Journal Pre-proof

Dietary composition of myctophid larvae OFF western Australia

Ainhoa Bernal, M. Pilar Olivar, Lynnath E. Beckley

PII: S0967-0645(20)30051-5

DOI: <https://doi.org/10.1016/j.dsr2.2020.104841>

Reference: DSR II 104841

To appear in: *Deep-Sea Research Part II*

Received Date: 1 April 2020

Revised Date: 14 July 2020

Accepted Date: 15 July 2020

Please cite this article as: Bernal, A., Olivar, M.P., Beckley, L.E., Dietary composition of myctophid larvae OFF western Australia, *Deep-Sea Research Part II* (2020), doi: <https://doi.org/10.1016/j.dsr2.2020.104841>.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2020 Published by Elsevier Ltd.

Author statement

Ainhoa Bernal: Formal Analysis, Investigation, Writing-Original Draft, Visualization.

Pilar Olivar: Conceptualization, Writing- Reviewing & Editing, Supervision, Project administration.

Lynnath Beckley: Conceptualization, Writing- Reviewing & Editing, Resources, Supervision,
Funding acquisition.

DIETARY COMPOSITION OF MYCTOPHID LARVAE OFF WESTERN AUSTRALIA

Ainhua Bernal^{1*}, M. Pilar Olivar¹, Lynnath E. Beckley²¹ Institut de Ciències del Mar, Passeig Marítim de la Barceloneta, Barcelona 08003, Spain² Environmental and Conservation Sciences, Murdoch University, 90 South Street, Perth, Western Australia 6150, Australia

* Corresponding author: bernal@icm.csic.es

Abstract

Mesopelagic fishes of the southeastern Indian Ocean are represented by a high number of lanternfish species (Myctophidae). The horizontal distribution patterns of their larvae have been previously studied; however, research on larval feeding habits is non-existent. The goal of this study was to describe the diet and trophic-based strategies of the most abundant myctophid larvae off Western Australia through stomach content analysis. Samples were collected in autumn 2007 off southwestern Australia when this oligotrophic area was under the influence of the seasonal Leeuwin Current, and in autumn 2010 on the tropical continental shelf of northwestern Australia. The species investigated during these periods were *Benthosema fibulatum*, *B. pterotum*, *B. suborbitale*, *Dasyscopelus asper*, *Diaphus* “deep” and “slender” morphotypes, *Hygophum hygomii*, *Lampadena luminosa*, *Lampanyctus alatus*, *Lampanyctus* spp., and *Myctophum* sp. Generally, myctophid larvae showed a diurnal feeding pattern. Only postflexion stages in *L. alatus*, *L. luminosa*, *B. pterotum*, *Diaphus* “slender”, and *Myctophum* sp. preyed at dawn or during the night. The highest feeding incidence was found in *L. luminosa* and the *Diaphus* “deep” morphotype, while the lowest, in *H. hygomii*. Generally, larvae were zooplankton feeders with nauplii and copepodites being the most abundant dietary groups, except for *B. suborbitale* and *Myctophum* sp., where the small non-calanoïd genus *Oncaea* was dominant. Soft organisms such as appendicularians were frequent items in most fish diets throughout their entire larval phase, and highly abundant in *Diaphus* “deep” morphotype. The wide prey-size spectrum indicates that the majority of the fish species were not size-specific feeders for most of their larval life. Nevertheless, *B. suborbitale*, *B. fibulatum*, and *L. alatus* preferred larger prey, ignoring the smaller items as they grew. Larval feeding patterns of similar genera from other ecosystems are discussed and compared with those in Western Australia.

Keywords: feeding behaviour, ichthyoplankton, marine fish larvae, Myctophidae, Indian Ocean

1. Introduction

Mesopelagic fishes, with an estimated biomass of 10 billion tons (Irigoién et al. 2014), dominate the total fish biomass on Earth (Gjøsæter and Kawaguchi 1980). Mesopelagic fishes are considered as organic carbon vectors between the surface and deeper waters and are an important intermediate link in the oceanic food web (Hidaka et al. 2001; Davison et al. 2013; Trueman et al. 2014; Hernández-León et al. 2019). Lanternfish (Myctophidae) constitute the most diverse family within this group of fishes (Paxton 1979; Olivar et al. 2017) and are particularly abundant and diverse in the oligotrophic southeastern Indian Ocean (IO) encompassing both temperate, subtropical and tropical species (Vipin et al. 2012). Different water masses modulate the existence of these heterogeneous larval fish assemblages (Muhling et al. 2008; Holliday et al. 2012), where the occurrence of tropical and subtropical species is attributed to the transport of fish larvae by the Leeuwin Current (LC) (Beckley et al. 2009, Pearce and Hutchins 2009). This oceanic area is of great importance since the recruitment of several commercial species depends on the strength of the LC (Lenanton et al. 1991, Lenanton et al. 2009).

The IO adjacent to the coast of Western Australia comprises two main bioregions, the North West (NW) characterised by tropical and subtropical biota and the South West (SW) characterised by subtropical and temperate biota (Fox and Beckley 2005; Australian Government 2012a, 2012b). The circulation in the NW bioregion is a complex interaction between large tides, wind, and regional forcing by currents along the shelf-break (Beckley et al. 2019). The anomalous LC is the dominant oceanographic feature off the west coast of Australia and it flows southward along the shelf-break transporting warm, low-salinity water of tropical origin and associated biota towards the SW, particularly during the austral winter (Beckley et al. 2009; Feng et al. 2010; Weller et al. 2011). The LC has strong kinetic energy and an associated eddy-field of both anticyclonic and cyclonic eddies (Waite et al. 2007a). The influence of these eddies on the pelagic ecology of different organisms has been investigated in several studies (e.g., Thompson et al. 2007; Waite et al. 2007b; Paterson et al. 2008; Sutton et al. 2015; Waite et al. 2019), some of which are specifically about larval assemblages of mesopelagic fishes (Muhling et al. 2007; Holliday et al. 2011a; Holliday et al. 2012).

Despite these studies on larval assemblages, there have been no investigations on the diet and trophic relationships of larvae of mesopelagic fishes such as myctophids in either the NW or SW. Most studies on the feeding patterns of myctophid larvae have

been conducted in the Pacific Ocean (Rodríguez-Graña et al. 2005; Sassa and Kawaguchi 2004, 2005, 2007, 2010), Atlantic Ocean (Contreras et al. 2019) or other regions (e.g., Gulf of Mexico: Conley and Hopkins 2004; Mediterranean Sea: Sabatés and Saiz 2000; Sabatés et al. 2003; Contreras et al. 2015). The southeastern IO is one of the most oligotrophic basins in the world, however, nutrient limitations for the zooplankton in the area remain unstudied. The pelagic ecology of the remote NW is even less studied than that of SW Australia.

The larvae of mesopelagic fishes are generally distributed in the epipelagic zone and are found from near the surface to about 200 m depth (Moser and Smith 1993; Sabates et al. 2003; Sassa and Hirota 2013). Once they attain the transformation stage, they descend to the mesopelagic domain (Badcock and Merrett 1976; Loeb 1979, Sassa et al. 2007; Bowlin 2016; Olivar et al. 2018) and start diel vertical migrations. Several studies have revealed that myctophid larvae feed on small zooplankton in the epipelagic zone (e.g., Sabatés and Saiz 2000; Rodríguez-Graña et al. 2005; Sassa and Kawaguchi 2005; Sassa 2010; Bernal et al. 2013; Contreras et al. 2015, 2019). In general, copepods constitute the main food source with nauplii and eggs being the predominant prey in the earliest larval phases of fishes. Nevertheless, the different myctophid species have diverse morphological characteristics and swimming abilities that can influence their diets (Sassa and Kawaguchi 2005; Contreras et al., 2019).

This study reports, for the first time, the feeding patterns of the larval stages of several species of myctophid inhabiting the coastal and adjacent oceanic waters of the NW and SW bioregions of Australia in the southeastern IO. Our research question was whether there are differences between the dietary compositions of the different species and, in that case, are they explained by distinct conditions in their habitats, their morphology or other factors?

2. Material and methods

2.1. Sampling locations and data collection

To obtain information on the diets of larval myctophids in the southeastern IO we selected larvae collected during two Australian research voyages carried out in different geographical areas. The first cruise was undertaken in May 2006 (austral autumn) in a region offshore of SW Australia dominated by an evolving anticyclonic eddy of the Leeuwin Current (30°S - 34°S, 112°E - 115°E) (Paterson et al. 2008; Holliday et al. 2011a), although the shelf stations near Perth were not in the LC or its anticyclonic eddy (see map in Fig 1A). The second research voyage was undertaken in

May 2010 across a coastal-oceanic gradient off NW Australia (Fig 1B; 13.5°S – 17.5°S, 120°E – 124°E) (Holliday et al. 2011b, Beckley et al. 2019). In both bioregions, fish larvae were collected with a Bongo net (diameter 0.6 m; 100 µm and 355 µm mesh sizes) towed obliquely for about 15 min from a maximum depth of 150 m up to the surface at a vessel speed of 2 knots, during both day and night. Zooplankton samples were fixed in seawater with 5% formalin and, in the laboratory, fish larvae were sorted out under a dissecting stereomicroscope and transferred to small vials containing 70% ethanol. The larvae were identified using appropriate literature (Moser 1984; Olivar and Fortuño 1991; Olivar et al. 1999; Moser and Watson 2006; Richards 2005). For each myctophid larva, standard length (SL), mouth width (MW) and the preflexion or postflexion notochordal stage were recorded employing an eyepiece micrometre. MW and SL were fitted to a power equation to obtain the slope of the function that represents the allometric growth coefficient.

2.2. Gut content analysis

Guts of 686 feeding larvae, mainly from catches obtained during daylight hours, were examined (Table 1). The myctophid larvae considered for this study from the SW area were: *Benthoosema fibulatum*, *Benthoosema suborbitale*, *Dasyscopelus asper*, *Diaphus* “deep” and “slender” morphotypes, *Hygophum hygomii*, *Lampadena luminosa*, morphotype similar to that of *L. pusillus*. From the NW area, *Myctophum* sp. (a “deep” morphotype) and *Benthoosema pterotum* were examined. Drawings of larval stages of each of these species are depicted in Fig 2 to show the general body morphology (gut and mouth shapes). Gut contents of other species besides the dominant species mentioned above, which occurred in low numbers, were also analysed, i.e. *Ceratoscopelus warmingii* (n=10, SW), *Diogenichthys atlanticus* (n=12, NW), *Hygophum proximum* (n=9, NW), *Myctophum nitidulum* (n=6, NW and SW), and *Notoscopelus resplendens* (n=3, SW).

Guts were removed from the larvae using a scalpel and placed in glass petri dishes with a mixture of water and glycerine. Feeding incidence (FI) was calculated for each species as the percentage of larval guts with at least one prey item, and only for individuals captured during the daytime (as in Vera-Duarte and Landaeta 2016). The low number of larvae that were analysed for gut contents during the night does not allow the calculation of the feeding incidence at night; instead, we provide evidence of night feeding in specific larval species. Prey items were counted and identified to the lowest possible taxonomic level, and their maximum body width and length were recorded with a precision of 0.001 mm. The percentage of abundance (%N) of each

prey taxon out the total number of prey items identified for a fish species was determined, and the frequency of occurrence (%F) was calculated as the number of guts containing at least one specimen of that prey taxon divided by the total number of guts with contents. The Index of Relative Importance (%IRI) was calculated to determine the importance of each prey type for each fish species as follows: %IRI = %F x %N (Sassa and Kawaguchi 2004).

For the most abundant species with at least one prey item in the gut, larvae were grouped into size classes of 1 mm-SL to evaluate changes in the size of prey consumed by fish larvae throughout their development according to Pearre's Trophic Niche Breadth (Pearre 1986), which was determined by the linear regression between larval body length and the standard deviation of the log₁₀-transformed prey sizes.

Multivariate analyses on prey abundance were performed to estimate the similarity of diets amongst species using PRIMER 6 (Clarke and Gorley 2006) after the construction of a Bray-Curtis similarity matrix. Prey abundances were squared-root transformed before analysis, and the species and notochordal stage used as main factors to group fish larval diets. Prey taxa with a representation <1% and undetermined organic matter (UOM) were not included as variables in subsequent statistical analyses. The SIMPER (one-way analysis) routine was applied to define the main contributions of prey taxa to the diet of each myctophid species and those prey taxa responsible for differences between species. PERMANOVA+ for PRIMER 6 (Anderson et al. 2008) was used to check the influence of the interaction between species and stage of development on their diet composition (unrestricted permutations: 999).

A scatterplot built with prey-specific abundance (%N) plotted against the percentage of occurrence (%F) was used to characterize the feeding behaviour of each species according to the Costello's diagram modified by Amundsen et al (1996).

3. Results

3.1. Feeding incidence

Myctophid larvae were daylight feeders, but larvae in postflexion stages of *L. alatus*, *L. luminosa*, *B. pterotum*, *Diaphus* "slender", and *Myctophum* sp. also fed at dawn or during the night. Individuals in postflexion stages appeared to feed with more frequency than preflexion stages (Table 1). The highest diurnal FI (78%) was found in *Diaphus* "deep" morphotype, and the lowest in *H. hygomii* (FI = 42.5%; Table 1).

3.2. Number of prey

Amongst preflexion larvae, *L. luminosa*, *L. alatus*, and *Lampanyctus* spp. from the SW showed the highest mean number of prey (2 - 3 prey items). In postflexion stages, although there was great variability in the number of prey ingested per larva, *Diaphus* “slender” morphotype showed the highest prey consumption (8 prey items in a postflexion larva of 4.2 mm SL). However, the most voracious larvae were the postflexion stages of *Myctophum* sp. from the NW, sometimes reaching >12 items in a single gut (Fig 3). There were significant differences in the mean number of prey between myctophid species and between preflexion and postflexion stages within a species (degrees of freedom: 9; square sum: 165.2; mean square: 18.36; F-value: 5.157; $p < 0.0001$). *Myctophum* sp. was the only species that showed a progressive increment of the number of prey items consumed as body size increased.

3.3. Relationships between the size of prey and fish larvae

Although all the species showed a positive allometric relationship between mouth width and standard length, it was only significant for larvae of *B. fibulatum* ($b = 1.68$, 95% CI = 0.49; b -range: 1.18 - 2.17) and *Myctophum* sp. ($b = 1.34$, 95% CI = 0.22; b -range: 1.12 - 1.55) (Fig 4). Mouth width increased throughout ontogenetic development, allowing the ingestion of larger prey items. All the species ingested larger prey when they were bigger, however, most continued to feed on small prey at the same time (Fig 5). Prey width ranges for *B. fibulatum*, *B. pterotum*, *B. suborbitale*, *Diaphus* “deep” and “slender” morphotypes were 64 - 320 μm , 80 - 367 μm , 112 - 496 μm , 16 - 480 μm , and 64 - 640 μm , respectively. Size ranges for the examined larvae of these species were similar (ca. 3 mm to 4.5 mm SL), except for *Diaphus* “slender”, which reached 9 mm SL and, at this size, ingested larger prey. Only *B. fibulatum* and *Myctophum* sp. shifted from the ingestion of small prey to the ingestion of higher proportions of larger prey with body growth. For the larval sizes studied, a slight decrease in the Trophic Niche Breadth (TNB) with larval length was observed in *L. alatus* and *B. pterotum* (lower standard deviation of the $\log_{10}$ of prey width once larvae attained the flexion stage), whereas the TNB did not change with larval body size for the remaining species.

3.4. Diet composition

About 40 prey taxa that belong to at least 18 genera were identified in the diet of the myctophid larvae (Table 2). Amundsen plots (Fig 6) suggest that none of the species was specialized in foraging on a specific category of prey. Nevertheless, nauplii dominated the diet of *B. fibulatum*, *L. alatus*, *Lampanyctus* spp., *D. asper*, and *H.*

hygomii. *Oncaea* sp. was a dominant genus in the diet of *B. suborbitale* and *Myctophum* sp. but it was observed in most fish larvae that adopted a generalist strategy.

PERMANOVA analysis of the diet matrix using Bray-Curtis distances revealed significant differences in composition of the diet between preflexion and postflexion stages of the 11 species studied (Table 3). There were high similarities between the diet of preflexion stages of different species whose diets were mainly composed of copepod nauplii (e.g., nauplii contributed 98% to diet similarity (66%) within the preflexion stages of *L. luminosa*). Dietary items in postflexion stages were more varied than in preflexion stages (see Supplementary Material for differences in the diet composition between larval stages).

The smallest larvae with food in their guts were 2 - 3 mm SL. In general, copepod nauplii and crustacean eggs were dominant in the smallest larval fish, with nauplii representing >33% by number in most examined species, except for those of *Diaphus* “deep” that fed mainly on appendicularians (Table 2 and Suppl. Mat.). The largest larvae ingested calanoid copepodites and adult copepods, mixed with other crustaceans. Appendicularia was the second taxon of importance for *Diaphus* “deep” (37% N; 20% IRI), *Lampanyctus* spp. (22.9% N; 12.1% IRI), *H. hygomii* (17% N, 4% IRI), *L. alatus* (13% N; 3% IRI), and *H. hygomii* (17% N, 4% IRI). For *Myctophum* sp., oncaeids were dominant (51% N; 28% IRI), and for *B. pterotum*, ostracods (20% N; 5% IRI).

Multivariate analyses of diet composition showed significant differences between the cluster composed of species collected in SW Australia plus *Benthoosema pterotum* (NW), and *Myctophum* sp. from the NW (Fig 7) ($p < 0.05$, >60% resemblance between the two groups). The average similarity in diet composition for the SW cluster reached 69%, where nauplii and appendicularians contributed 38.5% and 17%, respectively, to the group similarity. Interspecific average similarity between *Myctophum* sp. and *B. pterotum* from the same area (NW) was maximum, but <25%. The species of the same genus *B. pterotum* and *B. suborbitale* are grouped with ca. 84% similarity, and *Diaphus* “slender” and “deep” morphotypes, with <80%.

Larvae of a few other myctophid species were collected in very low numbers. For that reason, the results obtained from the analysis of their gut contents were not included in statistical tests. However, here we show a list of the prey items found in their guts: in *C. warmingii* and *D. atlanticus*, prey items were represented by 2 calanoid nauplii; in *H. proximum*, by 5 copepod nauplii, 2 appendicularians, and 1 radiolarian; in *M. nitidulum*

- 237 by 2 copepodites, 7 *Microsetella rosea*, and 7 Tintinnida; and in *N. resplendens* by 4
238 copepod nauplii and 1 appendicularian.

Journal Pre-proof

4. Discussion

This study focussed on feeding patterns of myctophid larvae from the southeastern IO as no previous reports have been published in this area on this topic, although there is an extensive literature from other oceanic regions.

4.1. Feeding incidence and trophic ontogeny

The diurnal incidence of prey in the guts of larvae was relatively high for all the myctophid species (> 42% FI), as previously found in other myctophid larvae (e.g., Sabatés and Saiz 2000; Sabates et al. 2003; Conley and Hopkins 2004; Sassa and Kawaguchi 2004, 2005; Rodríguez-Graña et al. 2005; Bernal et al. 2013; Contreras et al. 2015, 2019), indicating that they are visual feeders. A few larvae of myctophid species exhibited feeding activity at night. However, the low number of larvae analysed from the night period did not allow calculation of the night-time FI but, in a previous study, Sassa and Kawaguchi (2005) reported very low incidence of feeding at night in larvae of myctophids. Some species from the above-cited studies showed the onset of the feeding at night in postflexion stages or after transformation, which is when their anatomy and physiology change according to the energy requirements for performing diel migrations to deeper waters (Contreras et al. 2015, 2019). In the present work, *Myctophum* sp. and *B. pterotum* showed evidence of night-feeding similarly to *Myctophum selenops* and *Protomyctophum thompsoni* larvae from the Gulf of Mexico and North Pacific Ocean (Conley and Hopkins 2004; Sassa and Kawaguchi 2005). The larvae of the subfamily Myctophinae might be morphologically prepared to start feeding in low light intensities earlier during their development than those of the subfamily Lampanyctinae since they have stalked or narrow eyes that provide a greater field of vision (Weihs and Moser 1981; Conley and Hopkins 2004; Bozzano et al. 2007; Morote et al. 2011). Additionally, the large gut of this species may contribute to retaining prey for larger periods.

It might be expected that larvae with straight and tubular stomachs would have lower feeding incidences than those with saccular stomachs (longer food retention times), however, our study did not show a clear pattern between the shape of the gut and the incidence of feeding. *Diaphus* “deep” morphotype and *L. luminosa*, both with tubular and relatively short guts, had the highest food incidences (>70% FI). Other larvae with straight guts, namely, *Diaphus* “slender” morphotype and *H. hygomii*, showed the lowest feeding incidences (<42.5 - 50%), while larvae of *D. asper* and *Myctophum* sp., both with saccular guts, showed high incidences (ca. 70%).

According to the observation by Conley and Hopkins (2004), some of the early larvae with a straight/short gut consumed small prey, including tecate protists such as tintinnids. In our study, only *H. hygomii*, *L. alatus*, *B. fibulatum*, *Diaphus* “slender” and “deep” morphotypes, all with straight and/or short guts, preyed on tintinnids, but these prey items were not present in larvae with saccular guts. Nevertheless, the consumption of protists might not be strictly related to gut morphology, but mouth-gape size in correlation with the larval body size. These authors observed that those fish larvae with straight guts have elongated bodies with small mouth sizes, while species with stout and robust bodies are those with more saccular guts, and larger mouth gapes in relation to their body length, preferring larger prey. Other non-tecate protists were likely consumed by these larvae with straight guts but might be undetectable under the optical microscope. For this reason and because of technological advances, new studies will require the use of molecular techniques that allow expansion of knowledge on pelagic trophic relationships (see Young et al. 2015).

In larvae of most teleosts, the feeding behaviour changes with their ontogenetic development from the capture of few and small prey items in preflexion stages towards increasing numbers and sizes of prey in the postflexion stages (e.g., Sanchez-Velasco 1998, Sabatés and Saiz 2000, Contreras et al. 2015, 2019, Jackson and Lenz 2016). Similarly, in the myctophid larvae from the southeastern IO, we observed that they started fuelling themselves at very small body sizes (2 mm SL) with one small-sized item at a time, and an increase in both number and maximum prey size occurred in larger individuals. However, once attaining a specific length, the strategy of the myctophid larvae differed between species, with some of them showing greater ingestion of specific prey taxa (e.g., large calanoids), while others behaved as more generalist feeders on a larger variety of taxa (e.g., *B. pterotum* and *B. suborbitale*). Despite most myctophid larvae showed clear ingestion of larger prey with development, their TNB resulted independent of larval size, meaning that they still fed on small prey in postflexion stages, except for *B. pterotum* and *L. alatus* that showed certain feeding specialization towards the ingestion of larger prey whilst avoiding the smallest ones. No particular information on concurrent abundance and diversity of zooplankton was reported during the study surveys except for euphausiids (Sutton et al. 2015; Sutton and Beckley 2017a), the reason why prey selectivity could not be adequately assessed.

4.2. Diet composition

As expected from dietary studies of myctophid larvae elsewhere (e.g., Sabatés and Saiz 2000; Contreras et al. 2015, 2019), the southeast IO myctophids typically fed on different stages of copepods. In general, the diet was predominantly composed of copepod nauplii and copepod eggs in the smallest larvae, while copepodites and adult copepods comprised the diet of the largest larvae. In our study, copepod eggs were common in the diet of the earliest stages of all species, unlike the finding of Sassa and Kawaguchi (2005), who stated that copepod eggs would only be consumed by the myctophid *Tarletonbeania taylori* once its gut was fully developed to be able to digest them. The abundance of nauplii in the diet of all the myctophid species varied between 33% of the prey abundance in *B. pterotum* and 63% in *L. luminosa*. Ostracods only made an important contribution to the diet in larvae of the narrow-eyed subfamily Myctophinae, a feature that was first observed by Conley and Hopkins (2004). They attributed the occurrence of ostracods in the gut to the better vision capabilities of the larvae of this subfamily, which would allow them to improve the catchability of larger prey over other more abundant crustaceans (i.e. copepods). *Diaphus* “deep” morphotype fed on many appendicularians concurring with the findings by Sassa and Kawaguchi (2004, 2005) for larvae of *Diaphus garmani* from the North Pacific Ocean.

The species *Myctophum* sp. off NW Australia had a markedly different diet composition (Fig 7) (both in prey taxa and their abundance) compared to the species from the SW area. On the contrary, *B. pterotum* from the NW region had a diet similar to *B. suborbitale* from the SW, although the similar morphological traits of the genus may account for diet similarity. The presence of different taxa in the composition of the diet could be due to biogeography and different environmental characteristics of the area such as warmer water temperatures and higher productivity, as observed in other regions (e.g. Musialik-Koszarowska et al. 2019) and even in the anticyclonic eddies of the SW region (see Paterson et al. 2008, 2013). Additionally, the different proportions of prey taxa might be explained by dissimilar composition or distribution of the zooplanktonic prey items (spatial patchiness) between both areas (as in McKinnon et al. 2015). The diet of *Myctophum* sp. larvae from the NW showed the most diverse taxonomic composition, as for *Myctophum* sp. off East Australia (Rissik and Suthers 2000). The higher productivity of lower latitudes in Australia could lead to a greater diversity of zooplankton taxa that are potential prey resources for fish larvae, particularly over the shelf-break, where the tidal mixing contributes to enhance phytoplankton biomass, likely supporting food chains in the Kimberley oligotrophic waters (McLaughlin et al. 2019). Moreover, large postflexion stages of the two NW myctophids, *Myctophum* sp. and *B. pterotum*, preyed on larval-stage euphausiids,

absent in the other larval species of this study, at the time that higher concentrations of krill were reported in the NW bioregion (Sutton and Beckley 2017a, 2017b). Holliday et al. (2011b) also indicated that coastal waters off the NW study area showed a higher concentration of euphausiid larvae in the cross-shelf coastal waters than offshore associated with higher phytoplankton biomass bioregion.

Although the offshore region of WA can be considered as an oligotrophic region, the prevalent LC eddies exert a concentrating effect on marine organisms (Waite et al. 2019), causing an incremental abundance of zooplankton that might improve the chances of a predator-prey encounter for the myctophid larvae that inhabit the SW area. Waite et al. (2007c) demonstrated that LC eddies generated more productive areas with highly diverse and abundant zooplankton (Strzelecki et al. 2007), where higher densities of zooplankton and larval fish might be expected (Muhling et al. 2007). However, we need to distinguish between the warm-core anticyclonic eddies that occur mainly in autumn-winter in latitudes higher than 30°S, with entrainment of coastal phytoplankton, and the cold-core upwelling eddies that concentrate picoplankton, much more productive than diatoms, and with nutritious advantages for zooplankton (Säwström et al. 2014; Waite et al. 2019). Unexpectedly, Muhling et al. (2007) found higher chlorophyll biomass in a warm-core eddy than in a cold-core eddy. In addition, in the warm-core downwelling eddy, fish larvae extended deeper in the water column, which could favour vertical segregation in different trophic niches. To support if there is any potentially advantageous effect of eddies on zooplankton concentration for predators (fish larvae), it will be necessary to obtain data about the zooplankton composition in the study area and evaluate other factors beyond the direct seasonal influence of the LC, as proposed by Gaughan et al. (2009), such as nutrients or physiological responses. Fish larvae may displace along the first meters of the water column to match maximum prey abundances that often coincide with the chlorophyll maximum layer, however, Muhling and Beckley (2007) reported that larval fish vertical structure off the SW bioregion was more related to taxon-specific patterns rather than to the location of the chlorophyll maximum.

A final remark about the presence of appendicularians in fish guts is that these prey items are difficult to distinguish and count because of their soft gelatinous consistency and transparency. Yet, appendicularians were frequent and abundant in most species examined in the SW Australian samples. This agrees with the reliance of larval tunas on appendicularians in the unproductive habitat of the Florida Current (Llopiz et al. 2010) and of larval myctophids in oceanic waters of the western North Pacific (Landry et al. 2019; Sassa and Kawaguchi 2004). In these less productive habitats,

appendicularians might constitute an important source of food as they contain large amounts of filtered organic particles that remain in their houses. Some myctophid species, especially in their postflexion stages (*Diaphus* “deep” morphotype, *Dasyscopelus asper*, *Lampanyctus* spp.), showed a tendency towards the consumption of prey taxa such as appendicularians, which increases the partitioning of feeding resources between larvae of different species and developmental stages. Again, further study on the meso-zooplanktonic composition of the area is required to calculate selectivity indexes. Conversely, depth-stratified sampling is necessary to determine whether there is resource partitioning with depth, particularly between Myctophinae and Lampanyctinae, as already shown in other regions (Loeb 1979, 1980; Olivar et al. 2018) since they have dissimilar visual adaptations. Some of these questions may be addressed from samples obtained in the recent second International Indian Ocean Expedition carried out in May and June 2019 along the 110°E meridian (Beckley 2020; Olivar and Beckley *in prep.*).

5. Conclusions

Diverse copepod stages, appendicularians, and their houses, constituted an important part of the larval diet of most myctophid species of the southeastern IO. The diets were composed mainly of nauplii in the preflexion larvae but had greater variety and number of prey in postflexion individuals, suggesting a shift in the type of prey consumed throughout development. Both larval morphology and ontogenetic development are important factors to determine the diet composition and feeding niches of fish larvae, notwithstanding the influence of the geographic area of study (prey availability in each region). The most different dietary composition was that of *Myctophum* sp. larvae from the NW, which was also the most diverse in prey taxa, reflecting differences in the zooplanktonic composition of the two study areas (NW and SW bioregions). The specific dietary differences between the species in the SW likely implied partial partitioning of feeding resources.

6. Acknowledgements

This study was completed in the Fremantle Marine Laboratory of Murdoch University. Ainhua Bernal acknowledges access to the larval fish specimens collected during the voyages of the RV *Southern Surveyor*. Ainhua Bernal was the recipient of a PhD scholarship associated with the project CTM2008-04489-C03-02 awarded by the Spanish Ministry of Science and Innovation.

7. References

- Amundsen PA, Gabler HM, Staldvik FJ (1996) A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. *Journal of Fish Biology* 48: 607–614 doi: [10.1111/j.1095-8649.1996.tb01455.x](https://doi.org/10.1111/j.1095-8649.1996.tb01455.x)
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK
- Australian Government, Department of Sustainability, Environment, Water, Population and Communities (2012a) Marine Bioregional Plan for the North-west Marine Region (Australian Government: Canberra, ACT, Australia)
- Australian Government, Department of Sustainability, Environment, Water, Population and Communities (2012b) Marine Bioregional Plan for the South-west Marine Region (Australian Government: Canberra, ACT, Australia)
- ~~Bernal A, Olivar MP, Fernández de Puellas ML (2013) Feeding patterns of *Lampanyctus pusillus* (Pisces: Myctophidae) throughout its ontogenetic development. *Marine Biology* 160:81–95 doi: [10.1007/s00227-012-2064-9](https://doi.org/10.1007/s00227-012-2064-9)~~
- Badcock J, Merrett NR (1976) Midwater fishes in the eastern North Atlantic. I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. *Progress in Oceanography* 7(1): 3–58
- Beckley LE, Muhling BA, Gaughan DJ (2009) Larval fishes off Western Australia: influence of the Leeuwin Current. *Journal of the Royal Society of Western Australia* 92: 101–109
- Beckley LE, Holliday D, Sutton AL, Weller E, Olivar MP, Thompson PA (2019) Structuring of larval fish assemblages along a coastal-oceanic gradient in the macro-tidal, tropical Eastern Indian Ocean. *Deep-Sea Research Part II: Topical Studies in Oceanography* 161: 105–119 doi: [10.1016/j.dsr2.2018.03.008](https://doi.org/10.1016/j.dsr2.2018.03.008)
- Beckley LE, 2020, One Ten East voyage of the IIOE-2. The Indian Ocean Bubble (12): 3–4
- Bowlin NM (2016) Ontogenetic changes in the distribution and abundance of early life history stages of mesopelagic fishes off California. Advisor: Hastings PA. UC San Diego Electronic Theses and Dissertations

- 443 Bozzano A, Pankhurst PM, Sabatés A (2007) Early development of eye and retina in
 444 lanternfish larvae. *Visual Neuroscience* 24: 423–436 doi:
 445 [10.1017/S0952523807070484](https://doi.org/10.1017/S0952523807070484)
- 446 Clarke K, Gorley RN (2006) PRIMER v6: User Manual/Tutorial PRIMER-E, Plymouth
- 447 Conley WJ, Hopkins TL (2004) Feeding ecology of lanternfish (Pisces: Myctophidae)
 448 larvae: Prey preferences as a reflection of morphology. *Bulletin of Marine*
 449 *Science* 75: 361–379
 450 [https://www.scopus.com/inward/record.uri?eid=2-s2.0-](https://www.scopus.com/inward/record.uri?eid=2-s2.0-10344246599&partnerID=40&md5=48173f4d9dd03b871c5cf854ddef197)
 451 [10344246599&partnerID=40&md5=48173f4d9dd03b871c5cf854ddef197](https://www.scopus.com/inward/record.uri?eid=2-s2.0-10344246599&partnerID=40&md5=48173f4d9dd03b871c5cf854ddef197)
- 452 Contreras T, Olivar MP, Hulley PA, Fernández de Puelles ML (2019) Feeding ecology
 453 of early life stages of mesopelagic fishes in the equatorial and tropical Atlantic.
 454 *ICES Journal of Marine Science* 76(3): 673–689 doi: [10.1093/icesjms/fsy070](https://doi.org/10.1093/icesjms/fsy070)
- 455 Contreras T, Olivar M, Bernal Bajo A, Sabatés A (2015) Comparative feeding patterns
 456 of early stages of mesopelagic fishes with vertical habitat partitioning. *Marine*
 457 *Biology* 162: 2265–2277 doi: [10.1007/s00227-015-2749-y](https://doi.org/10.1007/s00227-015-2749-y)
- 458 Davison PC, Checkley DM, Koslow JA, Barlow J (2013) Carbon export mediated by
 459 mesopelagic fishes in the northeast Pacific Ocean. *Progress in Oceanography*
 460 116: 14–30 doi: [10.1016/j.pocean.2013.05.013](https://doi.org/10.1016/j.pocean.2013.05.013)
- 461 Feng M, Slawinski D, Beckley LE, Keesing JR (2010) Retention and dispersal of shelf
 462 waters influenced by interactions of ocean boundary current and coastal
 463 geography. *Marine & Freshwater Research* 61: 1259–1267
- 464 Gaughan DJ, Pearce AF, Lewis PD (2009) Does the poleward boundary current off
 465 Western Australia exert a dominant influence on coastal chaetognaths and
 466 siphonophores? *Estuarine, Coastal and Shelf Science* 83: 443–450 doi:
 467 [10.1016/j.ecss.2009.04.015](https://doi.org/10.1016/j.ecss.2009.04.015)
- 468 Gjøsæter J, Kawaguchi K (1980) A review of the world resources of mesopelagic fish.
 469 *FAO Fisheries Technical Paper*: I-VI:1–151
- 470 Fox NJ, Beckley LE (2005) Priority areas for conservation of Western Australian
 471 coastal fishes: a comparison of hotspot, biogeographical and complementarity
 472 approaches. *Biological Conservation* 125: 399–410 doi:
 473 [10.1016/j.biocon.2005.02.006](https://doi.org/10.1016/j.biocon.2005.02.006)

- 474 Hernández-León S, Olivar MP, Fernández-Puelles ML, Bode A, Castellón A, López-
 475 Pérez C, Tuset VM, González-Gordillo JI (2019) Zooplankton and micronekton
 476 active flux across the tropical and subtropical Atlantic Ocean. *Frontiers of*
 477 *Marine Science* 6: 535 doi: [10.3389/fmars.2019.00535](https://doi.org/10.3389/fmars.2019.00535)
- 478 Hidaka K, Kawaguchi K, Murakami M, Takahashi M (2001) Downward transport of
 479 organic carbon by diel migratory micronekton in the western equatorial Pacific:
 480 its quantitative and qualitative importance. *Deep-Sea Research I:*
 481 *Oceanographic Research Papers* 48: 1923–1939 doi: [10.1016/S0967-](https://doi.org/10.1016/S0967-0637(01)00003-6)
 482 [0637\(01\)00003-6](https://doi.org/10.1016/S0967-0637(01)00003-6)
- 483 Holliday D, Beckley LE, Olivar MP (2011a) Incorporation of larval fishes into a
 484 developing anti-cyclonic eddy of the Leeuwin Current off south-western
 485 Australia. *Journal of Plankton Research* 33: 1696–1708 doi:
 486 [10.1093/plankt/fbr064](https://doi.org/10.1093/plankt/fbr064)
- 487 Holliday D, Beckley LE, Weller E, Sutton AL (2011b). Natural variability of macro-
 488 zooplankton and larval fishes off the Kimberley, north-western Australia:
 489 Preliminary findings. *Journal of the Royal Society of Western Australia* 94: 181–
 490 195
- 491 Holliday D, Beckley LE, Millar N, Olivar MP, Slawinski D, Feng M, Thompson PA
 492 (2012) Larval fish assemblages and particle back-tracking define latitudinal and
 493 cross-shelf variability in an eastern Indian Ocean boundary current. *Marine*
 494 *Ecology Progress Series* 460: 127–144 doi: [10.3354/meps09730](https://doi.org/10.3354/meps09730)
- 495 Irigoien X, Klevjer TA, Røstad A, Martinez U, Boyra G, Acuña JL, Bode A, Echevarria
 496 F, Gonzalez-Gordillo JI, Hernández-León S, Agusti S, Aksnes DL, Duarte CM,
 497 Kaartvedt S (2014) Large mesopelagic fishes biomass and trophic efficiency in
 498 the open ocean. *Nature Communications* 5: 3271 doi: [10.1038/ncomms4271](https://doi.org/10.1038/ncomms4271)
- 499 Jackson JM, Lenz PH (2016) Predator-prey interactions in the plankton: larval fish
 500 feeding on evasive copepods. *Scientific reports* 6: 33585 doi:
 501 [10.1038/srep33585](https://doi.org/10.1038/srep33585)
- 502 Koslow JA, Pesant S, Feng M, Pearce A, Fearn P, Moore T, Matear R, Waite A (2008)
 503 The effect of the Leeuwin Current on phytoplankton biomass and production off
 504 Southwestern Australia. *Journal of Geophysical Research* 113: C07050 doi:
 505 [10.1029/2007JC004102](https://doi.org/10.1029/2007JC004102)

- Landry MR, Beckley LE, Muhling BA (2019) Climate sensitivities and uncertainties in food-web pathways supporting larval bluefin tuna in subtropical oligotrophic oceans. *ICES Journal of Marine Science* 76 (2): 359–369 doi: [10.1093/icesjms/fsy184](https://doi.org/10.1093/icesjms/fsy184)
- Lenanton RC, Caputi N, Kangas M, Craine M (2009) The ongoing influence of the Leeuwin Current on economically important fish and invertebrates off temperate Western Australia – has it changed? *Journal of the Royal Society of Western Australia* 92: 111–127
- Lenanton RCJ, Joll L, Penn JW, Jones K (1991) The influence of the Leeuwin Current on coastal fisheries in Western Australia. *Journal of the Royal Society of Western Australia* 74: 101–114
- Loeb VJ (1980) Patterns of spatial and species abundance within the larval fish assemblage of the North Pacific central gyre during late summer. *Marine Biology* 60: 189–200 doi: [10.1007/BF00389162](https://doi.org/10.1007/BF00389162)
- Loeb VJ (1979) Vertical distribution and development of larval fishes in the North Pacific Central Gyre during summer. *Fisheries Bulletin US* 77: 777–793
- Llopiz JK, Richardson DE, Shiroza A, Smith SL, Cowen RK (2010) Distinctions in the diets and distributions of larval tunas and the important role of appendicularians. *Limnology and Oceanography* 55(3): 983–996 doi: [10.4319/lo.2010.55.3.0983](https://doi.org/10.4319/lo.2010.55.3.0983)
- Mackas DL, Coyle KO (2005) Shelf–offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. *Deep-Sea Research Part II: Topical Studies in Oceanography* 52: 707–725 doi: [10.1016/j.dsr2.2004.12.020](https://doi.org/10.1016/j.dsr2.2004.12.020)
- Mackas DL, Galbraith MD (2002) Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: I. Transport and loss of continental margin species. *Journal of Oceanography* 58: 725–738 doi: [10.1023/a:1022802625242](https://doi.org/10.1023/a:1022802625242)
- McKinnon AD, Duggan S, Holliday D, Brinkman R (2015) Plankton community structure in the Kimberly-Browse region of NW Australia. *Estuarine, Coastal and Shelf Science* 153: 156–167 doi: [10.1016/j.ecss.2014.11.006](https://doi.org/10.1016/j.ecss.2014.11.006)
- Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL (eds) (1984) *Ontogeny and systematics of fishes. The American Society of Ichthyologists and Herpetologists* 1. 760 p

- 538 Moser HG, Smith PE (1993) Larval fish assemblages and oceanic boundaries. Bulletin
539 of Marine Science 53: 283–289
- 540 Moser HG, Watson W (2006) Ichthyoplankton In: Allen LG, Pondella DJ, Horn MH
541 (eds) Ecology of marine fishes: California and adjacent waters. University of
542 California Press. 269–319
- 543 McLaughlin MJ, Lourey MJ, Hanson CE, Cherukuru N, Thompson PA, Pattiaratchi CB
544 (2019) Biophysical oceanography of tidally-extreme waters of the southern
545 Kimberley coast, Western Australia. Continental Shelf Research 173(1): 1–12
546 doi: [10.1016/j.csr.2018.12.002](https://doi.org/10.1016/j.csr.2018.12.002)
- 547
- 548 Muhling BA, Beckley LE (2007) Seasonal variation in horizontal and vertical structure of
549 larval fish assemblages off south-western Australia, with implications for larval
550 transport. Journal of Plankton Research 29(11): 967–983 doi:
551 [10.1093/plankt/fbm072](https://doi.org/10.1093/plankt/fbm072)
- 552 Muhling BA, Beckley LE, Olivar MP (2007) Ichthyoplankton assemblage structure in
553 two meso-scale Leeuwin Current eddies, eastern Indian Ocean. Deep-Sea
554 Research Part II: Topical Studies in Oceanography 54(8–10): 1113–1128 doi:
555 [10.1016/j.dsr2.2006.05.045](https://doi.org/10.1016/j.dsr2.2006.05.045)
- 556 Musialik-Koszarowska M, Dzierzbicka-Głowacka L, Weydmann A (2019) Influence of
557 environmental factors on the population dynamics of key zooplankton species in
558 the Gulf of Gdańsk (southern Baltic Sea). Oceanologia 61(1): 17–25 doi:
559 [10.1016/j.oceano.2018.06.001](https://doi.org/10.1016/j.oceano.2018.06.001)
- 560 Olivar MP, Beckley LE (1995) Early development of *Diaphus* spp. (Pisces:
561 Myctophidae) of the Agulhas Current. South African Journal of Marine Science
562 16(1): 129–139 doi: [10.2989/025776195784156485](https://doi.org/10.2989/025776195784156485)
- 563 Olivar MP, Contreras T, Hulley A, Emelianov M, López-Pérez C, Tuset V, Castellón A
564 (2018) Variation in the diel vertical distributions of larvae and transforming
565 stages of oceanic fishes across the tropical and equatorial Atlantic. Progress in
566 Oceanography 160: 83-100 doi: [10.1016/j.pocean.2017.12.005](https://doi.org/10.1016/j.pocean.2017.12.005)
- 567 Olivar MP, Fortuño JM (1991) Guide to ichthyoplankton of the Southeast Atlantic
568 (Benguela Current Region). Scientia Marina 55(1): 1–383

- 569 Olivar MP, Hulley A, Castellón A, Emelianov M, López C, Tuset V, Contreras T, Molí B
 570 (2017) Mesopelagic fishes across the tropical and equatorial Atlantic:
 571 Biogeographical and vertical patterns. *Progress in Oceanography* 151: 116–137
 572 doi: [10.1016/j.pocean.2016.12.001](https://doi.org/10.1016/j.pocean.2016.12.001)
- 573 Olivar MP, Moser HG, Beckley LE (1999) Lanternfish larvae from the Agulhas Current
 574 (SW Indian Ocean). *Scientia Marina* 63(2): 101–120 doi:
 575 [10.3989/scimar.1999.63n2101](https://doi.org/10.3989/scimar.1999.63n2101)
- 576 Olivar MP, Palomera I (1994) Ontogeny and distribution of *Hygophum benoiti* (Pisces,
 577 Myctophidae) of the North Western Mediterranean. *Journal of Plankton*
 578 *Research* 16(8): 977–991 doi: [10.1093/plankt/16.8.977](https://doi.org/10.1093/plankt/16.8.977)
- 579 Ozawa T (1986) Early life history of the family Myctophidae in the ocean off southern
 580 Japan. In: Ozawa T (ed) *Studies on the oceanic ichthyoplankton in the western*
 581 *North Pacific*. Kyushu University Press, Fukuoka, Japan. pp: 114–188
- 582 Paterson HL, Feng M, Waite AM, Gomis D., Beckley LE, Holliday D, Thompson PA
 583 (2008) Physical and chemical signatures of a developing anti-cyclonic eddy in
 584 the Leeuwin Current, eastern Indian Ocean. *Journal of Geophysical Research*
 585 113, C07049:1-14 doi: [10.1029/2007jc004707](https://doi.org/10.1029/2007jc004707)
- 586 Paterson H, Heel K, Waite A (2013) A warm-core eddy linking shelf, Leeuwin Current
 587 and oceanic waters demonstrated by near-shelf distribution patterns of
 588 *Synechococcus* spp. and *Prochlorococcus* spp. in the eastern Indian Ocean.
 589 *Marine and Freshwater Research* 64: 1011–1021. doi: [10.1071/MF1227](https://doi.org/10.1071/MF1227)
- 590 Paxton JR (1979) Nominal genera and species of lanternfishes (Family Myctophidae).
 591 *Contributions in Science. Natural History Museum, Los Angeles County* 322: 1–
 592 28. <https://www.biodiversitylibrary.org/part/226854>
- 593 Pearce AF, Hutchins JB (2009) Oceanic processes and the recruitment of tropical fish
 594 at Rottnest Island (Western Australia) *Journal of the Royal Society of Western*
 595 *Australia* 92: 179–195
- 596 Pearre S (1986) Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and
 597 the size-efficiency hypothesis. *Marine Ecology Progress Series* 27: 299–314
- 598 Richards WJ (2005) *Early stages of Atlantic fishes - An identification guide for the*
 599 *western Central North Atlantic*. Taylor & Francis, Boca Raton, FL. doi:
 600 [10.1201/9780203500217](https://doi.org/10.1201/9780203500217)

- 601 Rissik D, Suthers IM (2000) Enhanced feeding by pelagic juvenile myctophid fishes
 602 within a region of island induced flow disturbance in the Coral Sea. Marine
 603 Ecology Progress Series 203: 263–273 doi: [10.3354/meps203263](https://doi.org/10.3354/meps203263)
- 604 Rodriguez-Graña L, Castro L, Loureiro M, Gonzalez HE, Calliari D (2005) Feeding
 605 ecology of dominant larval myctophids in an upwelling area of the Humboldt
 606 Current. Marine Ecology Progress Series 290:119–134 doi:
 607 [10.3354/meps290119](https://doi.org/10.3354/meps290119)
- 608 Sabates A, Bozzano A, Vallvey I (2003) Feeding pattern and the visual light
 609 environment in myctophid fish larvae. Journal of Fish Biology 63: 1476–1490
 610 doi: [10.1111/j.1095-8649.2003.00259.x](https://doi.org/10.1111/j.1095-8649.2003.00259.x)
- 611 Sabatés A, Saiz E (2000) Intra- and interspecific variability in prey size and niche
 612 breadth of myctophiform fish larvae. Marine Ecology Progress Series 201:261–
 613 271 doi: [10.3354/meps201261](https://doi.org/10.3354/meps201261)
- 614 Sánchez-Velasco L (1998) Diet composition and feeding habits of fish larvae of two co-
 615 occurring species (Pisces: Callionymidae and Bothidae) in the North-western
 616 Mediterranean. ICES Journal of Marine Science 55: 299–308 doi:
 617 [10.1006/jmsc.1997.0278](https://doi.org/10.1006/jmsc.1997.0278)
- 618 Sassa C (2010) Feeding ecology of *Symbolophorus californiensis* larvae (Teleostei:
 619 Myctophidae) in the southern transition region of the western North Pacific.
 620 Journal of the Marine Biological Association of the United Kingdom 90: 1249–
 621 1256 doi: [10.1017/S0025315409990464](https://doi.org/10.1017/S0025315409990464)
- 622 Sassa C, Hirota Y (2013) Seasonal occurrence of mesopelagic fish larvae on the
 623 onshore side of the Kuroshio off southern Japan. Deep-Sea Research I:
 624 Oceanographic Research Papers 81: 49–61 doi: [10.1016/j.dsr.2013.07.008](https://doi.org/10.1016/j.dsr.2013.07.008)
- 625 Sassa C, Kawaguchi K (2004) Larval feeding habits of *Diaphus garmani* and
 626 *Myctophum asperum* (Pisces: Myctophidae) in the transition region of the
 627 western North Pacific. Marine Ecology Progress Series 278: 279–290 doi:
 628 [10.3354/meps278279](https://doi.org/10.3354/meps278279)
- 629 Sassa C, Kawaguchi K (2005) Larval feeding habits of *Diaphus theta*, *Protomyctophum*
 630 *thompsoni*, and *Tarletonbeania taylori* (Pisces: Myctophidae) in the transition
 631 region of the western North Pacific. Marine Ecology Progress Series 298: 261–
 632 276 doi: [10.3354/meps298261](https://doi.org/10.3354/meps298261)

- 633 Sassa C, Kawaguchi K, Hirota Y, Ishida M (2007) Distribution depth of the transforming
 634 stage larvae of myctophid fishes in the subtropical-tropical waters of the
 635 western North Pacific. Deep-Sea Research Part I: Oceanographic Research
 636 Papers 54(12): 2181–2193 doi: [10.1016/j.dsr.2007.09.006](https://doi.org/10.1016/j.dsr.2007.09.006)
- 637 Strzelecki J, Koslow JA, Waite A (2007) Comparison of mesozooplankton communities
 638 from a pair of warm-and cold-core eddies of western Australia. Deep-Sea
 639 Research II: Topical Studies in Oceanography 54: 1103–1112 doi:
 640 [10.1016/j.dsr2.2007.02.004](https://doi.org/10.1016/j.dsr2.2007.02.004)
- 641 Sutton AL, Beckley LE, Holliday D (2015) Euphausiid assemblages in and around a
 642 developing anti-cyclonic Leeuwin Current eddy in the south-east Indian Ocean.
 643 Journal of Royal Society of Western Australia 95 (1): 9–18
- 644 Sutton AL, Beckley LE (2017a) Euphausiid assemblages of the oceanographically
 645 complex north-west marine bioregion of Australia. Marine and Freshwater
 646 Research 68 (11): 1988–1998 doi: [10.1071/MF16334](https://doi.org/10.1071/MF16334)
- 647 Sutton AL, Beckley LE (2017b) Species richness, taxonomic distinctness and
 648 environmental influences on euphausiid zoogeography in the Indian Ocean.
 649 Diversity 9(2): 23 doi: [10.3390/d9020023](https://doi.org/10.3390/d9020023)
- 650 Thompson PA, Pesant S, Waite AM (2007) Contrasting the vertical differences in the
 651 phytoplankton biology of a dipole pair of eddies in the south-eastern Indian
 652 Ocean. Deep-Sea Research Part II: Topical Studies in Oceanography 54:
 653 1003–1028 doi: [10.1016/j.dsr2.2006.12.009](https://doi.org/10.1016/j.dsr2.2006.12.009)
- 654 Trueman CN, Johnston G, O’Hea B, MacKenzie KM (2014) Trophic interactions of fish
 655 communities at midwater depths enhance long-term carbon storage and benthic
 656 production on continental slopes. Proceedings of the Royal Society B 281:
 657 20140669 doi: [10.1098/rspb.2014.0669](https://doi.org/10.1098/rspb.2014.0669)
- 658 Vera-Duarte J, Landaeta MF (2016) Diet of labrisomid blenny *Auchenionchus*
 659 *variolosus* (Valenciennes 1836) (Labrisomidae) during its larval development off
 660 central Chile (2012-2013). Journal of Applied Ichthyology 32: 46–54 doi:
 661 [10.1111/jai.12935](https://doi.org/10.1111/jai.12935)
- 662 Vipin PM, Ravi R, Jose Fernandez T, Pradeep K, Boopendranath MR, Remesan MP
 663 (2012) Distribution of myctophid resources in the Indian Ocean. Reviews in Fish
 664 Biology and Fisheries 22: 423–436 doi: [10.1007/s11160-011-9244-4](https://doi.org/10.1007/s11160-011-9244-4)

- 665 Young JW, Hunt BPV, Cook TR, Llopiz JK, Hazen EL, Pethybridge HR, Ceccarelli D,
 666 Lorrain A, Olson RJ, Allain V, Menkes C, Patterson T, Nicol S, Lehodey P,
 667 Kloser RJ, Arrizabalaga H, Anela Choy C (2015) The trophodynamics of marine
 668 top predators: Current knowledge, recent advances and challenges. Deep-Sea
 669 Research Part II: Topical Studies in Oceanography 113: 170–187 doi:
 670 [10.1016/j.dsr2.2014.05.015](https://doi.org/10.1016/j.dsr2.2014.05.015)
- 671 Waite AM, Thompson PA, Pesant S, Feng M, Beckley LE, Domingues CM, Gaughan
 672 D, Hanson CE, Holl CM, Koslow AT, Meuleners M., Montoya JP, Moore T,
 673 Muhling BA, Paterson H, Rennie S, Strzlecki J, Twomey L (2007a) The Leeuwin
 674 Current and its eddies: An introductory overview. Deep-Sea Research II:
 675 Topical Studies in Oceanography 54(8–10): 789–796 doi:
 676 [10.1016/j.dsr2.2006.12.008](https://doi.org/10.1016/j.dsr2.2006.12.008)
- 677 Waite AM, Pesant S, Griffin DA, Thompson PA, Holl CM (2007b) Oceanography,
 678 primary production and dissolved inorganic nitrogen uptake in two Leeuwin
 679 Current eddies. Deep-Sea Research Part II: Topical Studies in Oceanography
 680 54: 981–1002. doi: [10.1016/j.dsr2.2007.03.001](https://doi.org/10.1016/j.dsr2.2007.03.001)
- 681 Waite AM, Muhling BA, Holl CM, Beckley LE, Montoya JP, Stzelecki J, Thompson PA,
 682 Pesant S (2007c) Food web structure in two counter-rotating eddies based on
 683 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic analyses. Deep-Sea Research II: Topical Studies in
 684 Oceanography 54 (8–10): 1055–1075 doi: [10.1016/j.dsr2.2006.12.010](https://doi.org/10.1016/j.dsr2.2006.12.010)
- 685 Waite AM, Raes E, Beckley LE, Thompson PA, Griffin D, Saunders M, Swstrm C,
 686 O'Rorke R, Wang M, Landrum JP, Jeffs A (2019) Production and ecosystem
 687 structure in cold-core vs. warm-core eddies: Implications for the zooplankton
 688 isoscape and rock lobster larvae. Limnology and Oceanography 64: 2405–
 689 2423. doi: [10.1002/lno.11192](https://doi.org/10.1002/lno.11192)
- 690 Weihs D, Moser HG (1981) Stalked eyes as an adaptation towards more efficient
 691 foraging in marine fish larvae. Bulletin of Marine Sciences 31: 31–36
- 692 Weller E, Holliday D, Feng M, Beckley LE, Thompson PA (2011) A continental shelf
 693 scale examination of the Leeuwin Current off Western Australia during the
 694 austral autumn-winter. Continental Shelf Research 31(17): 1858–1868 doi:
 695 [10.1016/j.cr.2011.08.008](https://doi.org/10.1016/j.cr.2011.08.008)

Table 1 Summary of characteristics of the fish larvae dissected for gut content analysis. Body length ranges are also detailed. SL: Standard Length; FI_{day} : Daytime Feeding Incidence.

Table 2 Number of prey (N), percentage of abundance (%N), Frequency of occurrence (%F), and Index of relative importance (%IRI), determined as $\%F \times \%N$ for the main myctophid species collected off SW and NW Australia. UOM: Unidentified Organic Matter.

Table 3 PERMANOVA analysis based on Bray–Curtis dissimilarities of a square root-transformed matrix based on prey item numbers for preflexion and postflexion stages of 11 different myctophid species.

Supplementary material Abundance of zooplankton taxa in the guts of preflexion and postflexion stages of the main myctophid larvae analysed. Acronyms formed of two capital letters indicate the first letter of the compound scientific name of each fish genus+species (e.g.: BF for *B. fibulatum*), but “Myct” for *Myctophum* sp and “Lamp” for *Lampanyctus* spp. The number of guts analysed by preflexion (“pre”) or postflexion (“post”) stage is indicated within parenthesis.

Fig 1 A) Map showing the location of sampling stations where larval fishes were collected from shelf and oceanic waters off SW Australia. The dashed line parallel with the coast indicates the 200 m-depth contour and the dashed circles indicate the perimeter of an anticyclonic eddy of the Leeuwin Current as it evolved during the sampling period (modified from Holliday et al. 2011a). B) Sampling stations off NW Australia. The grey circles represent stations occupied for 2 h and the black circles represent stations that were occupied for 12 h over a complete tidal cycle. Dashed lines indicate bathymetry (modified from Beckley et al. 2019).

Fig 2 Sketches of the larval stages and their gut morphology of the myctophids in this study. Pigmentation was not included. a) *Benthosema fibulatum* (5.5 mm SL; modified from Olivar et al. 1999), b) *B. pterotum* (9 mm SL; modified from Olivar et al. 1999), c) *B. suborbitale* (6.6 mm SL modified from Olivar et al. 1999), d) *Dasyscopelus asper* (4.5 mm SL; modified from Ozawa 1986), e) *Diaphus* “deep” morphotype (5.5 mm SL; modified from Olivar & Beckley 1995), f) *Diaphus* “slender” morphotype (4.5 mm SL; modified from Olivar & Beckley 1995), g) *Hygophum hygomii* (5.3 mm SL; modified from Olivar and Palomera 1994), h) *Lampanyctus alatus* (4.3 mm SL; modified from Olivar and Beckley 1997), i) *Lampanyctus* sp. “deep” morphotype (4.8 mm SL; modified after *Lampanyctus pusillus* from Olivar and Beckley 1997), j) *Lampadena luminosa* (7.5 mm SL; modified from Olivar and Beckley 1997) and k) *Myctophum* sp. “deep” morphotype (4.5 mm SL; modified after *Myctophum obtusirostre* from Ozawa 1986).

Fig 3 Number of prey items per fish gut plotted against the standard length of each species. Each red dot indicates the number of prey items per gut. As specified in the methods, the mean number of prey and the corresponding SD are showed for size classes of 1 mm SL. The lower bar indicates the SL-range for preflexion individuals.

Fig 4 Allometric relationship between Mouth Width and Standard Length for larvae of the main myctophid species.

Fig 5 Prey Width plotted against the Standard Length of larvae of the main myctophid species.

Fig 6 Prey-specific abundance plotted against the frequency of occurrence of prey in the gut of each myctophid species, indicating trends in feeding patterns and TNB according to Amundsen et al. (1996).

Fig 7 Dendrogram showing the similarity between larval diet compositions of different myctophids. Myct: *Myctophum* sp.; HH: *Hygophum hygomii*; BP: *Benthosema pterotum*; BS: *Benthosema suborbitale*; BF: *Benthosema fibulatum*; DA: *Dasyscopelus asper*; LL: *Lampadena luminosa*; DS: *Diaphus* “deep”; DD: *Diaphus* “slender”; LA: *Lampanyctus alatus*; Lamp.: *Lampanyctus* spp. Significant clusters ($p = 0.05$) are denoted by the solid line and defined by the SIMPROF procedure.

Species	SL (mm)	Flexion boundary (cm)	No. larvae	Area	Gut morphology	Fl _{day} %	Mean No. prey	
							Preflexion	Postflexion
<i>Benthoosema fibulatum</i>	2.1-9.3	4	41	SW	straight and short	66	1.3±0.5	3
<i>B. pterotum</i>	2.3-8.2	3.8	44	NW	straight and short	68	2±1.7	1.3±0.5
<i>B. suborbitale</i>	2.0-8.0	4	51	SW	short and bent	58	1.5±0.8	1.9±0.9
<i>Dasyscopelus asper</i>	2.0-9.6	4.5	31	SW	saccular and bent	68	1.7±0.9	2.3±1.5
<i>Diaphus</i> "deep"	2.1-8.2	3.8	105	SW	straight and short	79	1.8±0.9	1.7±0.9
<i>Diaphus</i> "slender"	2.0-10.7	3.7	131	SW	straight and short	50	1.6±1.1	3.1±2.4
<i>Hygophum hygomii</i>	2.4-6.1	4.8	40	SW	straight and short	42.5	1.8±1.1	1.7±0.6
<i>Lampanyctus alatus</i>	2.0-7.0	3.9	57	SW	short and bent	69	3.1±3	1.5±0.8
<i>Lampanyctus</i> spp.	2.5-5.2	3.9	33	SW	short and bent	59	3.2±2.3	1.5±0.8
<i>Lampadena luminosa</i>	2.7-7.3	5.3	87	SW	straight and short	72	2.3±2	2.8±1.7
<i>Myctophum</i> sp.	2.0-8.0	4.3	26	NW	saccular and bent	67	2±1	9±5.7

Source	df	SS	MS	Pseudo-F	p	Component
Species*Development	21	2.85E+09	13558	59,819	0.001	Random
Residual	287	6.50E+09	2266.5			
Total	308	9.35E+09

Fig 2 Sketch of the myctophid larval stages and their gut morphology. Pigmentation was not included. a) *Benthosema fibulatum* (5.5 mm SL; modified from Olivar et al. 1999), b) *B. pterotum* (9 mm SL; modified from Olivar et al. 1999), c) *B. suborbitale* (6.6 mm SL modified from Olivar et al. 1999), d) *Dasyscopelus asper* (4.5 mm SL; modified from Ozawa 1986), e) *Diaphus* “deep” morphotype (5.5 mm SL; modified from Olivar & Beckley 1995), f) *Diaphus* “slender” morphotype (4.5 mm SL; modified from Olivar & Beckley 1995), g) *Hygophum hygomii* (5.3 mm SL; modified from Olivar and Palomera 1994), h) *Lampanyctus alatus* (4.3 mm SL; modified from Olivar and Beckley 1997), i) *Lampanyctus* sp. “deep” morphotype (4.8 mm SL; modified after *Lampanyctus pusillus* from Olivar and Beckley 1997), j) *Lampadena luminosa* (7.5 mm SL; modified from Olivar and Beckley 1997), and k) *Myctophum* sp. “deep” morphotype (4.5 mm SL; modified after *Myctophum obtusirostre* from Ozawa 1986).

Number of Prey items

Standard Length (mm)

Mouth Width (mm)

Standard Length (mm)

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: