 2004b, García-Seoane et al. 2013). The feeding behaviour of myctophids is commonly described as generalist, while some studies describe selective behaviour (Merrett & Roe 1974, Pusch et al. 2004b). Most trophic studies of myctophids have been performed in a limited area and time. Studying the diet composition and prey availability over a broad area can provide insights into their ability to adapt to different food availability or their degree of specialization for particular prey types, and assess their impact in the ecosystems they inhabit, namely the trophic interactions and their role in the trophic food webs. This information is particularly relevant since myctophids can remove more than 10% of the surface zooplankton biomass per night (Watanabe et al. 2002), and therefore exert an important top-down control of zooplankton communities.

Recent studies have analysed the diversity and distribution of mesopelagic fish in the Northeast and Central Atlantic, mostly on a regional scale (Pusch et al. 2004a, Wienerroither et al. 2009, Sutton et al. 2013, Ariza et al. 2016, García-Seoane et al. 2020, Olivar et al. 2022), but a few covered a large geographical scale (Olivar et al. 2017, Czudaj et al. 2021, García-Seoane et al. 2021, Kobyliansky et al. 2024). The family Myctophidae was the most diverse in the study area, and the most abundant species of myctophids in terms of numbers were *B. glaciale* and *Lobianchia dofleini* (García-Seoane et al. 2021). The fish community in the south (25 to 37° N) was more diverse than the north (42 to 48° N). *Notolychnus valdiviae* had a widespread distribution throughout the study area, while *Benthosema suborbitale*, *H. hygomii*, *H. taaningi*, *L. dofleini* and *Notoscopelus resplendens* showed a southern distribution (from the coast of Africa to off the Cape São Vicente) and *B. glaciale* were only registered in the north (along the Galician coast and Bay of Biscay) (García-Seoane et al. 2021). A detailed description of the main circulation patterns and hydrographic characteristics of the study area have also been described in García-Seoane et al. (2021)

Strategies for reducing competition for food, such as spatial segregation (Tyler & Pearcy 1975, Moku et al. 2000) or the synchronization of seasonal growth with their prey abundance (Young & Blaber 1986) have been suggested for myctophids. However, high food availability, characteristic of temperate and high latitude areas, has been related to a broad diet overlap (Young & Blaber 1986, Pakhomov et al. 1996), whereas the low food availability and high diversity of oligotrophic areas have been related to resource partitioning of mesopelagic fish assemblages (Hopkins & Gartner 1992, Hopkins & Sutton 1998). As postulated by the competition theory (Schoener 1974, Abrams 1992), lower food availability can lead to higher adaptation and specialization, to minimize competition and functional similarity (Aparecido et al. 2023). Knowledge of the large-scale patterns of diet variability is therefore essential to understand food web dynamics and resource partitioning.

The aim of this study was to examine and compare diet composition and feeding strategy of myctophids in oligotrophic and more productive coastal waters, and investigate species prey selectivity at a particular time of the year. This work covers a large geographical span that includes individuals inhabiting several areas, from oligotrophic open ocean deep waters off south Iberia to the coastal areas of western Morocco (Serret et al. 2015, Brotas et al. 2022), which are among the most productive areas of the world due to the permanent upwelling that occurs here. Due to the pivotal role of myctophids in the transfer of energy from zooplankton to higher trophic levels, analysis of the diet composition of these species is a fundamental source of information, necessary to inform ecosystem models and assist ecosystem management.

2. MATERIALS AND METHODS

2.1. Sampling

Samples were collected from 2 to 22 May 2019 during a multidisciplinary survey across the Northeast Atlantic Ocean (from Cape Verde to northern France) on board the RV 'Kronprins Haakon' (Fig. 1). Zoo-

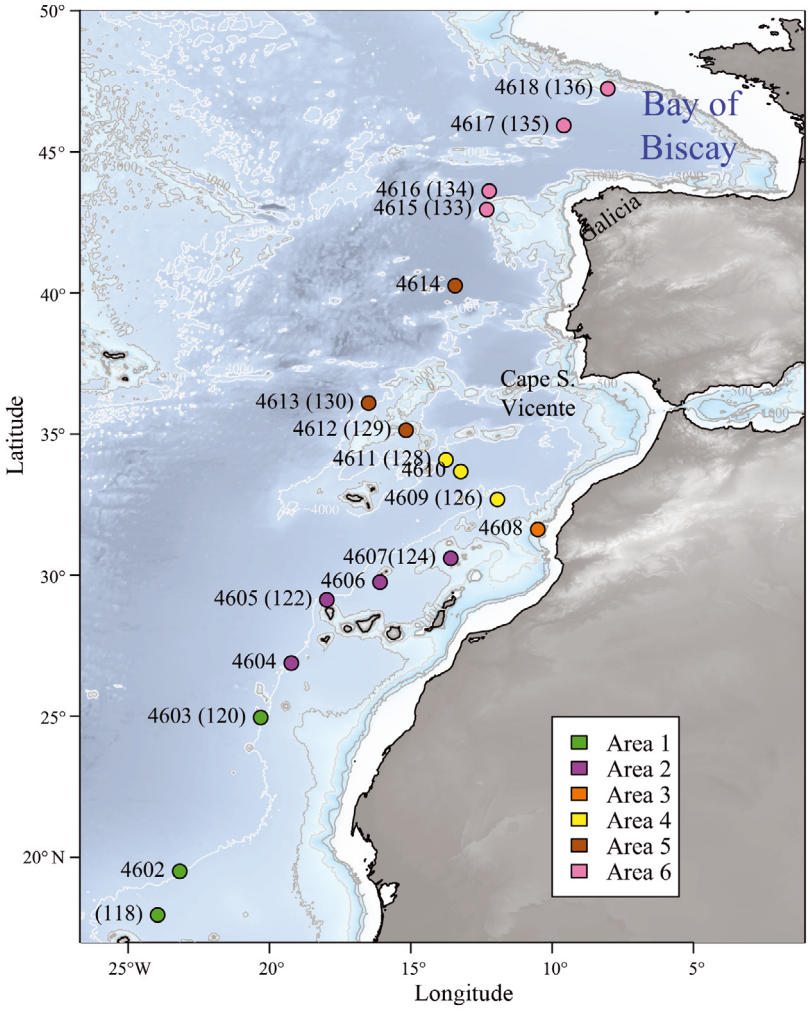

Fig. 1. Study area in the Northeast Atlantic showing location of the stations (circles, coloured by area). Stations with macroplankton trawls are numbered 4602 to 4618; Mammoth MultiNet stations are numbered 118 to 136 (in parentheses)

Table 1. Overview of the Mammoth MultiNet stations from which the zooplankton samples were obtained during May 2019. Dates are given as dd/mm/yy

MultiNet station	Trawl	Area station	Date	Starting time (UTC)	Day/ night	Maximum depth of the MultiNet hauls (m)
118		1	03/05/19	10:37	D	1148
120	4603	1	06/05/19	12:32	D	1147
122	4605	2	08/05/19	12:29	D	1148
124	4607	2	10/05/19	10:24	D	1148
126	4609	4	12/05/19	10:52	D	1148
128	4611	4	14/05/19	11:27	D	1148
129	4612	5	15/05/19	11:05	D	1147
130	4613	5	16/05/19	15:44	D	1148
133	4615	6	19/05/19	12:19	D	1148
134	4616	6	20/05/19	03:52	N	1148
135	4617	6	21/05/19	10:27	D	1148
136	4618	6	22/05/19	00:56	N	1148

plankton samples were collected with a Hydrobios Mammoth MultiNet that has a total of 9 nets with a 1 m^2 opening and 180 µm mesh size (Table 1). To monitor the filtering efficiency the MultiNet was equipped with 2 electronic mechanical flowmeters (measuring the internal and outside flow). The 4 first stations were obliquely hauled, with depth intervals of approximately 1150–1000, 1000–800, 800–600, 400–600, 400–200, 200–100, 100–50 and 50–0 m. Due to a winch problem on the aft deck, the rest of the stations were vertically hauled with the depth intervals of around 1150–1000, 1000–800, 800–600, 600–400, 400–300, 300–200, 200–100, 100–50 and 50–0 m. The sample of each net was split, filtered using a 180 µm sieve (eliminating the excess of water) and 1/4 of the sample was fixed in 4% formalin for later taxonomic analysis.

Mesopelagic fish were collected using 2 types of trawls. A 6 × 6 m mouth opening macroplankton net with square, 3 × 3 mm light opening mesh from the opening to the cod end and a graded, Multpelt trawl (pelagic fish trawl) with a mouth opening height of 35 m and 20 mm mesh in the cod end. Both the macroplankton and the pelagic trawl were obliquely towed from the surface to 1200 m and back to the surface during the daytime at an average trawling speed through water of 1 m s^{-1}, except for 2 trawls that took place in shallow water at night (Table 2). These samples were collected from a total of 17 stations, fish were identified onboard to species level, and frozen at −20°C. The sorting and subsampling of these organisms are detailed in García-Seoane et al. (2021), which also provides details of the spatial distribution of the myctophid species.

Six ecological areas have been defined based on information on hydrography and plankton distribution. These areas are smaller than the mesopelagic areas defined by Sutton et al. (2017) and Reygondeau et al. (2018) to also include potential differences in

Table 2. Overview of the trawl stations from which the myctophid species for stomach contents analyses were obtained during May 2019. Dates are given as dd/mm/yy

Trawl station	MultiNet	Area station	Type of trawl	Date	Starting time (UTC)	Day/night	Maximum depth for the trawl (m)
4602		1	Macroplankton trawl	04/05/19	09:30	D	1197
4603	120	1	Macroplankton trawl	06/05/19	09:54	D	1196
4604		2	Multpelt trawl	07/05/19	09:49	D	1183
4605	122	2	Macroplankton trawl	08/05/19	09:22	D	1200
4606		2	Multpelt trawl	09/05/19	08:28	D	1173
4607	124	2	Macroplankton trawl	10/05/19	07:55	D	1188
4608		3	Macroplankton trawl	11/05/19	14:37	D	1260
4609	126	4	Macroplankton trawl	12/05/19	08:18	D	1190
4610		4	Macroplankton trawl	13/05/19	08:20	D	1188
4611	128	4	Macroplankton trawl	14/05/19	03:02	N	173
4612	129	5	Macroplankton trawl	15/05/19	08:22	D	1191
4613	130	5	Macroplankton trawl	16/05/19	09:49	D	1190
4614		5	Multpelt trawl	18/05/19	07:44	D	1168
4615	133	6	Macroplankton trawl	19/05/19	09:26	D	1196
4616	134	6	Macroplankton trawl	20/05/19	00:52	N	288
4617	135	6	Macroplankton trawl	21/05/19	08:00	D	1192
4618	136	6	Macroplankton trawl	22/05/19	07:13	D	1196

plankton composition related to ocean versus coastal areas, proximity to islands and global patterns of plankton distribution in the Atlantic, described in Reygondeau & Dunn (2019). Area 1 (south of 25° N), with sampling stations located off the African coast, is characterized by the warmest waters. Sampling stations in Area 2 (from 25 to 31° N) are characterized by the influence of the Canary Islands and Area 3 (from 31 to 32° N), with only 1 sampling station, is located closest to the coast, in the productive coastal waters of western Morocco. Stations in Area 4 (from 32 to 34.5° N) are located offshore from the Moroccan coast and Area 5 includes the Central and South Iberian Peninsula offshore waters (from 34.5 to 42° N). Area 6 (from to 42 to 48° N) includes the northwestern Iberian waters and the Bay of Biscay, and is characterized by the coldest surface waters of the study area. To characterize the diet composition of myctophid species, we aimed to analyse at least 6 individuals per species and ecological area (Table 3), preferably 3 large and 3 small individuals from the available size range.

2.2. Laboratory analyses

Zooplankton samples were fractioned with a Folsom plankton splitter whenever needed, and 300 to 500 organisms were counted and identified under a Leica S8 APO stereoscopic microscope, to the lowest possible taxonomical level. The abundance of taxa was expressed as the number of individuals per cubic meter (ind. m^{-3}).

In the laboratory, myctophids were defrosted and standard length (SL) was measured to the nearest mm, and weight (both total weight and eviscerated weight) was recorded to the nearest 0.001 g. A total of 26 species of myctophids were selected for feeding studies based on their abundance, frequency and availability of the samples. Myctophid stomachs were removed (by cutting at the beginning of the oesophagus) and preserved in absolute alcohol for posterior stomach content analyses. Prey found in the fish mouth were discarded. Four species of myctophid (*Benthosema glaciale*, *Gonichthys cocco*, *Lampanyctus crocodilus* and *Taaningichthys bathyphilus*) that were sampled were not included in the analyses due to the low number of fish and high vacuity rate. Thus, a total of 417 stomachs from 22 different myctophid species were dissected under a stereomicroscope and all prey items were identified to lowest taxonomic level and quantified using a Zeiss IM35 inverted microscope with a 200× magnification. Copepods were identified to species level, when possible, Branchiopoda to genus, and the rest of the prey into broader taxonomic groups: Bivalvia larvae, Copepoda eggs, Crustacea eggs, Pteropoda, Cirripedia, Amphipoda, Euphausiacea, Decapoda, Ostracoda and fish.

2.3. Data analyses

In this work, prey was not measured. To determine the relative importance of prey, mean prey size per species or prey group were derived from literature,

Table 3. Number of individuals analysed for diet composition. Numbers in **bold** (1 to 6) correspond to the different areas. Max. SL: maximum standard length (in mm) following Sutton et al. (2020)

Species	Number of individuals per area						Length (mm)			Weight (g)		Empty
	1	**2**	**3**	**4**	**5**	**6**	Min.	Max.	Max. SL	Min.	Max.	
Benthosema suborbitale	6	6		6			17	32	39	0.038	0.377	4
Bolinichthys indicus	6	6	4	6	6	3	27	45	45	0.212	1.408	1
Ceratoscopelus warmingii	6	6		3	3		26	55	81	0.186	2.353	4
Diaphus mollis		6			3		32	49	66	0.526	1.94	0
Diaphus rafinesquii	3	6			3		28	67	90	0.361	5.046	0
Diogenichthys atlanticus		6		6			14	21	27	0.028	0.121	0
Hygophum benoiti				6	6		13	45	55	0.019	1.456	0
Hygophum hygomii	3	6		6	6		15	54	68	0.03	2.894	2
Hygophum reinhardtii	5	6		3			17	45	61	0.032	1.303	5
Hygophum taaningi	6	6		6	3		19	49	61	0.093	1.538	10
Lampanyctus alatus	6	6	6	3			26	55	61	0.108	1.718	5
Lampanyctus ater	3	6	5	6	6	6	27	117	130	0.112	14.241	11
Lampanyctus cuprarius		6	5	6	6		36	74	110	0.175	2.997	11
Lampanyctus pusillus			6	6			22	35	43	0.122	0.61	3
Lepidophanes gaussi	5	6		5	6		21	46	50	0.049	0.877	3
Lobianchia dofleini		6	6	6	6		18	35	78	0.102	0.727	0
Lobianchia gemellarii	6	6		4	4		20	86	60	0.107	8.971	1
Myctophum punctatum			6	6	6	2	18	72	110	0.039	5.231	6
Notolychnus valdiviae	6	6	3	6	6	3	14	24	25	0.008	0.128	13
Notoscopelus kroyeri			6	6		4	21	39	143	0.093	0.494	2
Notoscopelus resplendens		6		6	6		24	78	102	0.127	5.546	0
Symbolophorus veranyi				6	5		22	105	120	0.098	16.69	2

and the carbon content was estimated from prey length (Garrido et al. 2008, Garrido & van der Lingen 2014). The feeding incidence (FI) was estimated as the percentage of individuals with at least 1 prey item in the stomach in relation to the total number of stomachs analysed. Ivlev's electivity index (E) was used to determine prey selectivity of myctophid species in the diet by comparing zooplankton composition in the diet to that of the water in the sampled stations. The index was calculated using the formula:

$$E = \frac{r_i - p_i}{r_i + p_i} \quad (1)$$

where r_i is the proportion of prey item i in fish stomachs, and p_i is the proportion of prey item i available in the environment. The values of E range from −1 to 1, with values close to −1 indicating avoidance or inaccessibility of the prey, values around 0 indicating random selection from the environment and values close to 1 indicating active selection (Strauss 1979). To determine p_i, the abundances of zooplankton taxa were integrated for all of the water column at each sampled station, and only potential prey with a relative abundance above 3% were used for selectivity estimates. After the prey abundances from each MultiNet station were compared with the closest fish station, the mean prey selectivity estimate for all stations was calculated for each fish species. Most of the zooplankton and fish sampling were made in the same locations, with a few exceptions. In those cases, we used the nearest zooplankton sampling in the analysis.

The feeding strategy of each myctophid species was assessed by the Costello graphical method (Costello 1990) modified by Amundsen et al. (1996). This method plots the prey-specific abundance versus the frequency of prey occurrence.

Differences in the diet composition of the 22 myctophid species were investigated by multivariate analysis (Oksanen et al. 2020). Individuals with empty stomachs, with only digested material or with only uncommon prey (included in the category 'others') were not included in these analyses. Bray-Curtis similarities were calculated for each pair of predators to produce a similarity matrix. Uncommon prey (i.e. species that contributed less than 3% to the diet of the species), such as bivalve larvae, pteropods, cirripeds, crustacean eggs, *Pseudevadne* spp., fish, and the copepods *Eucalanus* spp., *Aetideus* spp., *Calanoides carinatus*, *Scolecithrix* spp., *Gaetanus* spp., *Paracalanus* spp., *Lubockia* spp., *Oithona* spp., and *Corycaeus* spp. (included in the category 'others') were not included in the matrix. Differences among species in the different areas were tested with permutational ANOVA (PERMANOVA) (Adonis routine; Anderson

2001) upon a Bray-Curtis similarity matrix, except for Area 6. Our data for this area contained insufficient information to model (most probably due to the low sample size). Between 2 and 4 stations were sampled in each area, apart from Area 3, which consists of only 1 station (Stn 4608). This station was considered as a separate area due to the short distance from the coast. We analysed the dispersion of prey among species per area with the Betadisper test because the PERMANOVA routine assumes homogeneity of the multivariate dispersion (Anderson et al. 2008). All these routines (PERMANOVA and Betadisper) were run with 9999 permutations. We performed multiple comparisons using the 'pairwise.adonis' function (Martinez Arbizu 2019) to identify the differences between each species pair. Multivariate analyses were performed using the vegan package (Oksanen et al. 2020) of the R software v 4.4.1 (R Development Core Team 2024). The package marmap (Pante et al. 2023) was used to create the map.

3. RESULTS

3.1. Zooplankton distribution

Maximum densities of zooplankton were recorded in the upper 100 m (Nets 8 and 9), with copepods being the dominant group in numbers (Fig. 2). The copepods *Oithona* spp. and *Oncaea* spp. generally dominated the water column from 100 to 1200 m depth. In terms of spatial distribution, maximum densities of zooplankton were recorded at the northernmost station (Stn 136, which belongs to Area 6), with densities above 10 000 ind. m^{-3} in the upper 50 m, followed by the southernmost station (Stn 118, from Area 1) and by the station off Cape São Vicente (Stn 130, from Area 5), with densities above 2000 ind. m^{-3} in the upper 50 m and 50–100 m depth, respectively. Minimum zooplankton density was recorded in Area 6, in the stations off the Galician coast (Stns 133 and 134), which had less than 250 ind. m^{-3} in surface waters (0–50 m depth).

Zooplankton composition changed along the cruise track, with lower diversity in the north (Area 6). The copepods *Oithona* spp., and *Paracalanus*/*Clausocalanus* copepodites were abundant in all areas, whereas the copepods *Oncaea* spp. dominated the surface waters of south Cape São Vicente (from Areas 1 to 5). *Clausocalanus* spp. were an abundant species in all areas (except for Area 4). In Area 1, the copepods *Acartia* spp. were also dominant, as well as the appendicularians *Fritilaria* spp. In Area 2, the branchiopods *Pseudevadne* spp. and *Evadne* spp., and organisms of the order Doliolidae were important at 1 station (Stn 124), whereas the copepods *Corycaeus* spp. were dominant in Area 4, and the copepod *Mecynocera clausi* was also important at Stn 126 and *Calocalanus* spp. and *Lucicutia* spp. at Stn 128. The copepod *Temora stylifera* was abundant at some stations of Areas 4 and 5, while the appendicularians *Oikopleura* spp. dominated at Stn 130 of Area 5. Chaetognatha were important at some stations of Areas 2, 4 and 5, and *Paracalanus* spp. were abundant at some stations of Areas 2, 5 and 6. In the northern stations, which belong to Area 6 (Stns 133 to 136), a few taxa dominated the surface waters in terms of number: *Oithona* spp., *Paracalanus* spp., *Clausocalanus* spp. and *Acartia* spp. Less dominant taxa, such as *Pleuromamma* spp. and *Candacia* spp., were present at all stations of each area, with higher abundances found in Area 6, particularly at Stn 136.

3.2. Feeding intensity and myctophid diet composition

The feeding incidence of the myctophid species analysed ranged from 33 to 100% during daytime (Table 4). The limited number of specimens collected during night-time revealed a higher feeding intensity in myctophids at night (feeding intensity of 100% for all the species, except *Notolychnus valdiviae*) than during the day. Most of the species sampled in Area 4 during daytime (80%) showed at least 1 prey in the stomach, followed by Area 5 with 63% of the species analysed with a feeding incidence of 100%. A feeding incidence lower than 30% was only recorded during daytime, and the species were *Hygophum taaningi* in Area 2 (0%, n = 6), *Lampanyctus ater* in Area 3 (20%, n = 5) and *N. valdiviae* in Area 6 (0%, n = 1). Six species (*Diaphus mollis*, *D. rafinesquii*, *Diogenichthys atlanticus*, *H. benoiti*, *Lobianchia dofleini* and *Notoscopelus resplendens*) had at least 1 prey in all stomachs analysed (FI = 100%). Feeding incidence lower than 60% was found for 3 species: *H. taaningi*, *Lampanyctus cuprarius* and *N. valdiviae*.

Myctophid species were mainly zooplanktivorous, preying on diverse meso- and macrozooplankton taxa. Copepods were the most important prey for most of these species (Fig. 3). The genus *Pleuromamma* made the largest average contribution to dietary carbon (49.6 ± 21.1%; mean ± SD), followed by *Candacia* spp. (16.8 ± 11.3%). Only 3 species (*H. benoiti*, *Myctophum punctatum* and *Symbolophorus veranyi*) had prey other than copepods as their main prey.

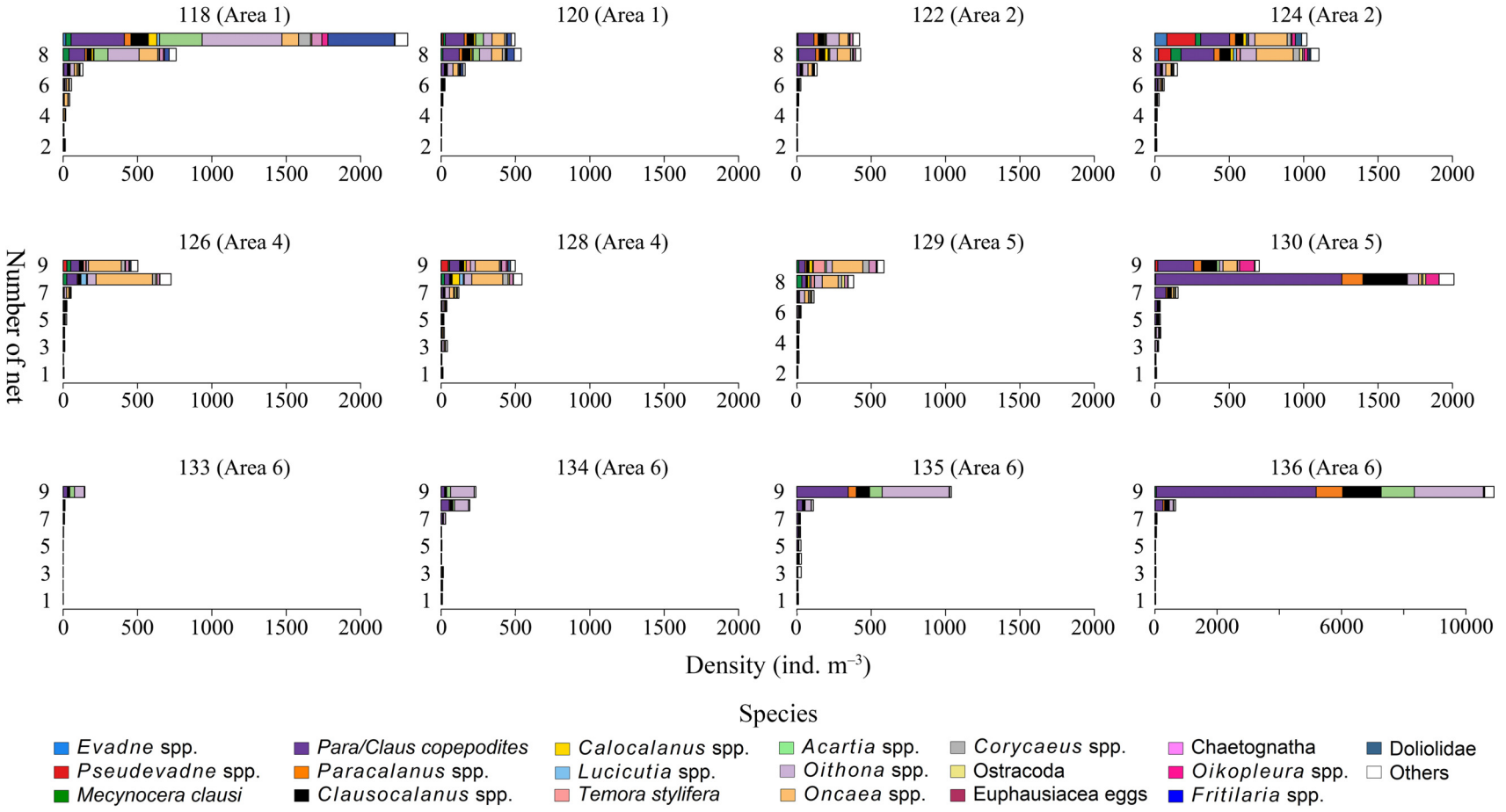

Fig. 2. Zooplankton composition of the samples collected in the Northeast Atlantic. Each panel shows the density of individuals for each Mammoth MultiNet haul for the depth strata (Nets 1 to 9). Net 9: ~0–50 m; Net 8: ~50–100 m; Net 7: ~200–100 m; Net 6: ~300–200 m; Net 5: ~ 400–300 m; Net 4: ~500–400 m; Net 3: ~700–500 m; Net 2: ~900–700 m; Net 1: ~1150–900 m. In the 4 first stations, Net 1 was not used and the Nets 2, 3, 4, 5 and 6 corresponded to ~1150–1000, ~1000–800, ~800–600, ~600–400 and ~400–200 m depth, respectively. Note that the *x*-axis has the same length in all the panels except for Stn 136 (Area 6)

Table 4. Feeding incidence of 22 myctophid species collected in the Northeast Atlantic during daylight and night-time

Species	Feeding incidence during day							Number of individuals examined for feeding incidence (day)	Feeding incidence during night			Number of individuals examined for feeding incidence (night)
	Area 1	Area 2	Area 3	Area 4	Area 5	Area 6	Total		Area 4	Area 6	Total	
Benthosema suborbitale	83	50		100			78	18				
Bolinichthys indicus	100	100	75	100	100		96	28		100	100	3
Ceratoscopelus warmingii	83	50		100	100		76	17	100		100	1
Diaphus mollis		100			100		100	9				
Diaphus rafinesquii	100	100			100		100	12				
Diogenichthys atlanticus		100		100			100	12				
Hygophum benoiti				100	100		100	10	100		100	2
Hygophum hygomii	67	83		100	100		90	21				
Hygophum reinhardtii	40	67		100			64	14				
Hygophum taaningi	33	0		100	100		52	21				
Lampanyctus alatus	83	67	67	100			75	20	100		100	1
Lampanyctus ater	67	50	20	50	100	100	66	32				
Lampanyctus cuprarius		67	60	33	50		52	23				
Lampanyctus pusillus			50	100			75	12				
Lepidophanes gaussi	100	67		100	83		85	20	100		100	2
Lobianchia dofleini		100	100	100	100		100	24				
Lobianchia gemellarii	100	100		100	75		95	20				
Myctophum punctatum			50	75	83	50	67	18	100	0	100	2
Notolychnus valdiviae	67	67	33	33	83	0	57	28	0	50	50	2
Notoscopelus kroyeri			100	100		50	88	16				
Notoscopelus resplendens		100		100	100		100	18				
Symbolophorus veranyi				100	60		80	10	100		100	1

The main prey for *Bolinichthys indicus*, *Benthosema suborbitale*, *Diaphus rafinesquii*, *H. hygomii*, *H. taaningi*, *Lampanyctus alatus*, *L. pusillus*, *Lobianchia dofleini*, *Notoscopelus kroyeri* and *Notolychnus valdiviae* were *Pleuromamma* spp., followed by *Candacia* spp. (Fig. 3). *Lepidophanes gaussi*, *Lobianchia gemellarii* and *Notoscopelus resplendens* also fed mainly on *Pleuromamma* spp., followed by krill, while *Ceratoscopelus warmingii*, *Diaphus mollis*, *H. reinhardtii* and *Lampanyctus cuprarius* fed mainly on *Pleuromamma* spp., followed by amphipods. Finally, *Diogenichthys atlanticus* fed mostly on *Pleuromamma* spp., which contributed to 32% of dietary carbon, followed by *Oncaea* spp. (21%) and *Candacia* spp. (18%). The copepods *Candacia* spp. were the dominant prey (contributing to 40.3% of the estimated dietary carbon) found in the stomachs of *Lampanyctus ater*. This species also fed on krill (25.1%) and *Pleuromamma* spp. (13.3%). Amphipods were the main prey for *H. benoiti* (39.0%), *M. punctatum* (58.4%), and *S. veranyi* (56.0%), and the next most important taxa were *Pleuromamma* spp. See Table 3 for an overview of the areas in which each species was collected.

3.3. Spatial variability of myctophid diet and prey selectivity

In general, myctophid species collected in the southern areas (1 to 5, i.e. from the coast of Africa to the Portuguese coast), mostly fed on copepods, particularly *Pleuromamma* spp. in most areas, followed by *Candacia* spp. in Areas 2 and 4 (Fig. 4). In southern stations (Area 1), krill contributed 17%, followed by amphipods with 13%, whereas in Area 5, the second and third most important prey were amphipods and *Candacia* spp. (contributing 21 and 10% to the diet, respectively). In the most coastal station (Area 3, note that there was no MultiNet station conducted in this area, see Table 1), *Pleuro-*

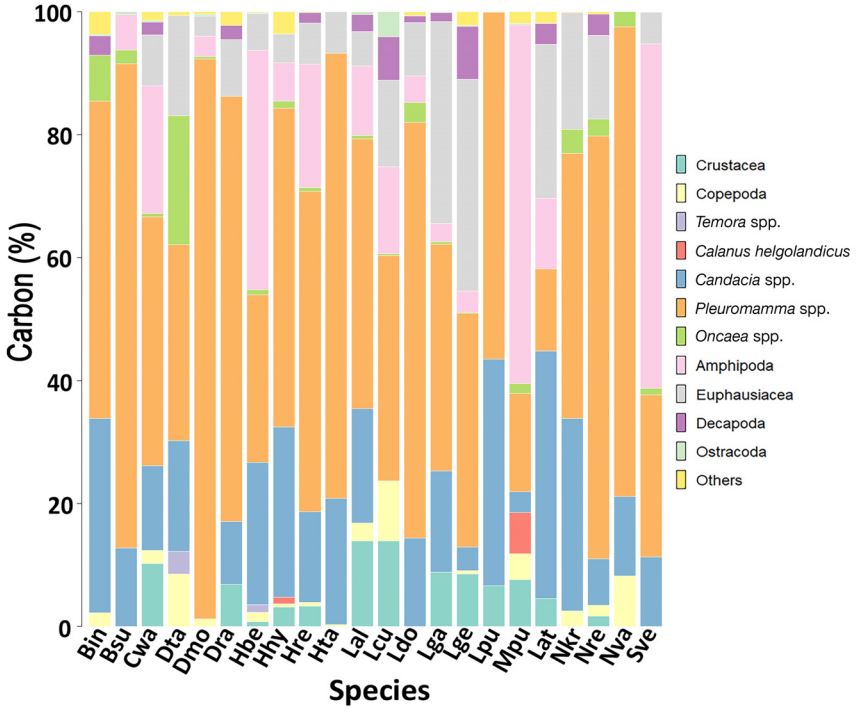

Fig. 3. Percentage of carbon content of the prey items found in the analysed stomachs of the 22 myctophid species. Bin: *Bolinichthys indicus*; Bsu: *Benthosema suborbitale*; Cwa: *Ceratoscopelus warmingii*; Dta: *Diogenichthys atlanticus*; Dmo: *Diaphus mollis*; Dra: *Diaphus rafinesquii*; Hbe: *Hygophum benoiti*; Hhy: *H. hygomii*; Hre: *H. reinhardtii*; Hta: *H. taaningi*; Lal: *Lampanyctus alatus*; Lcu: *Lampanyctus cuprarius*; Ldo: *Lobianchia dofleini*; Lga: *Lepidophanes gaussi*; Lge: *Lobianchia gemellarii*; Lpu: *Lampanyctus pusillus*; Mpu: *Myctophum punctatum*; Lat: *Lampanyctus ater*; Nkr: *Notoscopelus kroyeri*; Nre: *Notoscopelus resplendens*; Nva: *Notolychnus valdiviae*; Sve: *Symbolophorus veranyi*

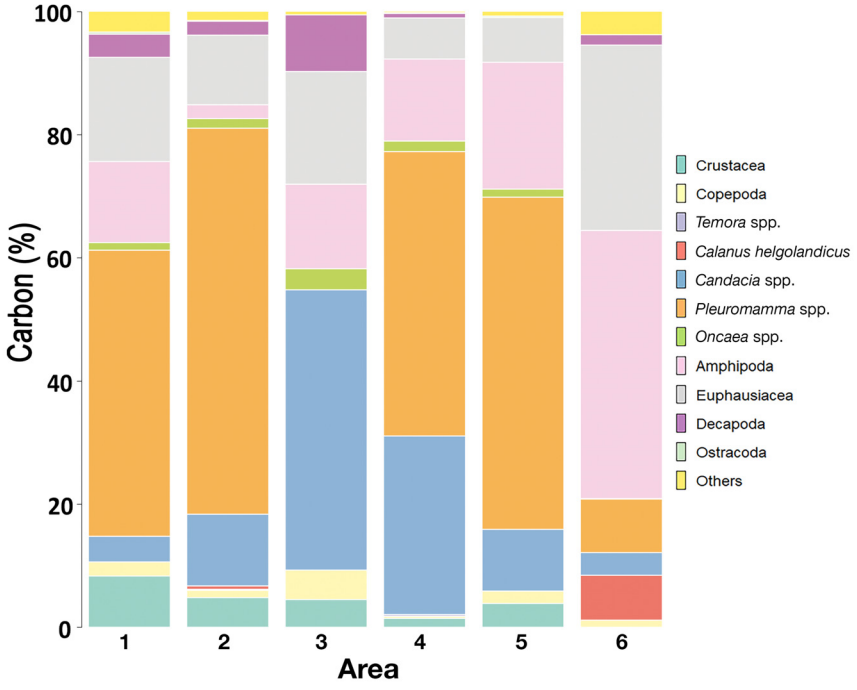

Fig. 4. Percentage of carbon content of the prey items found in the 6 areas analysed

mamma spp. were not identified in stomachs, and *Candacia* spp. were the main prey (45%), followed by krill (18%), amphipods (14%) and decapods (9%). Few myctophid species were collected in the northern stations (Area 6, i.e. along the Galician coast and Bay of Biscay). These individuals had a different diet to those in the other areas, and amphipods were their main prey (contributing 43% to the diet). The main copepods found in the stomachs of myctophids in this area were also *Pleuromamma* spp. (contributing 9% to the diet), followed by *Calanus helgolandicus* (contributing 7%).

Regarding prey selectivity, the copepods *Pleuromamma* spp. and *Candacia* spp., amphipods, euphausiids and decapod larvae were the most positively selected prey by all myctophid species, whenever these prey groups were present in the environment (Fig. 5). Although the copepods *Oncaea* spp. were found in the stomachs of several species, it was negatively selected in general, except by *Benthosema suborbitale*, *Bolinichthys indicus*, *Diogenichthys atlanticus*, *Lobianchia dofleini*, *Notolychnus valdiviae* and *Notoscopelus kroyeri*, which positively selected this prey (Fig. 5). Concerning other copepods, the calanoid *C. helgolandicus* was positively selected by *H. hygomii* and *M. punctatum*, *C. carinatus* by *B. indicus*, *Aetidaeus* spp. by *B. indicus*, *Scolecithrix* spp. by *C. warmingii* and *H. hygomii*, *Gaetanus* spp. by *L. gemellarii*, and the cyclopoids *Corycaeus* spp. by *L. dofleini*, and *Lubockia* spp. by *D. rafinesquii* and *N. resplendens* (Fig. 5). Pteropoda gastropods were also positively selected by fish species such as *Diaphus rafinesquii*, *H. reinhardtii*, *M. punctatum* and *Lampanyctus ater* (Fig. 5). The myctophid species *Benthosema suborbitale*, *Bolinichthys indicus*, *C. warmingii*, *D. mollis*, *L. ater* and *Lampanyctus cuprarius* positively selected ostracods (Fig. 5). Bivalve larvae and cyprid cirripeds were positively selected by *B. indicus* and *H. hygomii*, respectively (Fig. 5).

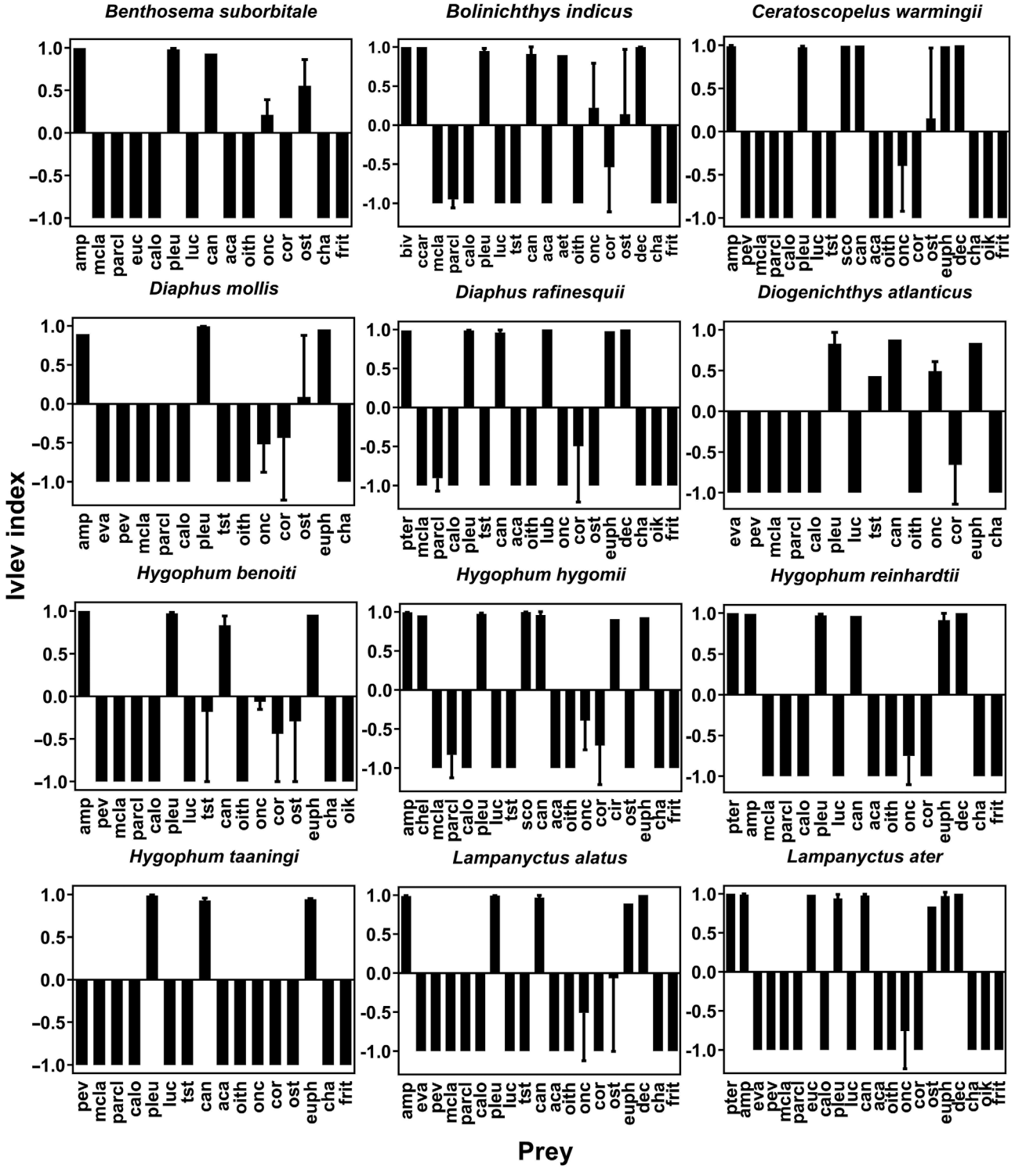

Fig. 5. (Above and next page.) Average Ivlev's electivity index (*E*) calculated for myctophid species according to the available zooplankton taxa in the environment. Error bars represent SD. pter: Pteropoda; biv: Bivalvia larvae; amp: Amphipoda; eva: *Evadne* spp.; pev: *Pseudevadne* spp.; ccar: *Calanoides carinatus*; chel: *Calanus helgolandicus*; mcla: *Mecynocera clausi*; parcl: *Para/Clausocalanus* spp.; euc: *Eucalanus* spp.; calo: *Calocalanus* spp.; pleu: *Pleuromamma* spp.; luc: *Lucicutia* spp.; tst: *Temora stylifera*; sco: *Scolecithrix* spp.; can: *Candacia* spp.; aca: *Acartia* spp.; aet: *Aetideus* spp.; gaet: *Gaetanus* spp.; oith: *Oithona* spp.; lub: *Lubockia* spp.; onc: *Oncaea* spp.; cor: *Corycaeus* spp.; cir: Cirripedia cyprid; ost: Ostracoda; euph: Euphausiacea; dec: Decapoda larvae; cha: Chaetognatha; oik: *Oikopleura* spp.; frit: *Fritilaria* spp.; dol: Doliolida

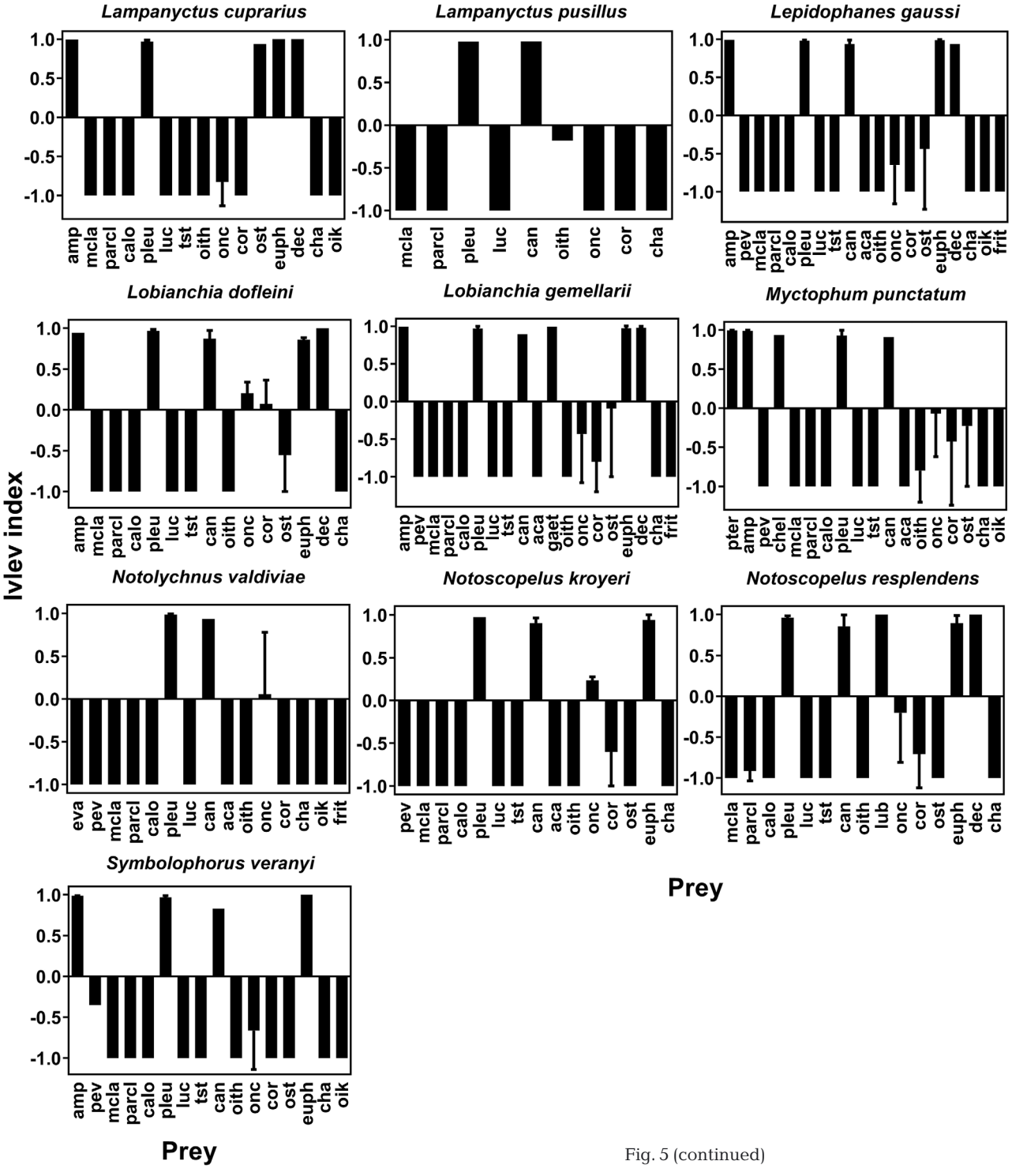

Fig. 5 (continued)

3.4. Feeding strategy

Most of the *Lampanyctus* species (*L. ater*, *L. alatus*, *L. cuprarius* and *L. pusillus*) and *M. punctatum* showed several prey located in the upper left of the Costello diagram (Fig. 6). This is indicative of specialization among individual predators, i.e. individual fish specialized on different types of prey, but each prey category was consumed by only a limited number of fish from the population (Fig. 6).

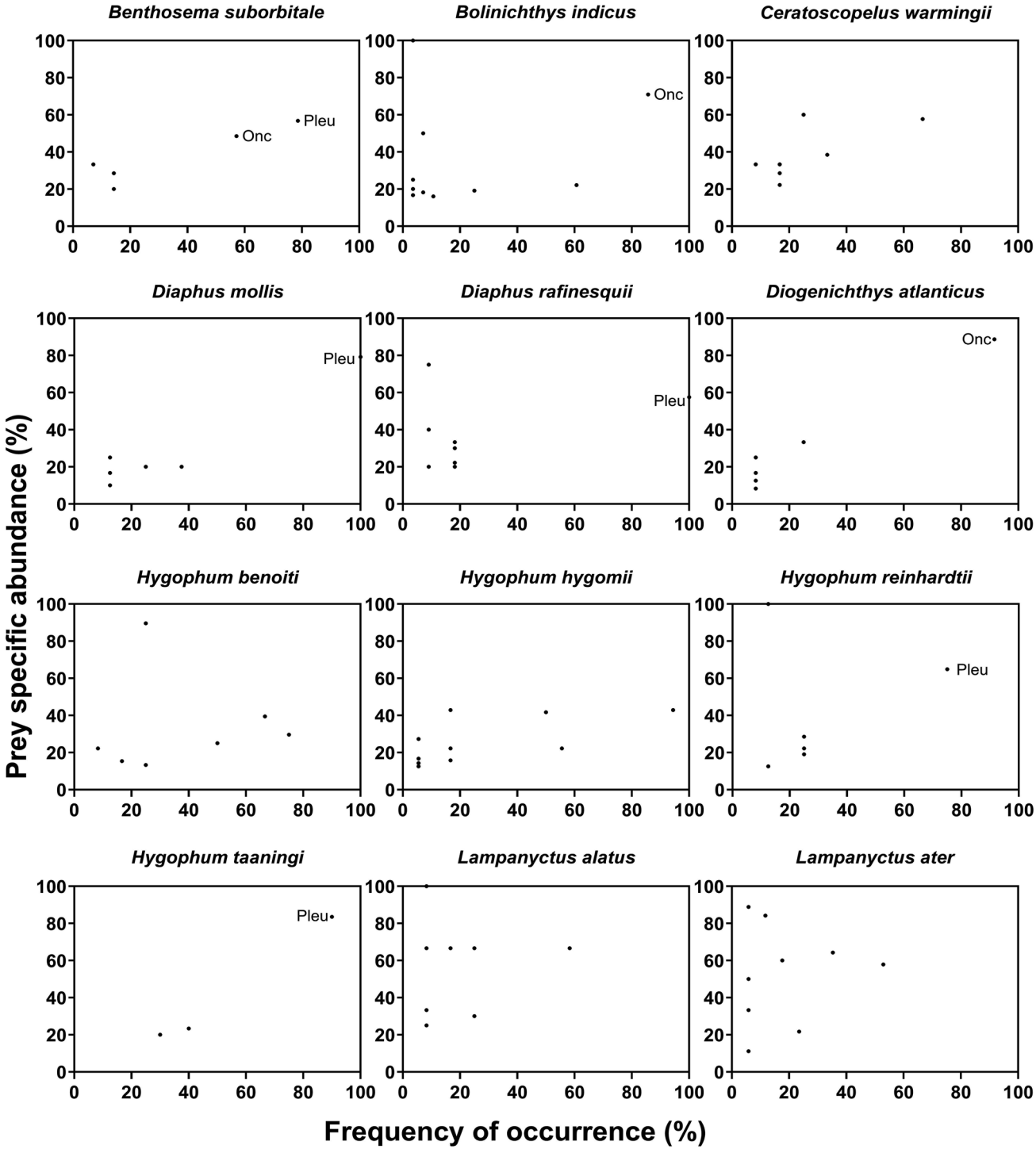

Fig. 6. (Above and next page.) Prey-specific abundance plotted against frequency of occurrence of prey present in the guts of Myctophidae species, indicating trends in importance of the prey, feeding strategy and niche width contribution according to Amundsen et al. (1996). These graphs allow inference of information on the importance of prey, feeding strategy and niche width contribution by analysis of the position of the different prey in the 2-dimensional plot. The importance of a given prey type is represented in the diagonal from lower left to upper right, corresponding to rare and dominant food items, respectively. Feeding strategy was assessed by analysing the vertical axis in terms of specialisation (upper part) or generalisation (lower part). The diagonal from upper left to lower right is indicative of the contributions of between- and within-phenotype components to the niche width, i.e. prey points located at the upper left correspond to individuals specialized on different resource types, and at the lower right means that most individuals use many resource types simultaneously. Onc: Oncaea spp.; Pleu: Pleuromamma spp.

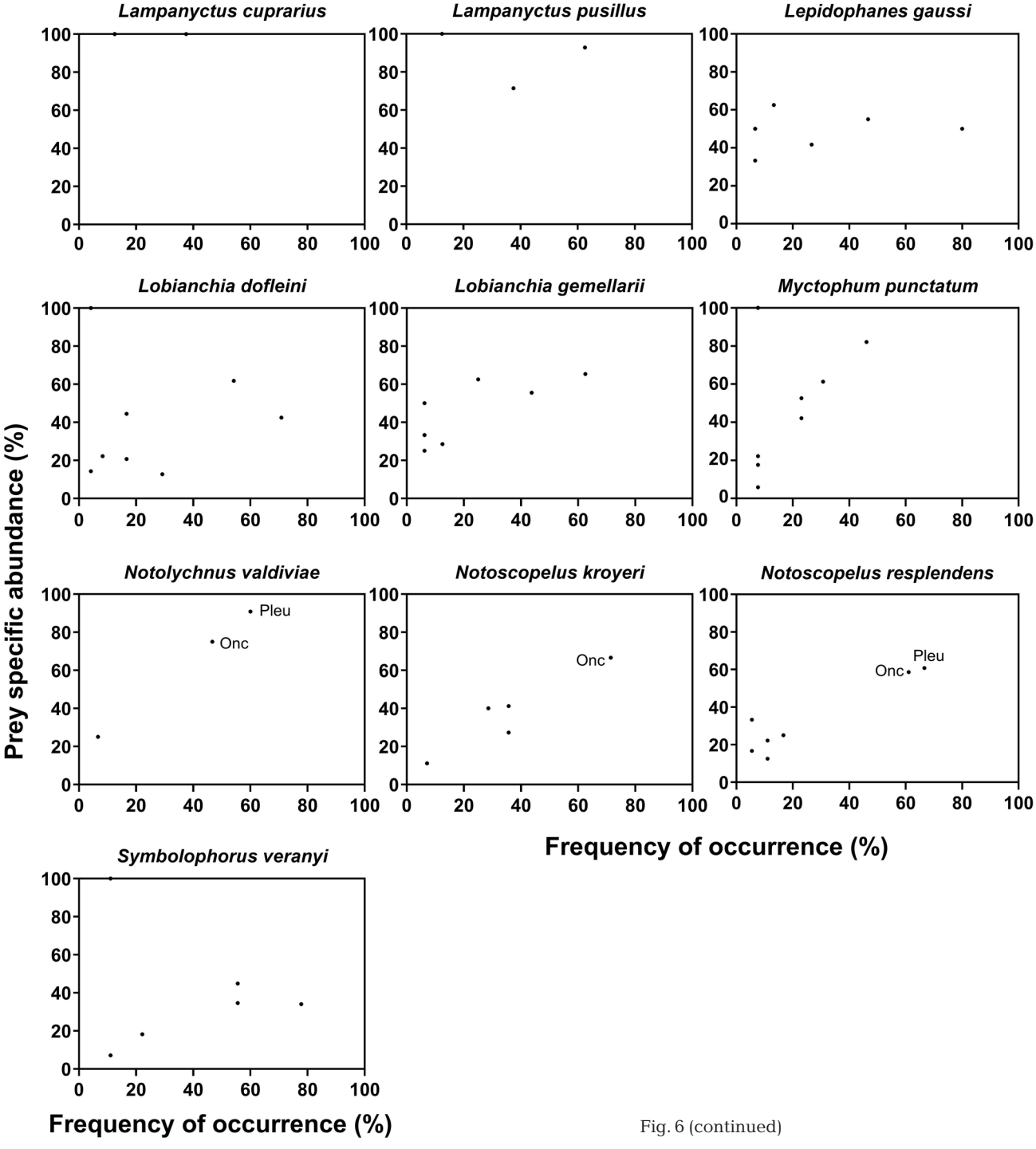

Fig. 6 (continued)

The *Diaphus* species (*D. mollis* and *D. rafinesquii*) and *H. taaningi* and *H. reinhardtii* specialized on *Pleuromamma* spp., and *Bolinichthys indicus*, *Diogenichthys atlanticus* and *Notoscopelus kroyeri* on *Oncaea* spp., whereas *Benthosema suborbitale*, *Notoscopelus resplendens* and *Notolychnus valdiviae* specialized on both prey items. Most individuals of these species fed on a dominant prey taxon and these prey points were located to the upper right of the Costello diagram (Fig. 6), while small proportions of other prey were occasionally included in the diet. These species showed specialization of the population with a narrow niche width.

Species such as *Ceratoscopelus warmingii*, *Lepidophanes gaussi*, *Lobianchia dofleini* and *Lobianchia*

gemellarii showed different degrees of specialization and generalization on several prey types, indicating a mixed feeding strategy (Fig. 6). *H. hygomii*, *H. benoiti* and *S. veranyi* prey points were mostly located towards the lower part of the diagrams, indicating that they fed on diverse zooplanktonic prey (Fig. 6). Thus, these species showed a generalized feeding strategy.

3.5. Diet overlap

Diet composition significantly changed among myctophid species in Areas 2, 4 and 5, even though there was a large overlap of the diets of some myctophid species (Fig. 7). In contrast, diet composition was not significantly different in Areas 1 and 3 ($p > 0.05$, $R^2 = 0.28$ and 0.34, respectively). Significant differences in diet composition were found in Area 2 ($F_{15,67} = 2.4124$, $p = 0.0001$, $R^2 = 0.41$), Area 4 ($F_{17,88} = 1.9693$, $p = 0.0001$, $R^2 = 0.32$) and Area 5 ($F_{15,63} = 2.1911$, $p = 0.0001$, $R^2 = 0.41$). In Area 2, pairwise comparisons revealed that diet composition was significantly different ($p < 0.01$) between *H. hygomii* and *Bolinichthys indicus* and between *H. hygomii* and *Notolychnus valdiviae*, whereas the other species showed similar diets. *N. valdiviae* (which is the smallest species of our samples) only fed on copepods. In contrast, pairwise comparison showed that diet composition of *Diogenichthys atlanticus* was significantly different ($p < 0.01$) from that of most *Hygophum* species (*H. hygomii*, *H. taaningi* and *H. benoiti*), *Lampanyctus pusillus* and *S. veranyi*. Also, the diet of *M. punctatum* was significantly different from that of most *Hygophum* species (*H. hygomii*, *H. taaningi* and *H. benoiti*) and *Lobianchia gemellarii*, and the diet of *H. benoiti* was significantly different from that of

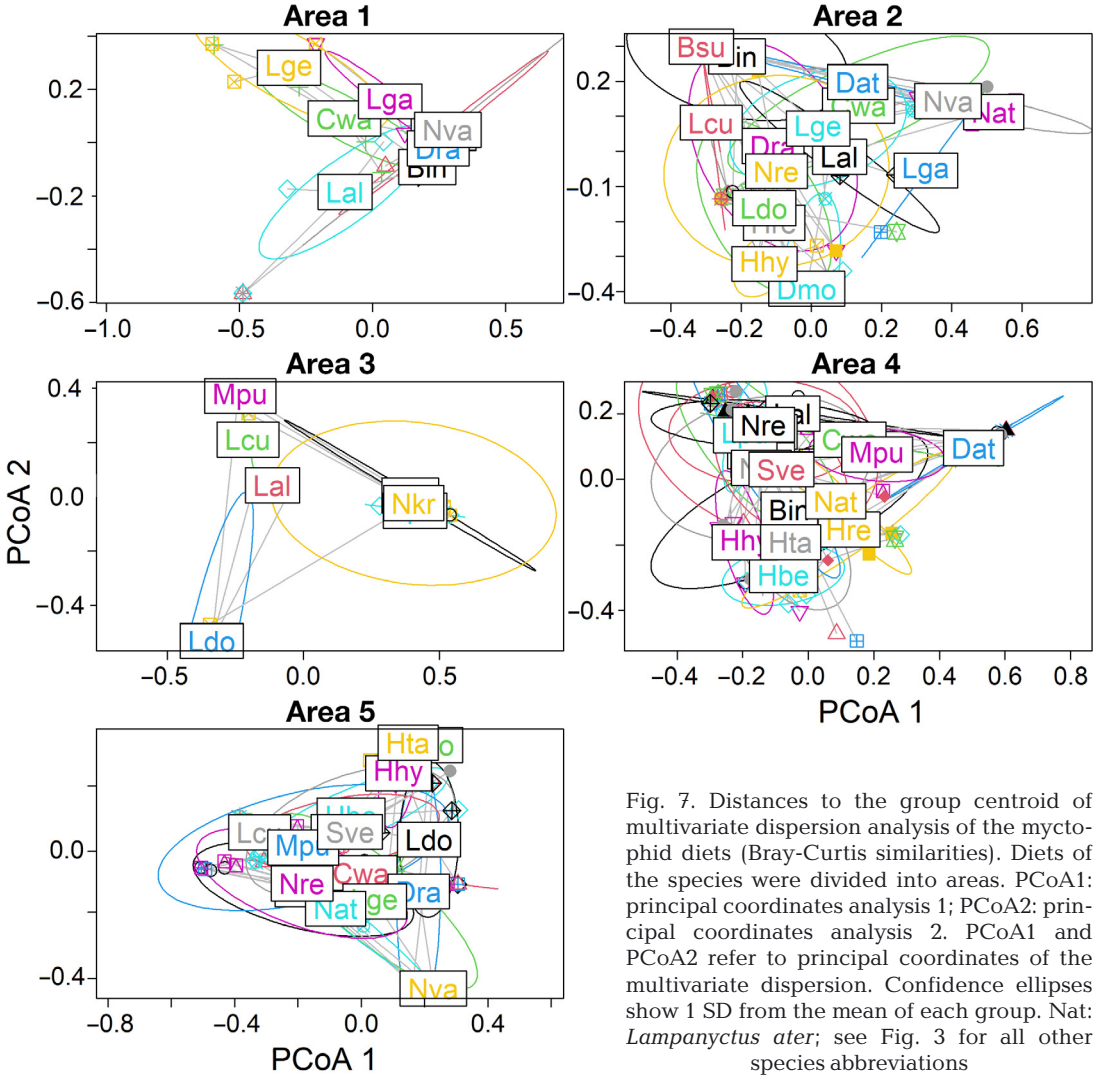

Fig. 7. Distances to the group centroid of multivariate dispersion analysis of the myctophid diets (Bray-Curtis similarities). Diets of the species were divided into areas. PCoA1: principal coordinates analysis 1; PCoA2: principal coordinates analysis 2. PCoA1 and PCoA2 refer to principal coordinates of the multivariate dispersion. Confidence ellipses show 1 SD from the mean of each group. Nat: *Lampanyctus ater*; see Fig. 3 for all other species abbreviations

Lampanyctus pusillus in Area 4. In this area, the 3 species with amphipods as main prey (*H. benoiti*, *M. punctatum* and *S. veranyi*) showed differences in diet when compared to other species, whose main prey were copepods (such as *H. hygomii*, *H. taaningi* and *D. atlanticus*). *H. hygomii*, and *M. punctatum* were the only species that fed on *Calanus helgolandicus*, while *D. atlanticus* and *H. benoiti* were the only ones that fed on the copepods *Temora* spp. (Fig. 3). Finally, the pairwise comparison showed that the diet of *H. hygomii* was significantly different ($p < 0.01$) from that of *B. indicus*, *Notoscopelus resplendens*, *Notolychnus valdiviae* and *Lampanyctus ater* in Area 5. However, the results of this area require cautious interpretation because the significance detected by the Adonis test in Area 5 could be an artefact of heterogeneous dispersions. In the other areas, Betadisper indicated homogeneity of the multivariate dispersions. Homogeneity of the dispersion between groups is an assumption for Adonis, thus confirming the results.

4. DISCUSSION

4.1. Methodological aspects

For logistical reasons, zooplankton collected by the opening/closing Mammoth MultiNet and the myctophid samples collected with the macroplankton and Multpelt trawls were not taken simultaneously, and sample positions were not exactly the same. Thus, the zooplankton samples do not necessarily represent the exact available prey of the myctophids analysed. Nevertheless, due to the proximity in location and time, we expect that our data are accurate enough for the analyses. Zooplankton was sampled from different depth strata, whereas trawls sampled the entire water column. We decided to analyse zooplankton from the whole water column and compared it with the myctophid diet, but it is important to note that the water layers where fishes are located during daytime may not necessarily correspond to the exact layer where they have been feeding. Most myctophid species undergo DVM (Sutton et al. 2013). The linkage between these DVMs and the peak of fish feeding activities is well known (Pusch et al. 2004b). In the present study, sampling was conducted mostly during daylight hours (Catul et al. 2011). Daytime feeding has been reported for some species, such as *Benthosema glaciale* (see Gjøsæter 1973, Kawaguchi & Mauchline 1982, Sameoto 1988), but myctophids are mainly nocturnal feeders (Catul et al. 2011). This is supported by results on feeding incidence despite the limited number of stomachs collected at night. The digestion process continues during the daytime and thus prey in our samples were not completely digested, allowing feasible results to be obtained from stomach content analyses. Considering that the capacity to identify prey depends on digestion rate, soft prey are probably underestimated in this study. Crustaceans (due to the exoskeleton) are digested more slowly than soft-bodied organisms, such as salps and other gelatinous plankton (Arai et al. 2003, Hays et al. 2018). Similarly, some prey types are easier to identify even in advanced stage of digestion, such as the *Pleuromamma* genus, which can be identified only the thoracic pigment spot.

A potential bias in stomach content analyses is net feeding, i.e. fish feeding inside the trawls. Although some degree of net feeding may occur, it is unlikely that this is extensive for many midwater fishes (Hopkins & Baird 1977, Moku et al. 2000). Finally, stomach content analyses provide information on the taxonomy of the prey and size composition but only a snapshot in time of the diet. Therefore, studies analysing diel and seasonal variability of prey composition or complementary analysis such as fatty acid biomarkers and stable isotopic composition are recommended.

4.2. Spatial diet variability

The myctophids analysed in this study are zooplanktivores. In general, most individuals mainly feed on copepods, krill and amphipods, which is consistent with the results of studies conducted in the Northeast Atlantic (e.g. Merrett & Roe 1974) and elsewhere (e.g. Shreeve et al. 2009). In general, the spatial variability of myctophid diets along the Northeast Atlantic was low. The fact that the diet of myctophid species did not significantly vary spatially, and most species depended on the copepods *Pleuromamma* spp. in oceanic areas, seems to be in accordance with the competition theory (Abrams 1992), which states that in deep environments with low plankton availability, there is greater adaptation and specialization.

The taxa that mostly contributed to myctophid diets in all the studied areas were the copepods *Pleuromamma* spp., with a few exceptions (particularly Areas 3 and 6). *Pleuromamma* is a very common epi-mesopelagic oceanic/neritic genus, comprising 7 possible species that can occur across the studied area (Razouls et al. 2005–2023). Although it was not the most abundant copepod in the water, it was often found inside the guts of most species. This copepod genus is also an important prey in other regions, such

as the eastern Gulf of Mexico, where it accounted for 40% of the copepod biomass consumed by low-latitude mesopelagic fish (Hopkins et al. 1996). The fact that this taxon performs DVMs, like most myctophid species (Hattori 1989, Hays 1996, Fernandez de Puelles et al. 2023), may explain the preference for this prey, besides other characteristics inherent to this genus (e.g. size, bioluminescence, pigment spot). Sameoto (1988) suggested that *B. glaciale* and *Pleuromamma* spp. vertically migrate in synchrony. Previous studies (Sameoto 1988, Pusch et al. 2004b) reported that some myctophids (*B. glaciale* and *Lobianchia dofleini*) and their prey (*Pleuromamma* spp.) were mainly concentrated at the same depths during both day and night, and thus, the preferred prey species of myctophid are available for them anytime. Conversely, other large copepod species (*Metridia* spp. and *Calanus* spp.), which were concentrated above the night-time depth of *B. glaciale*, were negatively selected (Sameoto 1988).

The absence of *Pleuromamma* spp. in all fish stomachs collected in Area 3 is probably due to its proximity to the coast of Morocco, where more oceanic taxa are less abundant (Somoue et al. 2005). In fact, according to Ettahiri et al. (2021), *Pleuromamma* is much less dominant during this period of the year. The copepods *Candacia* spp. were the highest contributor to fish diet in this area, followed by amphipods, euphausiids, decapods and other copepods such as *Oncaea* spp. No MultiNet hauls were performed in this area. However, data from the literature show that the abundance of *Candacia* spp. was low in this area, similar to *Pleuromamma* spp. (Somoue et al. 2005), but the former species are probably present at higher densities than the latter copepods. *Candacia* spp. were also an important prey in other areas, particularly in Areas 2, 4 and 5.

Oncaea is a neritic genus, very common and dominant off the coast of Morocco (Lidvanov et al. 2018), which explains the high contribution to myctophid fish diet in Area 3, when compared to other areas. The same occurred for decapods, which are also dominant in this area (Lidvanov et al. 2018). It is important to note that Area 3 only has 1 station, and this was sampled in the afternoon rather than in the morning as for most of the other stations. Thus, the results for Area 3 should be interpreted with caution. However, considering our data on feeding incidence and previous literature (e.g. Catul et al. 2011), the differences that are expected due to the time of sampling are in the degree of digestion, not in the diet composition.

Myctophid species that occurred in the southern areas (i.e. from the coast of Africa to the Portuguese coast), such as *Benthosema suborbitale*, *Hygophum hygomii*, *H. taaningi*, *L. dofleini* and *Notoscopelus resplendens* (García-Seoane et al. 2021), mostly fed on copepods. On the Galician coast and in the Bay of Biscay, amphipods were the most represented taxa in fish diets, followed by euphausiids, and surpassing copepods. The species collected in the northern area comprise ubiquitous species (e.g. *Lampanyctus ater*; García-Seoane et al. 2021) and other species recorded in northern and southern stations, such as *Myctophum punctatum* and *N. kroyeri*. It is important to note that the northern area (Area 6) corresponds with the lowest diversity of the study area (García-Seoane et al. 2021), and since this study targeted 6 individuals per area and species, few species corresponds to fewer stomachs. Conclusions about the main prey in Area 6 should be interpreted with caution due to the low number of stomachs from there. However, the few non-empty stomachs of *B. glaciale* (dominant species only registered along the Galician coast and in the Bay of Biscay; García-Seoane et al. 2021) analysed in this study are consistent with these results, showing that amphipods were also the most important prey in terms of numbers (Table A1 in the Appendix). In this study, the main prey for most species included in this work were copepods (except for large *M. punctatum* and *Symbolophorus veranyi*, for which amphipods were the dominant prey). Different prey composition has previously been reported for other areas. For example, in the Eastern Gulf of Mexico, decapods were the main prey of *H. hygomii*, while at the Great Meteor seamount, amphipods were their main prey (Pusch et al. 2004b). Amphipods were also the main prey of *Lampanyctus cuprarius* in the North Atlantic (30° N, 26° W) (Merrett & Roe 1974) and of *Ceratoscopelus warmingii* at the Great Meteor seamount (Pusch et al. 2004b). Fish have been documented as the main prey item for *B. suborbitale* off the Iberian Peninsula (off Lisbon and the Gulf of Cadiz) (Bernal et al. 2023) and for *S. veranyi* off the Grand Bank of Newfoundland and the Flemish Cap (Podrazhanskaya 1993). In contrast, euphausiids were the main prey for *N. kroyeri* (Gjøsæter 1981) in the Northeast Atlantic and for *Diaphus rafinesquii* and *M. punctatum* off the Grand Bank of Newfoundland and the Flemish Cap (Podrazhanskaya 1993). At the Mid-Atlantic Ridge, *H. hygomii* preyed mostly on euphausiids and copepods (Hudson et al. 2014). In the Gulf of Cadiz, the diet of *Lepidophanes gaussi* consisted almost exclusively of copepods, unlike our findings showing euphausiids as an important prey. Off Lisbon, *M. punctatum* fed mainly on calanoid copepods (*Euchaeta* spp. and *Centropages* spp.), whereas in the Alboran Sea, appendicularians were the main prey. One explanation for these

differences in diet composition might be variations in food availability in the different regions. In contrast, the individuals collected in this study were much smaller than in previous studies (except for *B. suborbitale*, *Lampanyctus cuprarius*, *D. rafinesquii*, *Lepidophanes gaussi* and *M. punctatum*) and diet composition varied ontogenetically. For instance, most specimens of *S. veranyi* sampled in this study were smaller than 50 mm SL, whereas the individuals sampled by Podrazhanskaya (1993) ranged between 65 and 120 mm SL. Another example is *N. kroyeri*: individuals of this species sampled by Gjøsæter (1981) ranged between 105 and 142 mm SL, while those in the current study ranged between 21 and 39 mm SL. In contrast, most of the specimens of *Lepidophanes gaussi* and *M. punctatum* sampled by Bernal et al. (2023) in the Northeast Atlantic and the Mediterranean Sea were smaller than our samples, and thus, the fact that smaller individuals feed on smaller prey is most likely due to an ontogenetic dietary shift in these species. The change in diet throughout ontogeny is likely related to the variability of energy requirements related to growth, reproduction and predator avoidance. In fact, deep pelagic fish species have been shown to either shift their food resources (larger prey or prey with a higher trophic level), while others just increase food intake (Loutrage et al. 2024).

Species-specific differences in diet composition related to body size have been previously reported, namely showing that myctophids with small body sizes (e.g. *H. benoiti* and *Protomyctophum arcticum*) feed mainly on copepods, whereas larger myctophids species (e.g. *M. punctatum*, *Notoscopelus bolini* and *N. kroyeri*) feed mainly on larger prey such as krill (Gjøsæter 1981, Podrazhanskaya 1993). Shreeve et al. (2009) analysed individuals from different myctophid species collected in the northern Scotia Sea and found that the smallest individuals (<75 mm SL) fed on significantly more copepods than larger individuals, amphipods were the main prey for medium-sized myctophids (76–100 mm SL) and krill was important for the largest individuals (>100 mm SL), independent of the species. The smallest species of our samples (*Notolychnus valdiviae*) only fed on copepods, and this constrained food spectrum has been previously reported (Kinzer & Schulz 1985). However, in the equatorial Atlantic, previous studies have also found other prey in *N. valdiviae* stomachs: mainly ostracods, but also euphausiid larvae (Merrett & Roe 1974, Kinzer & Schulz 1985). This could be explained by a seasonal variation in diet, probably due to changes in the available prey throughout the year. Seasonal variation in diet has been previously reported for myctophids; for example, Gjøsæter (1981) found that in the Northeast Atlantic (between 54 and 66° N), *Notoscopelus kroyeri* only feed on euphausiids during winter, whereas in spring, copepods were also found in their stomachs. To confirm if the patterns observed in this study during spring are characteristic annual patterns of the study area, it is necessary to sample during other times of the year. In addition, analyses of stomach contents provide only a snapshot of the diet, and thus, other analyses (such as stable isotope studies) are needed to reflect an integrated overview of the diet through time.

4.3. Selectivity and visual prey detection

Prey items identified in stomach contents did not fully match the zooplankton communities in the water column. Even considering the possibility that densities of larger zooplankton might be underestimated due to net avoidance, most myctophid species included in this study showed positive selection for amphipods, euphausiids and decapod larvae. This agrees with previous studies; for example, Merrett & Roe (1974), Pusch et al. (2004b), and Bernal et al. (2015) reported that *Lobianchia dofleini* and *H. hygomii* positively selected euphausiids and *H. benoiti* the cyclopoids *Corycaeus* spp., whereas Merrett & Roe (1974) found that *Lampanyctus cuprarius* fed selectively on amphipods and probably decapods. In contrast to our results, Pusch et al. (2004b) found that *Lobianchia dofleini* (sampled in the same length range as this study) preferably selected ostracods and Merrett & Roe (1974) suggested that it is a generalist feeder (but limited data were available in the former study).

Dominant copepods of ⩽1 mm (e.g. *Oithona* spp., *Paracalanus* spp. and *Clausocalanus* spp.) were seldom consumed, except for *Oncaea* spp., which were important prey for several myctophid species. Myctophids might be inefficient at capturing these small prey, or prey are too small to be efficiently retained by gill rakers (Shreeve et al. 2009). The larger copepod species *Pleuromamma* spp. and *Candacia* spp. were positively selected by almost all myctophid species analysed in this work. Previous studies have shown that myctophid species preferentially feed on the genus *Pleuromamma* (Scotto di Carlo et al. 1982, Sameoto 1988, Bernal et al. 2015). All species of the genus *Pleuromamma* exhibit bioluminescence (Herring 1988), which might explain the positive selection, as well as their large body size, or it might be related to the detection of the large thoracic pigment spot on the side of the body (Bernal et al. 2013). *B. gla-*

ciale tend to select large copepods species (>1 mm), such as *Pleuromamma* spp., but not *Calanus finmarchicus*, which was the most abundant copepod species at the Nova Scotia shelf (Sameoto 1988). Roe & Badcock (1984) suggested that the myctophid *Benthosema glaciale* selects its prey according to size, because *Metridia lucens* was positively selected but the abundant *Clausocalanus* avoided. However, it is important to note that *M. lucens* is also a bioluminescent copepod (Clarke et al. 1962), and this could be the cause of positive selection. This is supported by the fact that some other myctophid species (in particular, *H. benoiti* and *Myctophum punctatum* stranded in the Strait of Mesina, Mediterranean Sea) have been described as visual predators, oriented on suitable size classes and likely preying more intensively on more visible prey such as bioluminescent copepods (Scotto di Carlo et al. 1982). It has been suggested that copepod bioluminescence has a defensive function (Widder 1992). However, despite bioluminescence, our data show that myctophids are successful at capturing these copepods.

Myctophids have well developed eyes and light organs for counterillumination camouflage or intraspecific camouflage, and vision plays a key role in their life (Turner et al. 2009). In order to find a solution to the trade-off conflict between visual foraging opportunities and visual predation risk, many species of myctophids (like other mesopelagic fish species) migrate to a particular depth during the DVM (Røstad et al. 2016, Kaartvedt et al. 2019). The light comfort zone hypothesis suggests that this depth depends on the optical conditions of the environment, i.e. mesopelagic fishes living in a murky water column are expected to have a shallower and narrower depth distribution than those in a clear water column (Røstad et al. 2016). In addition, the sensitivity hypothesis assumes that the visual pigments of mesopelagic fish maximize the sensitivity of the eye to downwelling sunlight (Turner et al. 2009). However, in contrast to this hypothesis, Turner et al. (2009) suggested that the visual pigments of myctophids are well placed for the visualization of bioluminescence instead.

4.4. Feeding strategies (generalist vs. specialist) and prey taxa as a limiting resource (resource partitioning vs. diet overlap)

Our results on feeding strategy indicate that most myctophid species are specialists, with both narrow (specialization of the predator population) and wide width niche (specialization of individual predators). In agreement with our results, mixed feeding strategies for *Lobianchia dofleini* were found in the Mediterranean Sea and Northeast Atlantic (Bernal et al. 2015, 2023) and *H. benoiti* was classified as a generalist species in the Mediterranean Sea (Bernal et al. 2023). Previous studies on myctophid feeding strategies from different regions have shown evidence of both generalist predators (which are dependent on prey availability) and feeding specialization. In general, myctophid species from temperate and high latitudes exhibit a high degree of overlap in their food spectrum, showing a generalist strategy (e.g. Pakhomov et al. 1996, Battaglia et al. 2014) because of high regional food availability. As an exception, Moku et al. (2000) suggested spatial resource partitioning among 3 species of myctophid in the productive subarctic and transitional waters off Japan, but the competing pressure in this area is expected to be lower than in oligotrophic low-latitude regions. Among the 6 areas in our study, 5 correspond to tropical and subtropical latitudes, and a specialist strategy has been mainly reported for myctophids (e.g. Clarke 1980, Hopkins & Gartner 1992, Van Noord 2013, Watanabe et al. 2002) which reduces interspecies diet overlap and food competition pressure for the scarce resources characteristic of oligotrophic waters. This dietary specialization is probably due to several factors, such as fish size, filtering capacity of the gill rakers, gape size and vertical distribution of myctophids and prey (Shreeve et al. 2009).

In addition, our results indicated a large overlap of myctophid diet, in agreement with Bernal et al. (2015), who reported diet overlap between Mediterranean mesopelagic fish species. This is contrary to the general assumption of the strong selective feeding strategies in oligotrophic waters, like the Mediterranean Sea, or most of our study area, and thus food resources do not seem to be a limiting factor. A possible explanation is that the mesopelagic fish assemblage is nonsaturated (low number of species in comparison with other low and mid-latitude areas), and more species could coexist in the region (Bernal et al. 2015). In contrast, the resource partitioning in myctophids is not only accomplished through partitioning of the prey, but also through partitioning of vertical space (Hopkins & Gartner 1992). Thus, the feeding strategy of myctophids is closely related to their diel migration patterns and migrating myctophids specialize in different prey types from different vertical habitats to reduce the trophic competition (Moku et al. 2000, Watanabe et al. 2002). Myctophids feed in the epipelagic layers at night (Sutton 2013), whereas daytime feeding was also reported for some species, e.g. *Benthosema*

glaciale, *H. benoiti* and *H. hygomii*, and *Lampanyctus crocodilus* individuals living near the bottom (Bagøien et al. 2001, Bernal et al. 2015). Peaks in feeding time are different among the migrant myctophid species, usually corresponding with the highest prey densities in the area (Watanabe et al. 2002).

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Appendix

Table A1. Diet composition of the myctophid *Benthosema glaciale* sampled in the Northeast Atlantic (n = 4)

Food item	Number
Copepods	1
Amphipods	7
Krill	1

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