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Diet and feeding strategies of mesopelagic fishes in the western Mediterranean

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ABSTRACT

Myctophids, gonostomatids and sternoptychids are the most abundant teleosts worldwide and constitute an important assemblage of the mesopelagic ecosystem, functioning as vehicles of energy and matter through trophic webs. This study concentrates on the trophic ecology of the most abundant mesopelagic fishes of the western Mediterranean (WM) based on stomach content analysis. The myctophids (in this study: *Benthoosema glaciale*, *Ceratoscopelus maderensis*, *Lobianchia dofleini*, *Myctophum punctatum*, *Hygophum benoiti*, *Hygophum hygomii*, *Lampanyctus crocodilus*, *Lampanyctus pusillus* and *Notoscopelus elongatus*) perform extensive diel migrations across the water column, between the surface to as deep as 1000 m, interacting with plankton and micronekton at multiple depths, and generally feeding in the epipelagic layers at night. In contrast, the gonostomatids *Cyclothone braueri*, *Cyclothone pygmaea*, and the sternoptychid *Argyropelecus hemigymnus* remain below epipelagic layers, feeding at different times throughout the day and night. The diet composition, trophic niche breadth and prey selectivity of 11 of these fish species were determined for juvenile and adult individuals from two surveys performed in December 2009 and July 2010 in the western Mediterranean Sea. The number of prey items varied among species, e.g. *Myctophum punctatum* was the species with the highest feeding intensity, reaching ca. 700 prey items in a stomach, whereas the mean number of prey in *Cyclothone braueri* was low (usually 1 or 2 prey per stomach). A dietary shift towards larger prey was evident from juveniles to the largest and oldest adult individuals, despite trophic niche breadths did not increase with body length for any of these mesopelagic species. The diets of the small gonostomatids, sternoptychid and early juveniles of myctophids were dominated by non-calanoïd copepods, ostracods, and other small zooplankton, whereas medium-sized myctophids, e.g. *L. dofleini* or *H. benoiti*, preyed mainly on calanoids. The oldest stages of *L. crocodilus* and *N. elongatus* fed mostly on macrozooplankton and micronekton. There was high diet overlap among mesopelagic fish species and strong heterogeneity in diet composition at intraspecific level. Nevertheless, some species showed certain degree of segregation of food resources, determined by the developmental stage or spatial distribution, and positive selection towards particular prey items. The Chesson's electivity index showed that *L. dofleini*, *N. elongatus*, *L. crocodilus* and *L. pusillus* preyed selectively on euphausiids; *B. glaciale* was selective on the calanoid genus *Pleuromamma*, and *C. maderensis* preferred to feed on larvaceans in autumn. The two congeneric species of *Hygophum* consumed a high number of food items, but *H. hygomii* showed positive selection for euphausiids, whilst *H. benoiti* preferred small corycaeid copepods. Overall, the main trophic difference among mesopelagic fishes in the WM was observed between the small non-migratory species that do not evidence a diel rhythm, feeding during both day- and night-time on small zooplankton, and the largest-sized myctophids, which fed on meso- and macrozooplankton and, more occasionally, on small fishes. Mediterranean midwater fishes can be characterised by the adoption of mixed feeding strategies, with varying degrees of specialisation on different prey types that allow flexibility in a changeable environment.

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Introduction

The mesopelagic fish community includes those species that inhabit the portion of the water column from the surface to ca. 1000 m in the open ocean (Gartner et al., 1997). Myctophids,

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gonostomatids and sternoptychids form most of the substantial biomass of such assemblage, and have a ubiquitous occurrence worldwide (Gjøsæter and Kawaguchi, 1980). The vertical migratory behaviour of many of these fish species, from great depths up to the surface, makes them an important component of the food webs, constituting common prey for demersal and large pelagic fishes (e.g. Gibbs, 1984; Fanelli et al., 2009; Anastasopoulou et al., 2013), cephalopods, marine birds (Cherel et al., 1993) and marine mammals (Pereira et al., 2011). Most groups of zooplankton and micronekton, the latter dominated by mesopelagic fishes in terms of biomass, exhibit strong diel variations in their vertical distribution, increasing the possibilities of interaction amongst trophic levels and, therefore, enhancing the complexity of the food web structure. Information on the vertical food usage of midwater fishes is scarce, although it is generally accepted that most species perform nocturnal migrations towards the epipelagic layers to forage, following the ascension of potential planktonic prey (Watanabe et al., 1999; Benoit-Bird and McManus, 2014).

Mesopelagic fishes might exert notable feeding pressure in the oceanic ecosystem due to their high abundance, e.g. myctophids have been reported to remove more than 10% of the surface zooplankton biomass per night (Watanabe et al., 2002). Moreover, these fishes can be selective upon certain types of prey (e.g. Hopkins and Gartner, 1992; Van Noord et al., 2013), and consequently, constitute an important top-down control on the zooplankton community structure in the open ocean. Several studies claim that the assessments of the biomass of midwater fishes might be widely biased and underestimated due to both the generalised effect of net avoidance and fish escapement through the meshes, the latter which can reach proportions rivaling those of net avoidance for certain fish size ranges (Gartner et al., 1989; Watanabe et al., 1999; Kaartvedt et al., 2012). Thus, the efficiency of the energy transferred, from primary production to top predators, in the open ocean through these mesopelagic migrators might be higher than previously reported (Davison et al., 2013).

The western Mediterranean (WM) is an oligotrophic region characterised by high species diversity (Estrada, 1996); however, for mesopelagic fishes, the number of species is much lower than in large oceans (Hulley, 1984). Mediterranean myctophids migrate to the epipelagic zone at night, with the exception of the oldest and largest individuals of some species (*Lampanyctus crocodilus*, *Benthosema glaciale* and *Notoscopelus elongatus*) (Olivar et al., 2012). The gonostomatids *Cyclothone braueri*, *Cyclothone pygmaea* and the sternoptychid *Argyrolepecus hemigymnus* do not migrate to the epipelagic waters, being partly responsible for the permanent acoustic response at the 400–600 m, i.e., the Deep Scattering Layer (DSL) reported in the Mediterranean continental slope (Olivar et al., 2012). As in other regions, the distributions of these mesopelagic fishes extend from the continental slope, where they co-inhabit with many other pelagic and demersal species, to the open ocean, where they constitute the dominant fish biomass of this typically oligotrophic system. Low primary production in the open ocean may be expected to induce the mesopelagic fish community to exhibit partitioning of food resources by adopting alternative behaviours, feeding on different food items or showing a particular spatial distribution that minimises overlap (Hopkins and Gartner, 1992).

Studies on the feeding habits of juvenile and adult midwater fishes from the Pacific and Atlantic oceans (Hopkins and Baird, 1973; Clarke, 1974, 1978; Gorelova, 1974; Merrett and Roe, 1974; Tyler and Percy, 1975) showed that they constitute the intermediate trophic levels and, due to their high abundance, are key components of open ocean food webs. In contrast, the information about their feeding habits in the WM is very limited. The oldest work in the WM described the diet of stranded individuals of *Hygophum benoiti* and *Myctophum punctatum* (Scotto di Carlo

et al., 1982), thus, potential factors involved in their feeding dynamics could not be evaluated. Stomach content analyses of the near-bottom adult stages of *Lampanyctus crocodilus* (Stefanescu and Cartes, 1992), and from individuals occurring at depths from below the DSL to the bottom, have been also reported (Fanelli et al., 2014). Finally, the diet of *Lampanyctus pusillus* was studied throughout its complete life history from larvae to late adults in a recent study (Bernal et al., 2013). Data on the feeding ecology of the stomiiforms (which include both the gonostomatids and sternoptychids) in the WM are even more scarce and restricted to the gonostomatid *Cyclothone braueri* (Palma, 1990). All these studies supply valuable information on the feeding of particular species; however, they do not integrate feeding interactions for the whole mesopelagic fish assemblage. A recent study (Valls et al., 2014) based on the stable isotope analysis of Mediterranean mesopelagic fishes estimated their trophic positions (all the species occupying trophic levels between 3 and 4) and elucidated diet sources through isotopic mixing models, thus providing a complementary approach to the identified prey components in the diet of these fishes.

Determining the diet of mesopelagic fishes is important to establish the topology of pelagic food webs, the flows of biomass across compartments and, eventually, assess the impact of environmental changes on pelagic systems by means of ecosystem models such as Ecopath. Due to the key role of mesopelagic fishes and the paucity of data on their trophic ecology, the stomach content analysis of midwater fishes is a potential source of information required for modelling the active fluxes of matter from zooplankton and microbial loops to top predators and back in the pelagic environment.

This study focused on the diet of the most abundant and frequent mesopelagic fishes of the WM, based on the identification and quantification of the different prey items consumed and changes in the prey size spectra throughout fish ontogeny. Our main aims were: firstly, to define their diet composition, prey selectiveness and feeding strategies; secondly, to determine the factors responsible for significant differences in diet composition at both intra- and interspecific levels; thirdly, to examine the hypothesis of high partitioning of food resources expected for oligotrophic regions such as the WM; and finally, to compare our data with isotope analysis estimates from previous studies, which provided the trophic position of the species in a particular ecosystem.

Materials and methods

Area of study and sampling

The surveys were carried out in the western Mediterranean (WM) over the shelf-break and slope off Mallorca Island (39°N, 2°E) during two surveys conducted in December 2009 and July 2010 (Fig. 1). The WM is a semi-enclosed basin characterised by moderate oligotrophic condition and seasonal alternation of the hydrodynamic conditions; in late autumn, the mixing of the water column occurs and the highest productivity levels are reached in the first 50 m depth. The mixing period is followed by a marked stratification of the water column in summer, with the highest levels of phytoplankton and zooplankton biomasses in subsurface layers (Deep Chlorophyll Maximum) (Sabatés et al., 2007; Olivar et al., 2012). The study focused on the 9 most abundant and frequent fish species of the pelagic hauls (more than 90% of the total number of fish captures, and at least 50% of occurrence in the hauls) within the family Myctophidae (Table 1). The present study also included three stomiiforms, the dominant species of the family Gonostomatidae, *Cyclothone braueri*, as well as its congener *Cyclothone pygmaea*, and the most common species of the family Sternoptychidae, the hatchetfish *Argyrolepecus hemigymnus*

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