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### Myctophid feeding ecology and carbon transport along the northern Mid-Atlantic Ridge



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#### ABSTRACT

Myctophids are among the most abundant fishes in the world's ocean and occupy a key position in marine pelagic food webs. Through their significant diel vertical migrations and metabolism they also have the potential to be a significant contributor to carbon export. We investigated the feeding ecology and contribution to organic carbon export by three myctophid species, Benthosema glaciale, Protomyctophum arcticum, and Hygophum hygomii, from a structurally and ecologically unique ecosystem- the Mid-Atlantic Ridge (MAR). Similar to the results of previous studies, the diet of these fishes was primarily copepods and euphausiids, however, gelatinous zooplankton was identified in the diet of B. glaciale for the first time. Ridge section and time of day were significant explanatory variables in the diet of B. glaciale as determined by canonical correspondence analysis, while depth was the only significant explanatory variable in the diet of P. arcticum. Daily consumption by MAR myctophids was less than 1% of dry body weight per day and resulted in the removal of less than 1% of zooplankton biomass daily. Although lower than previous estimates of carbon transport by myctophids and zooplankton in other areas, MAR myctophid active transport by diel vertical migration was equivalent to up to 8% of sinking particulate organic carbon in the North Atlantic. While highly abundant, myctophids do not impart significant predation pressure on MAR zooplankton, and play a modest role in the active transport of carbon from surface waters.

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#### 1. Introduction

Fishes of the family Myctophidae are an important component of the marine pelagic food web due to their abundance and duality as both prey and predator in the epi- and mesopelagic zones. Myctophids are important prey for deep-sea and epipelagic piscivorous fishes, marine mammals, and sea birds (Hopkins et al., 1996; Beamish et al., 1999; Pusineri et al., 2008; Pereira et al., 2011). As predators, myctophids feed primarily on crustacean zooplankton, but are also known to feed on gelatinous zooplankton, pteropods, and other non-crustacean prey including fishes (Kinzer, 1982; Sameoto, 1988; Hopkins et al., 1996; Moku et al., 2000). Within midwater fish assemblages, myctophids can be the most important consumer (Hopkins et al., 1996), and have a significant impact on zooplankton populations, consuming 8–16% of the total copepod daily production and 2% of the overall zooplankton biomass each night in the Gulf of Mexico (Hopkins

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E-mail addresses: jeannak@vims.edu (J.M. Hudson), debbies@vims.edu (D.K. Steinberg). and Gartner, 1992), and 2–31% of the zooplankton standing stock daily in the equatorial Pacific (Gorelova, 1984).

In this study, we focus on the feeding ecology of myctophids from a structurally and ecologically unique ecosystem – the Mid-Atlantic Ridge (MAR). The MAR was the location of a project to describe and understand the patterns of distribution, abundance, and trophic relationships of organisms inhabiting the northern MAR between Iceland and the Azores (MAR-ECO; Bergstad, 2002). Sutton et al. (2008) characterized the midwater fish composition at the MAR during June–July, 2004 and reported that the family Myctophidae was the numerically dominant fish family (59% of all fishes collected), with one species, *Benthosema glaciale*, the most abundant species collected.

Diet studies of myctophids from seamounts (Pusch et al., 2004, Colaço et al., 2013) show elevated feeding, which is hypothesized to be due to turbulent mixing resulting from the unique hydrography associated with these structures (Pusch et al., 2004). Structurally similar to seamounts, mid-ocean ridges have the potential to increase food availability to benthic and planktonic consumers through resuspension of sediment (Genin and Boehlert, 1985; Dower et al., 1992; Muriño et al., 2001) and trapping of laterally advected and vertically migrating zooplankton by the raised bottom of the ridge

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(Genin and Dower, 2007; Porteiro and Sutton, 2007), which may sustain a unique community and trophic structure compared to offridge waters. Although several studies have reported on the feeding ecology of myctophid species from seamounts or other environments (Hopkins et al., 1996; Pakhomov et al., 1996; Pusch et al., 2004; Petursdottir et al., 2008; Dypvik et al., 2012), none exist for myctophids from mid-ocean ridge systems.

Furthermore, little quantitative data exist on the role of these abundant consumers in carbon cycling. Many myctophid species make daily vertical migrations to the epipelagic zone at night to feed on zooplankton, and migrate to deeper water ( $\sim 400$ – 1000 m) during the day where apparently most of the food is digested (Baird et al., 1975). By metabolizing this surface-derived food in the mesopelagic zone, myctophids actively transport organic and inorganic carbon to depth, a process which is an important component of the biological pump (Ducklow et al., 2001). Active transport of carbon via mortality, egestion of fecal pellets, respiration of CO<sub>2</sub>, and excretion of dissolved organic carbon at depth have been determined for vertically migrating zooplankton in a variety of environments (e.g., Longhurst et al., 1990; Steinberg et al., 2000; Al-Mutairi and Landry, 2001), but only two previous studies have quantified active transport by vertically migrating myctophids. Hidaka et al. (2001) reported myctophids in the equatorial Pacific actively transported the equivalent of 15-28% of passively sinking particulate organic carbon (POC) measured by sediment traps, and Davison et al. (2013) estimated myctophid vertical migration could account for  $\sim$  8% of passively sinking POC (as estimated from satellite data) in the northeast Pacific Ocean. There are no previous estimates of active transport by myctophids for the Atlantic Ocean.

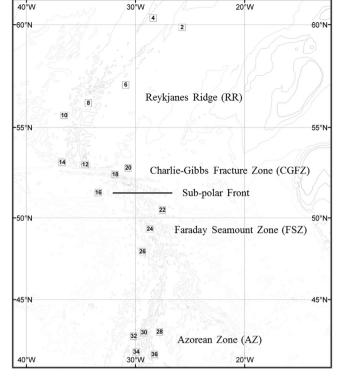
The first goal of our study was to describe and quantify the feeding ecology of three myctophid species from the northern MAR (*Benthosema glaciale, Protomyctophum arcticum*, and *Hygophum hygomii*) to investigate how the presence of a mid-ocean ridge may affect myctophid diet composition. Our second goal was to provide an estimate of active carbon transport by myctophids at the MAR, a first for the North Atlantic Ocean. Diet composition, daily consumption rates, and carbon export of these fishes were used to assess their role in the overall trophic structure and carbon cycle of this topographically and hydrodynamically unique ecosystem.

#### 2. Methods

#### 2.1. Sampling procedure

Myctophids were collected during the R/V G.O. Sars research expedition to the northern MAR (Iceland to the Azores) during June–July, 2004. Two double-warp, multi-cod end midwater trawls were used to sample the ridge fauna in discrete depth zones. The macrozooplankton trawl has a  $6 \times 6$  m mouth opening, 6 mm stretched mesh throughout its length, and was equipped with five opening and closing cod ends. The Åkra trawl has a 20–35 m vertical mouth opening, 110 m door-spread, graded mesh to 22 mm (stretched), and was equipped with three multiple opening and closing cod ends. Volume of water filtered was calculated using the trawl mouth area, towing speed, and distance traveled.

Predefined stations along the ridge were sampled discretely within five depth categories: 0-200, 200-750, 750-1500, 1500-2300, and > 2300 m in four ridge sections (Fig. 1). Samples were classified as day (D), dusk (DN), night (N), or dawn (ND) with dusk and dawn samples defined as the start time of the net being one hour before to one hour after sunset and sunrise, respectively (Sutton et al., 2008). Once on board, specimens were sorted and either frozen whole or preserved in 10% buffered formalin.



**Fig. 1.** Trawl sampling stations at four ridge sections along the northern Mid-Atlantic Ridge from Iceland to the Azores during the 2004 R/V *G.O. Sars* MAR-ECO expedition. Black line represents the approximate location of the Sub-polar Front ( $30^{\circ}W$ ,  $52^{\circ}N$ ) at the time of the cruise.

Preserved samples were identified and transferred to 70% ethanol in the laboratory. For additional details concerning net sampling aboard the R/V *G.O. Sars*, (see Wenneck et al., 2008).

Trawl gear provides measures of relative fish biomass (Koslow et al.,1997; Kaartvedt et al., 2012), which implies information on gear efficiency is needed for the estimation of any biomassnormalized rate processes. Using hydroacoustics, Kaartvedt et al. (2012) reported a value of 0.14 for the sampling efficiency of B. *glaciale* collected by a large ( $\sim$ 400 m<sup>2</sup> mouth area) Harstad trawl net. For the gears used in the present study, Heino et al. (2011) determined the Åkra trawl was more efficient at sampling fishes than the macrozooplankton trawl, with a relative catchability of 2.3. Despite the improved efficiency of the Åkra trawl, we elected to base our myctophid biomass and carbon transport calculations on data obtained by the macrozooplankton trawl since the fixed mouth area of this gear allowed for a more accurate calculation of volume of water filtered. For all calculations based on data collected by the macrozooplankton trawl, both the actual biomass and biomass corrected for an assumed sampling efficiency of 0.14 are reported.

#### 2.2. Sample selection, dissection, and prey identification

Three myctophid species were selected for analysis – *Benthosema glaciale, Protomyctophum arcticum,* and *Hygophum hygomii* – based on their diverse geographic distributions and availability of samples. A subset of specimens from the total cruise catch was selected for measurement and dissection from the available geographic-location, depth, and time-of-day combinations. A total of 380 fishes were processed for diet composition information broken down by species as follows: 265 *B. glaciale,* 76 *P. arcticum,* and 39 *H. hygomii.* The standard length of each fish was recorded to the nearest 0.1 mm and the stomach and intestines were excised. Prey was identified microscopically to the lowest possible

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