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Feeding ecology of three myctophid species at the Great Meteor Seamount (North-east Atlantic)

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Abstract

The feeding ecology of three abundant myctophid species was studied using individuals sampled at the Great Meteor Seamount during a cruise of RV "Meteor", M42/3, in September 1998. Different habitats defined by water depth were sampled with a pelagic trawl: the north-eastern and the south-western slopes of the seamount (bottom depths between 300 and 1500 m), and an oceanic deep-water station (bottom depth > 2300 m). The food composition of the three myctophids was analysed and showed interspecific differences. The diets of the larger myctophid species, *Ceratoscopelus warmingii* (standard length 20 to 76 mm) and *Hygophum hygomii* (SL 29 to 63 mm), were dominated by amphipods. In contrast, the major prey categories of the smaller sized myctophid *Lobianchia dofleini* (SL 21 to 34 mm) were ostracods and calanoid copepods. We found a shift in prey composition of *C. warmingii* with predator size. Individuals larger than 40 mm standard length fed on a higher proportion of amphipods and on a lower proportion of pteropods compared to smaller sized individuals. Comparison of the myctophid diets with zooplankton composition in multi-net samples showed that the examined species consume selected prey categories in disproportionate numbers to their environmental abundance. *L. dofleini* showed a pronounced selectivity for the copepod species *Pleuromamma xiphias*. The observed differences in the dietary compositions of *C. warmingii* and *H. hygomii* at different localities of the seamount was a result of local predator size variability rather than an effect of local food availability. Feeding intensity of the myctophids was enhanced over the seamount slopes compared to an oceanic reference station. This could be due to more favourable feeding conditions over the seamount slopes, where hydrographic conditions were characterised by enhanced turbulent mixing processes.

Kurzfassung

Die Ernährung von drei Myctophidenarten im Gebiet der Großen Meteorbank

Die Nahrungsökologie von drei häufigen Myctophidenarten im Bereich der Großen Meteorbank wurde untersucht, anhand von Individuen, die mit einem pelagischen Trawl auf der Forschungsfahrt M42/3 mit der FS „Meteor" im September 1998 gefangen wurden. Dabei wurden verschiedene bathymetrisch definierte Habitate beprobt: Der Seebergabhang im Nordosten und Südwesten des Seebergs (Wassertiefen 300 bis 1500 m) sowie eine ozeanische Tiefwasserstation (Wassertiefe > 2300 m). Die Nahrungszusammensetzung der drei häufigsten Myctophidenarten wurde analysiert und zeigte artspezifische Unterschiede. Die Nahrung der größeren Arten *Ceratoscopelus warmingii* (Standardlänge 20 bis 76 mm) und *Hygophum hygomii* (SL 29 bis 63 mm) wurde dominiert durch hyperiide Amphipoden, wohingegen die kleinere Art *Lobianchia dofleini* (SL 21 bis 34 mm) hauptsächlich Ostracoden

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und Copepoden fraß. Für *C. warmingii* wurde mit zunehmender Individuengröße eine Verschiebung des Beutespektrums von kleineren Organismen wie Pteropoden hin zu größeren wie Amphipoden beobachtet. Der Vergleich der Nahrungszusammensetzung der Myctophiden mit der Zusammensetzung des Zooplanktons in Multischließnetzfängen zeigte, dass bestimmte Beuteorganismen unverhältnismäßig häufig im Vergleich zu ihrer Abundanz gefressen wurden. *L. dofleini* zeigte eine ausgeprägte Selektivität für die Copepodenart *Pleuromamma xiphias*. Lokale Unterschiede in der Nahrungszusammensetzung von *C. warmingii* und *H. hygomii* in verschiedenen Habitattypen waren weniger auf die Variabilität der Zooplanktonzusammensetzung als auf Unterschiede in der Größenverteilung der Fische zurückzuführen. Die Fraßintensität der Myctophiden über den Seebergabhängen war im Vergleich zur ozeanischen Referenzstation erhöht, was auf eine bessere Nahrungsverfügbarkeit in diesem Habitattyp aufgrund erhöhter Turbulenz beruhen könnte.

Introduction

Mesopelagic fish represent an important component of the deep scattering layer (Salvanes and Kristoffersen 2001). The majority of these fishes exhibit extensive diurnal vertical migrations, bringing them from daytime depths below 500 m into the food-rich epipelagic layers during the night (Badcock and Merrett 1976; Kinzer and Schulz 1985). Midwater fishes represent an important link between predators of higher trophic levels (*e. g.*, seabirds, squids, piscivore fishes, marine mammals) and zooplankton. Due to their crucial role in the mesopelagic food web, there is extensive literature relating to the diets of mesopelagic fish, indicating that most of them feed on crustacean zooplankton such as amphipods, copepods, euphausiids and ostracods (Hopkins and Baird 1977; Gartner *et al.* 1997).

Many pelagic ecosystems are characterised by the absence of structural microhabitats and generally food-poor environments (Hopkins and Baird 1977). Mesopelagic fish feeding in the epipelagic layers of subtropical waters are assumed to experience competitive pressure towards the partitioning of limited food resources (Merrett and Roe 1974; Hopkins and Gartner 1992). The question of whether the feeding behaviour of mesopelagic fishes is opportunistic, *e. g.*, the composition of food in fish stomachs mirrors the composition of zooplankton in the environment, or whether fish feed selectively to reduce competition, is still under scientific discussion. Selectivity can be related to taxon, size, and distribution of predators and prey (Hopkins and Baird 1977; Gartner *et al.* 1997). Taxonomic selectivity may reduce interspecific competition if many individuals of a predator species take a specific prey taxa in disproportionate numbers to their environmental abundance, or it may reduce intraspecific competition if a specific size range (*e. g.*, juveniles) of the predator selectively ingest specifically sized prey taxa. The present study investigates whether the abundant myctophids *Ceratoscopelus warmingii*, *Hygophum hygomii* and *Lobianchia dofleini*, which co-occur in the upper water layer above Great Meteor Seamount (Pusch *et al.* 2004), have evolved mechanisms to reduce intra- or interspecific competition, *e. g.*, by the utilisation of different prey categories.

Seamounts are elevations of the seafloor and are known to alter the characteristics of the water masses surrounding them (Rogers 1994). Relatively little is known about the feeding ecology of mesopelagic fish in the vicinity of submerged topographic features like seamounts (Gartner *et al.* 1997). Numerous publications describe reduced abundances of vertically migrating organisms above shallow topographic features, such as mesopelagic fish larvae and euphausiids above Great Meteor Seamount (Nellen 1973; Weigmann 1974), and zooplankton above the summits of the eastern North Pacific seamounts (Genin *et al.* 1988; Genin *et al.* 1994; Haury *et al.* 2000). Pusch *et al.* (2004) observed a "thinned out" mesopelagic fish community above the NE slope of the Great Meteor Seamount and an almost complete lack of myctophids above the shallow plateau. As a possible reason, reduced food availability above the seamount summit was considered. However, the zooplankton distribution at Great Meteor Seamount showed no significant differences in total abundance between different topographic stations (Schnack-Schiel and Henning 2004), even though the relative abundances of specific taxa varied considerably. The present study investigates whether existing differences in the zooplankton distribution were reflected in the myctophids' diets and compares the feeding intensities of myctophids at different seamount localities.

Thus the main objectives of the present paper are the questions:

a) Is there a difference in dietary composition among three abundant myctophid species at the Great Meteor Seamount?
b) Is a shift in prey size and prey composition with increasing predator size observable?
c) Do the myctophid species feed selectively on specific prey species?
d) Does the Great Meteor Seamount influence the dietary composition and feeding intensity of myctophids at different topographic stations?

Material and methods

Sampling and laboratory analysis

Mesopelagic fishes and zooplankton were studied during cruise M42/3 of the RV "Meteor" in September 1998 to the Great Meteor Seamount (subtropical NE Atlantic). The fishes were sampled with a pelagic Young Fish Trawl (YFT) during the night. The estimated mouth opening of the YFT was 80 m^2 with a mesh size of 11 mm at the cod end. The YFT was towed at a ship's speed of 3.0 to 3.5 knots in a horizontal manner at selected depth horizons (Table 1), with the exception of Station 531, which was sampled in a double oblique tow. Zooplankton was sampled with a multiple opening/closing net system (Multi-Net) with a mouth opening of 0.25 m^2 and a mesh size of 100 mm. Stratified samples were collected at the 300 to 150 m, 150 to 50 m, and 50 to 0 m depth horizons (Schnack-Schiel and Hen-

Table 1: Sample data, YFT = Young Fish Trawl; Multi-Net = Multiple opening/closing net.

Station No.	Gear	Date	Latitude	Longitude	Time [UTC]	Habitat	Sample depth [m]	Water depth [m]
531	YFT	15 July 98	29°47.8' N	28°38.4' W	20:19–20:37	SW slope	0–300	325–1480
540	YFT	16 July 98	30°10.1' N	28°17.8' W	20:35–20:51	Deep water	100–250	2340–2475
541	YFT	16 July 98	30°09.0' N	28°16.9' W	22:40–23:00	Deep water	300–400	2348–2553
542	YFT	17 July 98	30°07.1' N	28°23.0' W	00:53–01:08	NE slope	120–135	452– 570
543	YFT	17 July 98	30°07.0' N	28°23.2' W	02:19–02:38	NE slope	140–250	568– 750
461	Multi-Net	5 July 98	29°47.8' N	28°38.4' W	02:20–03:30	SW slope	0–300	1002–1045
506	Multi-Net	12 July 98	30°12.3' N	28°14.4' W	02:30–03:05	Deep water	0–300	3009–3014
509	Multi-Net	12 July 98	30°07.2' N	28°22.8' W	20:51–21:51	NE slope	0–300	1005

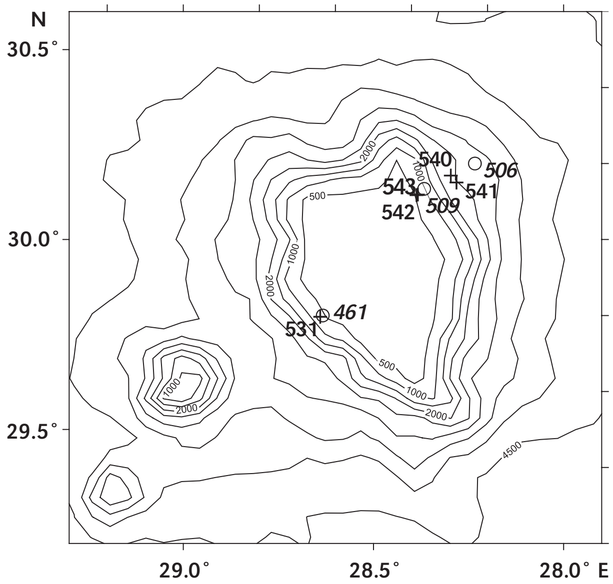

Figure 1: Stations at Great Meteor Seamount sampled with Young Fish Trawl (+, non-italic station numbers) and Multi-Net (○, *italic* station numbers).

ning 2004). YFT stations and Multi-Net stations were located at different sites of the seamount (Figure 1, Table 1). Four YFT and two Multi-Net stations were located on the north-eastern side of the seamount. Two YFT hauls (# 540 and 541) and one Multi-Net station (# 506) were sampled in areas with bottom depths > 2300 m, hereafter called "deep-water" stations. The YFT stations # 542 and 543 and Multi-Net station # 509 were located above the north-eastern slope of the seamount with soundings of < 1005 m ("NE-slope" stations), and YFT station # 531 and the corresponding Multi-Net station (# 461) were located over the south-western slope of the seamount ("SW-slope" stations).

Fish samples were preserved in buffered formalin (8 %) immediately after the catch and transferred to alcohol (80 %) after 24 h. In the laboratory fishes were identified, measured to the millimetre below and, after blotting adhesive water with tissue paper, weighed to 1 mg accuracy. The individuals of *Ceratoscopelus warmingii*, *Hygophum hygomii* and *Lobianchia dofleini* were grouped into 10-mm size classes. To study a potential shift in diet with increasing predator size at least 10 individuals of each size class were selected whenever available. The stomachs (anterior end of the esophagus to the pyloric constriction) of the myctophids were dissected. The whole stomach was weighed before and after removal of the stomach content to determine the food wet weight. Prey items were transferred to petri dishes and identified to higher taxonomic levels (*i. e.*, amphipods, copepods, ostracods, *etc.*). In consideration of the high number of copepods found in the stomachs of *H. hygomii* and *L. dofleini*, this prey group was analysed in more detail. For this purpose, 12, 33, and 38 individuals of *C. warmingii*, *H. hygomii* and *L. dofleini*, respectively, with high proportions of copepods in their stomachs were selected, and copepods were identified to species level.

Data analysis

To describe the main prey categories in the myctophid diets, three indices, the frequency of occurrence (F_i) of each prey item i in non-empty stomachs, the percentage of each food item *i* by number (N_i) to the total number, and the percentage by weight (W_i) were calculated. Ash-free dry-weight data for different prey categories were obtained from Fock *et al.* (2002). Using the following equation (1), all three indices have been combined to describe the prey utilisation by the "Relative Importance Index" (RI) for each prey item (George and Hadley 1979; Hyslop 1980).

$$\mathrm{RI_i} = \frac{(F_i + N_i + W_i)\times 100}{\sum_{i=1}^{S}(F_i + N_i + W_i)} \qquad (1)$$

To analyse whether the dietary compositions of the three myctophid species were significantly different, multivariate statistics were performed using the package of the Primer-5 programme. Stomach content data (number of prey items) were standardised and square-root transformed prior to calculation of similarity matrices using the Bray-Curtis similarity coefficient. This coefficient was adopted since it is not affected by joint absence and it is sufficiently robust for marine data (Field *et al.* 1982). Non-metric multidimensional scaling (MDS) was applied as an ordination technique for graphical representation of stomach content data. The interspecific differences between myctophid diets was tested by using the one-way analysis of similarity (ANOSIM), a non-parametric permutation test that can be thought of as a multivariate analogue to a one-way ANOVA (Clarke and Warwick 1994).

Feeding intensity at different topographic locations of the Great Meteor Seamount was analysed by the stomach content index (SCI):

(2) SCI (%) = (wet weight of stomach content/body wet weight) × 100

Preference of the myctophids for a specific prey category was calculated with the selectivity index (α) by Chesson (1978):

$$\alpha_i = \frac{(r_i / p_\mathrm{i})}{\sum_{i=1}^{N}(r_i / p_i)} \qquad (3)$$

where r and p are the proportions by abundance of prey type i in the diet of the myctophid (r) and in the environment (p). Chessons's α was first calculated for each myctophid examined and afterwards averaged for each length class. N is the number of different prey taxa, and selection for prey occurs when $\alpha_\mathrm{i} > 1/N$. The length of copepod species was estimated using average lengths from literature data (Bradford-Grieve *et al.* 1999).

Results

Dietary composition

The highest proportion (35.3 %) of empty stomachs was found in *C. warmingii* (Table 2). This ratio was clearly lower in *H. hygomii* (15.5 %) and almost negligible in *L. dofleini* (2.8 %).

The Relative Importance Index (RI) showed that the dietary composition of all three myctophids was dominated by crustacean zooplankton (Table 2). The most important prey category of *C. warmingii* was hyperiid amphipods, which contributed to an RI value of 51.6 %,

Table 2: Major prey categories and dietary importance in terms of "Relative Importance index" RI of *Ceratoscopelus warmingii*, *Hygophum hygomii*, *Lobianchia dofleini*. AFDW = ash-free dry weight.

	Ceratoscopelus warmingii				***Hygophum hygomii***				***Lobianchia dofleini***			
No. of fish examined	85				58				71			
No. of stomach empty (%)	30 (35.3)				9 (15.5)				2 (2.8)			
SL range [mm]	20 – 76				29 – 63				21 – 34			
Prey items	No. of stomachs with prey	No. of items	Biomass [mg] (AFDW)	% Ri_j	No. of stomachs with prey	No. of items	Biomass [mg] (AFDW)	% Ri_j	No. of stomachs with prey	No. of items	Biomass [mg] (AFDW)	% Ri_j
Chaetognatha					1	1	0.67	0.61	7	7	4.71	5.07
Amphipoda	30	141	155.31	51.60	32	194	213.69	45.20	5	5	5.51	4.41
Copepoda	13	30	1.47	9.75	37	204	10.00	29.40	40	135	6.61	29.70
Decapoda (larvae)	1	1	2.64	0.97	1	1	2.64	0.79				
Euphausiacea	4	4	3.64	2.91	12	17	15.47	8.22	18	20	18.20	15.40
Mysidacea					3	3	1.04	1.73				
Ostracoda	18	27	8.21	12.90	7	13	3.95	4.48	46	84	25.23	34.50
Non-ident. Crustacea[a]	9	5			25	25			7	7		
Pteropoda	34	41	5.78	21.90	15	33	4.65	9.50	17	20	2.82	9.42
Polychaeta									1	1	0.18	0.55
Pisces (larvae)									1	1	1.03	0.85
Non-identified items[a]	23	23			1	1			39	39		

[a] Not included in calculation of indices

followed by pteropods with 21.9 , ostracods at 12.9, and copepods with 9.8 %. The major dietary components of *H. hygomii* were hyperiid amphipods and copepods, with RI values of 45.2 and 29.4 %, respectively. The prey composition of the smaller sized myctophid, *L. dofleini* (21 to 34 mm SL), was predominated by ostracods and copepods, with RI values of 34.5 and 29.7 %, respectively.

Due to the lack of adequate biomass data, taxonomic composition of copepods was represented by their numerical occurrence in the myctophid diets (Table 3).

Copepods were represented in the stomach content of *C. warmingii* by 16 species belonging to 10 families and 14 genera. The most important copepod families were the luminescent Metridinae (27.6 % of all identified copepods), followed by Candaciidae (17.2 %) and Euchaetidae (13.8 %). In the stomach contents of *H. hygomii* 15 species belonging to 7 families and 10 genera were identified (Table 3). The most abundant copepod families were Euchaetidae (36.1 %) and Calanidae (27.2 %). The copepod assemblage found in the stomach contents of *L. dofleini* showed the highest diversity and was represented by 23 species belonging to 11 families and 16 genera. The copepod composition was clearly dominated by individuals of the family Metridinae, accounting for 51.2 %.

Interspecific comparison of diets

Multivariate ordination techniques were used to compare the diets of the three myctophid species. The MDS plot of individual stomach contents supports the result of the RI anal-

Table 3: Copepod composition in the diets of *Ceratoscopelus warmingii*, *Hygophum hygomii* and *Lobianchia dofleini*. Size range = Length of copepods after Bradford-Grieve *et al.* (1999), N = number of copepods, ( ) = percentage contribution).

			C. warmingii	*H. hygomii*	*L. dofleini*
		No. fish examined	12	33	38
Family	Species	Size range [mm]	N (%)	N (%)	N (%)
Calanoida					
Aetideidae	*Aetideus acutus*	1.22 – 1.8			1 (0.8)
	Chirundina streetsii	3.8 – 5.55			2 (1.5)
	Euchirella amoena	2.7 – 4	1 (3.4)	1 (0.5)	
	Euchirella messinensis	2.8 – 6.2		4 (2.1)	
	Gaetanus minor	1.7 – 2.4			1 (0.8)
	Gaetanus sp.	4.0 – 5.6		1 (0.5)	
	Undeuchaeta plumosa	2.85 – 4.2			4 (3.0)
Calanidae	*Nannocalanus minor*	1.2 – 2.25	1 (3.4)	6 (3.1)	1 (0.8)
	Neocalanus gracilis	2.3 – 4		4 (2.1)	1 (0.8)
	Neocalanus robustior	2.84 – 4.32	2 (6.9)	42 (22.0)	
Candaciidae	*Candacia longimana*	2.4 – 3.9	2 (6.9)	2 (1.0)	2 (1.5)
	Candacia sp.	2.39 – 2.94	1 (3.4)	1 (0.5)	1 (0.8)
	Paracandacia bispinosa	1.7 – 1.82	2 (6.9)		1 (0.8)
Eucalanidae	*Pareucalanus sewelli*	2.89 – 6.1		1 (0.5)	
Euchaetidae	*Euchaeta marina*	2.88 – 3.64		41 (22.0)	1 (0.8)
	Euchaeta media	3.56 – 4.58		2 (1.0)	2 (1.5)
	Euchaeta sp.	3.47 – 4.38	4 (13.8)	25 (13.1)	3 (2.3)
Heterorhabdidae	*Heterorhabdus* sp.	2.6 – 3.38			1 (0.8)
Lucicutiidae	*Lucicutia flavicornis*	1.3 – 2.0	1 (3.4)		
Metridinae	*Pleuromamma abdominalis*	2.4 – 3.7	6 (20.7)		1 (0.8)
	Pleuromamma gracilis	1.6 – 2.15			3 (2.3)
	Pleuromamma piseki	1.6 – 2			1 (0.8)
	Pleuromamma sp.	2.5 – 3.5			10 (7.5)
	Pleuromamma xiphias	4 – 4.9	2 (6.9)	18 (9.4)	53 (39.8)
Paracalanidae	*Calocalanus* sp.	0.71 – 0.78	1 (3.4)		2 (1.5)
	Paracalanus denudatus	0.7 – 0.93	1 (3.4)		
Scolecitrichidae	*Scolecithricella* sp.	1.2 – 1.9		1 (0.5)	1 (0.8)
	Scolecithrix danae	1.8 – 2.4		8 (4.2)	
Cyclopoida					
Oithonidae	*Oithona* sp.	0.7 – 1.0	1 (3.4)		1 (0.8)
Harpacticoida					
Miraciidae	*Miracia efferata*	1.4 – 2	1 (3.4)		
Poecilostomatoida					
Corycaeidae	*Corycaeus* sp.	1.2 – 1.6			7 (5.3)
	Farranula sp.	0.74 – 0.84	1 (3.4)		
Oncaeidae	*Oncaea* sp.	0.5 – 0.8	1 (3.4)		16 (12.0)
Unidentified			1 (3.4)	33 (17.3)	17 (12.8)

ysis that all three species consume different prey categories (Figure 2). The individuals of *H. hygomii* and *L. dofleini* formed more or less discrete groups on the MDS plot, while the symbols representing dietary samples of *C. warmingii* largely overlap with the other two species. The R statistic of the global ANOSIM test confirmed that the dietary compositions of the three myctophid species differed significantly ($R = 0.307$; $p < 0.001$). However, the pairwise ANOSIM test showed that the R value was lower (0.206) for the species pair *C. warmingii vs. H. hygomii* compared to *L. dofleini vs. C. warmingii* (0.387) and *L. dofleini vs. H. hygomii* (0.307).

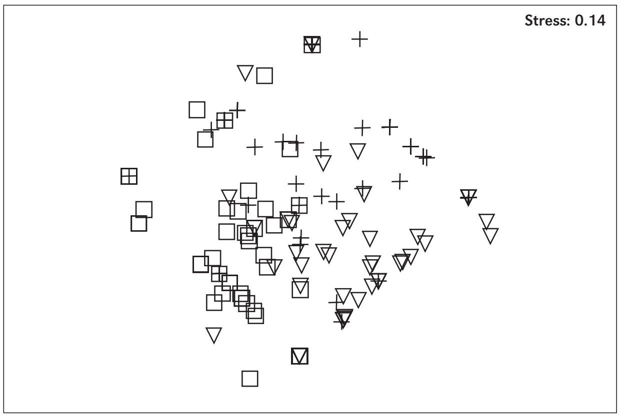

Figure 2: Ordination by MDS of Bray-Curtis similarities of standardized and square-root transformed stomach content data of *C. warmingii* (+) *H. hygomii* (▽), *L. dofleini* (☐).

Prey size

The size range of the examined *C. warmingii* specimens was 20 to 68 mm, with an average standard length of 38 mm. To investigate a potential shift in prey size with growth over the examined size range we compared the numerical proportion of amphipods (largest prey item) in different size classes. The proportion of amphipods in the diet of *C. warmingii* increased from 16 % in fish 20 to 29 mm to 90 % in the size class 60 to 69 mm (Figure 3). In order to test whether the observed increase was statistically significant, we compared the proportion of prey categories in individuals of fish smaller and larger than 40 mm. The ratio of amphipods was 21.2 ± 27.1 % ($\overline{x} \pm s$) in 20 to 37 mm sized individuals and 52.7 ± 45.1 for 41 to 68 mm SL fish. The difference was statistically significant (Mann-Whitney U-test; $p < 0.05$) and can be described as a shift towards larger prey size in individuals exceeding 40 mm SL. In contrast, the importance of pteropods, which represent a smaller sized prey category, decreased in larger individuals of *C. warmingii* (Figure 3). The ratio of pteropods to the total number of prey items was 46.6 ± 37.1 % ($\overline{x} \pm s$) for 20 to 37 mm SL individuals and 19.6 ± 26.0 % for 41 to 68 mm SL fish. The numerical decrease of pteropods in the diet of *C. warmingii* was statistically significant (Mann-Whitney U-test; $p < 0.01$), indicating a decreased importance of smaller prey items in larger fish. Copepods were of lower importance in the diet of *C. warmingii*, ranging from 6 % to 26 % of the ingested food without a significant shift over the length spectrum of the individuals examined.

The size spectrum of *H. hygomii* with identifiable stomach content ranged from 29 to 63 mm, with an average of 51 mm SL. *H. hygomii* showed an increase in the percentage of amphipods in higher size classes (Figure 3). The ratio of amphipods was 27.0 ± 30 % ($\overline{x} \pm s$) for individuals from 29 to 49 mm and 37.7 ± 36.3 % of 50 to 63 mm sized fish. The difference was not statistically significant (Mann Whitney; U-test $p > 0.05$). The proportion of copepods, which represent the smallest prey category in the diet of *H. hygomii*, decreased from 70 % in the size class 20 to 29 mm down to 33 % in fishes 50 to 59 mm (Figure 3). The ratio of copepods in individuals less than 50 mm SL was 51.4 ± 31.2 % and 39.9 ± 34.7 % for fish from 50 to 63 mm SL. Again this difference was not significant (Mann-Whitney U-test, $p > 0.05$).

L. dofleini was the smallest of the examined myctophids, with standard lengths ranging from 21 to 33 mm and an average SL of 28.3 mm. The food composition in both size classes

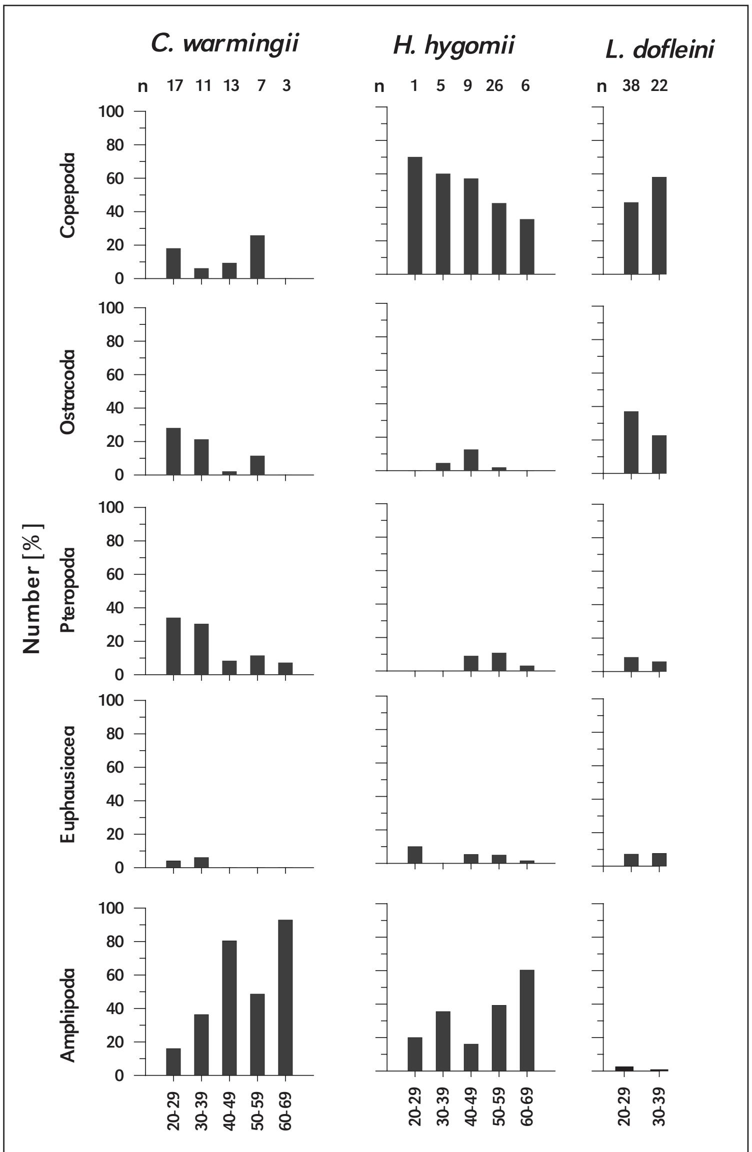

Figure 3: Food composition (by number) of various length groups of *C. warmingii*, *H. hygomii* and *L. dofleini.*

(20 to 29 mm and 30 to 39 mm) was dominated by copepods (Figure 3). Nevertheless, the proportion of copepods increased from 36.9 ± 36.3 % ($\overline{x} \pm s$) in the lower size class to 50.8 ± 35.9 % in fishes of the size class 30 to 39 mm. The difference was not statistically significant (Mann-Whitney U-test, $p > 0.05$).

Prey preferences

Prey preference was defined as the utilisation of prey taxa by many individuals of a myctophid species in disproportionate numbers to their environmental abundance. Prey preference of the three myctophid species was analysed for the taxonomic levels, major prey categories, and calanoid copepod genera.

The Chesson's α, based on the main prey categories (Table 4), indicated that *C. warmingii* in all size classes preferred to feed on amphipods ($\alpha = 0.55$ averaged over all size classes) and pteropods (0.29). *H. hygomii* showed in all size classes a strong preference toward amphipods (average $\alpha = 0.64$). *L. dofleini* preferably selected ostracods and euphausiids with average α values of 0.41 and 0.26, respectively (Table 4).

On the taxonomic level "copepod genera" (Table 5), *C. warmingii* selected for larger sized copepods of the genera *Candacia* (average $\alpha = 0.24$), *Pleuromamma* (0.22), and *Euchaeta* (0.18). *H. hygomii* preferred to feed, similar to *C. warmingii*, on the larger sized copepod genera, *i. e.*, *Euchaeta* (average $\alpha = 0.3$), *Neocalanus* (0.22), *Scolecithrix* (0.14) and *Euchirella* (0.1). *L. dofleini* showed a preference for copepods of the genera *Euchaeta* (average $\alpha = 0.08$) and, especially, *Pleuromamma* (0.66). Because of the high dietary importance of *Pleuromamma*, the selective feeding behaviour regarding this genus was analysed additionally on the species level (Table 6). Both size classes of *L. dofleini* strongly preferred *Pleuromamma xiphias*, while other *Pleuromamma* species were not taken in higher proportions compared to their occurrence in the zooplankton.

Prey size

Lengths of the copepods in the stomach content and in the ambient water column were analysed to provide evidence for size selectivity in the feeding behaviour of the myctophids (Figure 4). Due to the low number of copepods consumed by *C. warmingii*, conclusions about size selectivity should be interpreted with caution for this species. Nevertheless, in the food spectrum of this myctophid, smaller and medium sized copepods of the size classes 1.5 to 1.9 mm and 3 to 3.4 mm prevailed. *H. hygomii* fed most intensively on larger copepods of the size class 3.5 to 3.9 mm, which accounted for 54 % of its ingested copepods. *L. dofleini* showed a clear preference for larger copepods of the genus *Pleuromamma*, which were represented by the size classes 4.0 to 4.4 and 4.5 to 4.9 mm.

The average length of copepods consumed by *H. hygomii* was 3.25 ± 0.96 mm ($\bar{x} \pm s$) and 3.63 ± 1.08 by *L. dofleini,* far exceeding the average length of copepods consumed by *C. warmingii* (2.08 ± 1.04). The difference was statistically significant (Kruskal-Wallis test; $H = 11.3$; $p < 0.001$). A multiple post-hoc test after Dunn was performed to test for differences in the lengths of ingested copepods in the myctophid diets, and this revealed significant differences between all pairs of species ($p < 0.05$).

To examine the existence of size-selective feeding behaviour we compared the length composition of copepods in the stomach content with the length composition of copepods in the zooplankton (Figure 4). 97 % of all copepods in the upper 300 m of the water column were smaller than 1.5 mm. The average length of copepods in the zooplankton samples was 0.57 ± 0.39 mm and differed significantly from the size composition of copepods in the stomach contents of all three myctophid species (Mann-Whitney U-test, $p < 0.001$). This observation suggests a pronounced degree of size selectivity towards larger copepod species in the feeding behaviour of myctophids.

Table 4: Mean prey preferences (Chesson index) of different size classes of three myctophid species based on **main prey categories**. Preference indicated by *.

	Fish length class [mm]					
	20–29	30–39	40–49	50–59	60–69	Average
			C. warmingii			
No. of individuals	17	11	13	7	3	
Copepoda	0.00	0.00	0.00	0.02	0.00	0.00
Ostracoda	0.24*	0.04	0.00	0.33*	0.00	0.13
Pteropoda	0.37*	0.34*	0.08	0.37*	0.34*	0.29*
Euphausiacea	0.05	0.06	0.00	0.00	0.00	0.03
Amphipoda	0.34*	0.57*	0.91*	0.28*	0.66*	0.55*
			H. hygomii			
No. of individuals	1	5	9	26	6	
Copepoda	0.00	0.20	0.00	0.17	0.00	0.12
Ostracoda	0.00	0.01	0.02	0.02	0.00	0.02
Pteropoda	0.00	0.00	0.12	0.13	0.00	0.10
Euphausiacea	0.24*	0.00	0.23*	0.15	0.01	0.13
Amphipoda	0.76*	0.79*	0.63*	0.53*	0.99*	0.64*
			L. dofleini			
No. of individuals	38	22	0	0	0	
Copepoda	0.18	0.21*				0.19
Ostracoda	0.42*	0.39*				0.41*
Pteropoda	0.09	0.02				0.07
Euphausiacea	0.22*	0.33*				0.26*
Amphipoda	0.10	0.04				0.08

Spatial diet variability

The aforementioned results show inter- and intraspecific differences in myctophid diet composition. In order to determine the influence of the Great Meteor Seamount on the feeding behaviour we compared the diet compositions of the myctophid species at three (two in the case of *H. hygomii*) different topographic seamount locations.

The stomach content data of *C. warmingii* showed strong differences between the topographic stations (Figure 5A). For example, the percentage of numbers of amphipods in the diet of *C. warmingii* varied from 76 % at the deep-water station to 15 % at the NE-slope station.

As the present study reveals, the dietary composition was influenced by the specific predator size. The median standard length of *C. warmingii* differed significantly between sampling sites (Kruskal-Wallis test, $H = 17.4$, $p < 0.001$). Individuals sampled at the NE slope were significantly smaller (median SL 26.0 mm) compared to the deep water (SL 41.0 mm) and the SW slope (SL 48.5 mm). The diet composition of *H. hygomii* showed an increased numerical abundance of amphipods at the NE-slope station (59.7 % of all identified food items) compared to the deep-water station (17.2 %, Figure 5B). As the median standard length of NE slope individuals was significantly higher (55.0 mm) than the deep-water specimens (51.0 mm) (Mann-Whitney U test; $p < 0.05$), we assume that the diet

Table 5: Mean prey preferences (Chesson index) of different size classes of three myctophid species based on **calanoid copepod genera**. Preference indicated by *.

	Fish length class [mm]					
	20–29	30–39	40–49	50–59	60–69	Average
			C. warmingii			
No. of individuals	2	2	4	2	0	
Calocalanus	0.00	0.00	0.00	0.00		0.00
Candacia	0.89*	0.00	0.15*	0.00		0.24*
Euchaeta	0.00	0.50*	0.20*	0.00		0.18*
Lucicutia	0.00	0.00	0.25*	0.00		0.10
Nannocalanus	0.00	0.50*	0.00	0.00		0.10
Neocalanus	0.00	0.00	0.15*	0.00		0.06
Paracalanus	0.03	0.00	0.00	0.00		0.01
Paracandacia	0.00	0.00	0.00	0.50		0.10
Pleuromamma	0.08	0.00	0.25*	0.50*		0.22*
			H. hygomii			
No. of individuals	1	5	6	14	5	
Candacia	0.00	0.00	0.00	0.02	0.16*	0.03
Euchaeta	0.64*	0.62*	0.27*	0.13*	0.38*	0.30*
Euchirella	0.00	0.00	0.17*	0.09	0.19*	0.10*
Gaetanus	0.00	0.00	0.00	0.07	0.00	0.03
Nannocalanus	0.00	0.00	0.19*	0.11*	0.00	0.09
Neocalanus	0.25*	0.05	0.26*	0.32*	0.07	0.22*
Pareucalanus	0.00	0.00	0.00	0.04	0.00	0.02
Pleuromamma	0.00	0.00	0.06	0.14	0.00	0.07
Scolecithricella	0.12*	0.00	0.00	0.00	0.00	0.00
Scolecithrix	0.00	0.33*	0.05	0.09	0.20*	0.14*
			L. dofleini			
No. of individuals	21	15	0	0	0	
Aetideus	0.02	0.00				0.01
Calocalanus	0.00	0.00				0.00
Candacia	0.02	0.06				0.04
Chirundina	0.05	0.05				0.05
Euchaeta	0.01	0.17*				0.08*
Gaetanus	0.04	0.00				0.03
Heterorhabdus	0.03	0.00				0.02
Nannocalanus	0.05	0.00				0.03
Neocalanus	0.00	0.00				0.00
Paracandacia	0.04	0.00				0.03
Pleuromamma	0.66*	0.66*				0.66*
Scolecithricella	0.03	0.00				0.02
Undeuchaeta	0.04	0.06				0.05

composition of *H. hygomii* was affected by the predator size. The median standard length of *L. dofleini* showed no signifcant differences between sampling sites (Figure 5C). Accordingly, the dietary composition showed a low variability among the different stations.

Nevertheless, as shown by Pusch *et al.* (2004) all three myctophids showed a strong decrease in abundance above the seamount depths. In order to test whether the decreased abundance of myctophids over the slope and the plateau of Great Meteor Seamount was

Table 6: Mean prey preference (Chesson Index) of *L. dofleini* based on copepod genus *Pleuromamma.* Preference indicated by *.

	Fish length class [mm]		
	20–29	30–39	Average
No. of individuals	17	14	
P. abdominalis	0.00	0.07	0.03
P. gracilis	0.00	0.04	0.02
P. piseki	0.05	0.00	0.03
P. xiphias	0.95*	0.89*	0.92*

a result of reduced feeding success, we studied the feeding intensity of the three myctophids at different topographic stations (Figure 6). The stomach content weight of *C. warmingii* as percentage of body weight (SCI) ranged from 0 to 10.14 % with a median value 0.47 %. The feeding intensity was highest at the NE-slope station (median SCI 1.66 %), followed by the deep-water station (1.01 %) and the SW-slope station (0.18 %). The differences between the three sample locations were statistically significant (Kruskal-Wallis test; H = 19.7; $p < 0.001$). To detect differences between individual localities a multiple post-hoc test after Dunn was performed. It showed significant differences ($p < 0.05$) between the NE-slope and the SW-slope stations, as well as between the deep-water and the SW-slope stations, but no differences between the NE-slope and the deep-water stations. The SCI of *H. hygomii* ranged from 0 to 6.5 %, with a median value of 0.98 %. There was a significant difference in feeding intensity of *H. hygomii* (Mann-Whitney U-test; $p < 0.001$) between individuals taken at the deep-water station (median SCI 0.58 %) and the NE-slope station (median SCI 2.1 %). Feeding intensity was highest in *L. dofleini* with an SCI ranging from 0 to 5.17 % and a median value of 1.58 %. In contrast to the other two species, *L. dofleini* showed no significant differences in SCI at the different locations of Great Meteor Seamount (Kruskal-Wallis test; H = 1.05; $p > 0.05$). Nevertheless, *L. dofleini* did

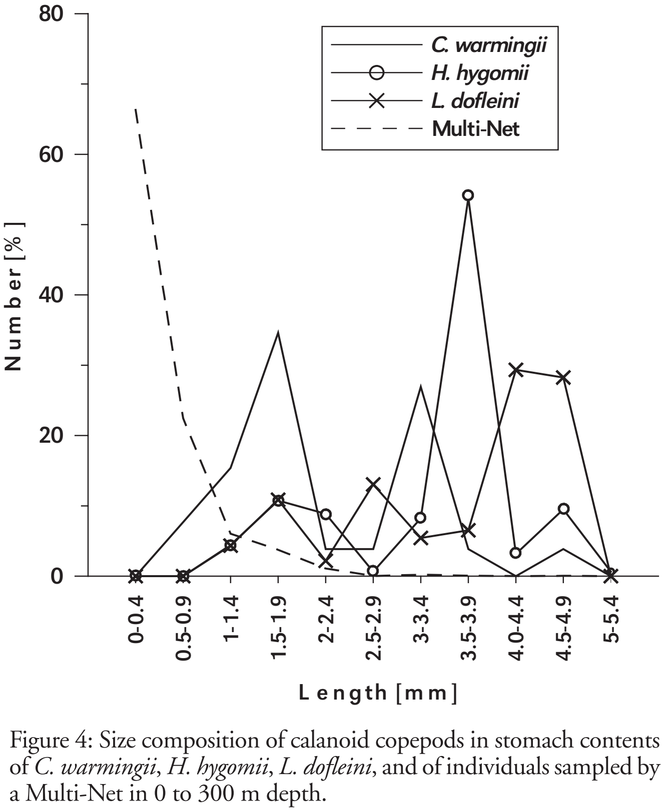

Figure 4: Size composition of calanoid copepods in stomach contents of *C. warmingii*, *H. hygomii*, *L. dofleini*, and of individuals sampled by a Multi-Net in 0 to 300 m depth.

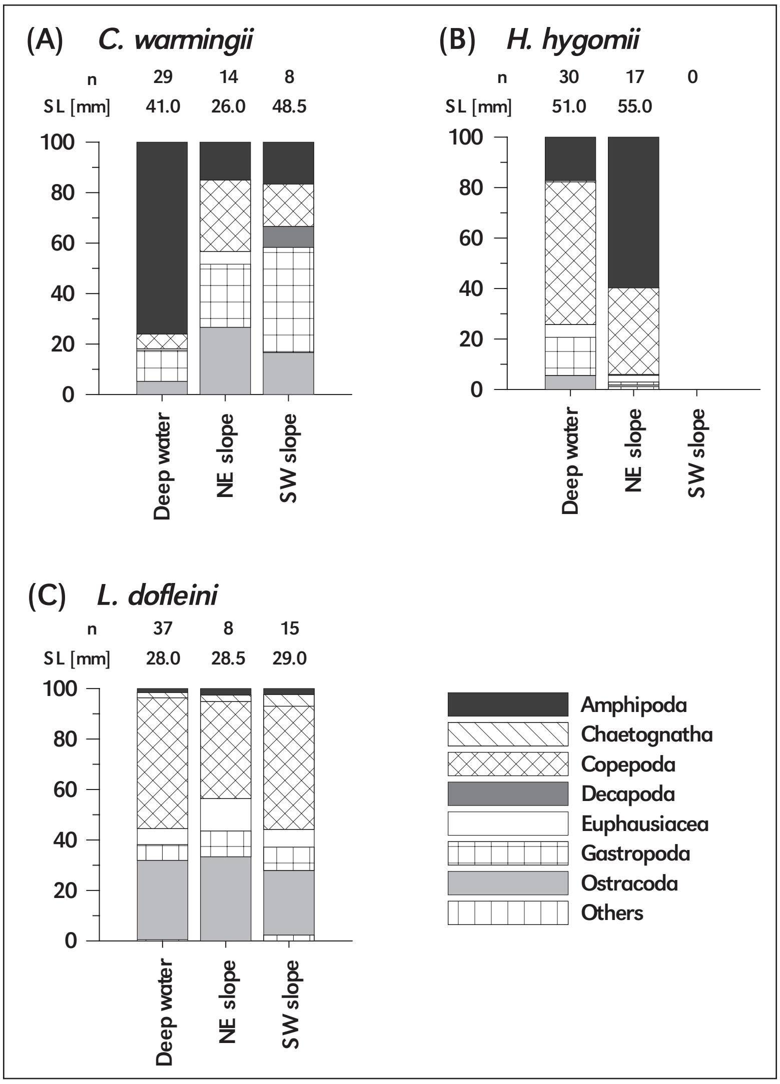

Figure 5: Food composition by percentage number at different stations. A = *Ceratoscopelus warmingii*, B = *Hygophum hygomii*, C = *Lobianchia dofleini*, n = number of individuals examined, SL = median standard length [mm].

show an increased feeding activity at the NE-slope station with a median SCI of 1.98 % compared to 1.63 % over the SW-slope and 1.56 % at the deep-water stations. We can assume that feeding activity was intensified in all three myctophids at the NE slope of Great Meteor Seamount.

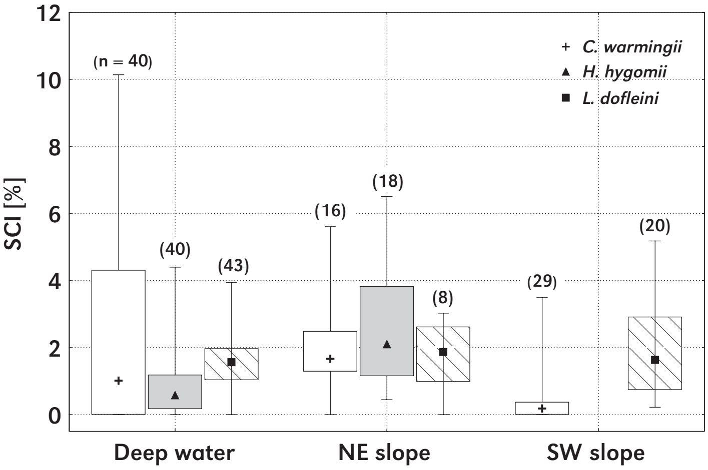

Figure 6: Stomach content index (SCI) of *C. warmingii*, *H. hygomii* and *L. dofleini* at three different topographic stations. Symbols represent median values, the hinges upper and lower quartiles; Box and Whiskers minimum and maximum values; ( ) = number of individuals examined.

Discussion

Methodology

Confirmation of selectivity in the feeding behaviour of oceanic midwater fish requires both adequate diet analysis and an accurate estimate of prey availability at the time and depth of feeding (Hopkins and Baird 1977). The fish samples taken with the YFT and the zooplankton samples taken with the multiple opening/closing net were not taken simultaneously. In addition, the sample positions and depths were not absolutely identical. Therefore, the zooplankton samples do not necessarily represent exactly the available food spectra of the examined myctophids. However, as sample-to-sample variability in Multi-Net samples was moderate (Schnack-Schiel and Henning 2004), we expect that our data regarding the zooplankton distribution at Great Meteor Seamount was accurate enough for the present analysis.

Mesopelagic fish, and to a lesser extent their zooplankton prey, undergo strong diurnal vertical migration. Therefore, the water layer the fishes were sampled in may not necessarily represent the precise layer at which the fishes ingested their food. The strong linkage between the diel migration behaviour of mesopelagic fish and peaks in feeding activity is well documented. The majority of tropical and subtropical myctophid species, including the species examined in the present study, feed during the hours of darkness, during their nocturnal stay in epipelagic layers (Merrett and Roe 1974; Kinzer and Schulz 1985). Because fishes were sampled during the night in the upper 400 m of the water column and most individuals contained fresh food, it is assumed that fishes were sampled during their active feeding period.

The determination of prey availability demands the accurate quantitative sampling of all size classes consumed by the predators (Hopkins and Baird 1977). The use of a single mesh size often results in a biased picture of the available prey spectrum. The mesh size of the multiple opening/closing net deployed in the present study was 100 mm and the mouth opening was restricted to 0.25 m^2. Therefore, the abundance of larger and more mobile zooplanktonic organism such as amphipods and euphausiids may have been underestimated. Thus, conclusions about feeding preferences of myctophids towards these larger prey organisms have to be viewed with caution.

The ability to identify individual prey items is dependent on the structure of the organism. Crustaceans are much easier to identify than gelatinous zooplankton because of their exoskeletons. Similarly, copepods of the genus *Pleuromamma* are easier to identify, even in an advanced stage of digestion, than other calanoid copepods because of their button-like luminous gland.

Dietary composition

The present study showed that the relative importance index (RI) of crustacean prey exceeded 78 % in the diet of each examined myctophid species, and reconfirmed the trophic classification of myctophids as crustacean zooplanktivores (Hopkins and Gartner 1992; Hopkins *et al.* 1996). This observation is in accordance with dietary studies of tropical and subtropical myctophids, which showed that copepods, euphausiids, ostracods, amphipods, and small decapods are the principal prey items (Merrett and Roe 1974; Clarke 1978; Kinzer 1982; Kinzer and Schulz 1985; Hopkins *et al.* 1996; Moku *et al.* 2000). Nevertheless, in the present study, ordination based on individual stomach content data showed a clear grouping by species. Accordingly, the results of ANOSIM indicated significant differences between the dietary compositions, as individual contributions of crustacean types varied markedly between myctophid species. For instance, the most important prey category of *C. warmingii* was hyperiid amphipods. This result is in agreement with findings by Clarke (1980), who reported the high dietary importance of large prey items like amphipods, euphausiids, decapods, and their larvae. The high number of pteropods in the diet of *C. warmingii* in the present study is in accordance with findings of Hopkins and Baird (1977), and supports the large contribution of non-crustacean invertebrate organisms in the diet of this species (Kinzer and Schulz 1985; Hopkins *et al.* 1996).

The major prey categories of *H. hygomii* were amphipods and copepods. A high proportion of large prey items was also recorded by Hopkins and Gartner (1992), who found that more than 50 % of the prey biomass in the diet of large *H. hygomii* (> 50 mm SL) consisted of decapods. The diet composition of *L. dofleini* was dominated by copepods and ostracods. This is in agreement with the data given by Merrett and Roe (1974) who studied the feeding ecology of this species in the subtropical NE Atlantic.

The observed differences in dietary composition of the three myctophids should not be taken as implying that each of these feeds on a completely different suite of prey organisms. However, our data support the hypothesis that co-occurring myctophid species at the Great Meteor Seamount reduce interspecific competition by the utilisation of different prey categories, as has been proposed for other subtropical mesopelagic fish species (Clarke 1980; Sutton and Hopkins 1996; Gartner *et al.* 1997).

Prey size

A frequent phenomenon is a shift of diet composition with increasing predator size, which has been documented for myctophids in numerous studies (Clarke 1978; Wörner 1979;

Clarke 1980; Duka 1986). Intraspecific resource partitioning of different myctophids size classes has been demonstrated by Hopkins and Gartner (1992) in the Gulf of Mexico. In our study, larger individuals of *C. warmingii* (> 40 mm SL) had fed on a higher proportion of amphipods (which represented the largest food item) and a lower proportion of pteropods, as compared to smaller sized individuals (< 40 mm). An ontogenetic shift of prey size for *C. warmingii* has been described by Gorelova (1978) and Duka (1986), who observed that individuals of 14 to 29 mm size fed predominantly on small copepods (*Microstellata*, *Macrosetella*, *Oncaea*, *Corycaeus*), while specimens measuring 30 to 70 mm switched to larger prey items like amphipods, larger copepods (representatives of the genera *Eucalanus*, *Gaetanus*, *Pleuromamma*), chaetognaths, appendicularians, and fish larvae. Hopkins and Gartner (1992) observed an increased dietary importance of decapods in *C. warmingii* individuals > 40 mm SL. Even though it was not statistically significant, we observed a shift towards larger prey items in *H. hygomii*. *L. dofleini*, a relatively small-sized myctophid, showed no dietary shift over the examined size range. We conclude that at least the dietary compositions of *C. warmingii* and *H. hygomii* showed shifts towards larger prey taxa with increasing predator size, reducing intraspecific competition for food resources.

Prey preference

C. warmingii and *H. hygomii* each showed a clear preference for amphipods. Even allowing for the probability that densities of some larger zooplankton taxa were underestimated due to net avoidance, the high Chesson index values for amphipods in the diet of *C. warmingii* and of *H. hygomii* indicate selective feeding behaviour. This result is in accordance with findings of Clarke (1980) who observed a preference of *C. warmingii* for larger prey items like amphipods, euphausiids, decapods, and fish larvae in epipelagic layers in the Gulf of Mexico.

Our data indicate that *L. dofleini* intensively fed on copepods of the genus *Pleuromamma*. This is in accordance with the results of dietary analysis by Merrett and Roe (1974) of *L. dofleini* in the NE Atlantic. Those authors found that *Pleuromamma piseki* and *P. gracilis* were the most important prey items of this myctophid, followed by ostracods of the genus *Conchoecia*. The same authors classified *L. dofleini* as a random feeder based on a comparison between fish dietary composition and zooplankton samples on a higher taxonomic level. In contrast, our data, analysed on the basis of copepod genera, suggested a clear preference for the genus *Pleuromamma*, and on the basis of copepod species for *P. xiphias*. This finding emphasises the advantage of detailed dietary examination. The ensuing results regarding actual selectivity in the feeding behaviour of a species have often been obscured by the use of broad taxonomic categories (Gartner *et al.* 1997).

However, our data reconfirms the high dietary importance of *Pleuromamma* in the diet of mesopelagic fish species as found by Hopkins et al. (1996), who showed that this genus made up 40 % of the total copepod biomass consumed by a low-latitude mesopelagic fish community in the Gulf of Mexico. The vertical distribution of *Pleuromamma* species at Great Meteor Seamount ranged from the surface to 1000 m depth, and they were concentrated at night in the upper 150 m of the water column (Schnack-Schiel, unpublished data). The vertical distribution of *L. dofleini* in the subtropical NE Atlantic ranges from 25 to 200 m at night and 300 to 500 m during the day (Hulley 1984). Therefore, the vertical distribution ranges of the two species largely overlap, and the preferred prey species of *L. dofleini* are available during day and night. The analysis of copepod size in the diet of *L. dofleini* revealed that > 45 % of copepods ingested were in the size range of 4 to 4.9 mm length, while approximately 97 % of the available copepods in the zooplankton were < 1.5 mm long. These results are in good agreement with findings by Hopkins and Gartner (1992), who showed that the predation pressure of a low-latitude myctophid community was highest on the prey size of > 4 mm length. Those authors calculated that the myctophids can consume one-fifth to one-half of the daily production of these zooplankton size classes, which represent the intermediate to late developmental stages of prey taxa (*e. g.*, *Pleuromamma* species). Therefore, our data on the selective feeding of *L. dofleini* on *P. xiphias* support the conclusion of Hopkins and Gartner (1992) that myctophids represent a substantial impact on the zooplankton community, because myctophid predation is heavily selective for particular size fractions and crucial life–history phases of important zooplankton taxa, *e. g.*, adult stages of the genus *Pleurommama*.

All species of the genus *Pleuromamma* are known to exhibit bioluminescence (Herring 1988). The function of bioluminescence in copepods remains under scientific consideration. It has been speculated that luminescence is a defensive tactic that does not necessarily prevent copepods being eaten by predators, but may alert conspecifics close by. However, the large thoracic pigment spot of *Pleuromamma* makes individuals of this genus conspicuous to visually oriented predators like myctophids (Hopkins and Baird 1977).

Spatial diet variability

Pusch *et al.* (2004) showed a significant decrease of myctophid densities in night hauls sampled over the flanks and the summit area of Great Meteor Seamount compared to hauls at an oceanic deep-water station. In contrast, Schnack-Schiel and Henning (2004) found no significant differences between invertebrate mesozooplankton abundances in the vicinity of the Great Meteor Seamount. Nevertheless, some zooplankton taxa showed significant differences in their densities at various seamount locations. The present study asks whether these differences are reflected in the dietary compositions of the three myctophids.

Dietary data indicated significant differences in prey composition of *C. warmingii* at three different stations. Previous studies have showed that the dietary composition of *C. warmingii* showed a higher regional variability than other myctophid species (Hopkins and Baird 1977; Kinzer and Schulz 1985; Duka 1986). In the present study, amphipods were of higher importance in individuals that were sampled at the deep-water station than those individuals sampled on the NE and SW slopes of the seamount. The analysis of fish length revealed that the low feeding incidence of amphipods at the NE slope was a result of the significantly smaller size of *C. warmingii* at this site. The reduced number of amphipods in the diet of *C. warmingii* at the SW-slope stations could not be explained by predator size, and may be a result of food availability. Schnack-Schiel and Henning 2004) described a reduced abundance of amphipods in samples taken above the flanks of Great Meteor Seamount.

However, the number of amphipods in the diet of *H. hygomii* was higher over the NE slope than at the deep-water station. Individuals at the NE slope were significantly larger, which supports the hypothesis that predator size was one of the main reasons for observed diet variability at different seamount locations. In accordance with these results, individuals of *L. dofleini* of similar size (no significant differences in median SL) showed no obvious variation in dietary composition at the three stations.

The stomach content index (SCI) values of the three myctophid species were in good agreement with those recorded for temperate and subtropical mesopelagic fish species (Clarke 1978; Duka 1986; Young and Blaber 1986; Moku *et al.* 2000). All myctophids exhibited a higher feeding intensity over the north-eastern slope of Great Meteor Seamount compared to the oceanic deep-water station. The zooplankton distribution studied by Schnack-Schiel and Henning (2004) showed no variations in zooplankton abundance between the two stations. These data suggest that the decreased abundance of myctophid species at the slope and a near lack of myctophids above the plateau of Great Meteor Seamount was not driven by a trophic gradient, *e. g.*, an active avoidance behaviour by the myctophids due to a decreased food availability in these habitats. Rather, the feeding rate was increased over the flanks of the seamount. A prominent hydrographic feature of the Great Meteor Seamount is an anticyclonic circulation of typically 6 $cm \cdot s^{-1}$ at the slope of the seamount, roughly aligned with the 2000 m isobath (Mohn and Beckmann 2002). It has been shown for zooplanktonic organisms that turbulent motion could increase the encounter frequency among nearby organisms (Rothschild and Osborn 1988; Mackas *et al.* 1993). Therefore, it could be speculated that myctophids find more favourable feeding conditions above the flanks of the Great Meteor Seamount compared to the surrounding deep water.

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