



Feeding patterns of transforming and juvenile myctophids that migrate into neustonic layers

T. Contreras¹, M. P. Olivar^{1,*}, J. I. González-Gordillo², P. A. Hulley^{3,4}

¹Institut de Ciències del Mar, CSIC, Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

²Instituto Universitario de Investigación Marina (INMAR), Universidad de Cádiz, 11510 Puerto Real, Spain

³Iziko – South African Museum, Queen Victoria Street, 8001 Cape Town, South Africa

⁴MA-RE Institute, University of Cape Town, Private Bag X3, 7701 Rondebosch, South Africa

ABSTRACT: Adult and juvenile myctophids feed at night in the epipelagic zone (<200 m) and are more dispersed in the mesopelagic zone (200–1000 m) during the daylight hours. In contrast, larvae inhabit the upper 200 m throughout a 24 h period and have daylight feeding patterns. Transforming stages occur both at the surface and in the mesopelagic zone and show less-defined feeding patterns. In this study, we analysed the trophic ecology of transforming and juvenile stages of 4 myctophids that occupy the neustonic layers (first 0–20 cm of the water column) during their nightly vertical migrations: *Dasyscopelus asper*, *Gonichthys cocco*, *Myctophum affine*, and *M. nitidulum*. Day and night neuston samples were collected across the equatorial and tropical Atlantic in April 2015. Transforming and juvenile stages occurred at night in the neuston, where they fed, but were absent from this layer during the day. The highest prey ingestion was observed between 01:00 and 04:00 h (UTC). Feeding incidence and the number of prey ingested increased from transformation stages to juvenile stages. Although the maximum prey size increased with fish body length, there was no significant increasing trend in mean prey sizes, but a great variability in the sizes of consumed prey. Diets of the 4 species mainly comprised a variety of copepod genera, usually dominated by *Oncaea* species. There was no evidence of resource partitioning among the 4 myctophid species. Estimates of daily feeding rations, based on the relationship between carbon content per gut and carbon content of fish body, throughout the night feeding period, showed that these species in these early stages ingested between 0.43 and 5.78 % of their body carbon weight daily. We suggest that the occurrence and feeding of these early stages in the neuston may contribute to reducing trophic competition between migrating myctophids by space segregation.

KEY WORDS: Myctophidae · Early life stages · Surface migration · Stomach content · Daily ration

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1. INTRODUCTION

Lanternfishes (family Myctophidae) are one of the most abundant fishes in the open ocean, and their larvae dominate ichthyoplankton samples from oceanic regions (Moser & Watson 2006, Ardura et al. 2016, Ayala et al. 2016, Priede 2017). Myctophids are a very species-diverse component of the mesopelagic fauna in all oceanic regions of the world (Backus et al. 1977, Gjøsæter & Kawaguchi 1980, Catul et al.

2011, Sutton et al. 2017). Vertical migration patterns for these species are quite consistent from different oceans of the world; adult and juvenile stages perform diel vertical migrations throughout the water column, while larvae are restricted to the upper epipelagic layers both day and night (Röpke 1993, Sassa et al. 2002, Olivar et al. 2014, 2018). Vertical ascent into the epipelagic/surface layer at night is associated with feeding (Gartner et al. 1997, Moku et al. 2000, Suntsov & Brodeur 2008, Bernal et al. 2013,

*Corresponding author: polivar@icm.csic.es

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2015, Duhamel et al. 2014), while the day descent to mesopelagic depths appears to be linked to predator avoidance (Robison 2003, Mehner & Kasprzak 2011, Sutton 2013).

Larval and adult features of these species are related to the environment they inhabit, i.e. the epipelagic and mesopelagic realms for larvae and adults, respectively. Briefly, larvae can be characterized by their transparency and limited sensorial and structural development, while adults are non-transparent, have photophores, and possess well-developed musculature and skeleton (Moser 1981, Moser & Watson 2006). The transformation stage is referred to the transition from larvae to juvenile (Kendall et al. 1984), which in addition to strong changes in morphology, pigmentation, and development of photophores demonstrates changes in habitat (Sassa et al. 2007, Moteki et al. 2017).

Success in recruitment is related both to the availability of prey and to foraging capabilities of the fish larvae, which directly or indirectly influence starvation and predation mortalities during early stages (Lasker 1975, Cushing 1990, Akimova et al. 2019). Most myctophids inhabit the pelagic environment (epi- and mesopelagic depths) throughout their entire life-cycle and forage on zooplankton populations, thereby becoming the energy conduit between secondary producers and upper trophic levels (Cherel et al. 2008, Valls et al. 2011, 2014, Battaglia et al. 2013, 2016, McClain-Counts et al. 2017, Navarro et al. 2017). One of the reasons for the high abundances of these species is related to their capacity to efficiently exploit lower trophic levels (Hopkins et al. 1996, Sutton 2013, Drazen & Sutton 2017). Quantification of such trophic connections in the marine environment can be achieved with a variety of analytical procedures, from stomach content analysis (until recently the most common type of analysis) (Hopkins et al. 1996, Sassa & Kawaguchi 2005, Sassa 2010) to isotopes, or molecular DNA studies (Valls et al. 2014, McClain-Counts et al. 2017, Olivar et al. 2019). While information on the adult diets of most myctophids is generally lacking due to the high species richness and extensive distributions in the family, dietary data do exist for a number species, especially those from the Southern Ocean (Gorelova 1975, Clarke 1978, Hopkins & Gartner 1992, Hopkins & Sutton 1998, Saunders et al. 2014, 2015, 2019, Bernal et al. 2015, Lourenço et al. 2017). Similarly, investigations for the early stages generally involve the most abundant species (Sabatés & Saiz 2000, Rodríguez-Graña et al. 2005, Sassa 2010, Bernal et al. 2013, Contreras et al. 2015,

2019). Investigations including estimations of feeding rates are even scarcer, spanning to a limited number of species (Gorelova 1984, Pusch et al. 2004, Drazen & Sutton 2017, Sassa & Takahasi 2018).

Here we study the feeding patterns of several myctophids (of subfamily Myctophinae) from the equatorial and tropical Atlantic, which occur at night in the neustonic layer. The diel vertical distribution of larvae, transforming, and adult stages of myctophids in this region have been recently investigated by Olivar et al. (2017, 2018) based on samples obtained with a midwater trawl and a plankton net throughout the water column. In general, species of this subfamily have been reported as the most common in neuston samples in other regions of the Atlantic, as well as in the Indian and Pacific oceans (Hopkins & Gartner 1992, Watanabe et al. 1999, 2002, Watanabe & Kawaguchi 2003, Olivar et al. 2016).

The trophic ecology of myctophids in the equatorial and tropical Atlantic has been studied from stomach content analysis for larval and transforming stages (Contreras et al. 2019) and from stable isotope analyses for adults (Olivar et al. 2019). Here we focus on the transforming and juvenile stages of those myctophine that migrate into the neustonic layers (*Dasyscopelus asper*, *Gonichthys cocco*, *Myctophum affine*, and *M. nitidulum*) to investigate their feeding patterns through the analysis of stomach contents, feeding chronology, and daily rations.

2. MATERIALS AND METHODS

2.1. Study region, sampling and target species

Samples were obtained on board the R/V 'Hesperides' in the equatorial and tropical Atlantic (April 2015), in a transect of stations from off the Brazilian coast to south of the Canary Islands (Fig. 1). Sampling at each station was repeated several times throughout the 24 h period and covered both day and night hours (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m650p239_supp.pdf). Hauls were performed with a neuston net with a mouth opening of 1 × 0.5 m and mesh size of 0.2 mm. The net sampled the upper 20 cm of the water column. The ship speed during sampling was 2 to 3 knots (1–1.5 m s⁻¹), and the net was fished for 10 to 15 min. Plankton samples were preserved in 5% buffered formalin for later processing in the laboratory. Juvenile and transforming stages of myctophids were sorted and identified using Hulley (1981, 1984)

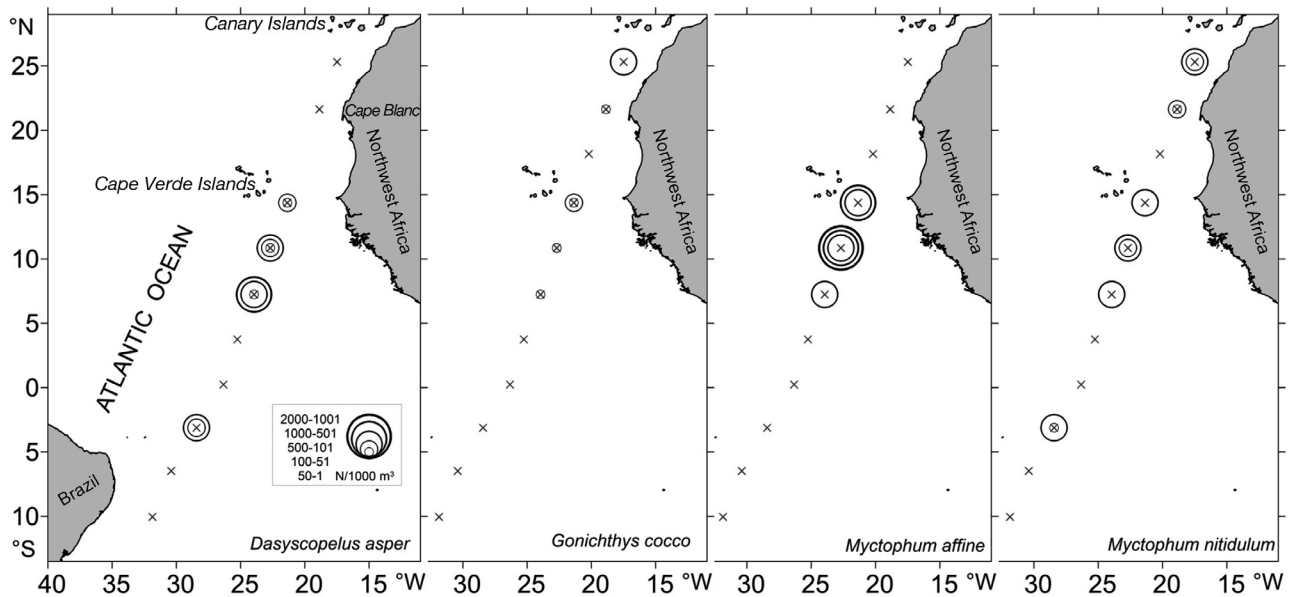


Fig. 1. Distribution of 4 species of myctophids occurring in the neuston samples across the equatorial and tropical Atlantic. Abundances in number of individuals per 1000 m³. Circle diameters indicate abundances from the repeated hauls at the same station but at different times

and Hulley & Paxton (2016a,b). The numbers of fishes collected at each station were standardised to reflect the number of individuals per 1000 m³.

The investigation focused on transforming and juvenile stages of the 4 most abundant species found in the neuston layers: *Dasyscopelus asper* and *Myctophum affine* (represented by transforming and juvenile stages), *Gonichthys cocco* and *M. nitidulum* (represented by juveniles). The specimens selected for stomach content analysis came from stations south of Cape Verde Islands. For *Gonichthys cocco*, specimens from the station south of Canary Islands were also included in order to increase the number of individuals for analysis. Stomachs from a total of 391 specimens were analysed: 45 *D. asper*, 45 *G. cocco*, 258 *M. affine*, and 43 *M. nitidulum*.

2.2. Stomach content analysis

Prior to dissecting the specimens for stomach content analysis, the standard length (SL) and mouth width (MW; the widest distance between the posterior edges of the maxillae) were measured to the nearest mm. Allometric relationships between MW and SL were analysed by fitting a power function with the slope of the function representing the allometric coefficient. Stomachs were then removed using a fine scalpel and the contents placed on a glass slide with a drop of glycerine:water (50:50) mix-

ture. The state of prey digestion was estimated as high, highly digested (completely transparent, soft and degraded items), or low, partially digested (body shape maintained, some colour remains). Prey items were counted, identified, and measured (length and width). The maximum prey width was taken along the maximum cross-section and measured to a precision of 0.001 mm with a Leica MZ12 stereoscopic microscope. Prey items were identified to the lowest taxonomic level using Vives & Shmeleva (2007, 2010) and Rose & Tregouboff (1957).

2.3. Data analysis

Feeding incidence was calculated for each species and stage as the percentage of individuals with at least one prey item in the stomach (Arthur 1976, Vera-Duarte & Landaeta 2016).

The relationships between prey size (prey width) and fish size (SL) were analysed by grouping fishes into 1 mm size-classes, each containing ≥ 3 prey items. The trophic niche breadth was analysed according to Pearre (1986) as the standard deviation (SD) of the log₁₀-transformed prey width for each of these size classes. Linear regression analysis was used to explore the significance of prey size (and prey number) to larval size relationships.

To characterize the diet and assess the importance of each prey type, the index of relative importance

(%IRI) of each prey type for each species and stage was calculated as the product of the frequency of occurrence (%F) in the specimens with food in the stomach and its relative abundance in relation to the total number of diet items examined (%N) ($\%IRI = \%F \times \%N$) (Sassa & Kawaguchi 2004). In addition, the index of relative importance in carbon units %IRIC was also calculated as $\%IRIC = (\%N + \%C) \times \%F$ (Pinkas et al. 1971), where %C is the relative contribution of each prey in carbon units, obtained from estimations of total carbon of each prey item in relation to total C per stomach.

2.3.1. Carbon estimations

Carbon was estimated by applying a conversion factor between eviscerated dried-weight (DW) and organic carbon content. The conversion factor between DW and organic carbon was set at 40% for all the species, except for *M. nitidulum*, for which a factor of 39.2% obtained for specimens from the same cruise was available (Olivar et al. 2017).

The relationships between eviscerated DW and wet weights (WW) were measured for 34 individuals of the *M. affine* used in stomach content analyses. The estimated parameters of the fitted equation ($DW = 0.2475WW^{1.0156}$) were then used to estimate DW from the measured WW for the rest of specimens.

For *M. nitidulum*, the conversion of SL (mm) to DW (g) was calculated from individuals collected at the same stations as those used in this study, but caught in subsurface layers with a midwater trawl (C. López-Pérez pers. comm.). The relationship used was: $DW = 3e^{-6}SL^{3.341}$.

Specimens of *D. asper* and *G. cocco* obtained in a previous cruise (Malaspina 2010 cruise, Olivar et al. 2016), and fixed in 5% buffered formalin, were used to determine the relationships between DW (g) and SL (mm). The fitted equation for *D. asper* was: $DW = 1e^{-7}SL^{3.7567}$. For *G. cocco*, the relationship was: $DW = 6e^{-7}SL^{3.4276}$.

Prey DW estimates were derived from their relevant metrics (maximum width, maximum length, or prosomic length) and species-specific length–weight relationships obtained from the literature (Deibel 1986, James 1987, Van Der Lingen 2002). DW were then converted to carbon content according to DW–C relationships from the literature (Deibel 1986, James 1987, Gorsky et al. 1988, Van Der Lingen 2002), or assuming carbon content equal to 40% of dry weight when relationships were not available from the literature.

2.3.2. Feeding chronology

Feeding chronology was analysed for each species as the mean number of prey per hour, by pooling data from all the stomachs for the same time interval. In this case, data from transforming and juvenile stages were combined in order to obtain a sufficient number of fish for each time interval.

The relative stomach carbon content index (%SSCI) was also calculated for each time interval, as $\%SSCI = 100 \times SC/BC$, where SC is the total carbon content per stomach obtained as the sum of carbon per prey, and BC is fish body carbon content. The significance of the relationships between number of prey or %SSCI and time of the day was assessed by linear regression analysis. %SSCI was used to estimate daily rations (DR) following Eggers (1977), with the modifications suggested by Pakhomov et al. (1996): $DR = \%SSCI \times FH/E$, where FH are the number of feeding hours, and E is the gut passage time from feeding to excreting faeces in hours. According to the time that the studied species remained in the neuston, we defined 10 h as the feeding period. Gut-passage time was calculated as in Hudson et al. (2014) using a temperature-based gut-evacuation rate $E = 0.0942e^{0.0708T}$, where T is the temperature in °C.

3. RESULTS

3.1. Species distribution

Transforming and juvenile stages of 8 myctophine species occurred in night samples from the study region, with *Dasyscopelus asper*, *Gonichthys cocco*, *Myctophum affine*, and *M. nitidulum* being the more abundant and frequent. The stations south of Cape Verde Islands showed the main concentrations (Fig. 1). While *M. affine* was restricted to this last zone, *D. asper* and *M. nitidulum* had a more widespread distribution across the station transect, and *G. cocco* was more abundant at the station south of the Canary Islands. The stations south of Cape Verde Island were placed in a transitional region from the warm and surface chlorophyll-depleted stations near the equator to the colder and more productive stations influenced by the Cape Blanc upwelling (Olivar et al. 2017). Sea surface temperatures (SST) at the stations south of Cape Verde Island ranged from 25.5 to 22°C, while those at the stations south of the Canary Island were 19°C.

3.2. Feeding incidence

The feeding incidence in transforming stages of *M. affine* and *D. asper* (<65%) was lower than in juveniles. Juveniles of the 4 species showed high feeding incidences that ranged from 66 to 100% (Table 1).

3.3. Prey number and carbon content

The highest number of ingested prey (Fig. 2A) was observed in *G. cocco*, with a maximum of 38 prey items in juveniles of 31 mm SL. In *M. affine*, the highest number of prey (32) was found in a transforming stage of 15.5 mm SL. In

Table 1. Feeding incidence (%FI) and size range of 4 species of myctophid occurring in the neuston samples. Numbers in parentheses indicate the total number of analysed specimens. T: transformation stage; J: juvenile stage; –: no data

Species	%FI		Size range (mm)	
	T	J	T	J
<i>Dasyscopelus asper</i>	61.5 (39)	100 (6)	13.6–16	17–24
<i>Gonichthys cocco</i>	–	73 (45)		19.5–44
<i>Myctophum affine</i>	63.7 (193)	66.2 (65)	12–15.5	15.6–43
<i>Myctophum nitidulum</i>	–	74.4 (43)		16.3–23.2

D. asper, 20 prey items were found in juveniles from 21 to 24 mm SL, and in *M. nitidulum*, 15 prey items were found in juveniles of 18 mm SL. The numbers

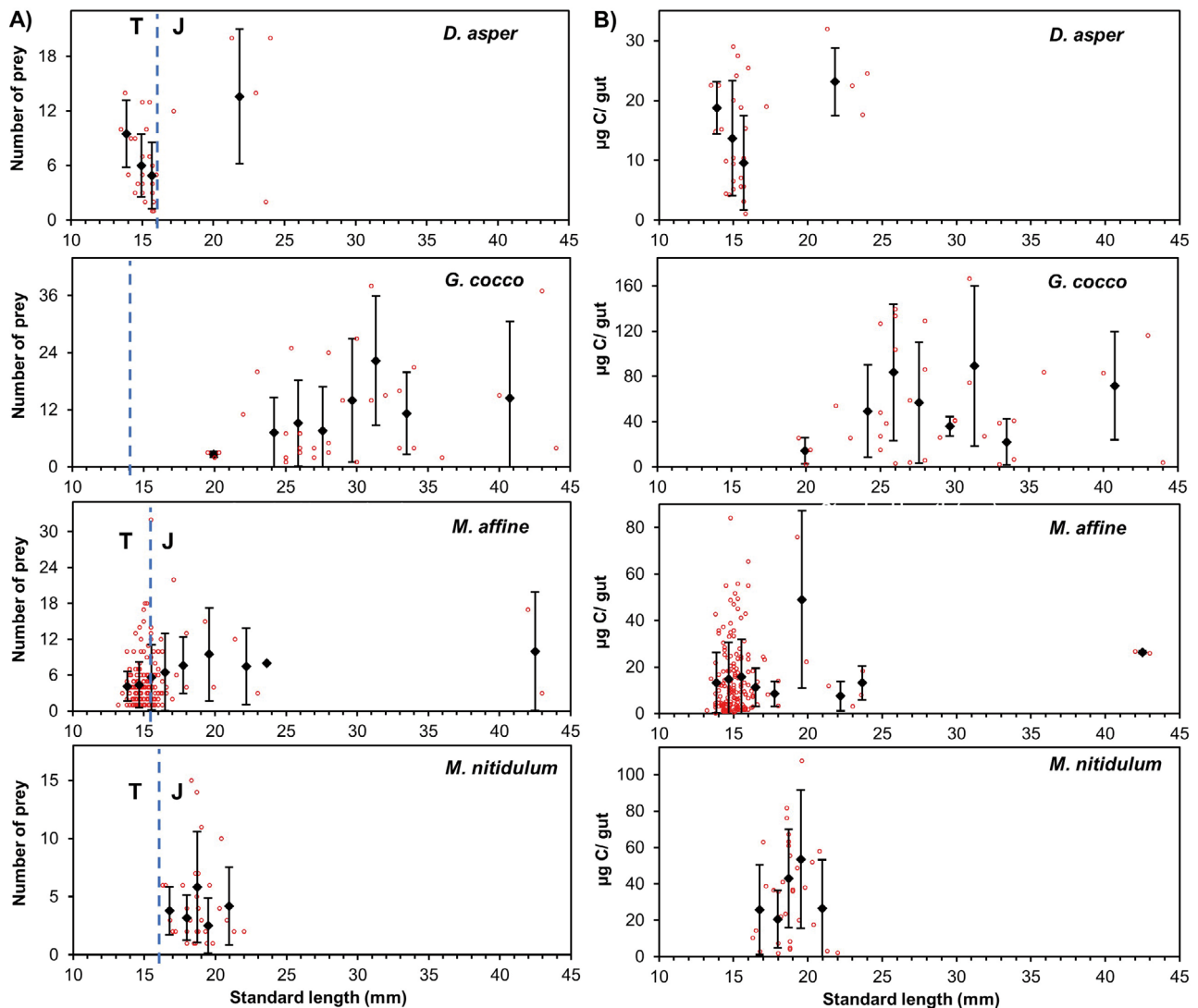


Fig. 2. Variation of (A) mean number (± 1 SD) of prey items per stomach and (B) mean (± 1 SD) carbon content per stomach with fish standard length. Open red circles: raw data. T: transformation stages; J: juvenile stages. See Table 1 for full species names

of prey were quite variable through transforming to juvenile stages, although in *M. affine* a significant increase was detected in the mean number through development ($p < 0.02$, $r = 0.75$, $t = 2.98$), with a maximum of 4 prey items at 14.5 mm SL and 9.5 prey items at 19.5 mm SL. In *D. asper*, there was a decrease with development within transforming specimens (9.5 prey items at 14 mm SL and only 5 prey items at 15.5 mm SL), although the overall mean number of prey was also higher in juvenile than in transforming stages. In juveniles of *M. nitidulum* and *G. cocco*, there was no significant increasing tendency in the number of ingested prey with increasing fish size.

Gut fullness in terms of carbon (Fig. 2B) also showed noticeable variability within species during development. Species comparisons showed that *G. cocco* presented the highest carbon content per gut (166 μg in a specimen of 31 mm SL). The highest contents for the other species were 107.6 μg in an *M. nitidulum* specimen of 19.6 mm SL, 84 μg in an *M. affine* specimen of 14.8 mm SL, and 31.9 μg in a *D. asper* specimen of 21.3 mm SL. In *M. affine* and *D. asper*, the mean carbon per gut increased from transformation to juvenile stages, with mean values of 14.9 and 12.9 μg in transformation stages and 15.7 and 21.8 μg in juveniles, respectively, although no significant overall increase in total carbon content per gut was observed throughout development.

3.4. Trends in prey size and trophic niche breadth

Mouth widths showed an isometric growth in relation to SL for *M. nitidulum* (allometric coefficient $b = 0.99$, $\text{CI}95\% = 0.2$). Negative allometric relationships of mouth widths with body length for the 3 remaining species were significant ($b = 0.84$, $\text{CI}95\% = 0.1$ for *D. asper*, $b = 0.66$, $\text{CI}95\% = 0.1$ for *G. cocco*, and $b = 0.78$, $\text{CI}95\% = 0.06$ for *M. affine*). The 4 species ingested a wide size range of prey throughout their transforming and juvenile stages: from 220–800 μm in *D. asper*, 240–1500 μm in *G. cocco*, 160–1600 μm in *M. affine*, and 230–1900 μm in *M. nitidulum*. Mean prey size did not show any significant trend in relation to fish size (Fig. 3A), and similar variabilities in prey sizes occurred throughout development. Trophic niche breadth did not reveal any significant trend, meaning there is no tendency towards specialization to particular prey sizes in any of the studied species (Fig. 3B).

3.5. Diet composition

The diets of the 4 myctophids are mainly composed of copepods (Tables 2 & 3), of which the genus *Oncaea* was the most important with %IRI ranging from 69–83% in transformation stages of *M. affine* and *D. asper* and 57–91% in juveniles of *M. nitidulum* and *M. affine*, or %IRIC of 48–75% and 52–82%, respectively. In particular, the diet in *D. asper* is exclusively composed of copepods. Prey items such as euphausiids, ostracods, and siphonophores were only represented in the diets of transforming stages and juveniles of *M. affine*, but with very low importance (<1% both in terms of %IRI and %IRIC). The hyperiids, which were present in the diets of the 4 species, were particularly important prey in juvenile individuals of *M. nitidulum* (23.6% as %IRI, and 29.3% as %IRIC). In terms of %IRIC, their contribution to the diet of *M. affine* was important (24% of %IRIC for transforming stages). Appendicularians were only observed in the diets of juvenile individuals of *G. cocco* and represented 7.6% of %IRI and 21.4% of %IRIC.

3.6. Feeding chronology and %SCCI

Feeding activity associated with the exclusive night occurrence in the neustonic layer extended from 20:00 to 04:00 h (UTC). The lowest numbers of prey were always found at the beginning and at the end of this time period. The species that showed the clearest pattern was *M. affine*, with an increasing trend in number of prey eaten up to 24:00 h, followed by a decrease thereafter (Fig. 4). Although most prey were in a low degree of digestion through the night, prey in advanced states of digestion were always present (Fig. 4).

The only species that showed a significant increasing pattern in %SCCI through the night was *M. affine* ($p < 0.001$, $n = 9$, $t = 5.05$), ranging between 0.02 and 2.04%. The greatest %SCCI were observed for *D. asper* (mean 1.16%, range 0.08 to 3.19%) (Fig. 5), with maximum values in individuals collected from 22:00 to 02:00 h (UTM). In *G. cocco*, mean values were 0.26% (range: 0.004 to 0.85%). The lowest mean %SCCI was for *M. nitidulum* 0.17% (range: 0.006 to 0.44%), and the highest mean values for this species occurred around midnight, from 22:00 to 24:00 h.

DRs, using our observation of 10 h of the feeding period and an excretion period of 2 to 4 h (calculated for the range of SST indicated above), were

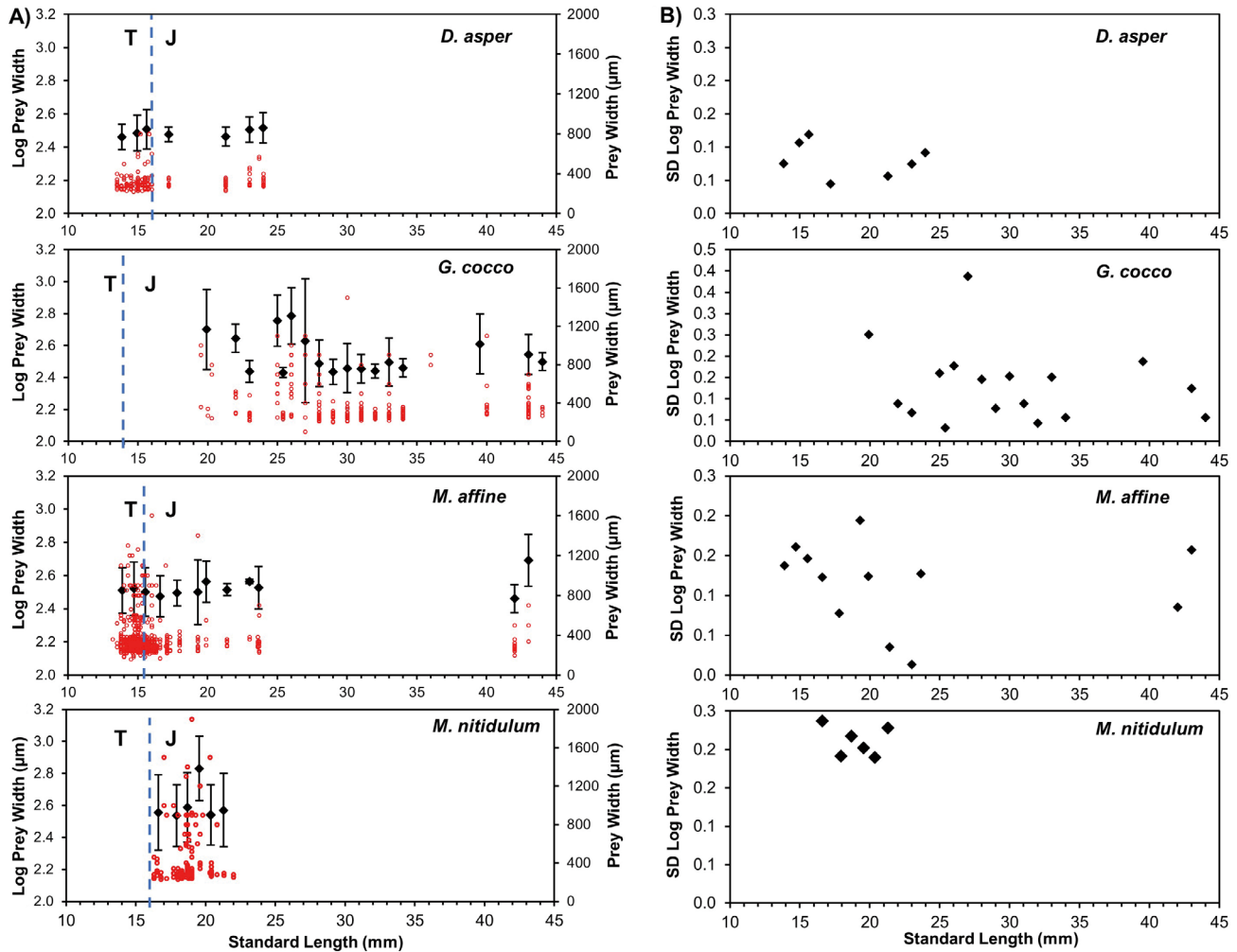


Fig. 3. Variation of (A) mean prey width (± 1 SD) and (B) niche breadth, expressed as SD log of prey width, with fish standard length. Open red circles: raw data. T: transformation stages; J: juvenile stages. See Table 1 for full species names

2.89–5.78 % for *D. asper*, 0.65–1.3 % for *G. cocco*, 0.99–1.98 % for *M. affine*, and 0.43–0.86 % for *M. nitidulum*.

4. DISCUSSION

4.1. Species distribution

The occurrence of transforming and juvenile stages of the studied species in the neuston coincides with the presence of their larvae in plankton samples from the epipelagic layers and of juveniles and adults from midwater trawls at the same stations (Olivar et al. 2017, 2018). In general, larval stages showed wider horizontal distributions than juvenile and adults. The observed distributions agree with the known geographical distribution of the species (Hul-

ley & Paxton 2016b, Olivar et al. 2016). However, it is worth mentioning that the presence of juveniles of *G. cocco* in the neuston samples from this study and in Olivar et al. (2016) proves their capacity to perform vertical migrations previously questioned (Hulley & Paxton 2016b).

4.2. Feeding patterns

According to gut content analysis, the presence of these 4 Myctophinae species in the neustonic layer can be associated with feeding. Previous investigations have indicated that feeding activity in migrating myctophids reaches a maximum when prey density is at its highest (Clarke 1978, Roe & Badcock 1984, Kinzer & Schulz 1985). This must have a direct relationship to feeding chronology. However, other

Table. 2. Index of relative importance (%IRI), determined as $\%F \times \%N$, of 4 species of myctophids occurring in the neuston samples. T: transformation; J: juvenile; %F: frequency of occurrence; %N: relative abundance; unid.: unidentified

Food items	<i>Dasyscopelus asper</i>			<i>Goniichthys cocco</i>			<i>Myctophum affine</i>			<i>Myctophum nitidulum</i>		
	T	J		T	J		T	J		T	J	
	%F	%N	%IRI	%F	%N	%IRI	%F	%N	%IRI	%F	%N	%IRI
Copepodites												
Calanoida												
Acartia				2.22	0.29	0.02				2.33	0.70	0.04
Calanus	10.26	3.27	0.83	13.33	6.34	3.11	1.05	0.33	0.03	4.65	1.41	0.17
Calanoida unid.	12.82	3.27	1.03	28.89	8.93	9.50	9.47	3.80	3.08	10.29	2.78	0.44
Centropages				2.22	0.29	0.02	11.58	4.63	4.58	17.65	5.16	1.41
Eucalanus				6.67	0.86	0.21	1.58	0.83	0.11			
Paracalanus	25.64	16.99	10.74	26.67	23.05	22.64	0.07	2.94	0.79	20.93	9.15	5.00
Temora				6.67	1.44	0.35	11.05	5.12	4.84	17.65	5.95	1.63
Cyclopoida							5.26	2.15	0.97	4.41	1.19	0.08
Corycaeus	17.95	6.54	2.89	24.44	11.82	10.63	16.32	6.78	9.45	19.12	8.73	2.58
Oithona	2.56	0.65	0.04				0.53	0.17	0.01	2.94	0.79	0.04
Oncaea	53.85	62.75	83.27	42.22	26.22	40.77	12.63	64.30	69.42	94.12	63.10	91.92
Harpacticoida												
Miracia efferata	10.26	3.27	0.83				2.63	1.16	0.26	9.30	4.93	1.20
Clytemnestra										1.47	0.40	0.01
Euphausiacea				11.11	8.07	3.30	2.11	0.66	0.12	1.47	0.79	0.02
Hyperida							12.11	5.12	5.30	14.71	5.16	1.17
Ostracoda	5.13	2.61	0.33	11.11	4.03	1.65	1.05	0.33	0.03	1.47	0.40	0.01
Mollusca							2.11	0.66	0.12	1.47	0.40	0.01
Siphonophora	2.56	0.65	0.04	4.44	0.86	0.14	2.63	0.83	0.19	1.47	0.40	0.01
Appendicularia				26.67	7.78	7.64				2.33	0.70	0.04

factors such as gut fullness and satiation must control the need to take in new food, thereby contributing to the variability in feeding activity during the night (Watanabe et al. 2002). Our results indicate that as soon as the fish reach the neuston layers, they start feeding on small organisms inhabiting these layers. The increase in the number of prey per gut in the night hours and the presence of prey in both a low and an advanced state of digestion suggest that the migrating population of myctophids remains in the neuston and feeds throughout the night. A similar result was observed for *Myctophum nitidulum* in the Kuroshio Current (Hattori 1964). The change from an exclusively epipelagic habitat and daily feeding pattern in larval stages (Sabatés & Saiz 2000, Sassa & Kawaguchi 2004, Bernal et al. 2015, Contreras et al. 2015) to a daylight mesopelagic habitat and nightly feeding ascension to the near surface in juvenile and adults (Clarke 1973, Baird et al. 1975, Hopkins & Gartner 1992, Watanabe et al. 2002, Bernal et al. 2015) might entail some period for adaptation. This may explain the differences in daily feeding patterns frequently observed between transforming stages when compared with juvenile and adults, e.g. both day and night feeding in transforming stages of *Benthosema glaciale* and *Ceratoscopelus maderensis*, or feeding only during the day in transforming stages of *Diaphus vanhoeffeni*, *Hygophum benoiti*, *H. macrochir* and *M. affine* (Contreras et al. 2015, 2019).

This study reveals an increase in %FI from transforming to juvenile stages in *Dasyscopelus asper* and *M. affine*. A comparison with larval stages also evidenced a higher feeding success in transforming than in larval stages. For instance, the %FI for *M. affine* larvae collected in the first 200 m of the water column in the same region and period was <55% (Contreras et al. 2019). In transforming stages, FI was always >60 %, both

Table 3. Index of relative importance (%IRIC), determined as $(\%N + \%C) \times \%F$, of 4 species of myctophids occurring in the neuston samples. T: transformation; J: juvenile; %F: frequency of occurrence; %N: relative abundance; %C: relative contribution of each prey in carbon units; unid.: unidentified

Food items	—— <i>Dasyscopelus asper</i> ——				<i>Gonichthys cocco</i>		—— <i>Myctophum affine</i> ——				<i>Myctophum nitidulum</i>	
	—— T ——		—— J ——		—— J ——		—— T ——		—— J ——		—— J ——	
	%C	%IRIC	%C	%IRIC	%C	%IRIC	%C	%IRIC	%C	%IRIC	%C	%IRIC
Copepodites							0.52	0.92	1.59	0.59		
Calanoida												
<i>Acartia</i>			3.4	0.49	0.22	0.02	0.28	0.03			0.08	0.04
<i>Calanus</i>	16.6	3.12			6.66	3.46	11.1	6.47	3.97	0.72	0.18	0.17
Calanoida unid.	9.58	2.52			16.9	14.9	4.67	4.93	13.7	3.45	1.54	11.1
<i>Centropages</i>					0.11	0.02	3.61	0.32				
<i>Eucalanus</i>					2.37	0.43	1.72	0.16	2.53	0.1		
<i>Paracalanus</i>	17.1	13.4	33.1	26.5	9.06	17.1	5.54	5.4	12.1	3.31	0.26	4.62
<i>Temora</i>			5.9	0.81	0.82	0.3	5.24	1.78	2.18	0.15		
Cyclopoida												
<i>Corycaeus</i>	3.84	2.85	11.9	11	5.88	8.63	1.87	6.46	1.72	2.07	0.07	0.98
<i>Oithona</i>	2.12	0.11	9.32	1.24			0.1	0.01	0.47	0.04		
<i>Oncaea</i>	28.1	74.8	26.3	57.1	5.22	26.5	19.4	48.4	21.7	82.8	0.58	52.3
Harpacticoida												
<i>Miracia efferata</i>	9.82	2.05	10	2.78			2.6	0.45			0.43	1.17
<i>Clytemnestra</i>					3.7	2.61				0.01		0.36
Euphausiacea								0.32	0.13	0.02	0.06	
Hyperiida		1.17			16.3	4.5	2.63	23.9	0.46	6.72		29.3
Ostracoda	12.3						38.1	0.03	38.9	0.01	7.79	
Mollusca		0.05			0.3	0.1	0.26	0.22	0.1	0.01		0.04
Siphonophora	0.61	0.2		0.01			1.64	0.2	0.12	0.01	0.02	0.01
Appendicularia					32.5	21.4	0.82		0.43			

in neustonic specimens from the present samples and those from the mesopelagic zone (Contreras et al. 2019). Increases in feeding incidence with ontogeny related to the apparent improvement in predation skills have been reported for other fish species (Sassa & Kawaguchi 2004, Morote et al. 2008).

From larval to transforming stages, there is always positive allometric mouth growth in relation to SL (Contreras et al. 2019, Sabatés & Saiz 2000), denoting the importance of mouth size as a constraining feeding factor (Zavala-Muñoz et al. 2019). However, in the subsequent stages, this tendency ceases. It seems that once the mouth reaches a size great enough to swallow meso-zooplankton items (mostly <2 mm width), an increase in the mouth width growth is no longer important.

Transforming and juveniles of the examined species ingested preys of a wide range of sizes. Consequently, trophic niche breadth did not show any tendency to specialization for a particular prey size between these life-stages. Therefore, diet cannot be explained entirely by predator-prey sizes, and other aspects, such as food availability, must play an important role (Pusch et al. 2004).

4.3. Diet

There was no ontogenetic shift in the composition of the diet from transforming to juvenile stages feeding in the neuston. The diets of the transforming and juveniles of the studied species comprised mainly copepods, as previously reported for juveniles and adults of other myctophids (Sassa 2001, Sassa & Kawaguchi 2004, 2005, Takagi et al. 2009). Similar results have been reported for other genera, namely *Diaphus*, *Hygophum*, *Gymnoscolecus*, and *Myctophum* from other regions (Pakhomov et al. 1996, Risik & Suthers 2000, Contreras et al. 2019) where *Oncaea* species dominate the diets. Large prey such as decapods, euphausiids, and amphipods are absent or extremely rare in these stages. Nevertheless, this diet overlap is likely compensated by the higher concentrations of migrating zooplankton in neustonic waters at night, rather than in intermediate layers, thereby making prey available to the myctophid population that ascends, as discussed by Takagi et al. (2009).

M. affine was the species that showed a more diverse diet, although this was dominated by *Oncaea* sp., as in the transforming stages collected in the sub-surface waters (Contreras et al. 2019). The dietary

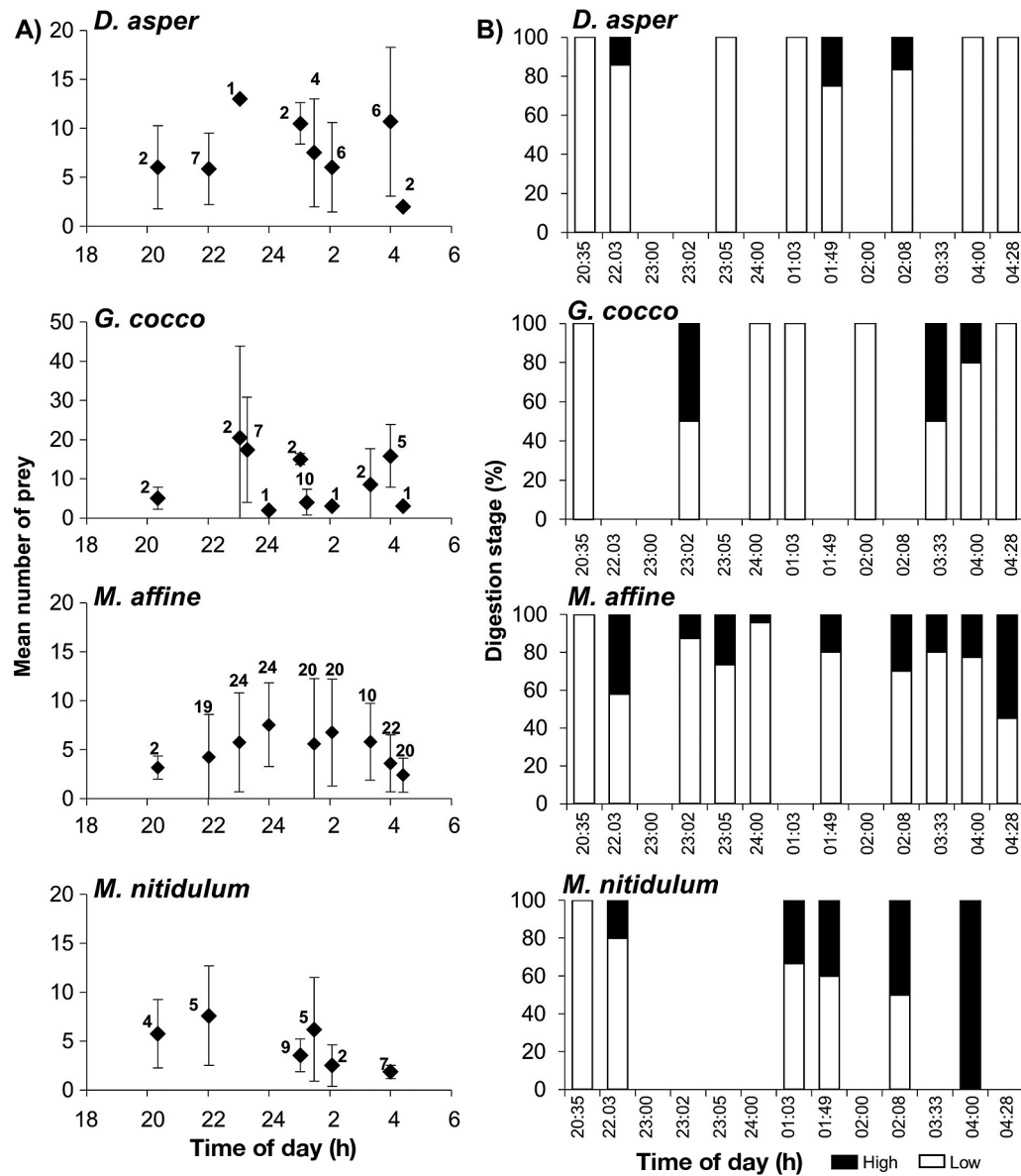


Fig. 4. (A) Mean number (± 1 SD) of prey per stomach. Numbers on top of the data points indicate the number of fishes in the group. (B) Digestion state (high/low) as a function of time (UTC). See Table 1 for full species names

shift observed from larval stages, dominated by small prey items such as copepod nauplii, ostracods, and molluscs, to transforming stages dominated by *Oncaea* sp. (Contreras et al. 2019, present study) should be noted. Other prey items such as ostracods, euphausiids, amphipods, or appendicularians have also been reported in the diets of juveniles of *D. asper* and *M. nitidulum* (Watanabe et al. 2002, Watanabe & Kawaguchi 2003, Sassa & Kawaguchi 2004, Van Noord et al. 2013). These preys occurred in the present study, but they did not constitute relevant items, except for the hyperiid amphipods in juvenile *M. nitidulum*. Stable isotope analysis indicates that

adults of the latter species also have, in addition to copepods, a significant contribution of macrozooplankton in their diets (Olivar et al. 2019). Interestingly, prey such as appendicularians, which have been reported as common in *D. asper* from neustonic layers in other world regions (Watanabe et al. 2002), did not appear in the stomachs of the species of this study but did occur in *Gonichthys cocco*. As far as we know, there are no previous studies on diet of this latter species, but the diet of the Pacific *G. tenuiculus* (Van Noord et al. 2013) is mainly composed of ostracods (not present in our specimens) and amphipods (in low proportion in our specimens).

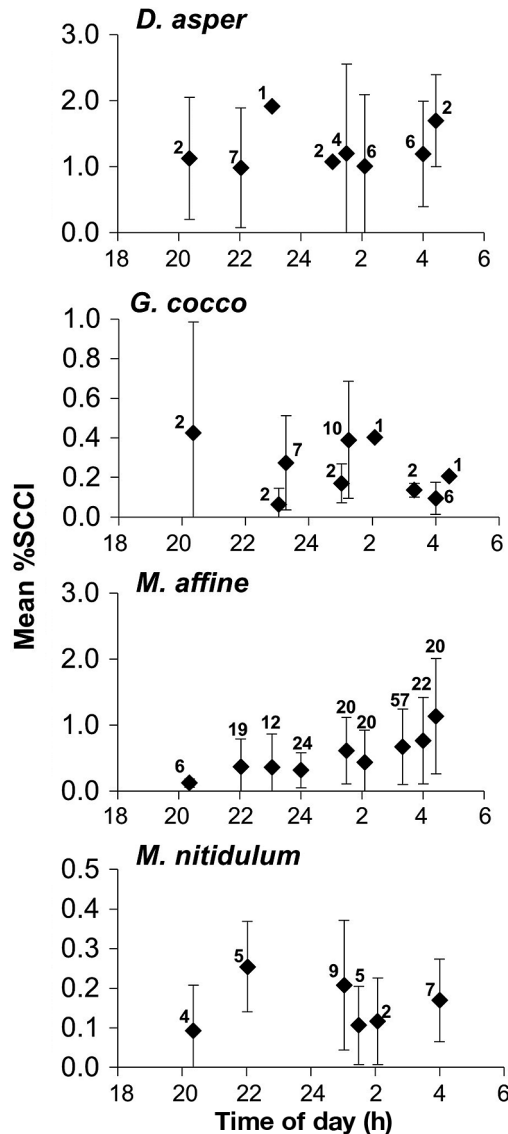


Fig. 5. Mean (± 1 SD) stomach carbon content index (%SCCI = $100 \times \text{SC}/\text{BC}$) as a function of time. SC: total carbon per stomach; BC: fish body carbon content. Numbers on top of the data points indicate the number of fishes in the group. See Table 1 for full species names

4.4. Daily rations

Our calculations of stomach filling as %SCCI (in carbon units) gave similar values to the indices calculated on the basis of dry or wet weight in other myctophids, with gut content representing from 0.4 to 3% of body weight (Gorelova 1984, Watanabe et al. 2002, Pusch et al. 2004). In addition to stomach-filling data, estimations of daily rations are dependent on the length of the feeding period, as well as on the evacuation rates. In our study, we considered the 10 h of presence of the species in the neuston as the length of the feeding period and therefore assumed

that no feeding occurred in the mesopelagic layers during the day. Because no direct measures of the evacuation time were available, gut-passage time was calculated using an evacuation rate equation dependent on temperature (Hudson et al. 2014) and set from 2 to 4 h, as for other tropical and subtropical myctophids (Gorelova 1975, Clarke 1978, Watanabe & Kawaguchi 2003, Hudson et al. 2014). DR values ranging from 0.4 to 5.8% of body weight per day were obtained, which are similar to estimates for other tropical species, e.g. *Benthosema pterotum* (Dalpadado & Gjøsaeter 1988), *Ceratoscopelus warmingii*, *Hygophum proximum* (Clarke 1978), *D. asper* (Takagi et al. 2009), and *Lampanyctus alatus* (Hopkins & Baird 1985), and slightly higher (although of the same order of magnitude) than those for colder species from the colder Southern Ocean (Pakhomov et al. 1996, Pusch et al. 2004, Drazen & Sutton 2017).

In summary, the present investigation confirms that the night migration of transforming and juvenile stages of *D. asper*, *G. cocco*, *M. affine*, and *M. nitidulum*, which extends into the neustonic layers, is related to their feeding behaviour. Diets of these 4 species are fairly similar to those of transforming stages of other myctophid species concurrently feeding in the near-surface waters at night. This suggests that the migration of part of the population to these upper surface layers represents a method for space segregation from the bulk of other myctophids also located in the subsurface layers and may contribute to the sharing of similar feeding resources among the various species. Information on trophic ecology and feeding chronology in fishes is not only a fundamental input for ecological models but is also a requirement for the explanation of the individual and community processes in food web interactions. Such information is relevant in assessing the role of a very abundant group of fishes, the myctophids, that play a major role in the active carbon flux of the ocean (Cavan et al. 2019, Hernández-León et al. 2019).

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