SHORT REPORT

Diet and prey selectivity in three surface-migrating myctophids in the eastern tropical Pacific

Joel E. Van Noord · Robert J. Olson ·
Jessica V. Redfern · Ronald S. Kaufmann

Abstract To test feeding selectivity, the diets of three surface-migrating myctophids [*Myctophum nitidulum* ($n = 299$), *Symbolophorus reversus* ($n = 199$), and *Gonichthys tenuiculus* ($n = 82$)] were compared to zooplankton prey collections at 32 stations in the eastern Pacific Ocean, August–November 2006. *Myctophum nitidulum* fed predominately on copepods (42.7 % by number) and ostracods (41.5 %), selected amphipods ($p = 0.002$) and ostracods ($p = 0.014$), and avoided copepods ($p < 0.001$). *Symbolophorus reversus* fed on copepods (32.5 % by number) and euphausiids (29.6 %) and selected euphausiids ($p = 0.002$) and amphipods ($p = 0.008$). *Gonichthys tenuiculus* fed on ostracods (34.6 %) and amphipods (27.3 %), but showed no significant selectivity.

Keywords Myctophids · Diet · Selectivity · Eastern tropical Pacific

J. E. Van Noord (✉) · R. S. Kaufmann
Marine Science and Environmental Studies Department,
University of San Diego, 5998 Alcalá Park,
San Diego, CA 92110, USA
e-mail: joel.van.noord@gmail.com

Present Address:
J. E. Van Noord
California Wetfish Producers Association, PO Box 1951,
Buellton, CA 93427, USA

R. J. Olson
Inter-American Tropical Tuna Commission,
8901 La Jolla Shores Drive, La Jolla, CA 92037, USA

J. V. Redfern
Southwest Fisheries Science Center, 8901 La Jolla Shores Drive,
La Jolla, CA 92037, USA

Introduction

Myctophids are voracious consumers of zooplankton, capable of removing as much as 10 % of the zooplankton biomass per night (Watanabe et al. 2002). In addition, myctophids are estimated to encompass the greatest biomass among any fish family (Gjosaeter and Kawaguchi 1980; Kaartvedt et al. 2012). Given this abundance and feeding intensity, myctophid prey selectivity can greatly influence zooplankton community structure and trophodynamics.

The purpose of this study was to test whether feeding selectivity occurs within common surface-migrating myctophids in the eastern tropical Pacific Ocean (ETP) and to assess which prey groups are selected. To accomplish this, we determined the major prey taxa of these myctophids, numerically quantified the zooplankton prey community, and compared diet to zooplankton at 32 stations.

Materials and methods

Samples were collected from throughout the ETP (Fig. 1), but most locations occurred within the north equatorial countercurrent, from approximately 10° to 5°N and 115°W to the coast of the Americas. Myctophid fishes were captured by dip-net (Coad 1984) 1–2 h after local sunset in surface waters using deck lights aboard the National Oceanic Atmospheric Administration's (NOAA) R/V *David Starr Jordan* and R/V *MacArthur II* from August to November 2006. Zooplankton were sampled using a bongo net (0.6 m mouth diameter, 333-μm mesh) 30 m after the conclusion of dip-netting and towed obliquely to 200 m at an average speed of 1.75 kts. An oblique net tow was used since myctophids can feed at depth during their migrations.
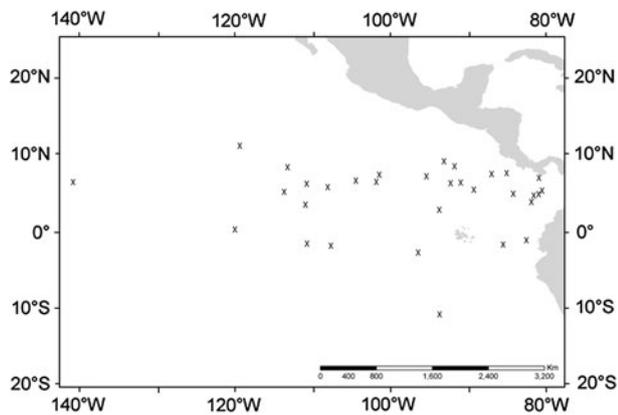
Fig. 1 Myctophid collection localities from 32 stations in the eastern tropical Pacific Ocean are indicated by an "*x*." Samples were taken from August to November, 2006

Myctophids were identified in the lab using published guides (Wisner 1974; Gago and Ricord 2005). The diets of the three most common myctophids were examined, *Myctophum nitidulum* (Garman 1899) ($n = 299$), *Symbolophorus reversus* (Gago and Ricord 2005) ($n = 199$), and *Gonichthys tenuiculus* (Garman 1899) ($n = 82$). Standard length (SL) was measured to the nearest mm. Stomachs were dissected from each specimen and the contents identified to order. Mean percentage by number (MN_i) was calculated using the following equation:

$$MN_i = \frac{1}{P} \sum_{j=1}^{P} \left(\frac{N_{ij}}{\sum_{i=1}^{Q} N_{ij}} \right) \times 100$$

where N_{ij} is the count of prey group i in fish j, Q is the number of prey groups in the stomach of fish j, and P is the number of fish with food in their stomachs (Chipps and Garvey 2007).

Net captured zooplankton were split to one-eighth volume using a Folsom Plankton Splitter and individuals were identified to order and enumerated. Zooplankton densities

were standardized to numbers of individuals per m³ of water filtered at each station (Smith and Richardson 1977) and converted to percentages for comparison with the MN_i index. Chesson's (1983) alpha (α_i) was used to evaluate selectivity for prey group i for each myctophid species j:

$$\alpha_i = \frac{\left(\frac{r_i}{n_i} \right)}{\sum_{j=1}^{m} \left(\frac{r_j}{n_j} \right)}$$

where m is the number of prey groups eaten by each myctophid species. r_i and n_i are the proportions of prey group i in the diet of each myctophid species and the proportion of that prey group found in the environment (as sampled by the oblique net tow), respectively. α_i is interpreted as the numeric proportion of the diet that would consist of prey group i if all prey groups were present in equal numbers in the environment (Chesson 1983). $\alpha_{neutral}$, defined as m^{-1}, is the proportion of a prey group out of all prey groups consumed by a myctophid species. Nonselective feeding occurs when $\alpha_i = \alpha_{neutral}$; positive selection occurs when $\alpha_i > \alpha_{neutral}$; and negative selection (prey avoidance) occurs when $\alpha_i < \alpha_{neutral}$ (Chesson 1983). A t test was used to compare mean α_i to $\alpha_{neutral}$ for each prey group (Chesson 1983).

Results

Collectively, these myctophids consumed copepods (37.7 % by MN_i), ostracods (34.9 %), euphausiids (13.7 %), and amphipods (9.1 %), with the remaining prey groups contributing less than 5 % by MN_i and consisting of pelagic molluscs (pteropods and heteropods), larval fishes, decapods, fish eggs, and squid paralarvae. *Symbolophorus reversus* had the greatest standard length (55.9 ± 8.8 mm, mean $\pm$ SD) and *Gonichthys tenuiculus* (37.8 ± 4.3) were the smallest, while *Myctophum nitidulum* were intermediate in length (47.9 ± 6.6). One of the 299 *M. nitidulum* stomachs, two of the 199 *S. reversus* stomachs, and 21 of

Table 1 Mean percentage by number (MN_i), Chesson's alpha (a_i), and p values from t tests for the four main prey groups consumed by *Myctophum nitidulum*, *Symbolophorus reversus*, and *Gonichthys tenuiculus*

	M. nitidulum $n = 299$, 1 empty stomach SL = 47.9 ± 6.6 $\alpha_{neutral} = 0.125$			S. reversus $n = 199$, 2 empty stomachs SL = 55.9 ± 8.8 $\alpha_{neutral} = 0.111$			G. tenuiculus $n = 82$, 21 empty stomachs SL = 37.8 ± 4.3 $\alpha_{neutral} = 0.250$		
	MN_i (%)	Mean a_i	p value	MN_i (%)	Mean a_i	p value	MN_i (%)	Mean a_i	p value
Amphipods	8.4	0.356	0.002*	7.6	0.269	0.008*	27.3	0.367	0.408
Copepods	42.7	0.046	<0.001*	32.5	0.077	0.424	18.6	0.106	0.094
Euphausiids	3.2	0.089	0.224	29.6	0.314	0.002*	19.4	0.347	0.441
Ostracods	41.5	0.316	0.014*	24.4	0.130	0.705	34.6	0.182	0.525

See text for explanation of a_i. Standard lengths (SL) are measured in mm $\pm$ SD

* Significance at $p < 0.05$

the 82 *G. tenuiculus* stomachs were devoid of prey material (Table 1).

Seventeen taxonomic groups were identified and enumerated ($n = 178{,}090$ individuals) in the zooplankton net samples. *Symbolophorus reversus* consumed nine of these groups, *M. nitidulum* eight, and *G. tenuiculus* four. Copepods were most abundant in the net tows (72.2 ± 10.7 % numerical percent, mean $\pm$ SD), followed by ostracods (8.7 ± 10.1 %), euphausiids (4.4 ± 3.2 %), and amphipods (1.4 ± 0.5 %) across all stations.

Myctophum nitidulum predominately consumed copepods (42.7 % by MN_i) and ostracods (41.5 %), significantly selected amphipods ($p = 0.002$) and ostracods ($p = 0.014$), and significantly avoided copepods ($p < 0.001$) (Table 1). *Symbolophorus reversus* primarily fed on copepods (32.5 % by MN_i) and euphausiids (29.6 %) and selected euphausiids ($p = 0.002$) and amphipods ($p = 0.008$) (Table 1). *Gonichthys tenuiculus* fed on ostracods (34.6 % by MN_i) and amphipods (27.3 %) (Table 1), but showed no significant selectivity.

Discussion

Myctophid feeding selectivity has the potential to influence zooplankton community structure. Collectively, myctophids primarily consumed copepods; however, all three species avoided them, with *Myctophum nitidulum* showing significant avoidance for copepods. Conversely, amphipods and euphausiids, which are calorically rich (Ikeda 1974, 1985; Morris and Hopkins 1983), were selected by these myctophids. Similarly, all three myctophids consumed ostracods in high proportions, while *M. nitidulum* significantly selected them. These preferences may provide a competitive advantage to copepods or other mesozooplankton, because despite consuming copepods in great proportions, these myctophids select other taxa.

Due to their feeding selectivity, myctophid species composition could influence trophodynamics in pelagic communities. *Myctophum nitidulum* and *Symbolophorus reversus* were most dissimilar in their preference for euphausiids. Although mesozooplankton diet is varied and can reflect ambient food conditions (Cowie and Hedges 1996; Nakagawa et al. 2001; El-Sabaawi et al. 2009), euphausiid diets can differ from those of other large mesozooplankton, such as amphipods and copepods (Kinsey and Hopkins 1994; Yamada and Ikeda 2003). In some cases, greater abundances of *S. reversus* could result in stronger bottom-up forces acting on the food web than greater abundances of *M. nitidulum*. Myctophid abundances, however, were not available for this study.

An ability to prey on a diversity of zooplankton would be advantageous for myctophids in a dynamic ecosystem. *Myctophum nitidulum* is abundant and widespread throughout the oceans (Wisner 1974). In most locations, such as the western Pacific (Watanabe et al. 2002; Van Noord 2013) and equatorial Atlantic (Van Noord, unpublished data), copepods are their primary prey. From the 1960s to the 1990s, however, Watanabe and Kawaguchi (2003) observed that the diet of *M. nitidulum* was alternately dominated by euphausiids, copepods, and larval sardines in the Kuroshio Current, possibly reflecting changes in prey availability. In this study, however, *M. nitidulum* were statistically selective for amphipods and ostracods, while statistically avoiding copepods. A flexible diet may help explain the diverse diet observed in the literature and wide distribution of *M. nitidulum*.

Diet can also reflect environmental conditions. *Symbolophorus evermanni* similarly focused on euphausiids and amphipods in the productive waters of the Kuroshio Current (Watanabe et al. 2002), but preyed on copepods (Van Noord 2013) in the more oligotrophic waters of the Mariana Trench (Furuya 1990). Additional spatial and temporal sampling could further elucidate the relationship between diet and environmental conditions.

Biases can influence selectivity estimates. The taxonomic resolution in identifying prey resources, for example, can lead to a conclusion that an entire order was selected for or against, while selection for species within that order may be different (Cortés 1997; Longenecker 2007; Robert et al. 2008). Net avoidance by larger organisms (Fleminger and Clutter 1965) can undersample certain taxa, leading to potential false positives. In addition, ontogenetic shifts in diet are common, with greater fish size generally corresponding to the incorporation of larger prey, such as euphausiids (e.g., Hopkins and Baird 1973; Hopkins and Gartner 1992; Suntsov and Brodeur 2008). Therefore, estimates of selectivity could differ if a greater range of juvenile or adult specimens were available for this study. This study focused on feeding patterns shortly after sunset, a time at which both myctophid species and mesozooplankton conduct diel vertical migrations (Haney 1988; Watanabe et al. 1999). Therefore, timing of sampling could affect feeding selectivity. Samples collected from different periods during the night, for example, may result in a different zooplankton community available to these myctophids.

This study contributed to the understanding of pelagic ecosystems by describing, for the first time, the major diet constituents of un- and understudied myctophids. In addition, significant selectivity and avoidance was observed, indicating these myctophids may influence zooplankton community structure.

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