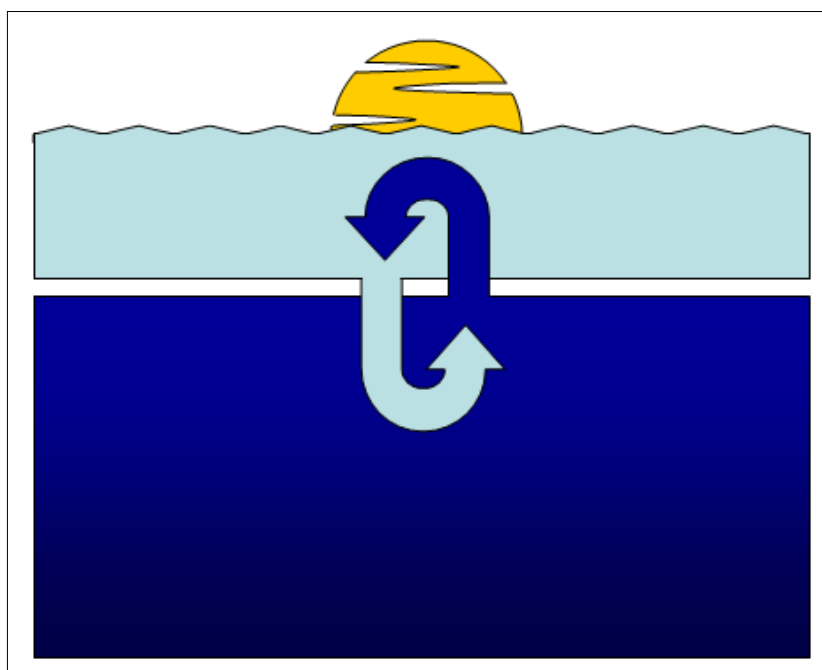# TESIS DE MÁSTER EN OCEANOGRAFÍA

Migration and feeding ecology of dominant diel vertical migrant fishes (myctophidae) in the Canary Islands waters: A combined study for the assessment of the active flux efficiency

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Migration and feeding ecology of dominant diel vertical migrant fishes (myctophidae) in the Canary Islands waters: A combined study for the assessment of the active flux efficiency.

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ABSTRACT: Diel vertical migrants (DVMs) are mainly zooplankton and micronekton migrating upward from 400-700 m depth every night to feed in the productive epipelagic zone and downward at dawn to the mesopelagic zone, where they release the ingested carbon. This is the so-called Active Flux, an important component of the Ocean Carbon Pump. Around 70% micronektonic DVMs biomass are lanternfishes (myctophidae). Therefore, myctophids might represent a pathway accounting for a substantial export of organic carbon to deeper waters. In order to assess the efficiency of the micronekton active flux, here we study the migration pattern and the feeding ecology in *Hygophum hygomii* and *Lobianchia dofleini*, two dominant myctophids in the Subtropical Eastern North Atlantic. Our results show that both populations are split in migratory and non-migratory individuals. The last ones were in a deprivation and post-digesting state with full stomachs of non-fresh food. This suggests that the evacuation rate is long enough to export efficiently most of the ingested food to the mesopelagic zone. The daily ration of the migratory individuals was 1.99 ±0.18 and 1.34 ±0.45 % of body dry weight of *H. hygomii* and *L. dofleini* respectively, feeding mainly on copepods and euphausiids. The feeding strategies and the migration patterns are discussed in order to provide further information concerning the micronekton active flux efficiency.

KEY WORDS: Diel Vertical Migrants · Myctophids · Micronekton · Active flux · Feeding ecology

INTRODUCTION

Diel vertical migration (DVM) is a particular adaptive behavior performed by many pelagic organisms around the world ocean. Nevertheless, this phenomenon is commonly attributed to large zooplankton and micronekton as they perform important displacements in terms of distance and biomass (Pearre 2003). During the day, they are concentrated in several deep scattering layers (DSL) around 400-700 m depth (Dietz 1948; Tucker 1951; Barham 1966) and at sunset they migrate upward to the surface. Up there they form migrant layers (ML) and spend the night feeding on the epipelagic zone

(Merrett and Roe 1974; Roe and Badcock 1984). Myctophids contribute up to the 70% of total biomass of those migrant layers (Hidaka *et al.* 2003) controlling around the 5-10% of the daily zooplankton production (Hopkins *et al.* 1996). Also, they are the most speciose and widespread family of midwater fishes in the world oceans (Moser and Ahlstrom 1972). They constitute the 75% of mesopelagic fish biomass caught by trawling, being the estimated global stock around 500-600 million tones (Gjøesaeter and Kawaguchi 1980; Lam and Pauly 2005; Catul *et al.* 2010). Thus, myctophids may represent a pathway accounting for a substantial export of organic carbon out of the surface mixed layer (Angel 1989; Angel and Pugh 2000; Hidaka *et al.* 2001; Hernández-León *et al.* 2010). This transport is called the active flux, a complex process which involves several physiological mechanisms of organic matter release such as the feces production (Robison and Bailey 1981),

the carbon dioxide respiration (Ikeda 1989; Longhurst *et al.* 1990), the dissolved organic carbon excretion (Steinberg *et al.* 2000) and also the death of any migrant below the mixed layer promoting a net downward transport (Zhang and Dam 1997).

The range of migration as well as the carbon releasing depth is a quite important issue concerning the effectiveness of the active flux. In order to guarantee some carbon sequestration, the DVMs must feed over the seasonal pycnocline and then cross it downward releasing the ingested carbon out of the mixed zone (Longhurst and Harrison 1989), in other words, they must perform an interzonal migration. The active flux efficiency is also dependent of the gut evacuation rate of migrants. It should be slower than the duration of the migratory phase in order to sequestrate the ingested organic matter (Angel 1985). Thus, the study of the migratory patterns and feeding chronology of DVMs is of importance for
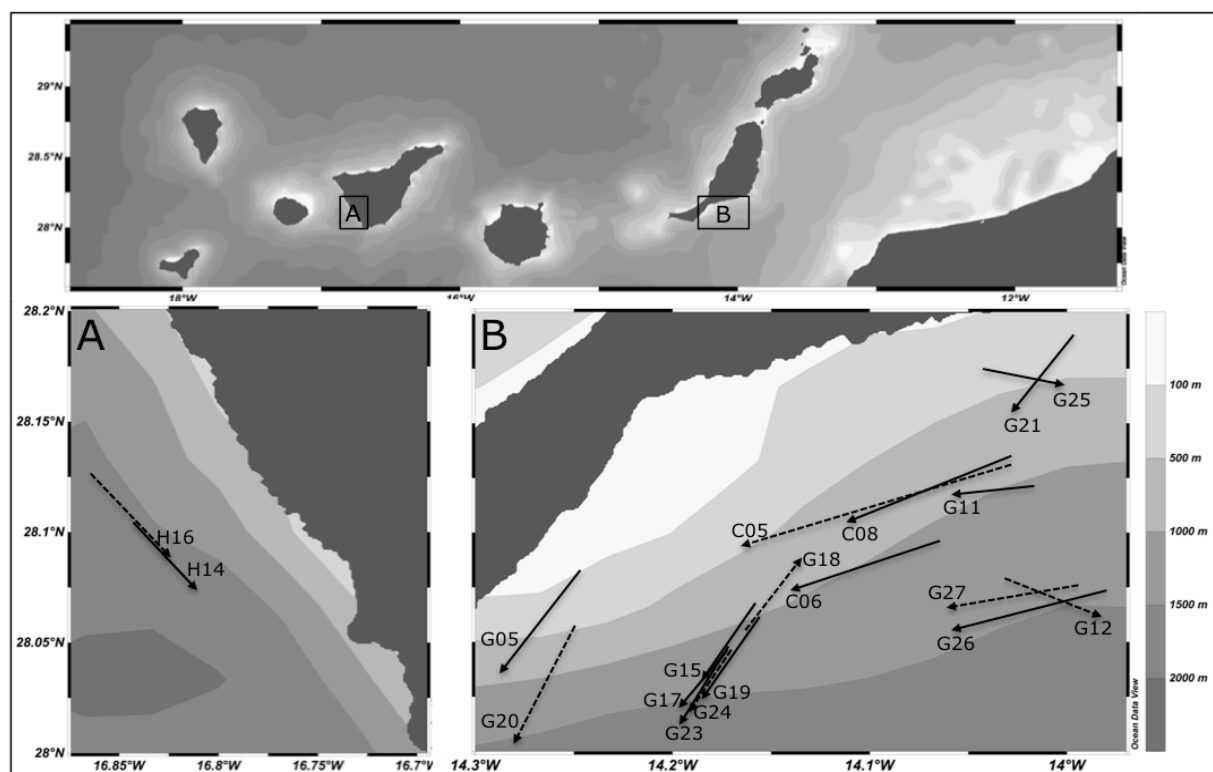

Fig. 1. Canary Islands Archipelago in the subtropical Eastern North Atlantic Ocean. The arrows indicate the position, length and direction of the profiles conducted at the SW Tenerife (A) and the SE Fuerteventura (B) islands. Dashed arrows are mesopelagic hauls, the rest are epipelagic.

the assessment of the biological pump efficiency.

Several authors have carried out these combined studies around the oceans (Tyler and Pearcy 1975; Clarke 1977; Dalpadado 1988; Moku *et al.* 2000) and frequently the conclusions concerning the feeding depth and time have been conflicting, although they were in well agreement that it depends on the migratory range of the studied species and the vertical distribution of its preys. In the Subtropical Eastern North Atlantic Ocean (SENAO) the vertical distribution and the diet of mesopelagic micronekton is well documented (Merrett *et al.* 1974; Roe *et al.* 1984) but most of the studied species were limited vertical migrants or non migrants and also the feeding chronology were partially approached. Recently, Pusch *et al.* (2004) made a thorough analysis of the diet of dominant interzonal migrants in the SENAO but unfortunately the feeding chronology neither was approached.

In order to assess active flux efficiency in the SENAO, in this manuscript we study the migration pattern in combination with the feeding chronology in *Hygophum hygomii* and *Lobianchia dofleini*, two dominant interzonal DVM fishes in this area (Wienerroither *et al.* 2009). In addition, we also show the prey composition and the daily ration. Samples were obtained from several surveys performed in the Canary Islands waters. The feeding strategies and the migration patterns are discussed in order to provide further information concerning the micronekton active flux efficiency.

MATERIALS AND METHODS

This study is based on data from 19 micronekton profiles conducted around the Canary Islands (Figure 1). The profiles were carried out during 3 pelagic trawling surveys on board the *B/E La Bocaina* (month and year follow the acronym for each cruise): ECOS-04/99, BOCAINA-03/02 and ZIFIOCAL-06/09. The hauls were towed horizontally throughout the daytime at different depths between the surface and 1000 m depth. A commercial pelagic trawl with an estimated mouth area of 2000 m^2 and a cod-end mesh size of 2 mm was used. Detailed data concerning date, time, duration, location, trawling and bottom depth of all the hauls are given in Table 1. Fishes were isolated from the rest of the catch and they were fixed in 4% formalin seawater and later transferred to 70% ethanol. The chosen targeted species for the migration and feeding study were *Hygophum hygomii* and *Lobianchia dofleini*, dominant diel vertical migrants fishes in the SENAO.

Diel migration was approached by the study of the vertical distribution of abundance between the ML and the DSL throughout the day. For this purpose, we collected the trawling data from several surveys performed between 1997 and 2002 around the Canarian Archipelago to find and select the appropriate hauls (see Bordes *et al.* 2009 and Wienerroither *et al.* 2009 for further information about the surveys). In order to reduce as much as possible the influence of the spatial and temporal oceanic variability we decided to compare only hauls which were carried out in the same area and similar date. According to these restrictions, the SE Fuerteventura area during March-April resulted the best choice, as it was the sampling place and period with more hauls performed throughout the day cycle. We also restricted our analysis to the hauls performed at the ML and the DSL. According to the scattering layers observed on the echograms obtained during the surveys (Bordes *et al.* 2009), the trawl tows performed in the upper 150 m depth line were considered as ML hauls and between 300 and 700 m depth as DSL hauls. The resulted selection was

Haul code	Strata E/M	Date dd/mm/yy	Time hh:mm	Duration min	Initial position Lat (N) - Lon (W)	Final position Lat (N) - Lon (W)	T. depth m	T. range m	B. Depth m
G05	E	09/03/02	00:10	62	28° 04.961 - 13° 14.802	28° 02.175 - 14° 17.210	50 ± 23	34 - 123	813 ± 84
C08	E	14/04/99	05:55	50	28° 08.100 - 14° 01.670	28° 06,330 - 14° 06.650	55 ± 8	47 - 67	1313 ± 41
G11	E	14/03/02	10:05	35	28° 07.298 - 14° 00.999	28° 07.296 - 14° 03.488	52 ± 36	33 - 140	1299 ± 33
G15	E	15/03/02	10:55	35	28° 04.083 - 14° 09.466	28° 02.023 - 14° 11.029	45 ± 24	30 - 98	1534 ± 85
G25	E	17/03/02	19:56	52	28° 10.482 - 14° 02.559	28° 09.900 - 14° 59.795	25 ± 4	20 - 33	134 ± 153
G21	E	16/03/02	20:10	42	28° 11.417 - 13° 59.819	28° 09.348 - 14° 01.681	22 ± 6	15 - 28	175 ± 200
G19	E	15/03/02	21:09	36	28° 03.693 - 14° 09.384	28° 01.493 - 14° 11.036	61 ± 34	30 - 139	1553 ± 68
G26	E	17/03/02	22:03	92	28° 04.363 - 13° 58.905	28° 03.308 - 14° 03.461	30 ± 10	25 - 61	1466 ± 66
C06	E	12/04/99	22:13	88	28° 05.760 - 14° 03.850	28° 04.430 - 14° 08.340	36 ± 13	20 - 52	1490 ± 36
G27	M	18/03/02	00:46	74	28° 04.556 - 13° 59.727	28° 04.002 - 14° 03.558	483 ± 62	310 - 525	1437 ± 50
G24	M	17/03/02	02:47	53	28° 02.856 - 14° 10.328	28° 00.787 - 14° 11.799	696 ± 101	565 - 980	1664 ± 72
C05	M	11/04/99	09:45	115	28°07.850 - 14°01.780	28°05.620 - 14°09.880	473 ± 37	382 - 511	1310 ± 23
G20	M	16/03/02	13:18	77	28° 03.424 - 14° 15.006	28° 00.255 - 14° 16.793	470 ± 46	308 - 498	1471 ± 108
G12	M	14/03/02	14:01	64	28° 04.741 - 14° 01.902	28° 03.746 - 13° 59.017	524 ± 76	323 - 570	1420 ± 14
G18	M	15/03/02	16:50	55	28° 03.369 - 14° 09.785	28° 05.292 - 14° 08.095	655 ± 66	470 - 695	1416 ± 46
H16	M	07/06/09	18:11	61	28° 07.617 - 16° 51.916	28° 05.365 - 16° 49.635	599 ± 44	461 - 627	1164 ± 89
H14	E	06/06/09	23:45	60	28° 06.358 - 16° 50.646	28° 04.573 - 16° 48.702	124 ± 6	117 - 135	1170 ± 89

Table 1. Characteristics of trawl stations of the 3 surveys. The first letter of the haul code indicates the survey (C = ECOS-04/99; G = BOCAINA-03/02; H = ZIFIOCAL-06/09). Next code indicates the sampling layer of each haul (E = epipelagic; M = mesopelagic); T. depth stands for Trawling depth, T. range for Trawling range and B. depth for Bottom depth. See Fig. 1 and Materials and Methods for further information.

17 profiles performed during the surveys ECOS-04/99 and BOCAINA-03/02 (see Figure 1 and Table 1 for further information). Abundance data of each haul were normalized per 10,000 m^3 of water filtered. The trawling filtered volume was estimated by multiplying the mouth area of the net by the trawling distance of each haul. Finally, the resulted density data were computed in a 24 hours time-scale histogram in order to visualize the diel migration.

The feeding of those organisms was approached by the study of the stomach contents. Because of the unavailability of samples from ECOS-04/99 and BOCAINA-03/02 surveys, an alternative sampling was chosen. We used samples from ZIFIOCAL-06/09 survey as it was the only one that had samples available and in good condition of preservation to perform the analysis. The feeding chronology was preliminary approached by the study of the fullness and digestion state of stomach contents from specimens caught before and after the migration. We selected specimens from the haul H16, performed at 18:11 around 600 m depth, as pre-migrant individuals and from the haul H14, performed at 23:45 around 120 m depth, as post-migrant individuals (see Figure 1 and Table 1 for further information). Twenty specimens per haul and species were taken. The stomachs were removed and their contents flushed into Syracuse dishes. The stomach fullness was estimated considering the filling degree and the rugae condition (folds in the internal wall of the stomach) on a scale from 0 to 3, where 0 = empty; 1 = partly full, rugae not distended; 2 = Full stomach, rugae partially distended; 3 = very full stomach, no rugae, stomach very distended (Tyler *et al.* 1975). The state of digestion was carried out with the most abundant taxon within the stomach contents, the subclass copepoda. Each

copepod were staged on a scale from 1 to 3, where 1 = fresh prey not digested; 2 = body shape of prey preserved, but some appendages separated from body; 3 = body shape of prey deformed, but identifiable to some higher taxa (Moku *et al.*, 2000). The contents used for the digestion assay came from the same stomachs used for the fullness assay (20 per species and per haul).

For the diet and daily ration study, all prey items within the stomachs were identified to higher taxa and the number of individuals of each taxon was recorded before weighting. We only used post-migrants individuals (20 stomachs from haul H14) because the contents were in better conditions for identification. For calculation of daily ration, we assume that it is equal to the amount of food found in very full stomachs during night at the migrant layer. The assumption is based on the well documented nighttime feeding activity reported in several studies (Clarke 1977; Hopkins and Baird 1977; Dalpadado 1988; Moku *et al.* 2000; Pearre 2003) and also based in the feeding chronology observations of the present study. Thus, the chosen content for weighting were those proceeding from stomachs staged as 3 in the stomach fullness scale in the haul H14. The daily ration was expressed as a percentage of body weight. It was calculated by dividing the dry weight of the stomach contents by the dry weight of the fish body.

RESULTS

Migrant pattern

Densities of *H. hygomii* and *L. dofleini* from the hauls performed at the epi- and the mesopelagic layers are shown in a 24 hours time-scale histogram. In the epipelagic hauls (Fig. 2a,b) no catches were found for both species during the daytime (G11 and G15), not even in
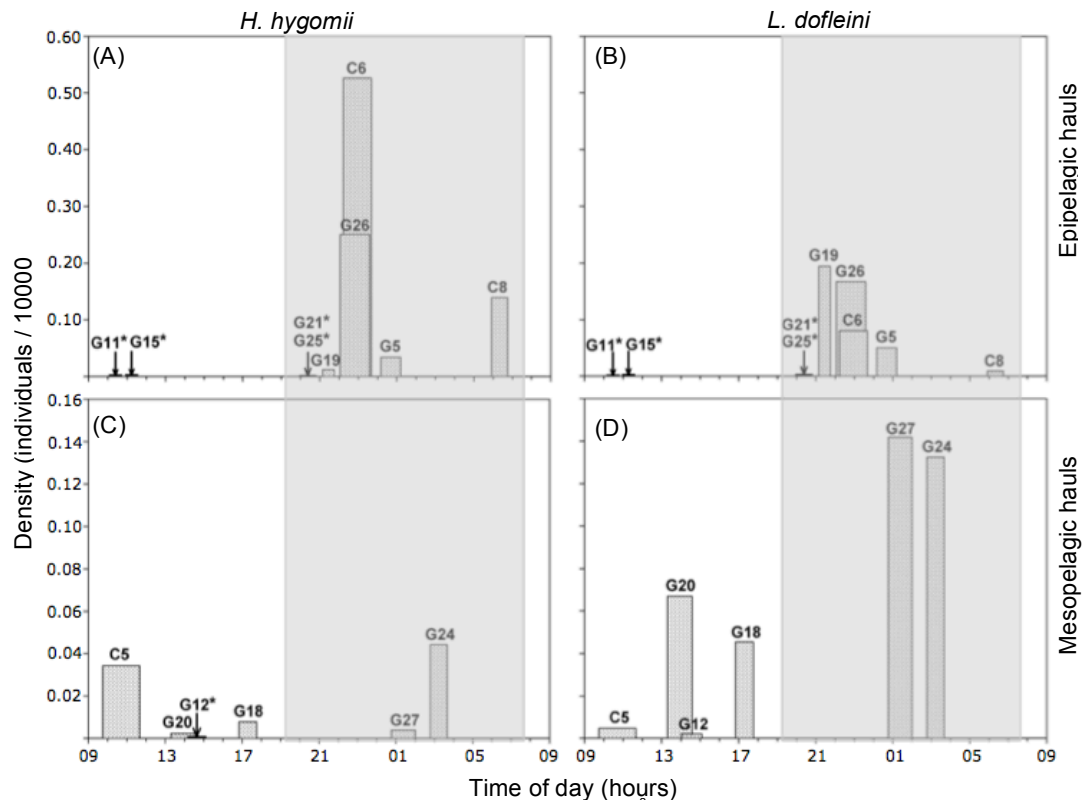
Fig. 2. Number of individuals per haul normalized per 10000 m³. The location of each bar indicates the time of day when the hauls were performed and the width indicates de duration. The names of the hauls are indicated above the bars. Asterisks mean that a haul was performed at this time but no individuals were found. The shaded area corresponds to the nighttime.

those performed during the first hours after sunset (G21 and G25). The highest density values were recorded during proper nighttime hours, between 21 and 01 h, and later abundance became progressively lower until the night was over. The mesopelagic hauls (Fig. 2c,d) showed catches of *H. hygomii* and *L. dofleini* both during the day and night (except haul G12, where no *H. hygomii* were caught), and no statistical differences were found between the two periods (Kruskal-Wallis test, $p > 0.05$). Comparing nighttime densities between epi- and mesopelagic hauls, values of *H. hygomii* resulted one order of magnitude greater at the epipelagic than in the mesopelagic layer, but not in the case of *L. dofleini*, as densities were similar in both layers.

Feeding chronology

Stomach fullness analysis for individuals caught at the epipelagic at midnight (Fig. 3a, b), shows that most of the stomachs were full or partly full for both species. Those captured at the mesopelagic layer during afternoon (Fig. 3c,d) also showed a similar pattern, dominating the full and partly full stomachs. In fact, no significant differences were found comparing the results from the epi- and mesopelagic layer for both species (Pearson's χ^2-test, $p > 0.05$).

Considering the state of digestion of copepods within the stomachs of *H. hygomii*, we observed that fresh copepods at the epipelagic layer were the most abundant prey item (Fig. 4a), while almost all preys at the mesopelagic were well digested (Fig. 4c). As expected, statistical differences were found between the stomach contents of *H. hygomii* from meso- and epipelagic layers (Pearson's χ^2-test. $p < 0.05$). A similar pattern was also observed in *L. dofleini* although a low
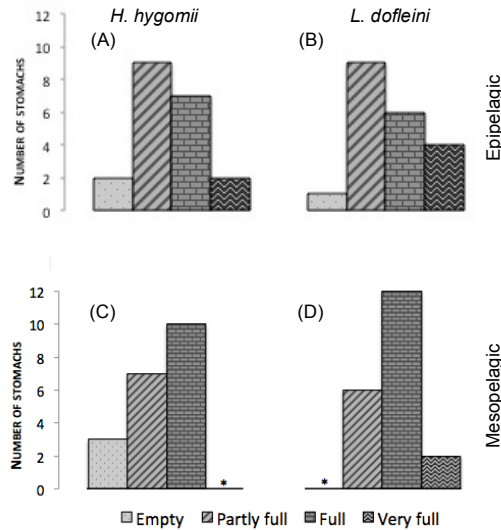
Fig. 3. Frequency of occurrence of each stage of stomach fullness. Twenty stomachs were examined per species and scenario: at afternoon at the mesopelagic layer (haul H16) and midnight at the epipelagic layer (haul H14). Asterisks = zero values.

number of identifiable copepods preclude any conclusion (Fig. 4b,d).

Diet and daily ration

We identified a total of 183 prey items in the stomachs of *H. hygomii* and only 30 in *L. dofleini*. Copepods were the commonest prey found within the *H. hygomii* stomachs, followed by amphipods and euphausiids (Table 2). Ostracods and decapod larvae were also found but in a quite low proportion. Most of the preys found in *L. dofleini* were euphausiids and copepods, although ostracods and amphipods were also significant. The obtained mean daily ration for *H. hygomii* was 1.99% ±0.18 (n=3) of the body dry weight, while in *L. dofleini* was 1.34% ±0.45 (n=6).

DISCUSSION

Migrant pattern

The density of *H. hygomii* and *L. dofleini* derived from the trawling tows is obviously underestimated due to the net associated problems of avoidance and escapement (Koslow *et al*. 1997; Ianson *et al*. 2004). However, the observed variability in abundance between the ML and the DSL throughout the diel cycle shows the effect of the vertical migration on the presence or not of both species. No individuals of *H. hygomii* and *L. dofleini* were found during the daytime in the shallower layers (Fig. 2a,b) supporting their diel migration behavior as several authors have reported (Badcock and Merrett, 1977; Roe, 1983; Roe and Badcock, 1984). Moreover, a decrease of abundance was observed along the night, especially in the case of *L. dofleini* (Fig. 2b). It could be an indicative of asynchronous midnight sinking. This mechanism was proposed by Pearre (2003) in contrast to the traditional hypothesis of synchronic descent at dawn, and it postulates that DVMs feed until their guts are full, and then asynchronously, return to the DSL to avoid predation. Because midnight sinking is a dispersed individual phenomenon, it is quite difficult to observe it with traditional vessel-mounted echosounders. Recently, however, the long-term and individual tracking acoustical observations are showing that the mechanism proposed by Pearre (2003) is a widespread behavior in DVMs (Giske *et al.* 1990; Torgersen and Kaartvedt 2001; Kaartvedt *et al.* 2009; Staby *et al.* 2011).

Our results also show individuals of *H. hygomii* and *L. dofleini* at the DSL during the nighttime (Fig. 2c,d). Their presence could be explained by asynchronous midnight sinking but also because a fraction of the same population is not migrating (Sutton and Hopkins 1996a,b). Recent results using newly systems of individual acoustic tracking supports the split of the population in migratory and no migratory individuals (Kaartvedt *et al*. 2009).
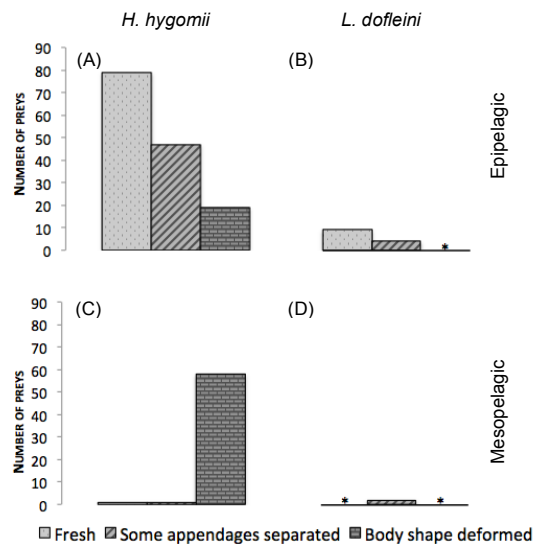
Fig. 4. Frequency of occurrence of each stage of digestion of copepods within twenty stomachs per species and scenario: at afternoon at the mesopelagic layer (haul H16) and at midnight at the epipelagic layer (haul H14). Asterisks = zero values.

Feeding chronology

Nighttime feeding at the epipelagic layer was clearly observed in both *H. hygomii* and *L. dofleini*, as most stomachs were full or partly full of fresh preys (Fig. 3a,b and 4a,b). Nocturnal feeding by myctophids in shallower waters is well documented, especially in the subtropical and tropical regions where the zooplankton production is lower and mainly restricted to the epipelagic zone (Baird *et al.* 1975; Clarke 1977). However, strikingly most stomachs were also full just before dusk at the mesopelagic zone (Fig. 3c,d). Pearcy *et al.* (1979) suggested daytime feeding at depth in productive regions where the presence of zooplankton preys in the mesopelagic zone is higher and therefore are available for non-migratory individuals. However this seems not to be the case for the non-migratory individuals of *H. hygomii* and *L. dofleini* as practically no fresh preys were found within their stomachs (Fig. 4c, d). The most feasible explanation is that stomachs remain full or partly full right before the sunset because it content

proceed from the last migration. This implies an extremely slow digestion and evacuation rate, something deserving further research.

Based on our results we agree with Sutton and Hopkins (1996a, b) who proposed that while migratory individuals are eating in upper layers, the non-migratory individuals are in a digesting or post-digesting state at depth. Recently, Drazen and Yeh (2012) documented by *in situ* respiration measurements that some deep-sea fishes have a substantially lower metabolic rate (up to one order of magnitude) than their shallow water relatives at the same temperature. This observation also supports the hypothesis of a quite slow evacuation rate in deep-sea organisms.

Diet and Daily Ration

The major prey categories found in the present work for *H. hygomii* (copepods and amphipods) agree with the finding by Pusch *et al.* (2004) in the Great Meteor Seamount (North East Atlantic). This author also studied the diet composition of *L. dofleini* and observed that it was dominated by copepods and ostracods. However, in our study, euphausiids were 43% of the diet in terms of abundance. These organisms should be an important fraction of the diet because of the high biomass of those individuals. The daily rations of both myctophids (*H. hygomii*: 1.99% ±0.18; *L. dofleini*: 1.34% ±0.45) were also in good agreement with those recorded for temperate and subtropical mesopelagic fishes. Pakhomov *et al.* (1996) listed the mean daily rations of several myctophids from the Southern Ocean and the values ranged between 1.48-2.28%. Pusch *et al.* (2004) also reported similar values (0.98 and 1.54% for *H. hygomii* and *L. dofleini*, respectively). Nevertheless, daily rations

obtained at the present study should be considered carefully, as the sample size resulted quite short because of the few very full stomachs found.

	H. hygomii	L. dofleini
Copepoda	87.43	40.00
Euphausiacea	2.73	43.33
Amphipoda	8.20	6.67
Ostracoda	1.09	10.00
Decapoda (larvae)	0.55	0.00
Total preys	n=183	n=30

Table 2. Percentage of occurrence of each recognizable taxon found within the stomachs of *H. hygomii* and *L. dofleini*.

Implications for the Active flux.

Our results suggest that the studied interzonal DVMs migrate to the DSL right after they are satiated and that they spend a long time digesting there the food. This implies that micronekton DVMs are efficiently transporting organic matter downward (1.99 and 1.34% of the dry body weight in *H. hygomii* and *L. dofleini*, respectively). Considering that they are dominant myctophids in the SENAO and that this family constitute around 70% of mesopelagic and migrant biomass (Gjøesaeter *et al*. 1980; Hidaka *et al*. 2003; Lam *et al*. 2005; Catul *et al*. 2010) we can conclude that they may represent a pathway accounting for a substantial export of organic carbon to deeper waters. Migrant biomass estimates using acoustic sampling around the Canary Islands showed a conservative value of 158.2 mmol C m^{-2} d^{-1} (Caldentey *et al*. 2012). Considering the average daily ration for both species in the present work (1.66%), the micronekton active flux would be 2.6 mmol C m^{-2} d^{-1}, much higher than the gravitational flux estimates given by Neuer *et al*. (2007) in the same region

(0.7 mmol C m^{-2} d^{-1}) and similar to those found in the oceanic water of Hawaii and Bermuda (Michaels and Knap 1996). Besides, Hernández-León *et al*. (2010) assessed zooplankton mortality rates in the Canary Current and estimated a consumption by micronektonic DVMs almost on the order of the mean gravitational flux.

In summary, we consider that micronekton DVMs play an important role in the ocean carbon pump and further research is recommended. The assessment of micronekton active flux requires an accurate knowledge about the migrant behavior, which only can be approached by *in situ* individual tracking and long-term acoustical observations. It is also important to obtain reliable values of migrant biomass and metabolism in order to know more accurate estimations of active flux.

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