Journal of Marine Systems 138 (2014) 160–170

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Trophic structure of mesopelagic fishes in the western Mediterranean based on stable isotopes of carbon and nitrogen

M. Valls [a,*], M.P. Olivar [b], M.L. Fernández de Puelles [a], B. Molí [b], A. Bernal [b], C.J. Sweeting [c]

[a] Instituto Español de Oceanografía, Centre Oceanogràfic de Balears, Moll de Ponent s/n, Apdo. 291, 07015 Palma, Spain
[b] Spain Institut de Ciències del Mar (CSIC), Passeig Marítim 37-49, 08003 Barcelona, Spain
[c] School of Marine Science & Technology, Newcastle University, Newcastle upon Tyne NE1 7RU, UK

ARTICLE INFO

Article history:
Received 21 June 2013
Received in revised form 4 April 2014
Accepted 9 April 2014
Available online 18 April 2014

Keywords:
Food web
Niche segregation
Myctophidae
Gonostomatidae
Sternoptychidae

ABSTRACT

Mesopelagic fishes play an important role in the transfer of organic material in the photic zone to depth although the trophodynamic partitioning amongst co-existing and presumably competing species is unclear. This study employs combined carbon and nitrogen stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) of the 18 most abundant western Mediterranean mesopelagic fishes to explore niche partitioning in this group. Sampling was conducted along the water column from the shelf and slope grounds of the Balearic Islands in two contrasting periods (late autumn and summer). Trophodynamics were explored at assemblage level and at inter- and intra-species resolutions respectively using Bayesian diet mixing models and size specific behaviour respectively. Seasonal $\delta^{13}C$ differences in near basal particulate organic matter (POM) and zooplankton fractions were almost directly replicated in higher fauna suggesting strong isotopic coupling between mesopelagic fishes and planktonic production. Despite reliance on similar basal production, species were segregated by trophic position with a graduation from 2.9 for the small Gonostomatidae *Cyclothone braueri* to 4.0 for the Myctophidae *Lobianchia dofleini*. Mixing model data reflected basic trophic position estimates with higher contributions of small fish and zooplankton/POM in higher and lower trophic level species respectively. Species could be categorized as showing preference for i) mesozooplankton/POM as for *C. braueri*, (in the lower TrL), ii) euphausiids and fish prey as for *L. dofleini* and the near bottom *Lampanyctus crocodilus* (in the upper TrL) and iii) mesozooplankton/euphausiids as *Ceratoscopelus maderensis*, *Lampanyctus pusillus* or the migrating *L. crocodilus*. There was little evidence of size based inter-population trophodynamics, with size-isotope trends explained by co-varying lipid content.

1. Introduction

Mesopelagic fishes nominally inhabit the water column between 200 and 1000 m (Gartner et al., 1997). For some species displacement is restricted to below the euphotic zone e.g. *Cyclothone* spp. (Badcock and Merrett, 1976) but many e.g. myctophids occur outside these depth bounds for short periods, even reaching surface layers during nyctimeral migrations (Hulley, 1986). Vertical migration follows prey movement and consequently mesopelagic fishes are important consumers of a wide variety of zooplankton (Pakhomov et al., 2006; Petursdottir et al., 2008) and in turn become significant prey for demersal, benthopelagic and other large pelagic fishes (Bulman et al., 2002; Cartes et al., 2009; Pakhomov et al., 2006), cephalopods (Phillips et al., 2001; Quetglas et al., 2010), seabirds (Hedd and Montevecchi, 2006; Navarro et al., 2009) and mammals (Cherel et al., 2008, 2010).

Species that migrate to the near surface layers at night have very high caloric, lipidic and proteic contents relative to phylogenetically close species and stages resident at greater depths (Bailey and Robison, 1986; Childress and Nygaard, 1973; Childress et al., 1990) and thus represent particularly valuable prey items. In the highly oligotrophic western Mediterranean, mesopelagic fishes also form an important dietary contribution to the deep sea ecosystem (Cartes et al., 2009; Quetglas et al., 2010; Valls et al., 2011). Therefore, mesopelagic fish migration plays an important role in the transfer of matter synthesized in the euphotic zone to demersal and benthopelagic species, and consequently it is of foremost importance to ascertain the trophic position of these species.

Exploration of trophic structure in the higher mesopelagic food web, particularly in the Mediterranean has dealt with a few species, mainly to the oldest life stages of mesopelagic fishes collected at the benthic boundary layer (Fanelli et al., 2009; Papiol et al., 2012; Stefanescu and Cartes, 1992) and just a few include species in the water column (Bernal et al., 2013; Palma, 1990). This is the first attempt to analyse trophic structure of the pelagic assemblage of mesopelagic fishes in the Mediterranean.

Marked oligotrophic condition of the western Mediterranean makes mesopelagic vertical transport especially important to the benthos on the insular slope where it depends more directly on planktonic and nektonic prey along the water column (Cartes et al., 2008; Maynou and Cartes, 2000). However, compared to the nearby northeast Atlantic,

* Corresponding author. Tel.: +34 971401561; fax: +34 971404945.
E-mail address: maria.valls@ba.ieo.es (M. Valls).

http://dx.doi.org/10.1016/j.jmarsys.2014.04.007
0924-7963/

Mediterranean mesopelagic fish assemblages are depauperate in species (Goodyear et al., 1972; Hulley, 1984; Olivar et al., 2012; Roe and Badcock, 1984). Although there are no estimates of the overall abundance of mesopelagic species in the Mediterranean, lanternfishes (Myctophidae) and lightfishes (Gonostomatidae) usually dominate in both number of individuals and number of species (Goodyear et al., 1972; Olivar et al., 2012), and analysis of acoustic echograms also point to dominance in biomass (Olivar et al., 2012, Peña et al., in press). Mesopelagic species therefore play important trophic functions in the Mediterranean marine system as a function of their abundance and in the interplay and transfer of energy between system components.

Mesopelagic fish may be grouped as vertically migratory to the epipelagic layers (mostly myctophids) and non-migratory (mostly the small size gonostomatid species) (Olivar et al., 2012). In addition to interspecies differences in vertical migration, intra-specific differences may also occur in relation to body size, with the largest individuals often remaining at depth (Olivar et al., 2012). Vertical migration has been advocated to follow the upper vertical migrating zooplankton, and the coincidence of large number of individuals performing the same behaviour and size based changes in behaviour imply competition for food and may involve intra- and inter-species variations in feeding pattern and niche partitioning. Information on gut contents of mesopelagic fishes indicates that they may be micronektonivores, zooplanktivores and generalists (Gartner et al., 1997). Whilst gut content approaches provide high dietary taxonomic resolution, the approach is restricted by short temporal representation, and includes substantial challenges in prey identification and biases from differential rates of digestibility (Hyslop, 1980). Such shortfalls may be mitigated by the use of alternative trophic techniques like stable isotope analyses (Miller et al., 2010).

Stable isotope analysis for food web studies is predicated on a stepwise change in the ratio of heavy and light atoms of carbon (^{12}C:^{13}C as $\delta^{13}C$) and nitrogen (^{14}N:^{15}N as $\delta^{15}N$) that generally occurs between consumer and dietary resource (Deniro and Epstein, 1981; Hobson et al., 1995; Minagawa and Wada, 1984; Petursdottir et al., 2008). $\delta^{13}C$ values are indicative of the food carbon source and habitat (Cherel et al., 2010). whereas $\delta^{15}N$ acts as an indicator or trophic level (Sweeting et al., 2007a).

Isotope based trophodynamic assessment of myctophiforms and or stomiiforms is limited. Existing data is dispersed globally and includes the sub-Antarctic (Cherel et al., 2010), Southern Ocean (Choy et al., 2012) and southern Tasman sea (Flynn and Kloser, 2012). Species have also been included in wider studies of food web structure (e.g., Cardona et al., 2012; Hedd and Montevecchi, 2006; Nilsen et al., 2008; Revill et al., 2009; Sugisaki and Tsuda, 1995) but were often sampled incidentally, for example in Mediterranean where mesopelagic species have been collected in association with bentho-pelagic and demersal food webs (Fanelli et al., 2009, 2011a; Navarro et al., 2011; Papiol et al., 2012; Tecchio et al., 2013). No work has systematically addressed the Mediterranean mesopelagic migrant community or explored trophodynamics at intra-population resolution.

The objectives of the present study are therefore to analyse trophic structure of the mesopelagic fishes at assemblage, and interspecific and intra-population resolutions in the Mediterranean and test generality in space and time. Specifically this study will use C and N stable isotope analyses of the 18 most abundant mesopelagic fishes and the associated likely preys, inhabiting the shelf-break and the slope of the western Mediterranean, and will examine inter-species variation in i) trophic level and ii) potential food sources. This will be undertaken in iii) contrasting periods (late autumn mixing period and summer stratification season) at iv) two locations with expected isotopic changes in baseline due to contrasting environmental conditions, to establish generality and stability of trophic behaviour in the mesopelagic assemblage. A subset of the most numerous fish species will be assessed further using v) Bayesian mixing models to compare utilisation of potential food sources amongst closely related species to test for niche partitioning and vi) drivers of trophodynamics within species, particularly body size.

2. Material and methods

2.1. Source of the samples

Mesopelagic fishes and zooplankton were collected in two cruises off Mallorca Island (Balearic Islands, Western Mediterranean) in late autumn (December 2009) and summer (July 2010) at two locations on the southern (Cabrera) and northwestern (Sóller) above two depth strata (shelf and slope).

Mesopelagic fishes were collected in horizontal midwater trawls carried out at the near surface (40–80 m) or 400 m-deep scattering layers (Olivar et al., 2012). After on board identification specimens were frozen to −20 °C until stable isotope analysis (SIA). Older life history stages of *Lampanyctus crocodilus* were collected contemporaneously from bottom trawls, the sampling and analytical methods of which can be found in Massutí et al. (2014–in this issue).

Microzooplankton samples were caught from vertical hauls along the first 200 m of the water column by a Calvet net fitted with a 53 μm mesh size and then sieved through a 200 μm mesh size. Macro- and mesozooplankton samples were obtained from vertical hauls with a WP2 net of 200 μm mesh size and then sieved through 500 μm mesh size to separate macrozooplankton from mesozooplankton. Samples were oven dried at 60 °C on board and kept in a desiccator until preparation for SIA. Adult stages of the euphausiid *Meganyctiphanes norvegica* were collected from the pelagic midwater trawl with fishes, and kept frozen until analysis.

Particulate organic matter (POM) samples used in this study were collected from year-round moored time-series sediment traps placed on the slope (800 m water depth and 30 m above the bottom) of the study region (Pasqual et al., 2014–in this issue). Only data taken a month before each survey (November and June) were considered to provide a better temporal match with macrofauna.

2.2. Stable isotope analyses

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analyses were conducted on the 18 most abundant mesopelagic fish species (Table 1) and their most probable preys, i.e., the bulk zooplankton by size fraction (micro-, meso- and macrozooplankton), the euphausiid *M. norvegica* (adults) and POM. Zooplankton samples were left unacidified as i) previous analysis suggest only limited inorganic carbon bias (Bode et al., 2003; Bunn et al., 1995; Letessier et al., 2012) and ii) to maintain standardisation amongst samples.

In larger fishes dorsal white muscle was extracted for isotope analysis. For small fishes whole individuals minus head and gut were analysed. Tissues were dried at 60 ºC for 24 h and ground to a fine powder. Samples consisted of just one individual except for the bulk of zooplankton or the smallest fishes (*Cyclothone braueri* and *Argyropelecus hemigymnus*) in which cases several specimens were pooled to obtain required sample volume.

Analyses were performed by continuous flow isotope ratio mass spectrometry (CF-IRMS) using a Thermo Delta X-Plus mass spectrometer. Data were expressed in δ notation as parts per thousand relative to global standard CO_2 for $\delta^{13}C$ and N_2 for $\delta^{15}N$. The analytical precision based on the standard deviation of replicates of a standard reference was $\leq$0.25‰ for both $\delta^{13}C$ and $\delta^{15}N$. C:N data are as percent element by weight.

2.3. Data analysis

As lipids are strongly ^{13}C depleted relative to proteins and carbohydrates (Sweeting et al., 2006), differential lipid contents can bias the interpretation of $\delta^{13}C$ values. Lipids of zooplankton and fishes samples were not removed to avoid loss of material of the often very small sample quantities and because they are low in most Mediterranean species. Potential lipid bias was explored using % elemental by mass C:N ratios